Taxonomy and phytogeography of the Cactaceae of eastern Brazil

Thesis

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TAXONOMY AND PHYTOGEOGRAPHY
OF THE CACTACEAE OF
EASTERN BRAZIL

Thesis for the award of 'Doctor of Philosophy'

Life Sciences

The Open University

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Royal Botanic Gardens, Kew
(Sponsoring Establishment)
Supplement 1*

FORMAL TAXONOMIC TREATMENT OF THE CACTACEAE OF EASTERN BRAZIL

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* This appendix is a work to which the thesis makes frequent reference. It is not part of the thesis itself and hence has not been presented in double-spaced format. Some of the data it contains have been compiled with the assistance of Dr Daniela C. Zappi.  

NPT.
FORMAL TAXONOMIC TREATMENT OF THE CACTACEAE OF EASTERN BRAZIL

Introductory notes
As its scope this account attempts to include all taxa of Cactaceae that are native, naturalized or commonly cultivated outdoors in North-eastern Brazil, and in South-eastern Brazil north of 22°S and east of 46°W (entries for non-native taxa are indicated by an asterisk [*] below). However, the focus from the start has been on the terrestrial, rather than epiphytic taxa, the former having a centre of high endemism in the dry environments comprising south-eastern Piauí, southernmost Ceará, the southern half of Paraíba, mainland Pernambuco, Bahia, Alagoas, Sergipe, Espírito Santo, most of Minas Gerais and the northern half of Rio de Janeiro (Map 1, Chapter 4). While epiphytic taxa native within this area are fully treated below, their main centre of diversity in SE Brazil, around 22–26°S, has been intentionally excluded, since a preliminary account of the all-important tribe Rhipsalideae was published quite recently (Barthlott & Taylor 1995).

Except where expressly limited, synonymy aims to be comprehensive for names based on Brazilian types (Southern Brazil excepted), but all relevant botanical nomenclature is included in the Index to names and epithets (page 208). Vernacular names are also included from various sources, e.g. Menezes (1949). The morphological descriptions do not aim in principle to account for all aspects of the plant, but are meant to be primarily diagnostic, supplementing details in the dichotomous keys to facilitate identification. In some cases they are comprehensive where the data have been available or when the differences between taxa are particularly subtle. Details mentioned in descriptions of genera, subgenera or other infrageneric categories, which apply to all subordinate taxa, are not always repeated in those of the included species etc. Unqualified measurements refer to length (or height in the case of erect plants); those connected by a multiplication sign ( x ) refer to length followed by width/diameter and, occasionally, also thickness, in the case of laterally compressed structures. Dimensions of the whole plant or its stem are always given exclusive of the spines; and distances between structures that themselves have a size, e.g. between areoles on a rib, are given from organ centre to centre.

Besides nomenclatural and diagnostic/descriptive details, bibliographical, phyto­geographical (see Chapter 4) and ecological data are provided, likewise distribution records and conservation assessments (IUCN 1994 Categories of Threat and conservation short-listing values, including Phylogenetic Distinction [PD], Ecological Importance [EI] and Genetic Diversity [GD] — see Chapter 5). Where appropriate, commentary is also provided on some historical aspects, other taxonomic treatments, relationships and the need for further studies.

A few cactus terms employed below need brief explanation:

(1) areoles are the felted cushions (actually highly telescoped short shoots) found on various parts of the cactus plant, bearing the spines (= modified leaves), hairs etc. and giving rise to new shoots and flower-buds;
(2) glochids are normally short, strongly barbed, specialized spines produced by the areoles of Opuntioideae and distinct from the generally much larger normal spines, which are also barbed in this subfamily;
(3) podaria (sing. podarium) are the swellings often subtending areoles that represent the points of attachment of leaves or bracts that have been lost, or almost lost, in the course of evolution of the highly succulent habit;
(4) pericarpe is the cactaceous structure comprising the specialized stem or receptacle into which the ovary of the inverted cactus flower is sunken;
(5) the flower-tube is the hollow or partially hollow structure above the pericarpe which comprises fused floral and receptacular tissues; the latter on the exterior, often bearing bract-scales; the former within and subtending the perianth-segments at its apex.
(6) a *cephalium* is a ± modified part of the stem, whether apical or lateral, whence the flowers and fruits are borne (cf. Barthlott & Hunt 1993: 164). It is in effect a kind of inflorescence structure in which the areoles may be enlarged or reduced relative to those in the vegetative part, and often compressed together, bearing abundant trichomes and/or dense spines/bristles, distinguishing the fertile part of the stem from the purely vegetative. It may be either a chlorophyllous or non-chlorophyllous part of the stem, whose cross-section in the case of lateral cephalia may remain normal (i.e. terete) or deformed, as in the case of so-called 'sunken' cephalia.

All materials cited have been seen unless indicated by 'n.v.' (*non vidi*). The cited records are organized by state and *municipio* (abbreviated to 'Mun.'), and mostly arranged from north to south and west to east. A minimum of at least one record per *municipio* has been included and, in the case of many taxa, all available records are cited, since Brazilian Cactaceae remain in general very poorly collected. For three extremely widespread, abundant and taxonomically well-defined taxa — *Tacanga inamoena*, *Epiphyllum phyllanthus* and *Cereus jamacaru* subsp. *jamacaru* — only a few representative *exsiccata* or records marking the limits of distribution etc. have been cited, since their abundance and range are otherwise not in doubt. Apart from herbarium *exsiccata*, whose locations are indicated by the standard *Index Herbariorum* codes, other field observations by the author (or from reliable sources), even if unsupported by vouchers, are mentioned in some cases; likewise published and unpublished illustrations and photographs of plants in localized habitats. A bracketed questionmark (?) preceding a record’s entry indicates uncertainty about the collection’s identity, whereas after the name of the municipio it indicates doubt about the correct municipal attribution of the locality cited.

**ARTIFICIAL KEY TO GENERA**

1. Actively growing stems bearing broad or awl-shaped leaves 2
1. Actively growing stems leafless or with only minute scale-like leaf primordia 7
2. Spines not microscopically barbed, not becoming strongly attached if allowed to penetrate the skin; glochids lacking; seed with black testa visible 1. *Pereskia*
2. Spines microscopically barbed, very difficult to detach if allowed to penetrate the skin, or true spines lacking and glochids present (at least on older stem-segments or the trunk); seed encased in a pale and sometimes fibrous/hairy funicular envelope (Opuntioideae) 3
3. Leaves broad (SW Bahia & Cent.-N Minas Gerais) 2. *Quiabentia*
3. Leaves awl-shaped (widespread) 4
4. Tree to 4 m or more with dimorphic stems, comprising a cylindric indeterminate leader shoot and flattened determinate lateral segments, the ultimate thin and leaflike; seed 8–10 mm 4. *Brasiliopuntia*
4. Trees to < 4 m, or shrubs, subshrubs or lianas; stems not as above; seed to c. 5 mm 5
5. Stamens and perianth spreading, the former sensitive, closing around the style when touched, the latter patent but never strongly reflexed, at least partly yellow; pollen exine reticulate 6. *Opuntia*
5. Stamens erect, clustered around the style, not sensitive; perianth erect, spreading or strongly reflexed, greenish, deep pinkish, red or purplish, or orange-yellow and plants not exceeding 50 cm; pollen exine not as above 6
6. Stamens long-exserted and perianth-segments erect, not spreading; spineless (introduced/cultivated) *5. Nopalea*
6. Stamens not as above or perianth-segments spreading to strongly reflexed and/or stems spiny 3. *Tacanga*
7. Flower > 10 cm long, or 8–10 cm and tube bract-scales bearing hairs (hair-spines) in their axils 8
7. Flowers < 8 cm long, or 8–10 cm and tube bract-scales naked in their axils or lacking or minute  
8. Fruit yellow, globose, surface weakly ribbed, > 5 cm diam., falling to the ground, smelling of pineapple and spineless when ripe; seed light brown when fresh, brown when old (N & E Bahia & NE Minas Gerais: caatinga-agreste)  
10. Pseudoacanthocereus  
8. Fruit not as above; seed blackish  
9. Stems flat, trigonous or 3-winged  
10. Pericarpel and flower-tube bearing conspicuous spines/bristles or broad-based bract-scales; perianth > 15 cm diam.  
10 Pericarpel and flower-tube with inconspicuous, narrow-based bract-scales, minute spines and/or trichomes only, or expanded perianth < 15 cm diam.  
11. Stems trigonous or 3-winged  
7. Hylocereus  
11. Stems flattened  
12. Epiphyte or garden plant with mostly flattened stems  
12. Terrestrial with mostly trigonous or 3-winged stems  
13. Perianth remains cleanly abscissing from young fruit or persistent and strongly blackened  
13. Perianth remains not as above (blackening only if attacked by fungi)  
14. Fruit > 5 cm, dehiscent; seeds 3–4 mm (Bahia northwards: caatinga)  
14. Fruit 1–5 cm, indehiscent; seeds 1–2 mm (Minas Gerais: campo rupestre)  
15. Epiphytic, or epilithic on coastal rocks, in Mata atlântica or at altitudes of > 1500 m, with flattened or 3–5-winged/angled stem-segments or stems < 2 cm diam., often only slightly succulent; flowers < 3 cm long or if larger then magenta and zygomorphic (tribe Rhipsalideae)  
15. Terrestrial, or epilithic in caatinga / campo rupestre and/or stems and flowers not as above  
16. Flowers ± zygomorphic, tube to 8 mm long or more (S Espírito Santo & SE Minas Gerais)  
14. Schlumbergera  
16. Flowers actinomorphic, tube 0 or < 3 mm long  
17. New stem-segments (excluding greatly elongated and usually basal extension shoots) arising mostly 2 or more together from the apices of older segments (branching acrotonic), old and diseased stems separating from the plant at the joints between segments  
17. New stem-segments arising only at base or singly from the sides of older segments (branching basi-/mesotonic), not separating at the segment joints when old or diseased  
11. Lepismium  
18. Flowers whitish or not strongly coloured, or developed laterally on stem-segments of ± indeterminate growth  
12. Rhipsalis  
18. Flowers bright yellow or orange, from composite areoles at the apex of ultimate or penultimate segments of strictly determinate growth  
13. Hatiora  
19. Plant unbranched, never segmented, shortly columnar, ± globose or depressed-globose, with or without a non-chlorophyllous bristly-woolly terminal cephalium  
19. Plant branched (at least basally), slender cylindric to tall columnar, or stems solitary with lateral cephalia, segmented with cephalia at the joints or bottle-shaped and the juvenile stem tapering into an elongate chlorophyllous terminal cephalium  
20. Flowers yellowish, diurnal (central Minas Gerais)  
20. Flowers not as above (widespread)  
21. Flowers to 4 cm long, tubular, deep magenta-pink to red at least without, diurnal to crepuscular  
21. Flowers > 4 cm long, salverform, whitish, nocturnal  
22. Flowers from a cephalium  
22. Flowers from the stem apex, cephalium lacking (Chapada Diamantina, Bahia: A. bahiensis)  
23. Pericarpel and tube clothed in conspicuous bract-scales and/or wool and bristle-spines  
23. Pericarpel and tube ± naked, bract-scales lacking, minute or very widely spaced
24. Fruit with red or purplish pulp when ripe, spiny at first; stems to 2 cm diam. 25. Leocereus


25. Pericarpel and tube with bract-scales but lacking bristle-spines; fruit not as above (widespread) 26

26. Flowers shortly funnelform, at least 4 cm diam. at full anthesis; seed 2-3 mm 15. Brasilicereus

26. Flowers tubular, to 2.5 cm diam. at full anthesis; seed to c. 1.5 mm 26. Facheiroa

27. Fruit depressed-globose (rarely globose), 2-6 cm diam., bursting open laterally or apically due to pressure from the expanding funicular pulp; stems never regularly segmented (widespread) 20. Pilosocereus

27. Fruit not as above, or < 2 cm diam.; stems various 28

28. Stems segmented, with bristly/woolly ring cephalia at the joints and apex of distal stem-segments 29

28. Stems not as above; cephalium, if present, lateral and ± continuous 30

29. Flowers green without, 8-10 cm long (Bahia, caatinga) 18. Stephanocereus subg. Stephanocereus

29. Flowers deep pink to bright red without, < 4 cm long (widespread) 19. Arrojadoa p.p.

30. Mature plant bottle-shaped, the upper part narrowed into a terminal chlorophyllous cephalium (Bahia, Chapada Diamantina) 18. Stephanocereus subg. Lagenopsis

30. Mature plant not as above 31


31. Flower-bearing areoles ± modified or comprising a lateral cephalium; fruit not as above 32

32. Fruit clavate, sometimes laterally compressed, > 11 mm diam., deep pink to red, expelled from within the deeply sunken lateral cephalium when ripe and with a small basal pore allowing ants to enter (plants of naked gneiss/granite inselbergs of SE Brazil; C. goebelianus also on other rocks and in stony soil of the caatinga in cent.-E to S Bahia) 22. Coleoccephalocereus

32. Fruit depressed-globose, globose or very shortly clavate, variously coloured or whitish, not expelled from a deeply sunken lateral cephalium or the latter lacking or fruit < 11 mm diam., not opening at base 33

33. Stem tissues almost lacking mucilage; shrub branched at base and above, not glaucous; perianth-segments white inside and out (N & E of the Chapada Diamantina, Bahia: caatinga) 27. Espostoopsis

33. Stem tissues highly mucilaginous and perianth-segments coloured, at least without (Minas Gerais & Bahia: campo rupestre), or plant a glaucous, single-stemmed column (W of Rio São Francisco, Bahia: Bambu limestone) 21. Micranthocereus
PERESKIOIDEAE

This subfamily comprises only one genus following the removal of Maihuenia (S Chile & S Argentina: Patagonia) to the Maihuenioideae Fearn (cf. Wallace 1995). The Pereskioideae are distinguished from the 2 broad-leaved genera of Opuntioideae by their unbarbed spines and unspecialized seeds lacking a funicular envelope (aril).

1. PERESKIA Miller

Gard. dict. abr. ed. 4 (1754). Type: Pereskia aculeata Miller.

Including Rhodocactus Backeberg & Knuth (1936).

Literature: Leuenberger (1986), Wallace (1995: 9, Fig. 10).

Leafy and spiny trees, shrubs or scramblers, 1–10 m. Areoles in the axils of deciduous leaves, sparsely to densely tomentose, always with felt and sometimes with long hairs, producing spines and sometimes brachyblast leaves. Leaves alternate, broad, extispulate, somewhat fleshy, deciduous. Spines solitary or clustered, or paired, claw-like and recurved (see no. 1), sometimes lacking on the flowering stems but increasing in number on the trunk. Flowers solitary or in paniculate to cymose inflorescences, sometimes developing by proliferation from the flower receptacle; flowers 2–7 cm diam., perigynous or epigynous, receptacle smooth or with prominent podaria and areoles, bract-scales leafy, fleshy, green or tinged like the sepaloids; perianth multiseriate, segments free, sepaloids lacking axillary areoles and partly tinged like the petaloids, these spreading, rotate or forming a campanulate-urceolate corolla; stamens numerous; filaments shorter than the perianth; ovary superior to inferior, unilocular, with septal ridges at the ovary roof only, or rarely seporate; stigma-lobes 3–20, erect to spreading. Fruit solitary or clustered-proliferous, pear-shaped, turbinate or globular, terete or angled, with a narrow to broad umbilicus and persistent or deciduous flower remnants / leafy bract-scales; pericarp mucilaginous. Seeds few to numerous, obovate to lenticular-reniform, 1.8–7.5 mm, black, smooth, shiny; hilum whitish.

A genus widespread in the neotropics with 17 species, of which 5 are native to Eastern Brazil (3 species and one heterotypic subspecies are endemic to the core area). Two further species are reported from western and southern Brazil, P. sacharosa (Mato Grosso do Sul) and P. nemorosa (Rio Grande do Sul), and are related to nos. 2–4 from Eastern Brazil. The E Brazilian taxa are restricted to various phases of the Mata atlântica, agreste and southern caatingas.

1. Scrambling or climbing plant, spines on branches generally paired, recurved; flower white or cream 1. aculeata
2. Flower bright yellow; fruit globose, 1–3-seeded 5. aureiflora
3. Leaves narrowly elliptic to obovate-lanceolate; lateral veins 7–10–13; seeds 5–7 mm (Mata atlântica, s.l., including brejo forest) 2. grandifolia
4. Flowers with campanulate to urceolate perianth; flower-buds orange; perianth-segments reddish pink, erect, recurving at apex only, stamens and style enclosed 4. stenantha
5. Flowers with rotate, widely opening perianth; flower-buds greenish or pinkish; perianth-segments pink or magenta-pink, spreading; stamens and style not enclosed 3. bahiensis

Three types of sclereids are found in the genus (Leuenberger 1986: fig. 22) and each is represented amongst the species treated here, dividing them into three groups as indicated below:
PERESKIA ACULEATA Group (no. 1): sclereids fusiform-simple; stomata present on stem; periderm formation early; brachyblast leaves 0.


VERNACULAR NAMES. Ora-pro-nobis, Azedinha, Lobolobô, Espinho-de-Santo-Antônio, Espinho-preto, Surucucú, Cipó-Santo.

Climbing shrub or liana, 3–10 m long; shoots scandent. Areoles initially 2 mm diam., with white long hairs, later accrescent, cushion-like, to 15 mm diam., producing claw-like, gernimate primary spines and secondary straight spines, but not brachyblast leaves. Leaves lanceolate to oblong or ovate, 4.5–7.0(–11.0) × 1.5–5.0 cm, shortly petiolate, base cuneate, attenuate or rounded; blade green, concolorous or purplish below; lateral veins 4–7, often inconspicuous. Inflorescence terminal and lateral on long shoots, racemose to profusely paniculate, with up to 70 flowers of more. Flowers 2.5–5.0 cm diam., white or creamy-white, strongly fragrant (diosmin); pedicels 5–15 mm; receptacle cup-shaped to turbinate, with 6–15 hairy areoles on inconspicuous to prominent podaria; bracts leaflike, filiform, base petiolate, base cuneate, attenuate or rounded; blade green, concolorous or purplish below; lateral veins 4–7, often inconspicuous. Inflorescence terminal and lateral on long shoots, racemose to profusely paniculate, with up to 70 flowers of more. Flowers 2.5–5.0 cm diam., white or creamy-white, strongly fragrant (diosmin); pedicels 5–15 mm; receptacle cup-shaped to turbinate, with 6–15 hairy areoles on inconspicuous to prominent podaria; bracts leaflike, fleshy, lower bracts 9–12, spreading to recurved, upper bracts 3–8, erect or adpressed in bud; outer perianth-segments 2–5, pale green to whitish; inner segments 6–11, obovate to spatulate, to 2.5 cm, delicate, white; stamens 1.5–2.5 cm, globular, yellow to orange, fleshy, usually bracteate and spiny when immature, mostly naked when ripe; locule with gelatinous tissue enclosing the seeds. Seeds 2–5, lenticular, 4.5–5.0 mm diam., laterally compressed. Chromosome number: 2n = 22 (Leuenberger 1986: 43).

Humid/subhumid evergreen forest element: scrambling over vegetation and inselbergs of gneiss/granite etc., Mata atlântica, including restinga, mata de brejo and agreste, rarely in carrasco (cent.-N Minas Gerais), Maranhão, eastern Pernambuco to central-eastern and south-eastern Bahia, eastern and southern Minas Gerais and Espírito Santo, from sea level to > 1000 m; Goiás, South-eastern and Southern Brazil; eastern Paraguay and Argentina, Mexico, Central America, Caribbean and northern South America (once recorded from Peru). Map 14B.


CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1×5) = 5.

This taxon is variable in leaf size and shape and in its inflorescence morphology, both within and between populations. Its leaves and those of the following (no. 2) are eaten as a potherb.

PERESKIA GRANDIFOLIA Group (nos. 2–4): scleroids fusiform-aggregated; stomata on stem present; periderm formation retarded; brachyblast leaves present. Fusiform-aggregated scleroids are also found in P. nemorosa and P. sacharosa (SE South America, see Map 7), which are indicated as potentially basal members of this Group in a molecular phylogenies produced by R. Wallace (1995) and C. Butterworth (in litt., 10 Feb. 2000) at Iowa State University, USA.


Shrub or tree, 2–10 m, forming a trunk to 80 cm diam.; main shoots erect to arching. Areoles rounded, cushion-like, initially 3–7(–8) mm diam., later to 12 mm diam., producing straight spines, and 1–4 brachyblast leaves. Spines 0–8(–11) on twigs, fasciculate to spreading, 1–4 cm, increasing in number and size on older branches. Leaves elliptic
or narrowly elliptic-oblong, narrowly ovate to obovate-lanceolate, (6--)9-26(-30) × (3--)4-6(-9) cm, petiole to 1 cm or more; base of lamina attenuate, apex acute to acuminate, sometimes recurved; lateral veins (7--)10-13 or more. Inflorescence terminal, densely cymose-paniculate by proliferation from the receptacle, 10-15- to sometimes 30(-50)-flowered. Flowers 3-6(-7) cm diam., rose-like, showy; pedicels 1-3 cm, stout; receptacle turbinate, with conspicuous furrows and podaria, areoles on the upper half only; bracts small or leaf-like, fleshy, lower bracts spreading to ascending, upper bracts 2-5, adpressed in bud; outer perianth-segments 2-5, asymmetric; inner segments 5-12, obovate to spathulate, delicate, rose, pale or purple-pink, apex often emarginate; stamens 5-10 mm, filaments white; ovary distinctly inferior, with conical roof narrowing into the style, which is 8-12 mm, cylindrical, stigma-lobes 5-8, suberect, white to pale pink. Infructescences large, usually pendent; fruit 5-10 × 3-7 cm, pyriform or turbinate, with conspicuous angles, green or reddish to yellowish, bracts usually deciduous when ripe. Seeds 20-60, obovate-elliptic, 5-7 × 4.5-5.0 mm, laterally compressed.

This species is divisible into two subspecies:

1. Receptacular bracts green, the lowermost ones rarely with recurved apices; outer perianth-segments greenish to pink, inner segments 15-33 mm; anthers golden yellow (NE & SE Brazil) 2a. subsp. grandifolia

1. Receptacular bracts and outer perianth-segments purplish-pink to dark purplish, the lowermost bracts with recurved apices; inner perianth-segments 10-18 mm; anthers pale yellow (cent.-S Minas Gerais to W Espirito Santo, cultivated in N Minas Gerais & S Bahia) 2b. subsp. violacea

2a. subsp. grandifolia

VERNACULAR NAMES. Sabonete, Ora-pro-nobis, Quiabento, Entrada-de-baile, Rosa-mole, Sem-vergonha.

Leaves thin, green, concolorous, shortly acuminate to acute. Inflorescence and receptacular bracts green, flat, rarely recurved; receptacular bracts shorter than the inner perianth-segments, outer segments greenish-pink, inner segments 15-32 mm, pink to deep pink; anthers golden yellow. Fruit variable, pyriform to obtriangular, angled; often nearly as broad as long; ovary locule cup-shaped to broadly obovate-triangular. Chromosome number: 2n = 22 (Leuenberger 1986: 43).

Humid/subhumid evergreen forest element: perhaps native in agreste and Mata atlântica (including that on the E slopes of the Chapada Diamantina, brejo and riverine forest), c. 100-1140 m, southermmost Ceará, Pernambuco (native and cultivated, fide Andrade-Lima 1966: 1454), central-eastern and south-eastern Bahia to southern Espirito Santo and south-western Minas Gerais, but widely cultivated; perhaps also native in Rio de Janeiro and São Paulo; commonly introduced in the neotropics. Map 14B.


RIO DE JANEIRO: Sertão de Cacimbas, on right embankment of Rio Itabapoana, 10 Oct. 1909, Sampaio 985 (R); between Morro do Coco and Campos, 8 Aug. 1964, Trinta 1051 (R); Monte Alegre, Feb. 1927, Vidal s.n. (R); Mun. Cantagalo, Peckolt 121 (W).

CONSERVATION STATUS. Lower Risk (1), but perhaps Vulnerable or Conservation Dependent; PD=I, EI=I, GD=1. Short-list score (1×3) = 3. It has been taken into cultivation (as a hedge plant) in the region where it may be native.

The natural range of this taxon remains poorly known, probably through early destruction of its habitat and for the uncertainty as to its native status caused by its widespread introduction as a cultivated ornamental.


VERNACULAR NAME. Ora-pro-nobis.

Leaves thickish, dark green above, often slightly discolorous and purple below, nearly always distinctly acuminate and with recurved apex. Inflorescence bracts all dark purplish to bright purplish pink, uppermost almost resembling open flowers from a distance; lower receptacular bracts thick, keeled, recurved, nearly as long as the inner perianth-segments, outer segments purplish to pink, inner segments 10-15(-18) mm, pale pink to purple-pink; anthers pale yellow. Fruit and ovary locule narrowly obtriangular, bracts purplish tinged with green or becoming nearly green. Chromosome number: 2n = 22 (Leuenberger 1986: 43).

Southern humid/subhumid forest element: drier phases of Mata atlântica, c. 50–1400 m, drainage of the Rio Doce, central-southern and eastern Minas Gerais to central Espírito Santo, apparently cultivated elsewhere. Endemic to the core area within South-eastern Brazil. Map 16A.


CONSERVATION STATUS. Data Deficient (1), but perhaps at Lower Risk; PD=I, EI=I, GD=1. Short-list score (1×3) = 3. It has been taken into cultivation (as a hedge plant) in the region where it is native.
Even though the native distribution of subsp. *grandifolia* is poorly understood, there are no records of it as other than a cultivated plant within the extensive area in which subsp. *violacea* is found, thereby justifying recognition of the latter as a subspecies rather than a variety. Indeed, a recent studies of plastid DNA gene sequences, conducted by Wallace (1995: 9) and Butterworth (ined.), have indicated that this taxon may be worthy of specific status and that it is the basal element amongst the East Brazilian taxa belonging to the *P. grandifolia* Group. Whatever the true status of subsp. *grandifolia*, it seems reasonably certain that subsp. *violacea* is native within the area drained by the Rio Doce, where it was observed regenerating from stumps remaining in recently cut primary forest.


**Conservation Status.** Lower Risk (I); PD=2, El=1, GD=1. Short-list score (1×4) = 4. It has been taken into cultivation (as a hedge plant) in the region where it is native.

The very close relationship between this species and the following deserves further investigation. A plant encountered near the border of municípios Piatã and Boninal, Bahia (Taylor & Zappi in Harley 25598, SPF, CEPEC, K), well beyond the known range of *P. stenantha*, had somewhat intermediate flowers, and in the region of Caetité the two species seem to hybridize or intergrade. As already noted by Leuenberger (1986), there are scarcely any vegetative differences to separate them, although *P. stenantha* seems capable of producing much larger leaves (especially in western Bahia where it inhabits a region of higher rainfall).


**Vernacular Names.** As for *P. bahiensis*.

Shrub to small tree, 2–4(–6) m, branching mostly near the base, sometimes forming a trunk to 15 cm diam.; main shoots erect to arching. Areoles rounded, cushion-like, initially 2–5 mm diam., later to 15 mm diam., producing straight spines, and 1–3 brachyblast leaves. Spines 0–7 on twigs, fasciculate to spreading, 1–5 cm, increasing in number and size on older branches. Leaves obovate to elliptic, often folded upwards along the midrib, (5–)7–11–(15) × (2–)4–6(–9) cm, petiole 2–10 mm, base of lamina cuneate to attenuate, apex broadly acute to rounded, lateral veins 5–7. Inflorescence terminal, densely cymose-paniculate by proliferation from the receptacle, c. 15-flowered, or flowers sometimes solitary. Flowers perigynous to epigynous, 1–2 cm diam., urceolate-campanulate, opening very little; flower-buds orange-red; pedicels hardly distinguishable; receptacle turbinate, with 5–8 areoles, bracteate in the upper half, bracts sepal-like, fleshy, lower bracts 3–5(–7), spreading, upper bracts (1–)3–5(–6), erect, green to reddish, keeled, outer perianth-segments 4–5, erect, concave, red to orange-red, inner segments 6–8, 20–25 mm, linear lanceolate, erect, spreading at the tip only, pink to purplish pink, acute to broadly acute at apex; stamens 12–15 mm, surrounding the slightly longer style, filaments white; ovary half-inferior to inferior, with septal ridges at the roof; style 13–20 mm, thick at base, stigma-lobes 4–7, suberect to spreading. Inflorescence a densely cymose-paniculate cluster of up to 15 fruits, erect or arching at maturity, or fruits solitary; fruit 3–7 × 2–6 cm, pyriform or turbinate, ± angled, otherwise like *P. bahiensis*. Seeds c. 30–50 per fruit, obovoid, 4.5–5.5 × 3.2–3.6 mm, laterally compressed. Chromosome number: 2n = 22 (Leuenberger 1986: 43).


CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=1. Short-list score (1×4) = 4. It has been taken into cultivation (as a hedge plant) in the region where it is native.

Almost indistinguishable from P. bahiensis (see above) when not in flower, but with a distinct range.

PERESKIA PORTULACIFOLIA Group (no. 5): stone cells present; stomata on stem 0; periderm formation early; brachyblast leaves present. Other members of this group are from northern South America (P. guamacho, sister species of P. aureiflora; see Map 6) and the eastern Caribbean islands (4 spp.).


VERNACULAR NAMES. Facho, Ora-pro-nobis-da-mata.

Small tree or shrub, to 6 m, trunk to 20 cm diam.; branches erect to arching. Areoles rounded, cushion-like, initially 3 mm diam., later to 6 mm diam., producing straight spines, and 1–3 brachyblast leaves. Spines 0–3 on twigs, fasciculate to spreading, 1–3 cm, increasing in number and size on older branches. Leaves obovate to elliptic-suborbicular in shade, elliptic to lanceolate and thicker in sun, flat or somewhat boat-shaped, dimorphic, auxoblast leaves to 11 × 2–3 cm, brachyblast 4–10 × 1.5–2.5–5.0 cm, petiole 2–4 mm, base of lamina broadly cuneate, apex acute, lateral veins 3–5–7–7. Flowers solitary, yellow, terminal or on short lateral twigs 3–13 cm, c. 3–4 cm diam., opening widely, showy; epigynous; pedicels short; receptacle turbinate, with areoles, bracteate; bracts leafy, fleshy, green, sometimes reddish at margin, lower bracts 5–8, spreading, upper bracts 5–8, erect, keeled; outer perianth segments c. 3, obovate, inner segments 10–12, 15–20 mm, obovate, spreading to reflexed, bright yellow, obtuse at apex; stamens 5–10 mm, filaments white; ovary half-inferior; style 10 mm, cylindric, stigma-lobes 4–7, erect. Fruit
10–15–(20) mm diam., globular, reddish green to brown or ‘chocolate-purple’ when ripe, bracts leafy, deciduous. Seeds c. 1–3, obovoid, (4–)5–5.5 × 4.2–5.1 mm, laterally compressed.

Southern caatinga (inselberg) element: in caatinga/agreste, especially in association with gneiss/granite inselbergs or derived substrates, 300–920 m, central-southern Bahia to central-northern and north-eastern Minas Gerais. Endemic to the core area of Eastern Brazil. Map 24A.


CONSERVATION STATUS. Vulnerable (2) [criteria A2c]; extent of occurrence = 60627 km²; PD=2, EI=1, GD=1. Short-list score (2×4) = 8. This species appears to be rare within its area of occurrence, except in north-eastern Minas Gerais (Rio Jequitinhonha valley), where considerable habitat modification is taking place.

In southern Bahia and central-northern Minas Gerais P. aureiflora grows in close proximity to, or sympatric with, P. stenantha and/or P. bahiensis, but seems to be much rarer than either. However, it is the commonest pereskia in the middle part of the Rio Jequitinhonha drainage system, north-eastern Minas Gerais (Itaobim/Itinga), whence it was originally described, and where its above-mentioned congeners are absent. Its status as sister species to P. guamacho (N South America) was earlier suspected on purely morphological grounds, but has more recently been confirmed by gene sequence phylogenies obtained by Wallace (1995: Fig. 10) and Butterworth (ined.).
OPUNTIOIDEAE

Areoles bearing barbed spines and/or glochids; pericarpel scarcely differentiated from stem segments; pollen mostly polyporate; seed enclosed in a pale, mostly bony funicular envelope (aril).

Cladistic analyses employing DNA gene sequence data (Wallace & Dickie 2001) and seed anatomical, gross morphological data and pragmatic considerations (Stuppy & Huber 1991, Stuppy 2001; Taylor & Stuppy 2001) indicate that between 13 and 16 genera deserve recognition in this subfamily. Austrocylindropuntia and its sister group Cumulopuntia (both Andean) appear to be basal amongst Opuntioideae. The first genus treated below is the only South American representative of a group of 4 genera native to Central & North America and the Caribbean, comprising Pereskia, Quiabentia, Cylindropuntia and Grusonia (Corynopuntia). The broad flattened leaves of Quiabentia and Pereskia may be a synapomorphy, since both Austrocylindropuntia/Cumulopuntia and the subfamily’s plesiomorphic sister group, the Maihuenioideae (Nyffeler, ined.), possess cylindric/awl-shaped leaves.

2. QUIABENTIA Britton & Rose

Cact. 4: 252 (1923). Type: Quiabentia zehntneri (Britton & Rose) Britton & Rose.

A genus of only 2 species, the second being Q. verticillata (Vaupel) Vaupel, a sometimes treelike plant (2–15 m high), from the western Chaco and its periphery, in Argentina, Paraguay and Bolivia. Its Brazilian counterpart, treated below, is of restricted and presumably relictual distribution, representing a marginal floristic element of the caatinga, since it occurs only near the south-western limits of this vegetation type.

1. Quiabentia zehntneri (Britton & Rose) Britton & Rose, Cact. 4: 252 (1923). Type: Brazil, Bahia, Born Jesus da Lapa, Rio São Francisco, 15–16 Nov. 1912, Zehntner 630 (US, lecto. designated here; NY, lectopara.).


VERNACULAR NAMES. Quiabento, Flor-de-cera, Espinho-de-Santo-Antonio.

Shrubby, erect, 2–3 m, leafy when growing; branches, to 30 cm (or more), 1–2.5 cm diam., cylindric, the stoutest sometimes faintly ribbed, especially towards apex when dry, grey-green to grey, glaucous; areoles 20–40 mm apart, with white felt. Leaves 20–55 × 5–25 mm, to 3.5 mm thick, elliptic-ovate, orbicular or elliptic-lanceolate, pointed at both ends, concave above, gradually decurved towards apex, sessile, fleshy, stiff, green. Spines 7 or more per areole, the longest to 50 mm, white, reddish or golden, flexible, glochids few, spine-like and poorly differentiated from the spines apart from their position at the upper edge of the areole. Flowers apical or subapical, 7 × 7–8 cm; pericarpel narrowly turbinate to cylindric, to 40 mm, grey-green, with areoles and fleshy bracts; tube short, to 1 cm; perianth-segments to 40 mm, ovate or spatulate, retuse at apex, dark-pink, spreading; stamens exposed; stigma-lobes exerted. Fruit 4–7.5 cm long, narrowly turbinate, umbilicus not very deep, greenish to reddish or purple outside; funicular pulp translucent, whitish, placenta yellowish. Seeds many per fruit, to 4 mm diam.
Southern Rio São Francisco *caatinga* element: on ± naked or thinly wooded limestone (Bambui) outcrops or gneiss/granite inselbergs amidst high *caatinga* forest, 450–750 m, both sides of the Rio São Francisco valley, west-central/southern Bahia and central-northern Minas Gerais. Endemic to the core area of Eastern Brazil. Map 26B.


CONSERVATION STATUS. Lower Risk (1); PD=3, EI=1, GD=1. Short-list score (1×5) = 5.

Rizzini & Mattos-Filho (1992) claim that this species is found in the ‘região de Brumado–Condeuba, Bahia’ and is there used as hedges. However, the plant commonly used for this purpose in this region and called ‘quiabento’ is *Pereskia bahiensis* and it may be doubted that *Quiabentia* is native there.
The following 4 genera form a monophyletic lineage culminating in *Opuntia, sensu stricto*, which is the most derived, possessing sensitive stamens and pollen with a reticulate exine. Other genera included in this lineage, but absent from Brazil, are *Miqueliopuntia* (N Chile), *Tunilla* (Argentina) and *Consolea* (E Caribbean). The following genus, together with *Miqueliopuntia*, appears to be a basal element of this lineage, with a relictual distribution almost confined to Eastern Brazil, where its extensive range does not overlap at any point with that of *Opuntia sensu stricto*:

### 3. TACINGA Britton & Rose


Shrubs, subshrubs and lianas, 0.2–5.0 m; branches not dimorphic, pith often ± chambered or quite hollow when > 1–2 years old; stem-segments cylindrical or compressed, then orbicular, obovate to elliptic or rhomboid in outline; areoles borne on non-existent to very low tubercles in the axils of caducous leaves, with abundant glochids and felt, spines present or absent. Leaves minute, subulate, sessile, fleshy, early deciduous. Flowers solitary, from the margin or apex of the stem-segments; flowers epigynous, pericarpel globose, turbinate or elongate, sometimes deeply depressed and forming a tube at apex, with areoles subtended by leaf-like, fleshy, green or coloured bract-scales; perianth multiseriate, tube relatively short, outer perianth-segments short, stiff, erect, patent or strongly reflexed, coloured, fleshy, inner segments coloured, delicate, erect, somewhat spreading or strongly reflexed; stamens numerous, erect, at least at first, sometimes strongly exerted, not sensitive, those adjacent to the perianth represented by hairlike staminodes in species nos. 1–3; pollen exine not reticulate, very finely punctate/spinulate. Fruit solitary or clustered-proliferous, globose, turbinate or elongate clavate, with a very deep umbilicus, flower remnants deciduous, fleshy, pinkish or coloured, fibrous or almost lacking; placenta white, greenish or coloured. Seeds few, globular to reniform, to 5 mm diam., enclosed in a hard, bony funicular envelope.

As recently amplified, a genus of 6 species named as an anagram of *caatinga*, the dry thorn forest of Eastern Brazil, where it is frequent, also ascending into the included *campos rupestres* (see no. 6) and extending slightly west of the core area into north-western Minas Gerais on limestone outcrops (no. 5). Species nos. 1–4 are endemic to the core area of Eastern Brazil as defined here. Hybrids between nos. 2 & 3, 3 & 6, 4 & 6 and 5 & 6 are known or suspected and sometimes not uncommon, but are not keyed out below.

1. Perianth-segments erect and forming a tube or only spreading slightly at apex, deep magenta-pink to orange-red
2. Perianth-segments ± spreading to strongly reflexed and lying against the pericarpel, yellow, orange-reddish, green or purplish
2. Stamens exerted (cultivated) *Nopalea cochenillifera* 4
3. Stamens included (eastern *caatingas*) 3
3. Fruit greenish to reddish or purple outside, to 3 cm, funicular pulp yellowish 4. palmadora 3. werneri
4. Plants low-growing, rarely exceeding 1 m, mostly subshrubs; stem-segments always flattened; spines 0 or fine and slender, to 15 mm (widespread, especially on rocks) 5
4. Plants taller, to 2 m or more, scandent, with at least the lower parts of stems perfectly cylindrical; spines 0 (NE Minas Gerais to SW Pernambuco, *caatinga*) 6
5. Joints spineless (present in some areoles of *T. xquipa*); areoles well spaced, 10–20 mm apart 6. inamoena 5. saxatilis
6. Joints with minute spines; areoles congested, 1–14 mm apart 1. funalis 6. All stem-segments perfectly cylindrical; flowers green to purplish (S Bahia to SW Pernambuco) 2. braunii
6. Ultimate stem-segments ± flattened; flowers green (Rio Jequitinhonha valley, NE Minas Gerais)

T. atropurpurea var. zehntneroides Backeb., Descr. Cact. Nov. [1: 10 (1956, publ. 1957). Type: Brazil, Bahia (assumed not to have been preserved).

VERNACULAR NAMES. Rabo-de-rato, Rabo-de-gato, Cipó-de-espinho, Quipá-voador, Trança-perna.

Shrubby, decumbent or scandent, stems to 12 m long, hollow inside and scarcely succulent once > 1 year-old. Stem-segments to 30–100 cm or more, 0.8–1.5 cm diam., cylindrical, grey-green to purplish or reddish, often somewhat glaucous. Aroeleus 5–20 mm apart, prominent, felt white to brownish, spineless. Flowers from near the apex of terminal segments, 57–80 × 20 mm, green to purplish; pericarp narrowly turbinate, to 30–50 mm, grey-green, with aroeleus; outer perianth-segments 10, 5–15 mm, narrowly ovate, acute, spreading to reflexed; inner segments c. 7, to 20–40 mm, acute, revolute; stamens exerted c. 17 mm or more, the outermost replaced by abundant hairlike staminodes; anthers sometimes reddish; style to 45 mm, stigma-lobes exerted beyond stamens.

Fruit translucent, whitish, placenta yellowish. Seeds 3–5 per fruit, to 4 mm diam.

Central-southern caatinga element: in caatinga, 380–950 m, south-western Pernambuco (also vaguely reported from adjacent Piauí) and western and northern to southern Bahia. Endemic to the core area within North-eastern Brazil. Map 22A.


CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1×5) = 5. Lower Risk at present, but habitat destruction is continuing.
This species remains poorly known as fertile material, but appears to be variable. Its flowers may be either green or purple, the latter colour variant apparently being restricted to the southern part of its range, but recorded northwards to at least Mun. Cachanaum, central Bahia. These variants do not appear to exhibit obvious vegetative differences and the flowers of Backeberg’s var. *zehnnerioides*, as described, seem to be of somewhat intermediate colour. More collections and observations during its late winter (August/September) flowering period are needed.


*[Opuntia rubescens* sensu K. Schum. in Martius, Fl. bras. 2(4): 306 (1890), quoad Glaziou 14865, non Salm-Dyck ex DC (1828).]*


**VERNACULAR NAMES.** Rabo-de-rato, Cipó-de-espinhos, Rabo-de-espinhos.

Shrubby or semi-scandent with the ultimate stem-segments sometimes pendulous, to 6 m, partially hollow inside; primary stem cylindric, erect, subsequent stem-segments rounded at base, somewhat flattened towards apex, ultimate segments to 35 × 1.5–3.5 × 0.5–0.8 cm, rarely broader, ± strongly flattened, grey-green to purplish, glaucous; areoles to c. 23 mm apart, prominent, felt white, with long hairs when young; spines 0 (seen only in a plant thought to show introgression with *T. werneri*). Flowers apical or subapical, c. 7 × 2 cm; pericarpel narrowly turbinate, to 40 mm, grey-green to purplish, bearing areoles; outer perianth-segments green, c. 10, 5–15 mm, narrowly ovate, acute, erect to ± reflexed; inner segments pale green, to 40 mm, acute, revolute; stamens erect, the outermost replaced by abundant hairlike staminodes; style to 45 mm, stigma-lobes exserted. Fruit 40 mm, narrowly urceolate, with a deep umbilicus, greenish; funicular pulp translucent, whitish, placenta yellowish. Seeds 4–5 per fruit, to 4 mm diam.

South-eastern caatinga (inselberg) element: on gneiss/granite outcrops/inselbergs in caatinga-agreste, 170–350 m, Rio Jequitinhonha valley, north-eastern Minas Gerais. Endemic to the core area within Minas Gerais. Map 33A.


**CONSERVATION STATUS.** Vulnerable (2) [criteria B1/2c]; extent of occurrence = 1515 km²; PD=2, EI=1, GD=1. Short-list score (2×4) = 8.

Although correctly named only in 1989, this distinctive species was in fact collected (see *Glaziou* 14865) before its better-known sister-species treated above. The early collection, made at least 115 years ago and claimed by Glaziou, was misidentified by Schumann in the Flora *brasiliensis* (1890) as *Opuntia rubescens* Salm-Dyck ex DC., which is the type of Consolea Lemaire, an opuntioid genus endemic to the Caribbean (the original description of *O. rubescens* erroneously suggested it might have come from Brazil, so Schumann can, perhaps, be forgiven). Glaziou himself should not be credited with the first collection, however, since his locality data are clearly false (the Serra de São José, where he is known to have collected other plants, is in
perhumid southern Minas Gerais). It seems that, as in other well-documented cases (Wurdack 1970), Glaziou appears to have appropriated material from an anonymous collector and given it his own number. For a further example of this deplorable practice, see *T. inamoena*, below.


Shrubby, mostly < 1 m high; stem-segments flat, elongate-ellipsoid to broadly ellipsoid, 10–20 × 4–10 × 0.5–2.0 cm, dark green, those of seedlings and juvenile growth nearly orbicular; areoles c. 3 mm diam., on scarcely raised podaria, mostly 12–18 mm apart, often displaying indeterminate growth near base of plant; glochids dirty whitish, few at first; spines (0–)3–8 at first (rarely remaining almost spineless), 3–63 × 1.5 mm near base, ash-grey tipped yellow to yellowish brown, diverging. Flowers c. 35–50 mm long; perianth-segments ± erect to slightly expanded, to c. 7 mm long, bright red, outer series rather fleshy, darker red; stamens numerous, the outermost represented by staminodes (with rudimentary anthers or these entirely lacking), filaments orange-yellow to orange above; style narrowly obclaviform, yellowish; stigma-lobes 4, white; pericarpel 28 × 20 mm, green, areoles with numerous glochids but spineless. Fruit elongate ovoid, broadly beaked at apex, 40–55 × 25–35 mm, with a narrow, deeply sunken umbilicus, pale greenish white to white, pericarp thick, pale green; funicular pulp pink when ripe. Seed c. 3 × 3.5 mm, nearly spherical, funicular envelope pale ochre.

Eastern caatinga element: margins of gneiss/granite outcrops and inselbergs in caatinga-agreste, 100–650 m, middle drainage of the Rios Paraguasu, de Contas and Jequitinhonha, eastern Bahia and north-eastern Minas Gerais. Endemic to the core area of Eastern Brazil. Map 32A.


**Conservation Status.** Vulnerable (2) [criteria B1/b2–c]; extent of occurrence = 24031 km², but area of occupancy estimated to be < 2000 km²; PD=2, EI=1, GD=2. Short-list score (2+5) = 10. This species has a local and rather disjunct distribution. Its habitat at Rui Barbosa (BA) is being destroyed by mining operations.

The flowers and fruit of this species provide a clear link between *T. funalis*, *T. braunii* and the following species. The first locality cited above (Eggli 1259, Taylor et al. 1568) represents a variant population with rather weak or almost absent spination.

A plant of probable hybrid origin, involving *T. werneri* and *T. inamoena*, has been observed near Pedra Azul, Minas Gerais.


*Opuntia palmadora* Britton & Rose, Cact. 1: 202 (1919).
Shrubby, to 2(-4) m tall, main stem flattened, transversely elliptic, sometimes with brownish bark, very spiny, the areoles showing considerable indeterminate growth. Branches erect, stem-segments 8–17 x 3–7 cm, elliptic to obovate, grey-green, glaucous. Areoles 10–20 mm apart, prominent, felt white; spines (2–)3–9, (7–)15–35 mm, pungent, golden at first, pale grey with age. Flowers from the apex of the terminal segments, 30 x 15–20 mm; pericarpel turbinate, to 20 mm, pale to grey-green, with orange, acute, fleshy bract-scales subending bristles; outer perianth-segments 10 mm, narrowly lanceolate, deep red or pinkish orange, erect; innermost 15 mm, spatulate, orange, spreading only at apex; stamens included; stigma-lobes exerted. Fruit to 3 cm long, turbinate to obovoid, greenish to reddish or purple outside; funicular pulp translucent, whitish, placenta yellowish. Seeds 3–5 per fruit, to 5 mm diam.

Eastern caatinga element: in caatinga, agreste and carrasco, frequent on deep sandy substrates but not restricted to these, c. 200–1020 m, Rio Grande do Norte to southern Bahia (from the Chapada Diamantina / northern Serra do Espinhaço eastwards). Endemic to North-eastern Brazil. Map 30A.

RIO GRANDE DO NORTE: Mun. Tangará (?), 58 km N of Guarabira (PB) on road to Tangará, 6°21'S, 35°40'W, 1 April 2000, E.A. Rocha et al. (K, photos); between Tangará and Currais Novos, 6°14'S, 35°51'W, 1 April 2000, E.A. Rocha et al. (K, photos).


**CONSERVATION STATUS.** Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1×5) = 5.

The pollination biology of this species has been studied by Locatelli & Machado (1999a). It exhibits considerable regional and local variation.


Shrubby, to 50 × 400 cm., without main stem. Branches erect, stem-segments 10–16 × 5–11 cm, 7–17 mm thick, obicular to ovate, grey-green, sometimes glaucous. Areoles 1–14 mm apart, to 0.5 mm diam., sunken in raised podaria, with felt, glochids immersed in the stem; spines 0–6, delicate, generally bristly, off-white to dark brownish, erect, 1–19 mm, very thin. Flowers at the apex and margins of the terminal stem-segments, 3–4 × 2.6–4.2 cm; pericarpe 17–25 × 17 mm, green, with yellowish or dull red, acute, fleshy bract-scales subtending bristles; perianth-segments 12–22 × 9–14 mm, outer narrowly lanceolate, deep red to yellow-orange, spreading; innermost spatulate, yellow to orange, spreading; stamens 2–9 mm, exposed; style 7–20 mm; stigma-lobes exerted. Fruit to 38 × 28 mm
diam., globose to depressed-globose, slightly beaked, the beak 2–6 mm, brownish green to wine-red or brownish red when ripe; funicular pulp translucent, greenish, placenta yellowish. Seeds many per fruit, to 4.8 × 3.6 × 2.8 mm.

The spiny sister-species of *T. inamoena* (see below), with which it is narrowly sympatric in western Bahia, replacing it in the Rio São Francisco valley further south on limestone outcrops. It links *T. inamoena* to the preceding species in its tendency to having somewhat beaked fruits. Its range extends westwards on limestone outcrops into north-western Minas Gerais, slightly beyond the limits of the core area covered here. Two subspecies are recognized:

1. Areoles 7–14 mm apart; perianth-segments spathulate (W & cent.-N Minas Gerais, and W of the Rio São Francisco in SW Bahia)  
2. Areoles very densely disposed, 1–6 mm apart; perianth-segments lanceolate (Mun. Iuiú, Bahia)

### 5a. *subsp. saxatilis*

**VERNACULAR NAME.** Palma.

Stem-segments 10–12 × 5–6 cm. Areoles 7–14 mm apart. Flowers to 30 × 30 mm, pericarpel 11 × 11–13 mm; perianth-segments spathulate.

Southern Rio São Francisco *caatinga* element: on ± forest-covered limestone (Bambuí) outcrops surrounded by *caatinga, mata seca semidecidua* and *cerradão*, c. 450–700 m, western Bahia (west of the Rio São Francisco) to north-western, northern and central Minas Gerais (to c. 17°55'S). Map 26C.


**CONSERVATION STATUS.** Lower Risk (1); PD=1, EF=1, GD=2. Short-list score (1×4) = 4. Lower Risk at present, but found only on limestone and therefore potentially threatened by quarrying activities in the long term.

At the first Bahian locality cited above the hybrid *T. saxatilis* subsp. *saxatilis × T. inamoena* has been observed and collected (*Taylor et al.* 1430, CEPEC, HRCB, K, ZSS) together with both parental taxa. This subspecies shows significant regional variation (cf. synonymy above).


Holotype: Brazil, Bahia, [Serra de Iuiú], 1984, *E. Esteves Pereira* 191 (UFG; ZSS, iso.).

Stem-segments to 16 × 11 cm. Areoles 1–6 mm apart, very densely disposed. Flowers 18–22 × 26 mm, pericarpel 17 × 15 mm; perianth-segments lanceolate.


CONSERVATION STATUS. Endangered (3) [criteria C2b]; PD=1, EI=1, GD=1. Short-list score (3×3) = 9. It is presently known only from the location cited above and could be affected by quarrying in the future.

Type: Brazil, Rio de Janeiro [fide Schumann]; ‘Minas Gerais, Serra dos Ilheos, Sitio’ [fide Glaziou 1909: 327, but see below; probably north-eastern Minas Gerais], ‘1883–84’, [anon. in] Glaziou 14864 (K, lecto. designated here).


VERNACULAR NAMES. Quipá, Guibá, Guipá, Palmatória, Palmatória-miúda, Iviro, Gogoia, Palma-de-ovelha.

Subshrub, 10–50 × 50–300 cm, without main stem; stem-segments erect or sprawling, very variable in shape, size and thickness, 5–15 × 4–12 cm, orbicular to ovate etc., light green, with ducts exuding sticky, whitish mucilage when cut; areoles 10–15 mm apart, sunken and expanded inwards. Spines absent (but see T. xquipa below), glochids numerous but mostly concealed inside the sunken areoles. Flowers from near the apex of terminal segments, c. 50 × 35–40 mm; pericarpel globose, to 10 mm, green, with orange-red, acute, fleshy bract-scales subtending bristles; outer perianth-segments 16 mm, narrowly lanceolate, deep red or pinkish orange, spreading, inner segments 18–20 mm, spathulate, orange, spreading to slightly reflexed at apex; stamens exposed, erect; stigma-lobes exserted. Fruit to c. 40 mm diam., globose to depressed globose, yellow or orange when ripe, the depressed umbilicus small in relation to fruit diameter, funicular pulp translucent, edible. Seeds many per fruit, to 3 mm diam.

Widespread Eastern Brazil element: usually on rocks (including inselbergs) or very stony ground, open caatinga and campo rupestre, c. 100–1550 m, from the middle drainage of the Rio Jequitinhonha (MG) northwards to northernmost Piauí, and westwards on sandstone outcrops in the cerrado of western Bahia. Endemic to Eastern Brazil. Amongst the commonest of cacti from the region. Only records marking its approximate eastern, western and southern limits are given below. Map 19.


MINAS GERAIS: NW Minas Gerais, Mun. Itacarambi/Januária, vale do Rio Peraçu, illustrated in Costa et al. (1998: Fig. 29); cent.-N Minas Gerais, Mun. Forteirinha, 8 km S of town towards Riacho dos Machados, 7 Nov. 1988, Taylor & Zappi (obs.); Mun. Grão Mogol, subida da Trilha da Tropa, 27 May 1987, Zappi et al. in CFCR 11973 (SPF); Mun. Cristalina, road to town from Grão Mogol, 14 Apr. 1981, Pirani et al. in CFCR 917 (SPF, K); NE Minas Gerais, Mun. Itinga, on road BR 367, 41°48'W, 15 Feb. 1988, W.W. Thomas et al. 5971 (SPF, NY); Mun. Itabirim, 1 km W of town, 0.5 km N of Rio Jequitinhonha, 18 Nov. 1988, Taylor & Zappi (K, photos).

CONSERVATION STATUS. Lower Risk (1); PD=2, EI=2, GD=2. Short-list score (1×6) = 6. This species is locally a co-dominant element of the caatinga flora.

The type locality, as given by Glaziou (1909: 327), is assumed to be false and probably an invention to disguise the fact that he was not the real collector (cf. Wurdack 1970). It may be no
coincidence that the Glaziou number for ‘Opuntia rubescens’ [sensu Schumann (1890), non DC.], Gl. 14865, which is Tacinga braunii (q.v.), immediately precedes that for T. inamoena (Gl. 14864) and both species grow together in the valley of the Rio Jequitinhonha, north-eastern Minas Gerais, where T. braunii is endemic. It seems probable, therefore, that the type of T. inamoena came from north-eastern Minas Gerais, where it reaches its southern limit.

Braun & Esteves Pereira (1989: 272) remark that Opuntia inamoena reaches the state of Espírito Santo, but have so far apparently failed to substantiate this claim by the mention of a definite locality.

The true T. inamoena has spineless stem-segments as in T. funalis and T. braunii, but, as in those species, its abundant fine glochids demand that it be treated with appropriate respect and handled only with forceps. Forms with stems bearing occasional spines are usually to be referred to the following hybrid:–

**Tacinga xquipa** (F. A. C. Weber) N. P. Taylor & Stuppy in Succulent Pl. Res. 6: 00 (2001). Type: Brazil, Pernambuco, without date or collector (P†).

Opuntia quipa F.A.C. Weber in Bois, Dict. hort.: 894 (1898).


[T. inamoena × T. palmadora]

**VERNACULAR NAME.** Quipa.

Like T. inamoena, but stem-segments with occasional scattered spines, mainly at apex. Flowers not seen. Fruit variable in shape and colour.

Caatinga, c. 200–700 m, of sporadic occurrence throughout the range of T. palmadora where T. inamoena is also present. Endemic to North-eastern Brazil.

PERNAMBUCO: without locality (locus classicus of accepted name).


**CONSERVATION STATUS.** Lower Risk.

Although previously treated as a synonym of T. (Opuntia) inamoena, Weber’s diagnosis of O. quipa mentions the presence of occasional spines indicating hybridity.

The commonest and most widespread hybrid amongst the cacti of Eastern Brazil, the two parental species being frequently found growing together or in close proximity.
4. BRASILIOPUNTIA (K. Schumann) A. Berger

Entwicklungslinien Kakt.: 94 (1926). Type: Cactus brasiliensis Willd.

A very distinct, highly specialized, monotypic, arborescent genus, which is allied to Opuntia sensu stricto on the basis of seed-morphology/anatomy (Stuppy 2001), but with a cylindrical, apical leader shoot of indeterminate (unjointed) growth and markedly different pollen (cf. Leuenberger 1976). The adult tree displays unique shoot-morphology, the erect, cylindrical leader, giving rise to progressively more flattened, lateral stem-segments, the ultimate of which are very thin, hardly succulent, almost leaf-like and drought-deciduous. However, the first shoot (plumule) of the seedling, which arises between massive cotyledons, is thin, clearly flattened and early-determinate (cf. Opuntia sens. str.), soon giving rise to one or more equally flattened, subapical secondary segments and sometimes supplanted by stronger shoots of indeterminate growth arising from the axes of the cotyledons. The cylindrical, indeterminate leader shoot(s) develop from either of these sources and may be cylindric from the beginning or remain ± flattened for some time. Such leader stems show very early periderm formation, but the production of glochids from their areoles begins only when they have attained at least 3 years of age.

1. Brasiliopuntia brasiliensis (Willdenow) A. Berger, l.c. (1926). Type: probably a living plant in the Berlin botanical garden; no material extant at B-W. Lectotype (designated here): W. Piso, Historia naturalis Brasiliae: illustration, p. 100, below (1648); cf. Willdenow, l.c. infra.


Cactus heteroclads St. Hilaire, Voy. Rio de Janeiro and Minas Gerais 2: 103 (1830). Type: Rio de Janeiro, not known to have been preserved.


Holotype: Brazil, Minas Gerais, Itinga, 17 Oct. 1984, Rizzini & Mattos-Filho 38 (RB; UFMT, iso.).

VERNACULAR NAMES. Urumbeba, Rumbebra, Cumbeba, Mumbeca, Mumbbeo, Facho-de-renda, Palmatória grande, Palmatória-do-diabo, Ambeba, Arumbeva, Gerumbeba, Jurubeba, Palmadora, Palmatória, Xiquexique-dos-sertão.

Tree to 10(-20) m, trunk to 35 cm diam., cylindric, with clusters of spines to 9 cm long; pith chambered. Branches dimorphic, patent; intermediate joints cylindric, 20–100 cm, ultimate joints (4–)6–15 × 3–6(–7) cm, rhomboid to obovate, irregular at base, thin, bright to dark green, deciduous. Areoles on the lateral stem-segments 15–30 mm apart, with white felt, spineless or with 1 spine to 40 mm, those on the leader shoot with 1–3 or more spines, or those that have given rise to lateral stem-segments spineless, producing brown glochids at 3 years old; leaves early deciduous, ovoid or more elongate on the leader shoot, fleshy, bright green. Flowers from near the apex of the leader shoot or terminal stem-segments, or by proliferation from the pericarps of old flowers, c. 2.5–3.5 × 4.5 cm; pericarp globose, obovoid, elongate or elongate-flattened, c. 8–28 × 9–12 mm, green, tuberculate, bearing scale leaves c. 1 mm long, subtending areoles with white wool; outer perianth-segments to 15 mm, ovate,
greenish to yellowish, erect to spreading, innermost to 20 mm long and 10 mm broad, lanceolate to spatulate, yellow, spreading; stamens to 7 mm, anthers c. 0.6 mm, whitish; style c. 9 × 1.5 mm, whitish, stigma-lobes 3–6, exerted, to 4.5 mm. Fruit 2–4 cm diam., solitary or clustered-proliferous, globose to obovoid or pear-shaped, purplish red, orange-red or pale yellow, with areoles bearing conspicuous clusters of dark brown glochids; funicular pulp fibrous, white, yellowish or deep red (fide Britton & Rose), placenta greenish. Seeds 1–5, mostly 2, per fruit, to 8–10 mm diam.

Widespread southern neotropical element: restinga, drier phases of *Mata atlântica*, agreste, caatinga, *mata de brejo, mata seca* (on limestone), *mata de galeria* and *mata do planalto*, especially on deep sandy substrates and as a lithophyte, near sea level to c. 1000 m, western Paraíba, eastern and central-southern Pernambuco, Alagoas, Sergipe, north-western, northern and eastern Bahia, north-eastern and central-southern Minas Gerais and Espírito Santo; semi-humid forests of extra-Amazonian Brazil; Atlantic drainage of Andes eastwards (Peru, Bolivia, northern Argentina, Paraguay). Map 12A.

PARAÍBA: Mun. Cazajéiras, plant seen growing outside pharmacy in the town on road near eastern access to highway BR 230, ex Fazenda Capoeiras, east of town, where said to be frequent and increasing (property of owner of pharmacy), 3 April 2000, E.A. Rocha et al. (K, photo).


CONSERVATION STATUS. Lower Risk (1); PD=4, EI=1, GD=2. Short-list score (1×7) = 7. Much of its habitat, especially the Atlantic Forest and agreste, has been destroyed in Brazil, but it does occur in some Parques Nacionais and has a wide distribution in the southern Neotropics, although its status outside of Brazil is little known.

This widespread species, which is broadly circumscribed here, is rather variable in fruit shape and colour and in the number, shape and colour intensity of its perianth-segments. In the population sampled as Erskine 132 (see above) pericarpel shape varied from globose to very elongate or flattened and across the full range of the taxon fruit colour does not appear to present a consistent geographical pattern (there are disjunct occurrences of both yellow and reddish to purple colorations). At least some forms from the Brazilian Nordeste have reddish, ovoid fruit, and one such was distinguished as Opuntia bahiensis by Britton & Rose (1919), whom, it seems, assumed that the type of Cactus brasiliensis came from Rio de Janeiro, where the species has globose to depressed, yellow fruit. Willdenow, however, did not state the origin of the plant grown at Berlin, but made reference to Piso, i.e. Historia naturalis Brasiliae (Piso 1648). One of Piso's illustrations is here designated as lectotype and, since Piso was based at the Dutch colony at Recife, Pernambuco (Stafleu & Cowan 1983: 276) and a coloured copy of the same illustration in the contemporary work of Marcgraf (see Whitehead & Boeseman 1989: t. 3a) shows red fruits, it is clear that the name C. brasiliensis should be applied in its strictest sense to a red-fruited form from the Nordeste. Therefore, Britton & Rose's Opuntia bahiensis would be a synonym, even if the species was interpreted in a narrow sense (likewise Brasiliopuntia subacarpa Rizz. & Mattos-F.).
*5. NOPALEA Salm-Dyck


Seed-morphology/anatomy indicates that this small genus is very closely related to *Opuntia sensu stricto* (Stuppy 2001), but it differs markedly in flower- and pollen-morphology (Leuenberger 1976). Only the following introduced species is found in Eastern Brazil:


*Cactus cochenillifera* L., Sp. pl.: 468 (1753). *Opuntia cochenillifera* (L.) Miller, Gard. Dict. ed. 8: no. 6 (1768).

**VERNACULAR NAMES.** Palmatória, Palma, Palma-miuda, Palma-doce.

Shrubby, to 3 m tall, main stem with segments flattened at first, cylindric in age. Branches erect, sometimes pendent, stem-segments (10–)12–26 × (3–)8–10 cm, narrowly elliptic or obovate, bright green, sometimes glaucous. Areoles 25–30 mm apart, with white felt; spineless. Flowers from the apex of the terminal segments, 5–6 × 2–2.5 cm; pericarpel obovoid, to 30 mm, green, with areoles with white wool and few, dull pink bract-scales; outer perianth-segments to 15 mm, lanceolate, deep pink, erect, innermost 20 mm, lanceolate to spatulate, deep pink, erect, clasping the stamen filaments, these exserted, dark pink; stigma-lobes long-exserted, green. Fruit rarely formed in Brazil, to 4 cm, solitary, obovoid, red; funicular pulp translucent, purplish, placenta greenish. Seeds few per fruit, to 4 mm diam.

Introduced: on cultivated land throughout North-eastern Brazil (native to Mexico and Central America). The following are representative records of the species and do not account for its extensive occurrence in NE Brazil:


Like *Opuntia ficus-indica* (see below), this species is cultivated as cattle fodder for use during drought and is also suitable as a host for the cochineal insect.
6. **OPUNTIA** Miller


Shrubs or occasionally treelike, 0.5–5.0 m; branches not dimorphic; stem-segments compressed, orbicular, obovate to elliptic or rhomboid in outline, sometimes becoming cylindric through prolonged secondary growth at base of plant; areoles in the axils of deciduous leaves, with glochids and felt, spines usually present or absent in some forms of no. 3. Leaves minute, subulate, sessile, fleshy, early deciduous. Flowers solitary, mainly on the margin of the joint or born by proliferation from the flower receptacle; epigynous, pericarpel globose or turbinate, with areoles and leaf-like, fleshy, green or coloured bract-scales; perianth multiseriate, tube 0, outer perianth-segments coloured, fleshy, inner segments coloured, delicate, spreading; stamens numerous, spreading, sensitive and closing around the style when touched; pollen with reticulate exine. Fruit solitary or clustered-proliferous; turbinate with a pedicillate base or globose, with a broad, not very deep umbilicus and deciduous flower remnants; funicular pulp translucent or opaque, fibrous; placenta white, greenish or coloured. Seeds few to numerous, lenticular reniform, to 5 mm diam., enclosed in a hard, bony funicular envelope.

A genus of at least 150 species, even when (as here) narrowly circumscribed, ranging from Canada to southern South America, but with only 1, marginally represented species native to sandy places in the *Mata Atlântica* zone within the core area of Eastern Brazil (plus 2 spp. introduced from the Northern Hemisphere).

1. Areoles with clusters of numerous golden spines; segments ± orbicular (cultivated / rarely naturalised) *2. dillenii*
1. Areoles spineless or with few or dark brownish spines; segments obovate, elliptic or rhomboid

2. Segments dark green; fruits proliferating (E Minas Gerais and occasionally cultivated elsewhere) 1. *monacantha*
2. Segments generally somewhat glaucous; fruits never proliferating (cultivated everywhere) *3. ficus-indica*


**VERNACULAR NAMES.** Urumbeba, Palmatória, Monducuru.

Shrubby, to 3 m tall, main stem flattened. Branches erect to decumbent; stem-segments 8–20 × 4–10 cm, rhomboid to obovate, narrow at base and irregular in outline, dark green. Areoles 20–40 mm apart, with white to pale brown felt; spines 0–1(–2), (5)–15–50(–60) mm, pungent, pale grey. Flowers arising at the apex of the terminal segments or born by proliferation from the flower receptacle, 7–10 × 3–6 cm; pericarpel narrowly turbinate, to 30–70 mm, bright green, with areoles with white wool and few, dull red bract-scales; outer perianth-segments to 20 mm, lanceolate, bright yellow with deep red shades outside, spreading; innermost 20 mm, spathulate, bright yellow, spreading; stamens exposed, sensitive; stigma-lobes exserted. Fruit to 5–10 cm, solitary or clustered-proliferous, narrowly
turbinate to obovoid, curved at base, greenish to reddish outside; funicular pulp translucent, whitish, placenta yellowish. Seeds many per fruit, to 4 mm diam.

Southern humid/subhumid forest element: sand-dunes in open carrasco, c. 1000 m, central-eastern Minas Gerais, and open restinga near sea level, southern Espírito Santo (and presumably northern Rio de Janeiro); South-eastern and Southern Brazil; Paraguay, Uruguay and northern and eastern Argentina; frequently naturalized or planted elsewhere (including North-eastern Brazil). Map 17A.


CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=1. Short-list score (1x4) = 4.

This species has previously been known as either Opuntia monacantha Haw. or O. vulgaris Miller, but both of these names are beset with nomenclatural difficulties. The former, which is maintained here, was unequivocally based on a collection from Barbados (Lesser Antilles), whence only O. dillenii (Ker-Gawler) Haw. is currently recorded as native (Howard 1989). In order to maintain its use for the plant now widely associated with Haworth’s name, a Brazilian neotype has been designated above. This assumes that the provenance data given by Haworth were erroneous, or that O. monacantha as now understood had been introduced to Barbados by the early years of the 19th Century. In any case, Haworth’s brief and unsatisfactory diagnosis does not agree with O. dillenii and so neotypification or rejection are the only realistic options open. The above action seems marginally preferable to taking up the next available, well-typified name, O. urumbeba (Vell.) Steudel, which unfortunately has never been used, even though its epithet repeats the distinctive, vernacular name for the plant. The name Cactus monacanthos Willd. (1814) was cited by Haworth with a question mark as a possible synonym of his Opuntia monacantha. This indication of doubt rules out any consideration of Haworth’s name as a combination based on that of Willdenow, which cannot be typified.

Opuntia vulgaris Miller has been used in two quite different senses (O. humifusa Raf. and O. monacantha), but is now considered to be a renaming of Cactus opuntia Linnaeus, a taxonomic synonym of O. ficus-indica (L.) Mill. (Leuenberger 1993).

O. monacantha has been recorded only rarely as a native plant within the core area covered here, where it is at its north-eastern limit. The collections from central-eastern Minas Gerais are rather disjunct on present knowledge, but at least that from Rio Vermelho was from a population which appeared to be native and in an edaphically appropriate sand-dune habitat. Similar disjunct populations are known from localities remote from the coast in the state of São Paulo and it is probably this species that is depicted growing near Lorena, São Paulo state, in Martius, Flora brasiliensis 1 (1, Tabulae Physiognomicae): t. VII (1841).


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Cactus ficus-indica L., Sp. pl.: 468 (1753).


Shrubby, to 6 m tall, main stem with segments flattened at first, cylindric and forming greyish bark in age. Branches erect; stem-segments 20-40 × 12-20 cm or more, elliptic or obovate, grey-green, sometimes glaucous. Areoles 20-50 mm apart, with white or brown felt; spineless or with minute occasional spines to 5 mm. Flowers from the apex of the terminal segments, 6-9.5 × 5-6 cm; pericarpel obovoid, to 50 mm, green, areoles with dull red bract-scales; outer perianth-segments to 20 mm, rounded, yellow to orange, sometimes reddish, spreading; innermost 30 mm, lanceolate to spathulate, yellow to orange, spreading; stamens exerted, filaments dark pink, sensitive; stigma-lobes exerted. Fruit 5-10 × 4-8 cm, solitary, obovoid, yellow or deep orange (sometimes reddish); funicular pulp usually...
orange or yellowish, placenta greenish. Seeds many per fruit, to 5 mm diam. Chromosome number: 2n = 66, 88 (fide Kiesling 1999).

Introduced and increasingly planted about houses and on farms everywhere in North-eastern Brazil, often at the expense of other cactus vegetation. According to Kiesling (1999) originally domesticated in Mexico about 9000 years ago, having back-crossed with its putative wild ancestors, such as *O. streptacantha* and *O. megacantha*; subsequently introduced throughout the warmer parts of the world and sometimes becoming a serious pest. The following are representative records only, the plant being found in all states in Eastern Brazil:


BAHIA: Mun. Iramaia, 27.5 km NW of Pê-de-Serra, 5 Feb. 1991, Taylor et al. (ZSS, photos); Mun. Poções, road BR 116, 9 km S from the town, Fazenda Boa Esperança, 800 m, 5 Apr. 1988, L.A. Mattos Silva et al. 2334 (K, CEPEC).


An important source of cattle fodder during drought in the *sertão*. Also producing delicious fruits for human consumption.
CACTOIDEAE

Stems leafless or leaves replaced by minute scales; glochids lacking, spines never barbed; pollen mostly tricolpate; seeds with the testa exposed.

The deletion of an approximately 700 base-pair intron in the chloroplast-encoded gene rpoC1 supports a monophyletic origin for the subfamily Cactoideae of the Cactaceae (Wallace & Cota 1996). The tribes and their generic composition adopted here is that employed by Barthlott & Hunt (1993) modified on the basis of unpublished cladistic analyses, derived from DNA gene sequence data, presented at IOS meetings or otherwise communicated by R. Wallace (Iowa State Univ., USA) since 1993.

Tribe HYLOCEREEAE F. Buxbaum

The circumscription of Hylocereus adopted here is influenced by an unpublished phylogeny, based on DNA gene sequence data, presented by R. Wallace (Iowa State Univ., USA) at the IOS Congress, Bologna, September, 1996. This indicates that when Selenicereus is circumscribed to include sect. Salmyckia D. Hunt (1989) it is paraphyletic in respect of Hylocereus. Hitherto Hylocereus has been distinguished from the very similar trigonous-stemmed members of Selenicereus sect. Salmyckia on the basis of large scales versus spiny areoles on the pericarpel, flower-tube and fruit. However, such a separation was weakened from the start by the occurrence of occasional pericarpel spines in the otherwise typical Hylocereus species, H. trigonos (Haw.) Safford (syn. Cereus plumieri Gosselin, C. pomifer Weingart; see Hunt 1984: 41 & fig. 12), native of the SE Caribbean. The gene sequence data imply that the shared trigonous stems, whose similarity has been the cause of confusion between the two taxa treated below, are in fact a character uniting them generically and that their floral differences are perhaps only significant at subgeneric or sectional level.

7. HYLOCEREUS (A. Berger) Britton & Rose


Sprawling and clinging to rocks or climbing in trees; freely producing aerial roots; stems stout, trigonous or 3-winged, irregularly constricted, the juvenile bearing numerous, fine bristle-like spines, the adult with few, very short, stout, conical spines per areole. Flowers nocturnal, very large, to 32 × 25-34 cm, the pericarpel and tube bearing conspicuous podaria subtending large bract-scales and/or spiny areoles, the scales and spines becoming more pronounced on the reddish, ± globose fruit. Seeds to 3 mm, testa smooth, black.
1. Pericarpel, flower-tube and fruit bearing conspicuous spines; stem edges green, never horny (native, widespread)

**1. setaceus**

1 Pericarpel, flower-tube and fruit bearing large bract-scales only; stem edges often with a horny margin

(introduced, common near habitations) *2. undatus*

**1. Hylocereus setaceus** (*Salm-Dyk*) **N. P. Taylor** comb. nov. Type: assumed not to have been preserved. Neotype (designated here): Pfeiffer & Otto, l.c. infra, t. 16 (1839).


*Cactus triangularis* Vell., Fl. flum.: 206 (1829), Icones 5: t. 24 (1831), non L. (1753).


[[Mediocactus coccineus** sensu (Salm-Dyck) Britton & Rose, Cact. 2: 211, fig. 290 (1920) non Cereus coccinus** Salm-Dyck ex DC.**; see Hunt (1989).]]

[[C. triangularis** sensu K. Schum. in Martius, Fl. bras. 4(2): 208–209 (1890), pro parte, tab. excl., non (L.) Haw.]]


**VERNACULAR NAMES.** Rainha-de-noite, Mandacaru-de-três-quinas, Espada-de-jacaré.

Scrambling, climbing or epiphytic on trees or on rocks, sometimes forming large clumps, with basitonic or mesotonic branching. Stems 3(-5)-angled, to 100 × 1–4.5 cm, sometimes constricted, very woody at base, margins straight or undulate, never horny; epidermis bright green, yellowish when exposed. Areoles 4–6 mm diam., 1.5–4.5 cm apart (in juvenile forms as close as 4 mm or less, with very slender, bristly spines and hairs). Central spines 3–6, conic, 1–6 mm, occasionally accompanied by bristly, more delicate radial spines. Flowers nocturnal, 20–32 × 22–25 cm; pericarpel greenish, densely covered in tubercles/podaria bearing areoles with 10–15 pungent spines; flower-tube infundibuliform, 10–13 × 1.5–2.5 cm, with scattered woolly areoles and acute, spreading bract-scales; perianth-segments to 12 cm, outer segments reflexed, lanceolate to linear, fleshy, dark red-green, inner segments to 43 mm wide, erect to spreading, lanceolate and fimbriate, delicate, white; stamens exserted in relation to the perianth-segments, curved, anthers linear; style 15–17 × 0.5 cm, stigma-lobes c. 16, exserted; ovary locule ovoid to oblong in longitudinal section. Fruit ovoid, to 9 × 7–8 cm, floral remnants deciduous; pericarp greenish then bright red when ripe, covered in spiny areoles at first, spines to 2 cm; funicular pulp white. Seeds c. 2.5–3.0 mm, cochlleariform, black, shiny; testa-cells flat, smooth.

Widespread neotropical element: epiphyte, climber or lithophyte (on limestone or on gneiss/granite inselbergs) in caatinga-agreste, cerradão, Mata atlântica, mata de brejo, mata de planalto and restinga, near sea level to c. 900 m, widespread in Eastern Brazil from northern Piauí southwards; Northern, Central-western and Southern Brazil (southern Pará southwards to Mato Grosso do Sul and Paraná); Central (?) and South America (southwards to E Bolivia, N Argentina and Paraguay). Map 11.


RIO DE JANEIRO: Mun. Santa Maria Madalena, access road to the town, 22°0'55"S, 42°7'30"W, 21 Nov. 1999, Zappi et al. 355 (K, UEC).

CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=1. Short-list score (1×4) = 4. Much of its presumed former habitat has been destroyed in North-eastern Brazil.

In its vegetative state this widely distributed, native species is sometimes confused with the introduced H. undatus (see below), but the pericarpel and immature fruit is spiny and the stem-margins never horny. Its fruits are edible when red and mature. It is a close relative of a taxon cultivated in Colombia for the export of its yellow, egg-shaped, edible fruit, and of another known from Roraima in Northern Brazil (A. R. Pontes s.n., K, photo.), which is probably also the same as the plant from the Guianas recently illustrated and discussed by Leuenberger (1997: 48–51) as possibly identifiable with H. extensus (Salm-Dyck ex DC) Britton & Rose (Cereus extensus DC, tantum quod typ.). The Colombian plant, known in the British supermarket trade as ‘Pitaya’, has been tentatively referred to Selenicereus (sect. Salmdyckia) megalanthus (Schumann ex Ule) Moran, though it is possible that this name, based on a collection from the Amazonian drainage of Peru, will prove to be a further synonym of the Brazilian species treated here (Hunt 1992a). Indeed, it is possible that, when better understood, Hylocereus setaceus will prove to be the oldest name for a widespread neotropical species comprising all of the above as regional subspecies, amongst which Selenicereus tricae D. Hunt (1989) might also figure, extending the range of this complex to Central America (including southern Mexico).

It is likely that H. setaceus, sens. str., is significantly under-recorded in the northern half of its range within Eastern Brazil, as is suggested by the isolated collections from northern Piauí and Ceará, which are more than 700 km distant from the next nearest records, in northern Bahia and eastern Pernambuco. Plants resembling the species have been seen in north-central...
Maranhão, near Peritoró, while travelling the road connecting Teresina (PI) with Belém (PA), and it may be expected to occur in Paraíba, perhaps in brejo forest.

*2. Hylocereus undatus (Haworth) Britton & Rose in Britton, Fl. Bermuda: 256 (1918); Cact. 2: 187–188 (1920). Type: a plant cultivated at the London Horticultural Society, originating from China, assumed not to have been preserved. Neotype (Taylor 1995: 119–120; superseding that designated by Scheinvar 1988): Curtis’s Bot. Mag. 44: t. 1884 (1817), as ‘Cactus triangularis’. Scheinvar’s earlier choice of a neotype from Oaxaca, Mexico is in serious conflict with Haworth’s protologue, which calls for a plant with green stems (not glaucous as in Scheinvar’s neotype, Kimnach & Moran 171, which on other characters also certainly does not represent Hylocereus undatus as universally understood; Kimnach, pers. comm.). Presence or absence of a glaucous waxy stem deposit is an important character for delimitation of species in this genus.

Cereus undatus Haw. in Phil. Mag. 7: 110 (1830).

Scrambling, climbing or epiphytic, forming large woody masses of branches, with basitonic or mesotonic branching. Stem-segments trigonous/3-winged, to 100 x 4–7(–8) cm, sometimes constricted, narrow and very woody at base, margins crenate, horny in age; epidermis bright green, yellowish when exposed to full sun. Areoles 4–6 mm diam., (2.5)–3–6(–8) cm apart, with 2–6 conic, c. 4 mm spines. Flower-bearing areoles in the axils of the stem’s marginal crenations; flowers nocturnal, very showy, to 30 x 34 cm; pericarpel greenish, densely covered in rounded, broad-based, green or reddish bract-scales, but lacking spines; flower-tube infundibuliform, c. 12 x 1.5–2.5 cm, covered in broadly triangular, adpressed, to acute, spreading bract-scales; perianth-segments up to 14 cm, outer segments reflexed, lanceolate to linear, fleshy, dark red with green bases, inner segments erect to spreading, spathulate and apiculate, fimbriate, delicate, white; stamens disposed in a broad ring around the style, sometimes curved, anthers linear; style 14–20 x 0.8 cm, stout, stigma-lobes c. 20 or more, exserted; ovary locule oval in longitudinal section. Fruit ovoid to globose, to 12 cm diam., flower remnants deciduous; pericarpel covered in broadly triangular, fleshy, orange-yellow to bright red bract-scales; funicular pulp white. Seeds c. 3 mm, cochleariform, black, shiny; testa-cells flat, smooth.

Introduced as garden plant and sometimes escaping into roadside trees and maritime scrub; perhaps native in Mexico and Central America, commonly introduced elsewhere in the tropics and subtropics worldwide.


Widely cultivated in South America, this species may be found at the sites of old houses, where it often scrambles to the tops of trees. However, it does not seem to be able to reproduce by means of seed in Eastern Brazil, perhaps because all or most individuals belong to the same clone.

Some published reports of this species actually refer to the native H. setaceus (see above).
• 8. SELENICEREUS (A. Berger) Britton & Rose


An ill-defined genus of c. 15 species, native of Mexico, the Caribbean and northern South America. Typically, the genus has cylindrical, scandent stems with 5 or more low ribs (sect. Selenicereus), but the species encountered in Brazil have flattened stems. One such is native of Northern Brazil, Selenicereus (sect. Strophocactus) wittii (K. Schum.) G. Rowley (Amazônia, igapó). A detailed account of this species can be found in Barthlott et al. (1997).

Only the following Mexican plant is encountered in Eastern Brazil:

*Selenicereus anthonyanus (Alexander) D. Hunt in Bradleya 7: 93 (1989), native of southern Mexico, is the cactus most frequently cultivated as a house plant (in pots and hanging baskets) in Eastern Brazil. It is more rarely planted outdoors, where it has been observed climbing trees in a semi-naturalized state in South-eastern Brazil, outside the area treated here. It resembles the following genus in its vegetative state (especially the Mexican Epiphyllum anguliger), but has flowers with a stouter, much shorter tube and bristly pericarpel.
9. EPIPHYLLUM Haworth

Syn. pl. succ.: 197 (1812). Type and only species native of Eastern Brazil:


Cactus phyllanthus L., Sp. pl. 1: 469 (1753).

Epiphytic, forming woody clumps, with basitonic and mesotonic branching. Stems flat, alate, sometimes trigonous at base, 15–100(–150) × 3–(6–)8 cm, to 1 cm thick, lanceolate, narrow at base, margins crenate, teeth 2.5–4.5 cm apart, apex obtuse, midrib rather woody; epidermis green, yellow-green to reddish or purplish when exposed, margins sometimes horny in age; areoles spineless, but sometimes bristly on old branches. Flower-bearing areoles in longitudina section. Fruit narrowly ovoid to pear shaped, apiculate, to 10 x 3.5 cm, dehiscent by lateral slit, flower

Widespread neotropical element: epiphyte in Mata atlântica, caatinga-agreste, mata do planalto, mata ciliar and cerrado, near sea level to at least 1300 m, ± common throughout the more humid parts of Eastern Brazil; Neotropics from Central America southwards. It is the most widespread cactus species in Eastern Brazil and only a few representative collections/observations are cited here. There are currently no records from Rio Grande do Norte.


RIO DE JANEIRO: Mun. Santa Maria Madalena, access road to the town, 22°0'55"S, 42°7'30"W, 21 Nov. 1999, Zappi et al. 356 (K, UEC).

CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1×5) = 5.

Widespread in South America in various habitats, this is perhaps the only epiphytic cactus likely to be found in, or bordering on cerrado vegetation.
*Epiphyllum oxypetalum* (De Candolle) Haworth from southern Mexico and Central America is occasionally cultivated and has been recorded planted or escaped outdoors in the states of Pernambuco: Mun. Moreno, 7 Mar. 1936, B. Pickel 4121 (IPA); Mun. Arcoverde, 14 May 1966, D. Andrade-Lima 66-18 (IPA); and Bahia: Ilha de Itaperica, Mun. Vera Cruz, 31 Mar. 1997, Aline 1 (ALCB). It is easily distinguished from *E. phyllanthus* by its very long, slender, cylindric to angled, basal extension shoots and flowers to 27 cm in diameter, the outer perianth-segments conspicuously reddish to deep pink.
Tribe ECHINOCEREEAE  F. Buxbaum

The tribal placement of the following genus is rather uncertain at present and awaits the results of analysis of DNA gene sequence data. It is placed in this tribe, including the former Leptocereeae, only because the genus from which it was separated, i.e. Acanthocereus, is currently placed there.

10. PSEUDOACANTHOCEREUS Ritter


An isolated genus of only two species, comprising *P. sicariguensis* (Croizat & Tamayo) N. P. Taylor (NE Colombia & NW Venezuela) and the following:


VERNACULAR NAME. Catana-de-jacare.

Shrubby, scrambling or decumbent, sometimes forming large clumps, with basitonic or mesotonic branching. Stems erect to decumbent, 1.5–4.5 cm diam.; 2–6(–7)-ribbed, ribs high, acute, somewhat undulate; epidermis dark green to greyish. Areoles 3–6 mm diam., 2–7 cm apart, felt white, soon glabrescent, areolar growth ± indeterminate. Spines 8–14, central and radial difficult to distinguish, 5–50 mm. Flower-bearing region of stem not differentiated; flowers nocturnal, 15–17 × 11–12 cm; pericarpel green with dull pink tinge, bearing tubercles/podaria and areoles with bristles/spines to 5 mm; flower-tube infundibuliform, 9–10 × 1.4–2.0 cm, bearing scattered areoles with minute spines; perianth-segments to 60 mm, outer segments reflexed, lanceolate, fleshy, dull pink to reddish brown, inner segments spreading, lanceolate to spathulate and fimbriate, delicate, white; stamens exerted in relation to the perianth-segments, curved, anthers linear; style c. 100 × 3 mm, stigma-lobes 8–11, exerted; ovary locule rectangular to oblong in longitudinal section. Fruit globose, to 5.5–8.0 cm diam., floral remnants deciduous; pericarp greenish, becoming yellow when ripe and falling to the ground, smelling of pineapple, bearing podaria and deciduous areoles with white to pale brown felt; funicular pulp white. Seeds c. 5 mm, cochleariform, brown, dull; testa-cells flat, elongate, cuticular folds coarse, dense.

Eastern *caatinga-agreste* element: within and at the margins of *caatinga-agreste*, 40–700 m, east of the Chapada Diamantina crestline in northern and central-eastern Bahia, and in the drainage of the Rio Jequitinhonha (associated with gneiss/granite inselbergs) of north-eastern Minas Gerais (apparently disjunct, but possibly under-recorded through destruction of habitat in intervening areas). Endemic to the core area of Eastern Brazil. Map 31A.


MINAS GERAIS: Mun. Pedra Azul, 8 km W of the town towards road BR 116, 18 Oct. 1988, Taylor & Zappi in Harley 25185 (K, SPF); Mun. Itinga, 2 km E of the town, S of Rio Jequitinhonha, 14 Dec. 1990, Taylor & Zappi 768 (K, ZSS, HRCB, BHCB); Mun. Itaobim, 1 km W of Itaobim, 0.5 km N of Rio Jequitinhonha, 16°34'S, 41°31'W, Taylor & Zappi in Harley 25531 (K, SPF); Mun. Coronel Murta, 5 km SE of the town on road BR 342 to Araçuai, 21 Feb. 1988, Supthut 8863 (ZSS).

CONSERVATION STATUS. Vulnerable (2) [criteria C1/2a]; PD=3, EI=1, GD=2. Short-list score (2×6) = 12. Much of its preferred habitat has been destroyed and its original range may have been more extensive and less markedly discontinuous than is seen today.

This inconspicuous and, when out-of-flower, rather ugly plant appears to be of erratic occurrence, which may in part be the result of the widespread destruction of the agreste/caatinga, under whose shade it prefers to grow. While it is a variable species, there are no reliable differences between plants from Bahia and Minas Gerais and P. boreominarum Rizz. & Mattos-F. cannot be justified even at infraspecific rank.

Uebelmann (1996), under the number ‘HU 1197’, reports ‘Pseudoacanthocereus sp.’ from Penedo, Alagoas [‘Sergipe’]. Apart from the doubts surrounding the location of this record, it seems unlikely that this plant would occur so close to the coast, and it is therefore to be discounted as a misidentification.
Tribe RHIPSALIDEAE DC.

In terms of numbers of species, this is the second largest tribe of Cactoideae in Eastern Brazil (after Cereeae). All the species treated here are epiphytes and/or lithophytes in the core area of Eastern Brazil, with flowers < 6 cm long.

11. LEPISMIUM Pfeiffer


Epiphytic, branching mesotonic or basitonic, or branching acrotonically only when damaged, freely producing aerial roots in the species treated here; stem-segments often angled or flat with the areoles subtended by crenate or serrate marginal teeth, not deciduous as units when old. Areoles sometimes densely hairy, scale leaves sometimes clearly visible; composite terminal areoles lacking. Flowers either immersed in the areole or pendent, often campanulate; stamens generally much shorter than the perianth-segments, never exserted; pericarpel ridged or angled, rarely almost terete; tube inconspicuous in the species treated below. Fruit globose, ellipsoid or turbinate; pericarp ridged when immature (except in no. 43), white, magenta, red, dark wine-coloured or blackish.

A genus of 14 species in the Andes (Peru to Argentina) and south-eastern South America, with a centre of diversity in Bolivia. Species of Lepismium can be distinguished from other Rhipsalideae by the combination of the basi- to mesotonic (not acrotonic) branching pattern and non-deciduous stem-segments. The genus is restricted to the Mata atlantica in Eastern Brazil.

1. Distal parts of stems flattened, with conspicuous marginal teeth to at least 4 mm long
   1. houlletianum
2. Stems flattened or 3–6-winged/angled/ribbed, with strongly adpressed marginal teeth/crenations to at most 2 mm long
   3. cruciforme
2. Areoles woolly at anthesis and subsequently; flowers immersed in the areoles, 1 or more per areole, whitish to deep pink (Pernambuco southwards)
   3. warmingianum
2. Areoles not woolly; flowers 1 per areole, not sunken, whitish (SE Brazil)


Rhipsalis houlletiana Lem. in Ill. Hort. 5, misc.: 64 (1858). R. houlletii Hook. f. in Bot. Mag. 100: t. 6089 (1874). Type: as above.


VERNACULAR NAME. Rabo-de-Arara.

Plant 1–2 m, pendent; basal shoots erect at first; stem-segments 15–40 × 2–7.5 cm (towards apex), cylindric and woody at base, flattened distally and only to c. 2.5 mm thick (away from the vascular midrib), margins strongly serratate-dentate, teeth mostly acute, not adpressed but sometimes incurved, to 6 mm or more long, epidermis dark

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green to glaucous, sometimes purple tinged at the stem margin; seedlings with stems flattened at first. Areoles in the axis of the teeth, glabrous or with 1–3 minute bristles. Flower-buds somewhat erumpent; flowers scented, pendent, c. 20 × 15–26 mm, perianth-segments 10–15, white (yellowish post anthesis), c. 17 × 3 mm, not expanding fully; stamens in two weakly defined groups, the innermost clustered around the style, the remainder spreading out against the perianth and the largest slightly > half as long as the inner perianth-segments, white, but strikingly orange reddish at base (yellowish at base in the forma regnellii); style white, exceeding stamens, stigma-lobes 3–6, to c. 3 mm, outspread, white becoming yellow in age; pericarpel cylindric, c. 6–8 × 2.5–4 mm, longitudinally ridged. Fruit 5–8 mm diam., ovoid to globose, magenta to deep pink or black. Chromosome number: 2n = 22 (Barthlott 1976).

Southern humid forest element: epiphyte in *Mata Atlântica*, including *mata de neblina*, 500–1900 m, central and south-eastern Minas Gerais; South-eastern and Southern Brazil; North-eastern Argentina (Misiones). Map 17B.


**CONSERVATION STATUS.** Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (lx5) = 5.

Lützelburg (1926, 3: 111) reports this species from eastern Bahia, but it has not been encountered subsequently and his record is very likely an error or misidentification.

As in the case of *Schlumbergera kautskyi* (see below), the pointed, marginal, stem-segment teeth (podaria) in this species are assumed to function as, and represent the equivalent of, leaf drip tips. It is rather variable in stem and floral characters.


*Rhipsalis warmingiana* K. Schum. in Martius, Fl. bras. 4(2): 291 (1890); G.A. Lindberg in Gartenflora 41: 8–12, figs 5–7 (1892).


*Rhipsalis gonocarpa* F.A.C. Weber in Rev. Hort. (Paris) 64: 427 (1892). Type: Brazil, São Paulo (assumed not to have been preserved).

Stems pendulous to 3 m; stem-segments 25–150 × 0.3–1.5(–2.5) cm, flat or 3–4-angled, flat segments only 1 mm thick away from the vascular midrib, margins serrate-crenate, teeth low, obtuse, to 2 mm proud of the stem and 1–2.5 cm apart on its margins, the pale, scarious scale leaves strongly adpressed, epidermis dark olive to yellow-green. Areoles in the axis of the scale-bearing teeth, felt 0 or very sparse prior to flowering, bristles 0. Flowers sweetly scented, pendent, to 27 × 23 mm; perianth-segments 8–12, largest to 15 × 5 mm, cream or white, not expanding fully; pericarpel green, 7–8 × 4 mm, distinctly angled; stamens white, yellow or reddish at base, arranged in two groups, the outermost longest, to c. 10 mm, the inner series clustered around the style; style c. 12 mm, stigma-lobes c. 5, 3 mm, cream. Fruit c. 12 × 10 mm, ridged and green to red when unripe, rounded, smooth, dark wine-coloured to black and opaque when ripe.

Southern humid forest element: epiphyte or lithophyte, *Mata Atlântica*, c. 750 m (MG), central-southern Minas Gerais and southern Espírito Santo (Domingos Martins); South-eastern and Southern Brazil; eastern Paraguay and north-eastern Argentina (Misiones). Map 17B.


CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1×5) = 5. Lower Risk taking its total range into account, but apparently rare in the region treated here.

Also reported from Bahia and Paraiba by Lützelburg (1926, 3: 111), but these are assumed to be misidentifications.

*Lepismium warmingianum* is the sister species of *L. lorentzianum* (Grisebach) Barthlott, from the eastern Andes of eastern Bolivia (Santa Cruz & Tarija) and north-western Argentina.


*C. tenuispinus* Haw. in Phil. Mag. 1: 125 (1827), *nom. rej.* Type: not known to have been preserved. Neotype (Taylor 1994): Lodgges, Bot. Cabinet 19: t. 1887 (1832).


*Lepismium radicans* Vochting in Jahrb. Wiss. Bot. Leipzig 9: 399 (1874); *Rhipsalis radicans* (Vochting) F.A.C. Weber in Bois, Dict. hort.: 1047 (1898). Type: not known to have been preserved.

*Note:* for further synonymy, see Britton & Rose (1923: 215). All synonyms relating to this species are included in the Index to names and epithets.

Stems pendent, creeping or trailing, to 3 m, 15–40(–60) × 1–3(–7.5) cm, flat or 3–6-angled/ribbed, crenate, often irregular, epidermis green, red tinged around the edges and areoles, or entirely red when fully exposed. Areoles in the axils of the marginal crenations, subtended by conspicuous scales prior to flowering, sunken, becoming rather large in age, with abundant wool in tufts to 5 mm or more long and weak bristles to 6(-10) mm, to 20 mm or more apart on the stem margins/angles. Flowers immersed in the areoles, to c. 15 × 10 mm; perianth-segments 5-6 visible from within, white, cream or pale to deep pink, opening widely. Fruit broadly turbinate to depressed-globose, to 8.5 × 8.5 mm, magenta to deep red, shiny. Chromosome number: 2n = 22 (Barthlott 1976).

Disjunct humid forest element: epiphyte or lithophyte, *Mata atlântica*, including *mata de brejo* (NE Brazil) and *restinga*, sea level to 1200 m, eastern Pernambuco to south-eastern Minas Gerais; South-eastern and Southern Brazil; south-eastern Paraguay and north-eastern Argentina. Map 15A.


CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1×5) = 5. Lower Risk taking its total range into account.

A common and highly variable plant in South-eastern Brazil, but apparently rare or seldom collected in the brejo forests of the Nordeste. Its sister species is L. incachacanum (Cárdenas) Barthlott, from Bolivia (Cochabamba & La Paz).
12. RHIPSALIS Gaertner


Including Erythrorhipsalis A. Berger (1920); Rhipsalis subg. Erythrorhipsalis A. Berger (1920).


Habit pendent when epiphytic, or erect to decumbent when on rocks; stems segmented, always ± acrotonically branched when apex undamaged (basal extension shoots excepted) and lacking sharp spines, though sometimes bristly; stem-segments terete (unribbed), ribbed, angled, winged or flat (2-ribbed), the non-basal segments deciduous when old. Areoles small to almost absent (R. pulchra) or sunken and conspicuous and/or woolly only after bearing flowers, subtended by small to minute scale leaves; terminal composite areoles often present. Flowers 1–13 per areole, whitish or tinged yellow or pink, rarely red, buds erumpent from sunken areoles or developing at the stem surface; pericarpel ± naked, tube almost 0, perianth-segments c. 5–18, reflexed or semi-patent (campanulate flowers); stamens strongly exerted or included. Fruit subspherical to ellipsoid, perfectly rounded (never angled), naked, white, orange, pink or purplish, pulp highly mucilaginous. Seeds small, mostly c. 1–1.5 mm, black-brown; testa surface ± smooth.

As currently circumscribed a genus of c. 35 species (Barthlott & Taylor 1995, Taylor & Zappi 1997) with a centre of diversity in South-eastern Brazil (especially southern Espirito Santo, Rio de Janeiro and Sao Paulo). The genus is divided into 5 subgenera, each of which is represented in Eastern Brazil, mainly distributed in the Mata atlântica and in humid forests associated with the campos rupestres. A minimum of 19 species is treated here (but see nos. 14 & 16, below), of which only 4 taxa (2 species, 2 subspecies) appear to be endemic, but the group remains poorly collected in North-eastern Brazil, where most of its habitat has been destroyed. Six species (nos 2, 13–16 & 18) only just enter the area covered, having the major part of their ranges further south and west.

Besides the taxa treated below, Lützelburg (1926, 3: 111) records R. clavata F. A. C. Weber (SE Brazil) and R. robusta Lemaire (= R. pachyptera Pfeiffer, SE to S Brazil) from eastern Bahia, which probably represent misidentifications (the former may be R. baccifera subsp. hileiaabaiana, the latter R. russellii). Lützelburg also records plants under the names R. cribrata (Lemaire) N. E. Brown and R. platycarpa Pfeiffer, both of which are of uncertain application.

1. Flower red; flower-buds conspicuously erumpent (splitting the stem’s epidermis); stems perfectly terete (S Espirito Santo) 19. hoelleri
   1. Flower not red and/or flower-buds not erumpent; stems various 2
   2. Stems flat, angled, winged, strongly to weakly ribbed or terete with ± raised podaria subtending ± fleshy scale leaves (or cylindric and smooth but with conspicuously erumpent flower-buds exposing floccose areoles after the fall of the fruit); flower-buds etc. 1–many per lateral areole after the fall of the fruit; flower-buds etc. 3
   3. Stems perfectly terete or only the shortest, ultimate segments somewhat angled; scale leaves minute, not fleshy or soon scarious; flower-buds etc. 1 per lateral areole or flowers terminal 11
   4. Flower-buds conspicuously erumpent from sunken, often very woolly areoles that were absent, hidden by scale-leaves or minute prior to flower development, solitary 4
   5. Flower-buds not erumpent or only so on close inspection, the areoles not more obviously woolly after flowering, or flowers 2 or more per areole, at least on the older stem-segments 7
   4. Stem-segments of indeterminate growth, branching often only subacrotomic, with numerous discontinuous ribs (S Espirito Santo) 7a. pacheco-leonis subsp. catenulata
4. Stem-segments of determinate growth, branching acrotonically from terminal composite areoles, terete, angled or with low ± continuous ribs
5. Stem-segments terete, not ribbed, but sometimes with raised podaria subtending the scale-leaves (widespread)

5. floccosa

5. Stem-segments ribbed or angled
6. Stems weakly 5-ribbed (S Espirito Santo)
7. Stems 3–4-angled in cross-section, the angles discontinuous and not forming ribs (widespread)

6a. paradoxa subsp. septentrionalis

7. Fruit white or faintly tinged pink in part; stems mostly flat
8. Ultimate stem-segments very thin, only c. 1 mm thick (excluding midrib) in living material, margins shallowly crenate, the areoles 2–4 mm from the outermost part of margin; flowers mostly 1 per areole, developing during the rainy season (S Bahia)
9. oblonga

7. Fruit entirely pink to red or purplish; stems flat or 3–4(-5)-angled/winged
8. Ultimate stem-segments stouter, to 5–6 mm from the outermost part of margin; flowers 1–5 per areole, developing during the dry season (Pernambuco)
9. sulcata

8. Stems weakly 5-ribbed (S Espirito Santo)
9. Stems 3-4-angled in cross-section, the angles discontinuous and not forming ribs (widespread)

8a. paradoxa subsp. septentrionalis

9. stems mostly pendulous or sprawling, > 25 mm wide, flat or 3–5-winged
10. stems mostly erect, to 25(-30) mm wide, 3-5-angled (S Espirito Santo)

9. cereoides

10. Flowers/fruits 1–5 per areole, flower 12–20 mm diam., yellowish, fruit globose to oblong
11. Flowers < 8 mm long, with 4–7, patent to reflexed perianth-segments visible from within
12. Flowers > 8 mm long, campanulate, with 8–15 concave perianth-segments visible from within

10. crispata

11. Flowers > 8 mm long, campanulate, with 8–15 concave perianth-segments visible from within
12. All stems of ± indeterminate growth, not forming composite areoles at apex; flowers and fruits always lateral (widespread)
13. Higher order stem-segments of determinate growth, forming composite areoles at apex; flowers/fruits both lateral and terminal
14. Basal and higher order extension shoots of indeterminate growth present and > 12 cm long, other stem-segments usually decreasing in size towards distal parts of plant; stamens yellow, red or purplish at base
15. Stem-segments > 7 cm long, extension shoots and shorter higher order segments not markedly different, terminal composite areoles mostly lacking; flowers lateral and subterminal (S Minas Gerais, > 1500 m) 13. pulchra
16. Ultimate stem-segments swollen and sometimes angled/ribbed; fruit white, rarely with reddish scales (fruit sometimes red outside Brazil)
17. cereuscula

16. All stems terete, never angled/ribbed; fruit purple, magenta, red, orange or greenish tinged maroon
17. Stems clothed in semi-adpressed, bristle-like spines; fruit bristly
18. Stems and fruit naked
18. Flower 20–25 ×20 mm; fruit globose-ovoid, c. 10 mm long; plant flowering when < 1 m long
19. Flower c. 15 × 12 mm; fruit truncate, c. 6 mm long; plant attaining 2 m before flowering

14. burchelli

15. juengeri

Subg. Phyllarthrorhipsalis F. Buxbaum (nos. 1–4): seedlings (where known) flattened/2-ribbed at first; adult stem-segments of determinate size and acrotonically branched (except secondary segments from the somewhat indeterminate basal extension shoots); new stem-segments and flower-buds scarcely erumpent; lateral areoles visible before flowering; stem-segments mostly flattened, or with 3–5 continuous angles or wings, relatively thin; flowers lateral and terminal, remaining open at night and day, one to many at a time per areole, pericarpel exposed, areoles
flowering repeatedly, enlarging and bearing more flowers each time; fruit white, pink or purplish. Central and South America. Type: *R. pachyptera* Pfeiffer.


**VERNACULAR NAME.** Mandacaru-da-serra.

Swaying lithophyte to 80 cm, or pendent epiphyte with mostly dichotomous branching, to 200 cm or more; stem-segments usually flattened in epiphytic plants, or mostly 3–4(-5)-angled in lithophytes, irregularly angularly, often narrowly so, to c. 15 × 3–5.8 cm, 2–3 mm thick away from the vascular midrib; areoles exposed from the start, indented 3–11 mm from the crenate stem margin and to c. 40 mm apart, with conspicuous felt and 0–2 minute bristle-spines. Flower-buds pinkish, flowers (1-)3-9 per areole, c. 6.5 x 5-8.5 cm, sometimes scarcely opening, with purplish/pinkish magenta or red. Central and Brazil, Bahia, Mun. Jaguaquara [Toca da Onça], 27–29 June 1915, *Rose & Russell* 20106 (NY, lecto.; US, lectopara.).

**Widespread humid forest / campo rupestre element: epilithic or epiphytic, campo rupestre, mata de brejo and Mata atlântica** and their ecotones with caatinga-agreste, 50–1050 m, from the Chapada Diamantina and Serra do Espinhaço eastwards, Bahia, Minas Gerais and (?) Espirito Santo; Central-western Brazil (Goiás and Mato Grosso). Map 12B.


**ESPIRITO SANTO:** reported from the vicinity of Domingos Martins by Rauh (*Rauh & Kautsky* 67568, det. W. Barthlott from living material grown at Univ. Bonn, Germany, n.v.).

**CONSERVATION STATUS.** Vulnerable (2) [criteria B1/2b–e]; area of occupancy estimated to be < 2000 km²; PD=2, El=1, GD=2. Short-list score (2×5) = 10. It is markedly disjunct and its habitat has contracted severely and especially in eastern/south-eastern Bahia, whence the most recent collection was obtained in 1971. Elsewhere, it is found within some reasonably secure protected areas (eg. Parque Nacional Chapada Diamantina, BA), but its ecological niches are invariably limited.

A distinctive species with flowers minute in relation to the stem-segments, which somewhat resemble those of the larger-flowered *R. elliptica* (see below) and *R. pachyptera* (Rio de Janeiro to Rio Grande do Sul). Its clustered fruits are quite variable in colour. In cultivation, at least, the collection from Minas Gerais sometimes produces flowers almost devoid of fertile stamens.

A living collection, at the University of Bonn’s botanic garden, said to be from Goiás (*P. J. Braun* s.n.), which is yet to flower, seems referable here, and unlocalised living material of this
species from ‘Mato Grosso’ (*Uebelmann* s.n.) has recently flowered at Zürich, ZSS (accn n° 82-1444; BONN, photo.). Clearly, its range westwards from Eastern Brazil is incompletely understood at present.


*R. chloroptera* F.A.C. Weber in Bois, Dict. hort.: 1045 (1898). Type: Brazil, São Paulo, Santos, assumed not to have been preserved.

Pendent to 1 m or more; basal extension shoots to 35 cm; higher order stem-segments mostly flattened, rarely 3-winged, broadly to narrowly elliptic, rounded to narrowly truncate at apex, mostly 8–14 × 3–6 cm, c. 2–2.5 mm thick away from the vascular midrib, green, but often turning a striking shade of magenta or purple when drought-stressed or in strong light, usually at least the margins purplish tinged, margins undulate to broadly crenate; areoles ± inconspicuous or hidden prior to anthesis, glabrous or bearing minute bristles, indented up to c. 3 mm from the crenate stem margin and to 2 cm apart. Flowers 1–5 per areole, buds sometimes pinkish, at anthesis to 14 mm long (from tips of reflexed perianth-segments to stigma-lobes), 12–20 mm diam. before full anthesis, perianth-segments pale to golden yellow, the mostly 5 principal to 9 × 4.5 mm, strongly reflexed hiding the pericarpel, bluntly rounded at apex; stamens conspicuous to 8 nun, white; style white, scarcely exserted from the stamens, stigma-lobes 3–4, to 3.5 × 1 mm, white; pericarpel 3.5–4.0 × 3.5–4.0 mm, pale green. Fruit deep reddish pink, globose to elongate.

Southern humid forest element: epiphyte in *Mata atlântica*, including *mata de neblina*, near sea level to c. 1500 m, south-eastern to southern Minas Gerais; common elsewhere in South-eastern and Southern Brazil. Map 17C.


**CONSERVATION STATUS.** Lower Risk (1); PD=2, EI=1, GD=1. Short-list score (1×4) = 4. Lower Risk taking its total range into account.

Lüttzelburg (1926, 3: 111) reports the synonymous *R. chloroptera* F. A. C. Weber from Sergipe, but in the absence of documented material this record must remain rather doubtful, especially since no other species of subg. *Phyllarthrorhipsalis* is known from that state.

This may be the sister species of *R. russellii*, which it replaces to the south of the latter’s range.


Pendent to 1 m or more; stem-segments pale green or yellow-green, the margins sometimes tinged reddish when exposed to sun, frequently emitting aerial roots along the vascular midrib; basal or sub-basal extension shoots to 10–20 × 1–2 cm, gradually cuneate towards the almost cylindric base, ultimate segments to 12(–23) × 2–6(–7) cm, cuneate to truncate at base, ± truncate to rounded at apex, only c. 1 mm thick away from the vascular midrib, often
contorted, margins crisped and tortuous, crenate beneath the areoles; areoles c. 1 mm diam., 14–35 mm apart, sunken 2–4(–10) mm from stem margin, bearing 1 or more fine, bristly, pale, inconspicuous spines. Flowers 1–2(–3) per areole, to 15 × 18 mm when fully expanded (maximum diameter of perianth-segments when patent, but before full expansion when the spreading stamens reach a maximum of 15 mm diam., at which stage perianth-segments are strongly reflexed back and hiding pericarpel); perianth-segments c. 8, the 5 largest to 8–4 mm, greenish-yellow or sometimes tipped reddish in bud, turning yellow post-anthesis; stamens to 6–8 mm, white, conspicuous; style to 7 mm, white, stigma-lobes (3–)4–5, to 2–3 × 1 mm, white; pericarpel c. 4 × 4 mm, ovoid (narrowed to apex), greenish yellow. Fruit c. 6–7 × 7–8 mm, entirely white or pale pink at apex.

Humid forest element: epiphyte in perhumid Mata atlântica, low elevations, south-eastern Bahia (and Espirito Santo?); to South-eastern Brazil (São Paulo, Serra do Mar). Map 17C.


CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1×5) = 5. Lower risk taking its total range into account, but much of its former habitat in southern Bahia has been destroyed since the above cited collections were made in 1971.

*R. oblonga* is very similar to *R. goebeliana* from Bolivia (Yungas) and to *R. occidentalis* from northern Peru, southern Ecuador and Suriname. They differ from *R. oblonga* in their stem-segments being consistently narrowly cuneate at base, the pericarpel of *R. goebeliana* being more elongate and the flowers of *R. occidentalis* generally smaller than those of the Brazilian species.


*Epiphyllum crispatum* Haw. in Phil. Mag. 7: 111 (1830).

*Rhipsalis rhombea* sensu Löfgren in Arch. Jard. Bot. Rio Janeiro 1: 89, t. 16 (1915) non *Cereus rhombeus* Salm-Dyck. Like the preceding but aerial roots produced mainly from the junctions of the stem-segments, extension shoots larger, to 40 cm or more, ± erect or ascending at first; ultimate segments to 7(–10) cm wide, yellow-green to dark green, much stouter, c. 2 mm or more thick, the areoles sunken 5–6 mm or more (to 20 mm exceptionally) into the marginal crenations; flowers 1–5 per areole, 12–20 mm diam., greenish white; stamens shorter than perianth-segments; stigma-lobes 2–4; fruit 6 × 5 mm, white or greenish, ripening slowly. Chromosome number: 2n = 22 (Barthlott 1976).

Humid/subhumid forest element: epiphyte in mata de brejo, Mun. Caruaru, eastern Pernambuco; South-eastern Brazil (coast E of Rio de Janeiro between Niterói and Cabo Frio, and inner São Paulo). Map 15B.

CONSERVATION STATUS. Vulnerable (2) [criteria B1/2a–d]; area of occupancy estimated to be < 2000 km²; PD=2, EI=1, GD=1. Short-list score (2x4) = 8. Apparently wide-ranging but rarely observed and Vulnerable despite its range in view of the widespread destruction of the habitat it favours. The above cited population may no longer be extant, but needs to be checked!

The single record from Pernambuco is markedly disjunct from other known sites in Rio de Janeiro (Cabo Frio, Silva Jardim, Saquarema & Itacoatiara) and São Paulo (Rio Claro & Altinópolis), but similar disjunctions are known in Araceae from Pernambuco (e.g. Philodendron eximium Schott and P. corcovadense Kunth, fide S. Mayo, pers. comm.). Rhipsalis crispata is a species of more markedly seasonal or drier habitats, where it has been found as an epiphyte or lithophyte, both near the coast and far inland, but it can also grow in the sand of the restinga (Cabo Frio, RJ). It is closely related to R. oblonga, but has thicker and often broader stem-segments, which are deeply crenate-sinuate at the margin and, in cultivation, appears to flower following a dry or cool period, whereas R. oblonga flowers during the warm, humid growing period. Another possible relative is the recently rediscovered but still poorly known, R. cuneata, from Bolivia (Yungas), which differs in its consistently cuneate stem-segment bases.

The use of the name R. crispata for the plant described here is clearly supported by early herbarium records from the last century in Europe, where it was becoming widespread in cultivation under Haworth’s epithet (e.g. in the garden at Leuven (Louvain), Belgium, 1837, ex Herb. Martens [BR!], and from Munich, 3 Jan. 1850, ex Herb. Kummer [M!]).

Subg. Epallagogonium Schumann (including Subg. Trigonorhipsalis A. Berger and Subg. Goniorhipsalis Schumann) (nos. 5–9): stems ± angled to ribbed or terete with raised podaria, never flattened (except in the first shoot of seedlings of no. 5 and very rarely in shade forms of no. 8); all adult stem-segments determinate, except in R. pacheco-leonis; flower-buds 1 per areole (except in R. cereoides), strongly erumpent and the pericarpel sunk into the stem (less so in nos. 8–9), areoles rarely flowering > once. South America. Type: R. paradoxa (Pfeiffer) Salm-Dyck.


Pendent to 3 m or more; basal stems to 1.5 cm thick, new stem-segments arising singly or in groups of 2–5 from the apex of existing segments, at maturity to 30 cm long, pliable and rubbery in feel, but not flaccid; primary stem of seedling flattened, subsequent segments angled, mature growth terete but commonly with prominent podaria subtending the scale leaves, c. 6–10 mm thick, grey-green, matt, minutely roughened, podaria to c. 25 mm apart; areoles sunken and hidden until flowering, to 4 mm diam. and floccose after bearing fruits. Flowers to 12–18 mm diam. or slightly larger, perianth-segments pale green to greenish white, pericarpel immersed in the sunken, woolly areole. Unripe fruits light green, sometimes dark reddish above, ripe fruit turbinate, c. 7 × 6 mm, white, with a faint reddish ring around the perianth scar.

Together with R. lindbergiana, the most widespread and commonest Rhipsalis species in Eastern Brazil, from Pernambuco southwards, but rather variable and requiring further study in the field.
The following, which includes the type of the species (subsp. floccosa) is a frequent plant of the Mata atlântica and brejo forest.

5a. subsp. floccosa

Ultimate stem-segments to 10 mm thick, podaria subtending the leaf-scales very prominent. Flowers to c. 12 mm diam. Fruit white, half-immersed in stem.

Widespread humid forest element; epiphytic or epilithic in Mata atlântica, including mata de brejo and eastern foot of the Chapada Diamantina (Bahia) near sea level to c. 900 m, eastern Pernambuco to Espirito Santo; extending south-westwards into the interior of South-eastern Brazil (Minas Gerais and São Paulo); replaced by subsp. oreophila in the East Brazilian Highlands, by subsp. pulvinigera in mountains and coastal zones of South-eastern and Southern Brazil, by subsp. hohenauensis in eastern Paraguay and north-eastern Argentina, by subsp. tucumanensis in the eastern Andes of Argentina, Bolivia and Peru (Junín) and by subsp. pittieri in northern Venezuela. Map 14C.


CONSERVATION STATUS. Lower Risk (1); PD=1, EI=1, GD=2. Short-list score (1×4) = 4. Although much of its former habitat has been destroyed, it has managed to colonize cultivated trees such as mangoes and other long-lived species, planted as street trees and in village squares.

Variable in the length and especially thickness of its stem-segments.

Rhipsalis monteazulensis Ritter, Kakt. Südamer. 1: 42 (1979). Type (Taylor & Zappi, l.c.): as above.

Ultimate stem-segments to 6 mm thick, almost perfectly cylindrical, without obvious podaria subtending the scale-leaves. Flowers to c. 12 mm diam., greenish white. Fruit white, scarcely immersed in stem.

Northern campo rupestre element: epiphytic or epilithic in mata de neblina (capão de mata), campo rupestre, c. 1200-1750 m, Chapada Diamantina and Serra do Espinhaço, Bahia and northern Minas Gerais. Endemic to the core area of Eastern Brazil. Map 28C.


CONSERVATION STATUS. Lower Risk (1); PD=1, EI=1, GD=1. Short-list score (1×3) = 3.

The forms of this species from above 1200 metres in the northern sector of the East Brazilian Highlands (Chapada Diamantina, BA, and northern Serra do Espinhaço, MG) have almost perfectly cylindrical stems devoid of podaria and seem sufficiently distinct to treated as subspecifically different from those of the lowland forests and South-eastern campos rupestres. They have smaller flowers than plants from the latter area, which are provisionally referred to the following:


VERNACULAR NAME. Dedinho.

Like subsp. floccosa, but with generally smaller stem-segments and larger flowers; fruit usually deep pink, pink rarely white.

Southern humid forest element: epiphytic and epilithic, to 1850 m, southern Serra do Espinhaço, Serra da Mantiqueira and Serra do Caparaó, central and southern Minas Gerais to southern Espirito Santo; South-eastern and Southern Brazil. Map. 18B.

Typical *R. floccosa* subsp. *pulvinigera* is distinguished from its northern relatives by its generally smaller and more evenly sized, somewhat shiny, smoother, purple mottled stem-segments (usually to only 20 cm), larger, more expanded flowers (18–20 mm diam. or more), less woolly flower-bearing areoles and strongly exserted fruits, usually turning bright pinkish red when ripe (more rarely whitish). Beyond Eastern Brazil it ranges from Rio de Janeiro (Serra dos Orgãos) to Rio Grande do Sul (Mun. Guaiba) and replaces subsp. *floccosa* in the coastal regions of Southeastern and Southern Brazil. They can be reliably distinguished only on the basis of fertile material.

The following, above-cited collections from Minas Gerais and Espírito Santo are judged to represent a form of subsp. *pulvinigera*, but strongly imitate *R. dissimilis* (Lindberg) Schumann: Zappi & Scatena in CFCR 10931 (SPF), Zappi et al. 241 (K, HRCB, BHCB, SPF), Rauh 67567. These are more slender-stemmed than the true *R. dissimilis*, which is known from rock outcrops in São Paulo and Paraná.


Only the following heterotypic subspecies is found in the area covered here:


Pendent to 3 m or more; branching strictly acrotonic from terminal composite areoles; stems of seedlings of indeterminate growth, with 4–5 continuous ribs bearing closely set areoles and fine bristly spines, new stem-segments arising singly or in groups of 2–5 from the apex of existing segments, to c. 30 × 0.7–1.1 cm, determinate, with prominent winglike angles subtending each scale-leaf/areole, these alternating giving the stem a ± triangular cross-section, epidermis yellow-green to pale grey-green, matt, markedly roughened to the touch, areoles sunken and hidden before flowering, subtended by minute, adpressed scale leaves positioned 1.5–3.5 cm apart, areole scar to 5 mm diam. after bearing fruit, but almost glabrous. Flower-buds strongly erumpent, flowers yellowish, 15 mm diam., perianth-segments to 7 × 2–3 mm; stigma-lobes 5, white. Fruit turbinate, to 7.5 × 7.5 mm, white.
Humid forest element: epiphyte in *Mata atlântica*, low elevations to c. 900 m, eastern Pernambuco, eastern Bahia, central-eastern Minas Gerais and Espírito Santo. Endemic to Eastern Brazil. Map 14C.


**CONSERVATION STATUS.** Endangered (3) [criteria A2b/B1/2]; PD=1, EI=1, GD=1. Short-list score (3x3) = 9. Endangered in view of continuing forest destruction throughout the region of its occurrence, in which it is apparently a rarity. Only tiny fragments of its original habitat remain.

This taxon differs from subsp. *paradoxa* (SW Rio de Janeiro to Santa Catarina) in its consistently narrower vegetative parts and darker flowers.


Only the following heterotypic subspecies is found in the area covered here:


Like *R. paradoxa* subsp. *septentrionalis*, but smaller in all its parts, stem-segments indeterminate, to only c. 0.7 cm diam., branching sub-acrotonic, terminal composite areoles only rarely produced, the winglike stem angles more crowded and compressed, giving the stem a ± quadrangular cross-section; areolescale-leaves to only 1 cm apart, some bearing bristle-spines, or these developing post-anthesis, the scar left after fruit production being c. 3 mm diam.; flowers < 10 mm diam., brownish salmon without, pinkish salmon to orange within, anthesis associated with conspicuous production from extra-floral nectaries on pericarpel (ant-pollination syndrome?); fruit to 5 × 4.5 mm, white with a pink circle marking the perianth scar.

Southern humid forest element: at c. 900 m, southern Espírito Santo (Domingos Martins); Rio de Janeiro (Mun. Nova Friburgo). Endemic to South-eastern Brazil.

CONSERVATION STATUS. Data Deficient; known from only two localities, neither of which have been visited by the author.

The homotypic subspecies, *R. pacheco-leonis* subsp. *pacheco-leonis*, is known from the regions of Macaé, Cabo Frio and Pedra da Gávea, Rio de Janeiro. It has often rather weakly developed stem angles, bears deep pinkish fruit and was confused with *R. dissimilis* by Britton & Rose (1923).


Shrubby, forming dense clumps of ± upright axes (or pendulous when rarely epiphytic); stem-segments all of determinate size, to 14 × 3 cm, (2-)3-5-angled, new stem-segments arising singly or in groups of 2-3(-4) from the apex of existing segments. Flowers 1-4 per areole, 18-20 mm diam. or more, whitish, with 6 or more perianth-segments visible from above. Fruit ovoid-oblong, to 10 × 7 mm, but usually smaller, pink to whitish. Chromosome number: 2n = 22 (Barthlott 1976).

Southern humid forest (inselberg) element: lithophyte on gneissic inselbergs (rarely epiphytic on nearby trees), southern Espirito Santo (Domingos Martins); Rio de Janeiro (both sides of the Baía de Guanabara).


CONSERVATION STATUS. Vulnerable (2) [criteria B1/2c]; area of occupancy estimated to be < 2000 km²; PD=2, EI=1, GD=1. Short-list score (2×4) = 8. Apart from the above-cited collection, known from only a few localities close to the cities of Rio de Janeiro and Niterói and therefore potentially affected by urban expansion and coastal tourism.


Stems ± pendent, apparently all of determinate growth, the basal segments to c. 8–10 mm diam., new stem-segments arising singly or in groups of 2–5 from the apex of existing segments, vigorous segments to 250 × 6–7 mm, matt grey-green, weakly but recognizably (4–)5-angled/ribbed whether turgid or drought-stressed, shorter segments sometimes almost terete, the weakest ultimate segments tapering to c. 3–4 mm diam. near their apices, scale-leaves minute, upon raised podaria, often subtending inconspicuous, pale bristles to 1 mm, podaria/scales to 70 mm apart on the same angle/rib, 2–4 clustered around the small, terminal composite areoles at the stem apices. Flowers like those of the preceding species but c. 15 mm diam. Fruit pinkish.

Southern humid forest element: ecology and range poorly understood; only the following collection of documented provenance has been seen: **ESPIRITO SANTO:** Mun. Domingos Martins, 8 May 1986, *Rauh & Kautsky* 67562, cult. Univ. Bonn, Germany, accn. no. 04490, 1996 (K).
Until recently this species was known only in cultivation, where it was often misidentified as *R. micrantha* (central Andes to Central America). It seems to be a member of the *R. pacheco-leonis* / *R. pentaptera* complex, although it strongly resembles *R. jloccosa*, differing most obviously in its clearly angled/ribbed stem-segments, less conspicuously erumpent flower-buds and scarcely woolly fertile areoles post-anthesis. It is probable that it was first collected in the vicinity of Rio de Janeiro and is thus unlikely to prove to be an endemic of the core area of Eastern Brazil, although its range is presently documented only from the above-cited collection from southern Espírito Santo.

Scheinvar (1985) misapplies the name *R. sulcata* to specimens of *R. trigona* Pfeiffer (São Paulo to Santa Catarina).

Subg. *Rhipsalis* (nos. 10-12): seedlings 3–6-ribbed/angled; adult stems usually terete, branching ± acrotonic, but producing indeterminate, greatly elongated, basal extension shoots, the ultimate stem-segments usually the shortest; new stem-segments and flower-buds inconspicuously erumpent; flowers lateral and sometimes terminal, one per areole, areoles flowering once only, pericarpel fully exposed; fruits as above. Tropical America eastwards to Sri Lanka.


VERNACULAR NAME. Enxerto.

Pendent to 4 metres or more, forming a dense mass of closely adjacent stems; branching sub-acrotonic, new stem-segments arising singly or in groups of 2–5 from near the apex of existing segments, of indeterminate growth, lacking terminal composite areoles, to 60–90 × 3–6(-12) mm, cylindric, but sometimes longitudinally ridged when drought-stressed or when dried for the herbarium, light grey-green to dark green; the soon scarious scale-leaves marking the position of the hidden areoles often arranged in whorls, these to c. 10 mm apart; areoles apparent only after flowering, developing sparse wool and usually a few bristle-spines, areole scar c. 1.5 mm diam. Flowers to 9 mm diam.; perianth-segments 5–9 visible from above the flower, greenish white, strongly reflexed to show off the stamens; stigma-lobes 3–4, white, c. 1 mm. Fruit 3–5 × 2.5–4 mm, white or pink.

Disjunct/widespread humid/subhumid evergreen forest element: epiphyte (very rarely a lithophyte) in high restinga forest, *Mata atlântica*, *mata de brejo* and edges of *caatinga-agresta* (rare), near sea level to c. 1000 m, southern Pernambuco southwards, mostly within 150 km of the coast and on the lower eastern flanks of the Chapada Diamantina (Serra da Jacobina) and Serra do Espinhaço (MG), rarely on the western flanks in the south; to Southeastern Brazil (to W Rio de Janeiro & SE São Paulo). Map 12B.


BAHIA: cent.-N Bahia, Mun. Saude, 68.5 km S of Campo Formoso on road to Jacobina, 12 Jan. 1991, Taylor et al. 1396 (CEPEC, HRCB, K, ZSS); Mun. Jacobina, Barraço de Cima, 11°17'S, 40°32'43"W, 6 July 1996, H.P. Bautista et al. in PCD 3465 (K, ALCB, HUEFS); Mun. Mundo Novo, 2 km E of town on road BA 052,
Unfortunately, these species are less easy to separate in the herbarium and have often been confused, although this can be easily avoided on the basis of provenance, since they have discrete ranges, being sympatric only in parts of the Hileia Baiana of eastern Bahia. 

CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1x5) = 5.

In Eastern Brazil this species can be readily distinguished from *R. baccifera* in the living state by its very long shoots lacking composite terminal areoles and giving rise to subacrotonic secondary segments. Its fruits are generally smaller than those of *R. baccifera* and sometimes pinkish. Unfortunately, these species are less easy to separate in the herbarium and have often been confused, although this can be easily avoided on the basis of provenance, since they have discrete ranges, being sympatric only in parts of the Hileia Baiana of eastern Bahia. *R. lindbergiana* is somewhat variable in stem thickness, the stoutest forms including that described as *R. densiareolata*.

*R. lindbergiana* most closely resembles *R. baccifera* subsp. *shaferi* (Britton & Rose) Barthlott & N. P. Taylor, which ranges westwards and south-westwards from inner São Paulo (Campinas) to Paraguay, northern Argentina and (?) southern Bolivia.

A variable and complex taxon like *R. baccifera*, of which it is assumed to be the southern sister-species. Plants from the core area of Eastern Brazil are referred to the following form:


Like the following and especially *R. baccifera* subsp. *hilelabaiana*, but basal extension shoots to 100 cm, ultimate stem-segments only 1.3–2.0 mm thick; flowers apparently self-incompatible, pericarpel c. 2–2.5 × 2–2.5 mm, smaller than the perianth during most of the bud’s development, flowers borne laterally, laterally and terminally, or rarely terminally only, c. 7 × 7 mm or wider before the perianth-segments become strongly reflexed, these c. 3.5 mm or larger, often turning yellow post-anthesis; stamens more numerous, 3–4 mm or more; stigma-lobes 3–5; fruit globose to shortly barrel-shaped, to 4–5 × 4 mm, white or pink to deep purplish red, leaving a more prominent scar on the stem. Chromosome number: 2n = 22 (Barthlott 1976).

Southern humid forest element: epiphyte or lithophyte in *Mata atlântica*, to 1600 m; common everywhere in the Serra do Mar of South-eastern and Southern Brazil (to Rio Grande do Sul). Map 18A.

**CONSERVATION STATUS** (of species). Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1×5) = 5.

It is probable that *R. teres* will be found elsewhere in the southern part of the core area.


*Cassyta baccifera* J. S. Mueller, Ill. syst. sex. Linnaei. class IX. ord. 1, t. 29 (1770–77).


VERNACULAR NAMES. Enxerto, Conambaia, Tripa-de-galinha.

Pendent to 2 m or more, freely producing aerial roots, pale to dark green; all stems slender cylindric, naked except for minute whitish scale-leaves occasionally subtending very fine whitish bristles, basal extension shoots to 500 × 3–5 mm, eventually rather woody, subsequent branching acrotonic from felted terminal composite areoles, the secondary segments arising in clusters of 3 or more, subsequent orders of segments decreasing in size, the penultimate c. 90 × 2 mm, giving rise to clusters of 2 or more ultimate segments measuring 20–65 × 2 mm. Flowers self-compatible, terminal or subterminal from or around the composite areoles of the ultimate and lower order stem-segments, sometimes 2 or more clustered together, often also lateral, especially on the extension shoots; buds minutely erumpent, the pericarpel at least twice the size of the developing perianth until shortly before anthesis; flowers 6–7 × 4–5 mm, principal perianth-segments 4–6, to 3 mm, patent to reflexed, greenish white; stamens 1–2.5 mm, relatively few, whitish; style 3 mm, stigma-lobes 3, 1 mm, white, exserted; pericarpel barrel-shaped, 3 × 2 mm, pale green. Fruit translucent white, sometimes pinkish to violet near apex, ovoid, to 7.5 × 6 mm, juice extremely mucilaginous and sticky.

Note: the type of R. baccifera is assumed to have come from the Caribbean, whence it was introduced to England by Philip Miller in 1758 (Stearn, I.c.). The above description accounts only for what appear to be typical, slender-stemmed forms found in Northern and North-eastern Brazil and the Caribbean (eg. Jamaica), since it is clear that the species represents a complex entity requiring further detailed study. Thicker-stemmed forms, such as are known from the Guianas and elsewhere (as well as Old World plants referred to its various heterotypic subspecies) are not accounted for above, although some of these from the Americas were previously included with subsp. baccifera by Barthlott & Taylor (1995: 63).

In Eastern Brazil this species is divisible into the following subspecies:

1. Higher order stem-segments short, densely clustered, 6 or more axes arising from the apex of the longer lower order segments (coastal region of E Bahia at up to 500 m, and region of Catolés, Chapada Diamantina, 1650–1800 m) 12b. subsp. hileiabaiana

1. Stem-segments not as above (Amazonia; and Maranhão to E Pernambuco) 12a. subsp. baccifera

12a. subsp. baccifera

Higher order stem-segments 40–90 mm, solitary or in clusters of 2–3 from the apex of previous segments. Flowers with perianth-segments mostly patent; stamens 1–2 mm.

Amazonian forest element: epiphyte in mata de brejo and mata de tabuleiro, near sea level to c. 600 m, North-eastern Brazil southwards as far as coastal Pernambuco; replaced by subsp. hileiabaiana in central & eastern Bahia; throughout humid parts of the neotropics, northwards to eastern Mexico and Florida (replaced by subsp. erythrocarpa, mauritiana & horrida in the paleotropics). Map 15C.


**CONSERVATION STATUS.** Lower Risk (1); PD=1, EI=1, GD=2. Short-list score (1x4) = 4.

Records of *R. baccifera* from South-eastern and Southern Brazil refer to *R. lindbergiana* and *R. teres*; see above. However, *R. baccifera* subsp. *shaferi* (Britton & Rose) Barthlott & N. P. Taylor is known from the state of São Paulo, where it has been collected in Mun. Campinas.


Higher order stem-segments to c. 30 mm, in dense clusters (to 10 or more from the apex of vigorous, lower order segments), strongly differentiated from the much longer extension shoots. Flowers with perianth-segments reflexed to expose the 2–2.5 mm stamens.

Disjunct Bahian humid forest element: epiphyte (rarely lithophyte) in *Mata atlântica* (*Hileia Baiana*), at low elevations to c. 500 m, and in *mata de neblina*, 1650–1800 m, region of Catolés (Mun. Abaira), Chapada Diamantina, eastern and central Bahia. Endemic to Bahia. Map 12C.


**CONSERVATION STATUS.** Vulnerable (2) [criteria B1/2a–d]; area of occupancy estimated to be < 2000 km²; PD=1, EI=1, GD=1. Short-list score (2x3) = 6.

This endemic subspecies, which is restricted to the region of Bahia receiving most rainfall (within the 1750 mm annual isohyet along the coast and from very humid woodland in the highest part of the Chapada Diamantina), strongly resembles forms of *R. teres* in habit, but has flowers and fruits typical of *R. baccifera*.

Subg. *Erythrorhipsalis* A. Berger (nos. 13–18). Like Subg. *Rhipsalis*, but flowers campanulate (except sometimes in no. 18), pendent, one or more at a time from or around the margins of the terminal collective areole of ultimate and sometimes lower order stem-segments (also commonly lateral, but obliquely oriented on the segments in *R. pulchra*); perianth-segments 8–18 or more; stamen filaments usually highly coloured at base giving the flower a coloured throat; fruit white, pink, purplish, red or orange. South-eastern South America. Type: *R. pilocarpa* Löfgren.


Pendulous to 3 metres or more, stems eventually always pendulous, weak and pliable, almost as if flaccid, emitting aerial roots, to 5 mm diam., plain green, the scales sometimes with reddish marks below; branching acrotonic, subacrotonic or sometimes mesotonic, the stem-segments of indeterminate size but generally decreasing in length further away from the rootstock, their apices often not forming recognisable composite areoles, when present these very inconspicuous, actively growing segments gradually tapered to a fine point at apex; areoles almost 0, represented by a few minute trichomes visible at the distal edges of the inconspicuous scales, these < 0.25 × 0.5 mm, truncate, apiculate, pale at maturity, triangular and reddish when young. Flower-buds inconspicuously erumpent, leaving a glabrous scar to 1.5 mm diam. on the stem, pinkish to dark reddish; flowers downwardly directed, lateral and aligned with the stem and/or ± terminal and sometimes in groups of 3, in lateral flowers the pericarpel attached sublaterally, with a distinctive sweetish scent; perianth not expanding fully, ± campanulate, 15 × 15–20 mm; perianth-segments c. 11, 8–9 visible from within the flower, outermost ovate, c. 6 × 5 mm, whitish tinged purplish-pink at apex, inner segments 10–11 × 4 mm, creamy white, concave (boat-shaped) from within; stamens in two groups, the outer series spreading towards the perianth, the inner adpressed to style and varying from very short to equalising the style, all except the outermost with dark orange filaments, anthers pale yellow; style 5 mm, stigma-lobes 3–6, to 3 × 0.7 mm, white, spreading; pericarpel 4–5 × 4.5 mm, pale green to pinkish, naked or with 1–2 fleshy bract-scales. Fruit slightly depressed-globose, to c. 7 × 7.5 mm, translucent whitish or purplish red.

Southern humid forest element: epiphyte in *mata de neblina*, > 1500 m, Serra da Mantiqueira, southern Minas Gerais; South-eastern Brazil (Rio de Janeiro & São Paulo).

**CONSERVATION STATUS.** Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1×5) = 5. Possibly Conservation Dependent, since it is found within various protected areas.

This poorly known species was originally described with and commonly bears purplish magenta fruits and deep pink flowers, but the population cited here from southern Minas Gerais (Zappi 260) has white fruits and rather pale flowers. However, there can be no doubts about its identity.


Plant to 2 m or more; stems freely emitting aerial roots; primary shoots to 50.0 × 0.5 cm, crimson-red, secondary to fifth order to 2.5–7.0 cm, terminal segments 2.5–3.5 cm × 1–2 mm, sometimes slightly thickened at the tips; flowers terminal, 1–3 together, or appearing at the joints of the subterminal stem-segments, campanulate, only half-expanded, to 20–25 × 20 mm, pale silvery pink; stigma-lobes 4–5, to 5 mm, whitish. Fruit ovoid, c. 10 mm, magenta.

Southern humid forest element: epiphyte in *mata de neblina/galeria*, c. 900 m, southern Espírito Santo; South-eastern and Southern Brazil.

CONSERVATION STATUS. Not evaluated in view of taxonomic uncertainties (see below).

This complex of species, amongst which *R. burchellii* has the oldest typifiable name, is difficult to resolve from herbarium materials alone, and it is possible that as many as 5 species of this relationship are present in the area. The following, recently described species is one of these, as is no. 16.

The oldest name within this complex is *R. cribrata* (Lemaire) N. E. Brown (*Hariota cribrata* Lem. 1857), but this is too poorly typified to be applied with confidence and has been variously misapplied by previous authors.


Like *R. burchellii* and *R. clavata*, but plant pendulous to at least 3 m and sometimes much longer; stems scarcely succulent, plain green or tinged dull red; primary long extension shoots to 200 x 0.3 cm, terminal segments 1.25–1.75 mm thick; flowers solitary or two together, sometimes appearing at the joints of the subterminal stem-segments, campanulate, only half-expanded, c. 15 x 12 mm, stamens yellow at base; fruit globose-truncate, c. 6 mm or more, purplish to translucent greenish tinged maroon.

Southern humid forest element: epiphyte in *Mata atlântica*, c. 1500–1600 m, south-eastern/southern Minas Gerais; range and/or endemic status uncertain. Map 18C.


CONSERVATION STATUS. Not evaluated in view of taxonomic uncertainties.

Of the above, only the collection by Zappi and that from the Serra Negra have been seen as living plants and suggest the above identity, although neither has been seen in flowering condition. The other collections from Ibitipoca are referred here with considerable doubt, since it is likely that *R. burchellii* and the easily confusable *R. juengeri* can grow together, and there is also the recently described *R. ormindoi* Taylor & Zappi (1997), from the adjacent parts of Rio de Janeiro, to take into account.


Pendent to 3 m or more, basal extension shoots of indeterminate growth rare, but when present to c. 12 cm; primary determinate segments 3–7 cm long, secondary to fifth order segments often swollen at tips, up to 2.5–(6.0) cm long, terminal segments 1–4 cm long, 1.0–1.5 mm thick, thickened at the tips to 1.5–3.0 mm, up to 10 or more arising at once from the collective areole at apex of the previous segment. Flowers terminal, 1–3 together, sometimes appearing at the joints of the subterminal segments, pendent, campanulate to fully expanded, 13–15 x 13–23 mm; perianth-segments oblanceolate, to 10 x 2.5 mm, pure white, (7–}8–11 visible from within; stamens differentiated into long and short, not coloured at base; style 8 mm long, stigma-lobes 3–5, 2–3 mm long, slender, spreading; pericarpel pale whitish green, c. 2–3 x 2.5 mm; fruit (excluding withered perianth remains) c. 4 x 5 mm, greenish white, rarely red. Chromosome number: 2n = 22 (Barthlott 1976).

Southern humid forest element: epiphyte in Mata atlântica, c. 800–1140 m, southern Espírito Santo and northern Rio de Janeiro (and perhaps south-eastern Minas Gerais); South-eastern Brazil, from sea level to high elevations (westwards to Ilha São Sebastião, São Paulo). Map18C.

MINAS GERAIS (all of the collections from this state are only provisionally identified as this species in the absence of studies based on living material): SE Minas Gerais, Parque Nacional do Caparaó, 15 Oct. 1988, M. Brugger et al. in FPNC 328, 330 (CESJ, HRCB), Oct. 1941, Brade 17115 (RB); l.c., Cachoeira Bonita, 18 Sep. 1988, Krieger in FPNC 233 (CESJ, HRCB, SPF).


The collections cited above from Rio de Janeiro and Espírito Santo are definitely *R. clavata*, but those from Minas Gerais cannot be confidently identified at present from dried specimens and may include representatives of the preceding species as well as the orange-fruited *R. campos-portoana* Löfgren, which appears to be wide-ranging in Southern and South-eastern Brazil. A specimen of *R. clavata* said to have been collected in the grounds of CEPLAC, between Itabuna and Ilhéus, Bahia (coll. 1975, G. Daniels, cult. Huntington Bot. Gard.) and conserved in HNT is suspected as having incorrect provenance data (probably due to switched labels during cultivation). This Bahian locality is amongst the most well-collected by local botanists, who presumably would have obtained *R. clavata* by now, if it occurred there.

17. *Rhipsalis cereuscula* Haworth in Phil. Mag. 7: 112 (1830). Type: Brazil, a living plant not known to have been preserved or illustrated. Neotype (Barthlott & Taylor 1995: 69): Brazil, São Paulo, Mun. Piracicaba, campus of ESALQ, 3 Dec. 1993, V. C. Souza 4970 (ESA; K, isoneo.).


Stems pale green, freely emitting aerial roots, these attaching the basal extension shoots and terminal clusters of stem-segments to the trunk and branches of the host tree in new positions; extension shoots to c. 60 cm x 3 m, erect then spreading and finally pendent, densely clothed in fine adpressed bristle-spines at first, later mostly caducous, these subtended by minute reddish scales, the bristles forming a small erect tuft at the stem-segment
apices, second order segments arising in clusters of up to 10 or more at or near apex of extension shoots, c. 4–10 cm, or these lacking and extension shoots bearing specialized ultimate segments directly; highest order stem-segments densely clustered, sausage-like to ± globose, of irregular thickness and shape, 5–15 × 2–4 mm or thicker, sometimes slightly angled or ribbed, often partially shrunken or appearing swollen with sap, branching strictly acrotonic, with 1–5 new segments developing at apex from the bristly composite areole. Flowers in early spring, c. 17 × 16 mm, campanulate, whitish or very pale creamy yellow, ± Together from the terminal areole or its vicinity; pericarpace obovoid, c. 5.5 × 4.0 mm, pale yellow-brown to pale green, ± naked or bearing reddish bract-scales with trichomes and/or occasional bristles in their axes; perianth-segments c. 15, to 9 × 4 mm, partially differentiated into an outer somewhat spreading series and an inner series remaining erect and tending to enclose the stamens and style at the start of anthesis; stamens whitish, ± reddish at base, the innermost clustered around the whitish, exserted style, some of the outermost almost as long as the perianth-segments; stigma-lobes 3–5, c. 1 mm, whitish, exserted well beyond the perianth and stamens. Fruit c. 7 × 6 mm, white (or sometimes red outside Brazil), sometimes marked with reddish bract-scales. Chromosome number: 2n = 22 (Barthlott 1976).

Disjunct humid forest element: epiphyte in Mata atlântica, including mata de brejo (NE Brazil) and mata do planalto, c. 500–950 m, north-eastern Pernambuco, eastern Bahia and central-southern to southern Minas Gerais; South-eastern and Southern Brazil; Bolivia, Argentina, Paraguay and Uruguay. Map 15B.


CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=1. Short-list score (1×4) = 4. Lower Risk in terms of its overall range, but likely to disappear from Eastern Brazil as defined here due to destruction of its habitat.

This is another good example of a Rhipsalideae with a markedly disjunct distribution in the brejos of North-eastern Brazil. The irregularly swollen ultimate stem-segments may function as a water store, permitting the development of flowers at their apices during the close of the dry winter season, when they become visibly shrunken through water loss.


Like the preceding in overall habit, but all stem-segments cylindric, of ± uniform thickness and conspicuously white or yellowish bristly, seldom emitting aerial roots, often strongly tinged with dark red, otherwise dark green except the actively growing pale green apices, the lower parts of basal extension shoots c. 5 mm or more diam., the penultimate and ultimate flower-bearing segments c. 35 × 3.5-4.0 mm, lateral areoles bearing c. 8–15 strongly adpressed bristle-spines to 6 mm, these forming an erect cephalium-like tuft at the terminal collective areole and becoming displaced and patent at the joints of the earlier-formed segments (forming and performing like the terminal and ring cephalia of Arrojadoa rhodantha); flowers in early winter, mostly 1–4 together at or around the terminal composite areole, fragrant (moth-pollination syndrome?), buds densely bristly, the perianth strongly tinged pinkish red at first, flowers rather variable in size and form, c. 10–30 mm diam., pendent, all perianth-segments

66
67

patent to reflexed, silvery cream, tinged pink to purple at apex, c. 18 or more in total, to 9 × 2.5 mm, linear-tapered, minutely apiculate, pericarpel ± obconic, clothed in areoles and bristles identical to the stem-segments, green with minute reddish scales, stamens numerous, to 7 mm or more, whitish, reddish at base, expanded as in a loose brush and very conspicuous when the perianth-segments are strongly reflexed (cf. Subg. Rhipsalis & Subg. Phyllarthrorhipsalis etc.), the innermost shorter, tightly clustered around the style and effectively protecting the nectar-chamber around its base, style and 6–8 spreading, whitish 2 mm stigma-lobes exceeding the brush of stamens by 1–2 mm; fruit spherical, to 8–12 mm diam., pericarp bright red to crimson, bearing numerous areoles and whitish bristles. Seed 1.5–1.7 mm. Chromosome number: 2n = 22 (Barthlott 1976).

Southern humid forest element: epiphyte (rarely lithophyte) in Mata atlantica, 500–900 m, southern Minas Gerais (Rio Preto) and southern Espírito Santo (Domingos Martins); South-eastern and Southern Brazil (to Paraná). Map 18A.


CONSERVATION STATUS. Vulnerable (2) [criteria B1/2a–d]; area of occupancy estimated to be < 2000 km²; PD=2, EI=1, GD=2. Short-list score (2×5) = 10. Known from only 8 localities throughout its entire range and apparently rare (Taylor, l.c.).

This is the rare and geographically more restricted and variable sister species of R. cereuscula appears to have evolved the stamen-brush floral syndrome convergently with Rhipsalis subgenera Rhipsalis, Epallagognium, Trigonorhipsalis & Phyllarthrorhipsalis, and contrasts strongly with other members of Subg. Erythrorhipsalis in lacking truly campanulate flowers. As in its sister species, the bristly stem-segments may assist in the collection of moisture from mists and night-time dews.

Subg. Calamorhipsalis Schumann (no. 19): seedlings 3–4-ribbed/angled; adult branching sub-acrotonic or acrotonic; flower-buds and new stem-segments conspicuously erumpent; trichome-bearing, composite terminal and normal lateral areoles apparently lacking or hidden at first, visible only after flowering, scale-leaves minute, not fleshy; stem-segments perfectly terete, of indeterminate growth in the species treated below; flower-buds strongly erumpent, leaving a prominent scar on the stem, lateral to subterminal, solitary, areoles flowering only once; fruit red, magenta or orange. Lectotype (Backeberg 1942): R. neves-armondii Schumann.


Pendent, to 150 cm or more; stems perfectly terete, limp and growing vertically downwards, only 3–4 mm diam., green with faint purplish marks at the minute and very inconspicuous scales, growth indeterminate. Flowers c. 10 mm diam., not opening widely; perianth-segments, style and stigma-lobes intense carmine red, stamens colourless, at least distally. Fruit subglobose, 8 mm diam., not translucent, dull olive-red when immature, ripening to intense tomato red.

Southern humid forest element: habitat details unknown; awaiting rediscovery in the region indicated below.

CONSERVATION STATUS. Data Deficient, but to date collected only once.

This recently described species is closely related to *R. puniceodiscus* (Rio de Janeiro to Santa Catarina), which it strongly resembles in vegetative characters. Its red flowers are presumed to be an adaptation for pollination by hummingbirds.
13. HATIORA Britton & Rose


A genus of 5 species endemic to the *Mata atlântica* zone of Brazil, between Bahia and Rio Grande do Sul. Only a single species (from Subg. *Hatiora*) is represented here, although *H. epiphylloides* (Campos-Porto & Werdermann) F. Buxbaum (Subg. *Rhipsalidopsis*) may occur in southern Minas Gerais (Bocaina de Minas), just outside the southern limits of the core area of Eastern Brazil.


Epiphyte or lithophyte, stems erect, to 2 m, acrotonically branched. Stems articulate, basal segments thick, with brownish bark, apical segments 1–3.5 cm, globose to bottle-shaped or cylindric, all segments of strictly determinate growth, epidermis bright green, with red shades or spots and minute areoles at the sides, sometimes bearing up to 6 bristly spines, terminated by a large composite areole with felt and minute bristles. Flowers terminal from the composite areole, solitary or 2-3 together, orange or bright yellow, c. 15 x 10–15 mm; pericarpel pale greenish, obconic, smooth, c. 3.5 x 4 mm; tube inconspicuous, almost 0; inner perianth-segments erect, to 11 x 3 mm, others sometimes more expanded, ovate, broader, to 4 mm wide; stamens all at the same level, anthers rounded; style 5 mm, stigma-lobes 4–7, ± exserted; ovary locule obtriangular in longitudinal section. Fruit globose to turbinate, c. 10 x 5–8 mm, translucent, whitish to reddish; funicular pulp transparent, very mucilaginous. Seeds ovoid, black, shiny; testa-cells flat, smooth. Chromosome number: 2n = 22 (Barthlott 1976).

**CONSERVATION STATUS.** Lower Risk (1); PD=3, EI=1, GD=2. Short-list score (1x6) = 6. Rare in NE Brazil.

This species presents very diverse phenotypic manifestations, partly related to the conditions under which it grows (Zappi 1991). Its flowers are also rather variable, especially in the degree to which the outer perianth-segments expand, some forms scarcely opening except to reveal the anthers and stigma-lobes. Most of these variations appear to be determined genetically. Two somewhat different forms of this relatively widespread species are recognized in the area studied and are partially separated geographically, at least in Eastern Brazil. However, taking the whole range of the species into account it does not seem feasible to recognize these poorly understood variants as subspecies at present (Map 12C).

1. Segments globose, ovoid or inverted bottle-shaped
   1. Segments uniformly cylindric, or somewhat thicker at base

1. *f. salicornioides*

1. *f. cylindrica*
1a. forma salicornioides

Stem-segments globose, ovoid, or bottle-shaped and then very narrow at base, often with an irregular outline and presenting bristly spines at apex, 10–25 × 0.8–3.0(–5.0) mm.

Disjunct humid forest element: epiphytic or lithophytic, *Mata atlântica, mata de grotão and mata de neblina*, c. 800–1750 m, Bahia (E Chapada Diamantina), central-southern Minas Gerais (S Serra do Espinhaço and Serra da Mantiqueira), Espírito Santo and northern Rio de Janeiro, but northern records markedly disjunct; South-eastern and Southern Brazil (to Paraná).


Stem-segments almost perfectly cylindrical, or thickened at base, smooth, 11–35 × 2–3(–5) mm.

Disjunct humid forest element: epiphyte and (?) lithophyte, *mata de brejo* (*Mata Higrophišla Sul Baiana*) and *Mata atlântica*, c. 600–1200 m, eastern Bahia and southern Espírito Santo; south-western Minas Gerais (Camanducaia), Rio de Janeiro (Ilha Grande & Parati-Mirim) and São Paulo (Serra da Bocaina).


CONSERVATION STATUS. Vulnerable (2) [criteria B1/2c]; area of occupancy estimated to be <2000 km²; PD=3, EI=1, GD=1. Short-list score (2×5) = 10. Bahian localities have protected, but all of the *brejo* forest
vegetation in that state is severely threatened. Despite its substantial range, only collected 8 times to date and apparently rather rare.

The stem-segments of ± constant size, bearing conspicuously felted and often bristly, composite areoles only at their apices, readily distinguish non-flowering plants from superficially similar *Rhipsalis* spp., eg. *R. cereuscula*. Its distribution seems markedly disjunct on present knowledge.

A single collection of the magenta-flowered sister-species, *Hatiora herminiae* (Campos-Porto & Castellanos) Backeberg ex Barthlott, made in October 1942, from the Estação Experimental Coronel Pacheco, Minas Gerais (*E. P. Heringer* 911, SP), is assumed to represent a plant that was in cultivation and not a second locality for this rare species, which is otherwise known only from south-eastern São Paulo (Campos do Jordão), at higher elevations (> 1600 m), epiphytic on *Araucaria*. 
14. SCHLUMBERGERA Lemaire


Including *Epiphyllanthus* A. Berger (1905)


Epiphytic or epilithic; stems terete, few-ribbed, 2-3-winged or flattened, segmented, all stem-segments of determinate growth, oblong to obovate, sometimes truncate. Areoles scattered over the surface of the joints or confined to the ribs or to the crenate or serrate margins, crowded into composite areoles at the apex of segments and there originating new joints and flowers (except in *S. opuntioides*). Spines bristly, short or absent. Flowers scarcely to strongly zygomorphic, red, pink or purplish (rarely white); pericarpel terete or ribbed, greenish to brownish, naked, flower-tube elongate, with bract-scales only at its very base, straight to oblique at apex; perianth-segments spreading or recurved, in various series, giving the impression of a flower inserted within a flower; stamens numerous, comprising an outer and a distinct inner series united at their bases to form a short tube around the style and partially enclosing the nectar-chamber; style and stamens exserted; stigma-lobes erect, connivent. Fruit globose to obconic, ribbed or terete, the perianth deciduous. Seeds subreniform to ovate in outline, 1-1.7 mm, testa dark brown-black, shiny, with intercellular depressions.

An endemic Brazilian genus of 6 species, ranging from southern Espirito Santo (Domingos Martins) and adjacent Minas Gerais (Serra do Caparaó) to Rio de Janeiro, southernmost Minas Gerais and south-eastern São Paulo, in the mountains of the Serra do Mar and Serra da Mantiqueira (*Mata Atlântica*, to 2700 metres altitude). Three species are native to the area covered here, the first being endemic.

1. Terminal segments globose, short-cylindric or linear, rounded in cross-section 2. microsphaerica
1. Terminal segments orbicular to obovate or truncate in outline, laterally compressed 2. kautskyi 3. opuntioides
2. Joints almost unarmed, but margins toothed; flowers scarcely zygomorphic
2. Joints covered in areoles with pungent, very thin spines; flowers strongly zygomorphic


Epilithic or less often epiphytic, pendent; stem-segments 2.2-3.5(-4) × 1.4-1.8(-2.5) cm; compressed, truncate, with 1-2 sharp teeth on each side, or at least at apex on either side of the composite areole; epidermis dark green, often with reddish marks around the margins; primary stem of seedling flattened. Areoles in the axils of the marginal teeth and at apex; spines bristly or absent. Flowers self-compatible, scarcely zygomorphic, to c. 5 × 2.7 cm; pericarpel 12 × 5-6 mm, narrow, cylindric, 4-angled, green to dark reddish; flower-tube pink, with magenta outer perianth-segments, inner segments spreading or recurved at anthesis, lanceolate, magenta-pink. Fruits 25 × 19 mm, turbinate, 4-angled, pericarp yellow-green when ripe, with a reddish tinge. Seed 1 mm.


CONSERVATION STATUS. Endangered (3) [criteria B1/2c]; area of occupancy estimated to be < 500 km²; PD=2, EI=1, GD=1. Short-list score (3x4) = 12.

Disjunct from its nearest relatives in the Serra dos Órgãos (RJ) by over 250 kilometres.


Epiphytic or epilithic, ± erect, to 40 cm, densely branched; stem-segments 5–40 × 2–5 mm, globose, short-cylindric, angled or not, or linear, sometimes the terminal segments compressed, epidermis bright green, often with reddish markings or entirely reddened. Areoles scattered over the surface, or mainly at apex of the terminal segments; spines bristly, to 5 mm, brown or yellowish. Flowers self-compatible, zygomorphic, to 4–4.5 cm; pericarpel rounded, smooth or ridged; flower-tube pale pink, with pink bract-scales; perianth-segments spreading at anthesis, lanceolate, pale or deep pink; pericarpel reddish brown. Fruits 5–10 mm diam., turbinate to rounded, indistinctly 5-ribbed, green or white. Seed c. 1 mm.

Southern humid forest element: lithophytic or epiphytic, *mata de neblina*, at > 2000 m, Serra do Caparão, Minas Gerais / Espírito Santo; Rio de Janeiro (Serra de Itaitiaia). Map 18D.


CONSERVATION STATUS. Data Deficient, but much of its range is within protected areas.
The name *S. microsphaerica* must be used in preference to the more familiar *S. obtusangula*, since the former, as *Epiphyllanthus microsphaericus*, was the name accepted by Britton & Rose (1923: 181), the first authors to treat these two equally priorable names as synonyms.

Scheinvar (1985) reports *S. obtusangula* from northern Santa Catarina in Southern Brazil, but this is assumed to be an error and it has not been possible to locate the collection she cited. It is probably no coincidence that the locality she cites is a site for *Hatiora rosea*, which sometimes develops cylindric, ribbed stem-segments like those of *S. microsphaerica*.

The distribution of *S. microsphaerica* is markedly disjunct between the localities cited above and its *locus classicus* on Itatiaia, by some 350 kilometres. Living plants from these two areas should be compared in view of the distances involved, but photographs of flowering plants in habitat at the eastern locality, shown to the author by Inês Ribeiro in July 2000, have confirmed the identity accepted here.


*Epiphyllum obovatum* Engel. ex Schumann, Gesamtb. Kakt.: 224 (1897), nom. inval. (provisional name based on *Sellow 884, B†*).

Epiphyte or lithophyte, pendent, to 50 cm; stem-segments 15–70 × 5–30 mm, to 9 mm thick, orbicular to obovate, compressed, epidermis dark green to purplish. Areoles woolly, scattered over the surface of the segments, composite terminal areoles lacking; spines to 5 mm, pungent but delicate, golden, more densely developed on the older segments where up to 80 per areole. Flowers self-incompatible, 1–3 per stem-segment, strongly zygomorphic, to 6 × 4.5 cm; pericarpel obconic or 4-angled, smooth, red or white; flower-tube c. 3–4 cm, pale pink, with magenta outer perianth-segments, inner segments spreading at anthesis, those on the lower side of the flower reflexed, lanceolate, magenta-pink; stamens red, anthers bearing red-brown pollen; stigma-lobes 4–7, white; pericarpel slightly 5–7-angled, red. Fruits c. 10 mm diam., spherical to 4–5-angled, green. Seed c. 1.7 mm. Chromosome number: 2n = 22 (Bardlott 1976).

Southern humid forest element: lithophytic/epiphytic, *mata de neblina*, c. 1700 m, Serra da Mantiqueira, southern Minas Gerais; to north-western Rio de Janeiro (Itatiaia) and eastern São Paulo (Campos do Jordão). Map 18D.


**CONSERVATION STATUS.** Vulnerable (2) [criteria B1I2c]; area of occupancy estimated to be < 2000 km²; PD=2, EI=1, GD=1. Short-list score (2×4) = 8. Included within some protected areas.
Tribe CEREEAE Salm-Dyck

Columnar, treelike to shrubby or semi-erect, to low-growing and ± globose; stems ribbed; pericarpel (and tube) of flower and fruit with minute bract-scales or naked, glabrous and lacking bristles/spines (except in 2 Cipocereus spp. and Cereus subg. Mirabella), but sometimes immersed in a woolly/bristly, lateral or terminal cephalium. Type: Cereus Miller.

The most important tribe in Eastern Brazil. Its circumscription, as defined here, follows that employed by Taylor & Zappi (1989) and Barthlott & Hunt (1993), but until now this has not been supported by recent DNA gene sequence studies (Wallace 1995 & ined.). These have failed to resolve the tribes Cereeae, Trichocereeae and Browningieae as distinct units in cladistic analyses due to the synapomorphic deletion of 300 base-pairs from the ITS (internal transcribed spacer), which represent the most active part of the genome so far investigated. However, another recent survey of the family, utilizing surface waxes (n-alkanes), lends strong support to the distinctiveness of tribe Cereeae as employed here (Maffei et al. 1997). The following genus is somewhat aberrant within Cereeae, having a conspicuously scaly pericarpel:

15. BRASILICEREUS Backeberg


Erect plants, usually branched above the ground, 0.5–5.0 m, roots fibrous. Stems erect or inclined and partly supported by surrounding vegetation, with seasonal growth increments separated by slight constrictions, giving a jointed appearance; ribs 7–14, low, sinuses straight; central cylinder very woody, cortex ± lacking mucilage. Areoles felted, longer hairs absent, developing golden to brownish, adpressed to spreading spines, central spine(s) porrect, much longer than radials. Flower-bearing region of stems not differentiated, apparently quite random; flowers nocturnal, shortly tubular, to 7 cm; pericarpel and tube ridged, usually covered in acute or broad, rounded bract-scales; pericarpel and ovary locule depressed; stamens inserted in two series, the uppermost forming a ‘throat ring’ (cf. Echinopsis, Trichocereeae), filaments slender, mobile; pollen 16-colpate (in B. phaeacanthus, Leuenberger 1976). Fruit ovoid, indehiscent, floral remnants persistent, erect, pale brown (!) when not decayed (not strongly blackening as in other Cereeae), deeply sunken into fruit apex, pericarp somewhat ridged and bearing large, rounded, greenish, red, brownish or purplish bract-scales; funicular pulp white. Seeds black, cochleariform, applanate, shiny; testa-cells flat.

An endemic genus of 2 species, related to Praecereus F. Buxbaum (with 2 widespread South American species, P. euchlorus ranging into Central-western & South-eastern Brazil) and replacing it in Eastern Brazil (Taylor 1992a: 25). Like its probable closest ally, it is by no means certain that Brasilicereus really belongs in tribe Cereeae, and their conspicuously scaly flowers are suggestive of the primarily Andean tribe Browningieae (which may prove to be a part of the Trichocereeae). The genus is restricted to the South-eastern campos rupestres and southern caatingas-agrestes.

1. Shrubby to tree-like, branched above ground; flowers with ovate, truncate bract-scales; pericarpel c. 2–3× wider than long; stems 2–6 cm diam.; hilum-micropylar region forming an angle of 20–30° with the long-axis of seed (caatinga/agreste etc., E to S Bahia & N Minas Gerais) 1. phaeacanthus

1. Stem solitary or poorly branched at base; flowers with acute to acuminate bract-scales; pericarpel < 2× wider than long; stems 1.5–2.0 cm diam.; hilum-micropylar region forming an angle of 60° with the long-axis of seed (campo rupestre / carrasco, near Grão Mogol, MG) 2. markgrafii


Shrubby to tree-like, mostly somewhat branched above ground level, to 5 m. Stems erect, inclined on surrounding vegetation or sometimes semi-decumbent on rocks, 2–6 cm diam.; ribs 7–14, to 5 × 6 mm; epidermis dull or dark to grey-green. Areoles 2–3 mm diam., 4–8 cm apart on the ribs. Central spines 1–3, to 3 cm; radials few; flowers 4–7 × 4–5.2 cm; pericarpel very strongly depressed, 5–7 × 15–18 mm, greenish white; flower-tube infundibuliform, c. 3.2 × 1.7–2.0 cm, pericarpel and tube bearing broad, ovate, truncate, reddish to purplish bracts; perianth-segments to 2.7 cm, outer segments spreading, lanceolate, fleshy, dark red at tips, inner segments spreading to erect, spathulate, delicate, white to very pale green; nectar-chamber 11 × 13 mm; style 40–48 × 2 mm, stigma-lobes c. 10, exserted in relation to the anthers; ovary locule strongly depressed in longitudinal section. Fruit globose to ovoid, to 3.5 cm diam.; pericarp greenish to dull red or slightly purplish. Seeds c. 2–3 × 1.4 mm, cochleiform, hilum-micropylar region forming an angle of 20–30° with long-axis.

Southern *caatinga* element: in *caatinga-agreste*, often on or associated with granite/gneiss inselbergs, 40–920 m, central-eastern to central-southern Bahia and central-northern and north-eastern Minas Gerais. Endemic to the core area of Eastern Brazil. Map 24B.


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This species is rather variable in stem thickness and rib-number, but this variation seems to lack any kind of geographical pattern. A form with unusually short flowers has been described from near the Rio Jequitinhonha, north-eastern Minas Gerais (B. breviflorus Ritter), but it is otherwise unremarkable and does not merit recognition at any rank when the overall variation of the species is taken into consideration. A rather different and erroneous impression is given in a recent article by Hofacker & Braun (1998), in which they distinguish two subspecies in a key and illustrate each by a single collection. Their key implies that these two entities are geographically separated, the heterotypic subsp. breviflorus (Ritter) P. J. Braun & E. Esteves Pereira representing the species in Minas Gerais, while the homotypic subspecies is restricted to southern Bahia. However, this is not so, since the short-flowered population named by Ritter is only one amongst a number of variants found in Minas Gerais, none of which differs significantly from contiguous Bahian populations. The Bahian form illustrated from Jequié under the number ‘HU 746’ is very far from typical of the species, having a peculiar naked pericarpel.


Shrubby, solitary or poorly branched, to 2.5 m. Stems ± erect, 1.5–2.0 cm diam.; ribs 8–14, 2 × 3 mm; epidermis bright to grey-green. Areoles 2 mm diam., 4–8 cm apart on the ribs. Central spines 1–2(–3), to 4(–5) cm, radials 10–12, to 1 cm. Flowers 6 × 4 cm; pericarpel greenish, 11–12 × 8–9 mm; flower-tube infundibuliform, 4 × 1.5–1.8 cm, pericarpel and tube bearing broad, triangular, acute to acuminate bract-scales, green to strongly reddish at tips; perianth-segments to 2.8 cm, outer segments spreading, lanceolate, fleshy, dark red at tips, inner segments spreading to erect, spatulate, delicate, white to very pale green; stamens with greenish filaments; nectar-chamber 7–8 × 10–12 mm; style 60–65 × 3 mm, stigma-lobes c. 8, at the same level as the anthers; ovary locule hemiglobose to depressed in longitudinal section. Fruit globose to ovoid, to 3 cm diam.; pericarp greenish to dull red or slightly purplish. Seeds c. 2.4 × 1.8 mm, black, shiny; hilum-micropyle region forming an angle of 60° with long-axis.

South-eastern campo rupestre (Grão Mogol) element: carrasco, 850–1000 m, region of Grão Mogol, northern Minas Gerais. Endemic to the core area within Minas Gerais. Map 36D.


CONSERVATION STATUS. Vulnerable (2) [criteria C2a]; extent of occurrence = 434 km²; PD=3, EI=1, GD=1. Short-list score (2×5) = 10.

This species is clearly differentiated from the widespread and variable B. phaeacanthus by the acute bract-scales on its pericarpel and its curved seeds.
16. CEREUS Miller


Tree-like, shrubby or semi-scandent, with (2-)3-10-ribbed, triangular to cylindric or constricted-cylindric stems; rootstock tuberous or fibrous; vascular tissues becoming very woody; epidermis and cuticle thick and tough, often covered in whitish or bluish wax; areoles well-spaced along the ribs, usually rather spiny at least in young plants. Flowers large, elongate funnelform to salverform, nocturnal, sweetly scented, pericarpel and tube terete or somewhat angled, naked except for few minute scales, glabrous or with small tufts of trichomes in their axils; perianth white inside; floral remnants strongly blackening post-anthesis. Fruit ovoid to barrel-shaped, splitting laterally or opening at apex, pericarp deep pink to reddish or yellow, sometimes strongly glaucous until ripe, floral remnant persistent or early-deciduous leaving a depressed scar. Seeds c. 2–3 mm, black, testa smooth to ruminate.

A genus of some 20 poorly understood, South American species, divided between 4 subgenera, of which two are represented in Eastern Brazil (Subg. Cereus & Subg. Mirabella) by a total of 6 species. A third subgenus (Subg. Ebneria (Backeb.) D. Hunt) is represented in Central-western Brazil by at least three described species, C. spegazzinii F. A. C. Weber, C. kroenleini N. P. Taylor (1995b) and C. adelmarii (Rizz. & Mattos-F.) P. J. Braun, and a possible fourth, C. saddianus (Rizz. & Mattos-F.) P. J. Braun, which, however, bears more than a passing similarity to C. horrispinus Backeberg (Subg. Oblongicarpi (Croizat) D. Hunt & N. P. Taylor) from northern Colombia and Venezuela. Subgenera Ebneria and Mirabella are considered to be vicariant groups, the latter replacing the former in Eastern Brazil (Taylor 1992a).

In Eastern Brazil the genus has one or more representatives in all of the major vegetation types (see subgenera, below).

1. Floral remnant early-deciduous, leaving a well-defined scar at the apex of the ± terete (not strongly angled) developing fruit; rootstock fibrous, not rhizomatous-tuberous (in Brazilian spp.); semi-decumbent shrubs with branches to > 5 cm diam. or erect and tree-like to > 4 m (Subg. Cereus) 2
2. Fruit (when undamaged) opening from apex into c. 3 segments (S Minas Gerais) 6. hildmannianus
3. Fruit opening by a single lateral split 3
4. Tree-like, often with a well-defined trunk and to > 4 m; fruit pinkish- purplish-red (caatinga/agreste and on limestone etc. in other ecosystems, NE Brazil to cent. Minas Gerais) 5. jamacaru
5. Semi-decumbent or low shrub, 0.5–4.0 m; fruit pinkish red (coastal sand & rocks) or yellow (gneiss/granite outcrops in Mata Atlântica, W Espírito Santo, S edge of Minas Gerais & N Rio de Janeiro) 4
6. Ribs 3–5; flowers 14–25 cm (mainland Brazil) 3. fernambucensis
7. Ribs 5–9; flowers c. 13 cm (Fernando de Noronha) 4. insularis
8. Ribs (2–)3–4(–6), acute; wood yellow beneath the bark (caatinga, Piauí, Ceará, Pernambuco, N & S Bahia to cent.-N Minas Gerais) 2. albicaulis
9. Ribs (3–)4–6, rounded; wood whitish beneath the bark (cerrado & cerrado-caatinga ecotone, SW Maranhão, W Bahia, N & cent.-E Minas Gerais) 1. mirabella

Subg. Mirabella (Ritter) N. P. Taylor (nos. 1 & 2): rootstock tuberous; stems semi-scandent, slender; bract-scales of pericarpel and tube with conspicuous trichomes and sometimes fine
spines in their axils; fruit bearing persistent floral remnant at apex. More or less restricted to sandy substrates in *cerrado* and *caatinga*.

Kiesling (1994) has recently transferred the two species treated here to *Monvillea* Britton & Rose, which is typified by *Cereus cavendishii* Monv. ex Lemaire. Hunt (1988) drew attention to the view already expressed by others that this name and its better-known synonym, *C. paxtionianus* Monv. ex Salm-Dyck, had been misapplied by J. D. Hooker, and later by Britton & Rose, to plants now correctly known as either *Praecereus euchlorus* (F. A. C. Weber) N. P. Taylor or *P. saxicola* (Morong) N. P. Taylor (both from central South America). As to type, Hunt suggested that *C. cavendishii* and, therefore also *Monvillea*, were referable to *Acanthocereus* Britton & Rose. Heath (1992a) characteristically disagreed with Hunt’s view and neotypified *C. cavendishii* with an illustration published by J. D. Hooker (1899), to maintain the usage established by Britton & Rose. Heath argued that the type locality given for *C. cavendishii*, namely Cartagena, Colombia, was an error. However, photographs of *Acanthocereus tetragonus* (L.) Hummelinck from northern Colombia preserved at NY, showing juvenile growth stages, strongly suggest that *Cereus cavendishii* could have been based on a juvenile *Acanthocereus*, or possibly *Pseudoacanthocereus*, from the region of Cartagena, rather than a *Praecereus* from central South America, and that Heath’s neotypification should be superseded. It also should be noted that the genus *Praecereus*, represented by *P. euchlorus* subsp. *smithianus* (Britton & Rose) N. P. Taylor, does occur in northern South America (Colombia & Venezuela), but this subspecies has stems with 8-15 ribs (not 4-6 as required by the original description of *C. cavendishii*).

   Holotype: Brazil, Minas Gerais, c. 15 km W of Água Boa, Ritter 1238 (U).


Rootstock tuberous, with a large yam-like taproot; plant shrubby, usually ± decumbent on or scrambling over other vegetation, stems ascending to 1 m above the ground, to 2 m long and 3 cm diam. strongly glaucous when new, wood whitish beneath the bark; ribs (3-)4-6, rounded (5-6 in seedlings); areoles 3 - 5 mm diam., with blackish glandular trichomes at first, later whitish, 2-4 cm apart on the ribs; spines 3-6 (more in seedlings and young basal shoots), needlelike, brownish, paler tipped, the longest ± central, to 25 mm. Flower (Taylor 1992a: 21, Fig. F) narrow funnelform, c. 18.5 × 10 cm; tube angular, c. 12 × 1.3-1.5 cm, bearing occasional bract-scales with trichomes in their axils, stamens inserted in uppermost 2-2.5 cm, to 5 cm; style c. 14 cm, stigma-lobes c. 10, to 9 mm, whitish; perianth-segments c. 4-5 cm, narrow, white; pericarpel oblong, c. 22 × 15 mm, angular, bearing minute bract-scales with trichomes and occasional minute spines in their axils. Fruit 3.5-4.0 × 2-3 cm, tapered at apex, with a few minute scales bearing trichomes and sometimes minute spines near base, pinkish, bearing the blackened perianth remains. Seed c. 2.4 × 1.6 mm, testa ± smooth, shiny black.

*Cerrado* element: mostly in sandy phases of the *cerrado* and more open places of the *cerrado-caatinga* ecotone, c. 150-750 m, south-western Maranhão and western Bahia to cent.-N and W Minas Gerais (Rio São Francisco drainage), and disjunctly in E-cent. Minas Gerais (Rio Doce / Rio Jequitinhonha watershed); eastern Goiás (?). Map 34.


**Conservation Status.** Vulnerable (2) [criteria B1/2a–d]; area of occupancy estimated to be < 2000 km²; PD=2, EI=1, GD=1. Short-list score (2x4) = 8. *Cerrado* habitats in Eastern Brazil are suffering considerable modification by agricultural development.

Together with *Arrojadoa dinae*, *Cipocereus crassisepalus* and 3 *Discocactus* spp., this is one of the few terrestrial cacti that inhabits *cerrado*, although it cannot be said to be a common component of this vegetation, being of erratic occurrence, mostly in sandy places. The record of *C. mirabella* from south-western Maranhão is separated from those from western Bahia by c. 500 km, which in turn are some 425 km from the nearest in northern Minas Gerais, but this may reflect the lack of collections from these relatively inaccessible regions and it is possible that its distribution is ± continuous in the cerrados in between. Of greater interest is the apparent disjunction in its distribution across the Serra do Espinhaço, between central-eastern (the type locality) and central-northern Minas Gerais (c. 250 km). Nevertheless, it is possible that geographically intermediate populations await discovery, since it inhabits a vegetation type of little interest for cactus enthusiasts and has probably been ignored by botanists for the usual reasons.


Very similar to the preceding, but scrambling to 3 m high; tuberous taproot to 40 cm; stem to 5 cm diam., cortex yellow beneath the bark; ribs (2–)3–4–(-6), usually sharply triangular-acute; central spine better defined. Flower (Taylor 1992a: pl. III) nocturnal, 13.5–18.3 cm (more slender in all its parts than *C. mirabella* in the few examples seen), stamens c. 20 mm. Fruit to 7.5 × 4 cm, funicular pulp white. Seed c. 2 × 1.4 mm.

Widespread *caatinga* element: in *caatinga de altitude*, *caatinga* and *carrasco*, often on sandy substrates of the Cipó soil series, c. 470–1000 m, northern and south-eastern Piauí, north-western Ceará, western and central-southern Pernambuco to western, northern and eastern Bahia and southwards through the Chapada Diamantina to the Serra do Espinhaço, southern Bahia and (?) northernmost Minas Gerais. Endemic to the core area of Eastern Brazil. Map 19.

This species has a patchy geographical distribution, being widely spread in the *caatinga* towards its northern limits, but more or less restricted to the East Brazilian Highlands in the southern two-thirds of its range. This distribution pattern may in part correspond with that of the 'Cipó' soil series, upon which a distinct type of *caatinga* vegetation is found (type no. 5 of Andrade-Lima 1981: 159), but it has also been seen growing upon inselbergs. It is variable in the robustness of its stems.

It was originally described as an *Acanthocereus* by Britton & Rose, whose species it vaguely resembles in vegetative characters, although not in flower and fruit-morphology, which Britton & Rose unfortunately did not know.

Subg. *Cereus* (nos. 3–6): rootstock fibrous (in Brazilian taxa); treelike, semi-decumbent or creeping, stems stout; bract-scales of pericarpel and tube glabrous in their axils (rarely with inconspicuous trichomes in *C. fernambucensis*); floral remnant early-deciduous from fruit apex.

This is the least understood subgenus, species delimitation being hampered by lack of data on fruit and seedling morphology. Found in various phases of the *Mata atlântica, caatinga-agreste, cerrado* (but only on limestone outcrops) and South-eastern *campo rupestres* (rare).
3. Cereus fernambucensis Lemaire, Cact. gen. nov. sp.: 58 (1839). Type: 'patria est Fernambuco' [Pernambuco = Recife]; not known to have been preserved. Neotype (designated here): Brazil, Pernambuco, Mun. Jaboatão dos Guararapes, Candeias, by the sea, 20 Feb. 1990, Zappi 228 (HRCB) – the nearest extant population, since already extinct in Mun. Recife.


? 'C. neotetragonus' Backeberg, Die Cact. 4: 2363 (1960), nom. inval. (Art. 37). Supposedly based on a plant from Brazil (Rio de Janeiro?), but not typified. The plant in the plate 77 that Backeberg cites from Werdermann, Blühende Kakt. und andere Sukk. (1934), does not match his description and probably represents the Andean C. hankeanus F.A.C. Weber. [C. variabilis auct. non Pfeiffer, Enum. cact.: 105 (1837), nom. illeg. (Art. 52.1).]
[C. pitajaya sensu Hook. in Bot. Mag. 70: t. 4084 (1844), non (Jacq.) DC (= Acanthocereus tetragonus (L.) Hummelinck).]

Shrubby or caespitose, erect or sprawling, always branched at or very near base, 0.5–4.0 m; stems with numerous constrictions, pale green to glaucous, non-mucilaginous; ribs 3–5, to 65 × 10–30 mm; areoles to 10 mm diam., 15–35 mm apart on mature stems, rather woolly, felt often blackish at first, hairs whitish and conspicuous on young growth. Spination variable, pale yellow-brown to brown when young, later grey, sometimes almost lacking; central spines 1–4, to c. 50 mm; radials to 8 or more, to c. 25 mm. Flowers slender funnel-form, 14–25 × 9–15 cm, white, sometimes pinkish without; pericarpel bract-scales sometimes bearing trichomes in their axils, tube pale green. Fruit 5–7.2 × 3–6 cm, pinkish red or yellow, laterally dehiscent by a single split, the base of the floral nectar-chamber forming a deep depression (to 8 mm) at apex. Seed c. 2–3 × 1.5 mm, black, shiny, cuticular folds almost absent.

The specific epithet is correctly spelled with 'f' and should not be corrected to 'pernambucensis' as advocated by various authors, since Pernambuco was written Fernambuco by some Europeans during the last century (see Brummitt & Taylor 1990: 302–303; Werdermann 1933: 89–90). The illegitimate name C. variabilis Pfeiffer as to type belongs in the synonymy of Acanthocereus tetragonus (L.) Hummelinck, a Caribbean taxon, and cannot be used even though Pfeiffer's concept included elements referable to the Cereus treated here (cf. ICBN Arts 7.5 & 52.1/2). Haworth's C. obtusus has also been used for this species, but its original description and typification are unsatisfactory and its provenance is uncertain. Prior to conservation of the name C. jamacaru DC with a new type (see below), this name was in fact based on an illustration of C. fernambucensis.

Two subspecies are recognized and are quite separate geographically, except in the lowlands of the northern half of Rio de Janeiro:

1. Fruit pinkish-red; flower to c. 17 cm (sand & rocks by the sea) 3a. subsp. fernambucensis
1. Fruit yellow; flower to c. 25 cm (rocks inland, W Espirito Santo & S Minas Gerais) 3b. subsp. sericifer

3a. subsp. fernambucensis

VERNACULAR NAMES. Cardo-anamá, Cardo-de-praia, Cardo-vinagre, Figueira-do-inferno.

Low-growing, caespitose, mostly < 80 cm tall, occasionally semi-pendent or scrambling through vegetation and reaching 2.5 m high; stems very variable in size, 4–11 cm diam., pale to blue-green but not strongly glaucous; areoles spiny. Flowers c. 14–17 × 9–11 cm; pericarpel 13–18 × 7.5–12.0 mm, tube narrowed to 7–8.5 mm, then
flared to 13–30 mm diam. at apex; perianth-segments to 4.5–6 × 1.4–2.0 cm; style 11–16.5 cm; stigma-lobes 8–13, 8–15 mm, green. Fruit pinkish red.

Humid/subhumid forest (restinga) element: on sand-dunes, rocks and growing through shrubs of the restinga, sometimes within reach of the sea spray, to c. 100 m, throughout the coast of Eastern Brazil from Rio Grande do Norte southwards (to São Paulo: Ilha do Cardoso). Endemic to North-eastern and South-eastern Brazil. Map 14D.


RIO DE JANEIRO: Mun. Quicamã (Quissamã), road to Barra do Furado, 22°65′S, 41°26′W, 23 Nov. 1999, Zappi et al. 396 (K, UEC).

CONSERVATION STATUS. Lower Risk (1); PD=1, EI=1, GD=2. Short-list score (lx4) = 4.

The above key and description of this variable subspecies does not account for southern forms from western Rio de Janeiro and São Paulo, which are considerably larger in their stems and flowers. Its pollination biology has been studied by Locatelli & Machado (1999b).


Erect or semi-decumbent shrub to 4 m tall, branching mainly near base or from decumbent parts of the branches; stem 10 cm diam. or more, green to strongly glaucous; areoles almost naked to very spiny. Flowers to c. 25 x 15 cm; pericarpel c. 25 x 20 cm, tube narrowed to not < 10 mm, then flared to 35 mm or more at apex; perianth-segments to 11 x 4 cm; style c. 20 cm; stigma-lobes c. 15, 15–20 mm, pale yellow. Fruit yellow.

Southern humid/subhumid forest (inselberg) element: on ± naked rock outcrops (especially gneiss/granite inselbergs) inland in the Mata atlântica zone, 50–400 m, western and central Espirito Santo and southernmost Minas Gerais, to adjacent Rio de Janeiro (Rio Paraiba drainage). Endemic to South-eastern Brazil. Map 16B.


CONSERVATION STATUS. Lower Risk (1); PD=1, EI=1, GD=1. Short-list score (1x3) = 3.

This subspecies represents a distinct inland race of the otherwise littoral C. fernambucensis. Apart from its yellow fruit it differs from subsp. fernambucensis, as seen in Eastern Brazil, by being larger in all its parts, although forms of the latter from further south approach it in their stems and flowers.


Like C. fernambucensis, but stems more evenly cylindrical (less obviously constricted/jointed); ribs 5–9, 1–2 cm high, spines usually more numerous, to 15 or more, partially hiding the stem; flowers very similar, but to only c. 13 cm.

Humid/subhumid forest (restinga) element: rocky habitats and cliffs, Fernando de Noronha, North-eastern Brazil. Endemic. Map 15C.

PERNAMBUCO: Archipelago of Fernando de Noronha, 1887, Ridley et al. 23 (K, BM; IPA, photos), 1987, Duranton s.n. (K, SPF 48093, 48094, 48095); l.c., próximo a salina, 20 Oct. 1955, Andrade-Lima 55-2222 (IPA); Praia do Bode, 3°50'S, 32°25'W, 3 June 1993, A.M. Miranda et al. 999 (PEUFR); l.c., Praia Ataleia, 4 June 1993, A.M. Miranda 1042, 1043 (PEUFR, HUFE).

CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1x5) = 5. Probably Conservation Dependent (the Archipelago of Fernando de Noronha is a protected area).
This taxon may represent a further subspecies of *C. fernambucensis*, from which it is separated by c. 350 km of Atlantic Ocean, but careful field studies are required. *Cereus insularis* is apparently very variable in habit and spination, some forms being completely covered in fierce spines, the stems 5–9-ribbed (cf. Duranton s.n.). Its flowers, which are known from carefully preserved material, are very similar to those borne by smaller forms of *C. fernambucensis*, such as are found along the coast of Pernambuco. *C. ridleii*, which was discovered by the respected Dárđano Andrade-Lima, is known only from his original habitat photograph, depicting a distinctive tree-like plant (c. 3–5 m), and from its holotype preserved at Recife (IPA). Contrary to Backeberg's statements, this specimen, collected in October 1955 (*Andrade-Lima 55-2221*), is 6-ribbed and bears flowers. (It is possible that wild material was cultivated at Recife until it flowered, but the label does not give any clue about this.) Were it not for the photograph and the 6-ribbed stem, the holotype could easily be identified as *C. fernambucensis*. The photograph published by Backeberg (1960: Abb. 2247) shows the tree-like *C. ridleii* surrounded by plants of the low-growing *C. insularis*. It is therefore tempting to suppose that *C. insularis* is some kind of stabilized juvenile, yet reproductive, neotenic form, which occasionally develops into the erect adult stage represented by *C. ridleii*, such behaviour being known, for example, in the Madagascan cactus relative, *Didierea trollii* (Rowley 1992). Unfortunately, plants corresponding with *C. ridleii* have not be seen recently in habitat (Braun 1990) and so its true nature seems likely to remain a mystery for the time being.


VERNACULAR NAMES. Mandacaru, Mandacaru-de-boi, Mandacaru-facheiro, Mandacaru-de-faixo, Cardeiro, Jamacaru, Jamaracunl, JumuCunl, Jumarucu, Cumbeba, Urumbeba.

Tree-like, to at least 10 m, with a spread of up to 8 m or more, often with a short but well-defined, bark-covered, greyish trunk 50–200 × 30 cm or more (but regrowing from base to form a shrub when cut down), densely branched; stems 7–20 cm diam., often strongly glaucous when young, later dark blue-green, epidermis very tough, vascular cylinder extremely woody when old; ribs 4–10, sometimes only 3 in juvenile plants < 1.5 m tall, to 60 × 18–45 mm, high and narrow to broader and more rounded, with or without transverse fold lines alongside the areoles, margin weakly to more strongly crenate; areoles ± circular, 4–8 mm diam. at first, 15–40 mm apart, dirty white to grey woolly felted and hairy at first, often showing marked indeterminate growth in age, to 15 mm diam. Spination very variable, often ± absent on mature branches high above the ground, but sometimes spiny throughout and/or very spiny near base and then with many more spines per areole than described below, spines pale yellow-brown to reddish brown at first, later grey to blackish; central spines 1–4 or more, very variable in size, occasionally to 150 × 3 mm; radials 7–12, to c. 35 mm. Flowers developing from areoles almost anywhere on the branches, funnel-form, 21–30 × c. 10–20 cm; pericarpel 20–28 × 12–18 mm, like the tube bearing green or reddish bract-scales glabrous in their axils, apex of tube to 50 mm diam.; nectar-chamber to 65 mm; perianth-segments 50–100 × 20–27 mm, outer greenish sometimes tinged crimson near apex, inner pure white; style white to pale green, stigma-lobes 12–16, 11–19 × 1 mm, greenish. Fruit 6–10 × 4–8 cm, crimson to pinkish red, dehiscent by a lateral split to reveal white funicular pulp. Seed black, testa with cuticular folds.
This well-known name, which has already been conserved for purely nomenclatural reasons so that it can continue to be used in its familiar sense (Taylor & Zappi 1992c), may now be threatened by taxonomic union with C. hexagonus (Linnaeus) Miller. The Linnaean species is traditionally known from Venezuela southwards to the Guianas and northernmost Brazil (Roraima), but there exist populations further to the south-east, in the states of Pará and Maranhão, whose identity has not been determined. Since, on present knowledge, there do not appear to be any clear characters to distinguish between this pair of taxa, the absence of any significant geographical disjunction makes it tempting to suppose that there may be only a single widespread and variable species involved. Nevertheless, the name C. jamacaru, is maintained for the time being, at least until the situation in the field has been thoroughly researched.

Even in the restricted sense adopted here, this is a very wide-ranging and rather variable species divisible into the following subspecies:

1. Juvenile plants (between 10 cm and 1 m high) passing through a stage with only 3–7 ribs and yellow to orange-brown spines of variable length; mature stem-segments variously shaped; flower 15–20 cm diam. or more; pericarpel and tube to c. 16 cm, bract-scales red, conspicuous; largest perianth-segments 8–10 cm (NE Minas Gerais northwards, from c. 18°25'S in the drainage of the Rio Jequitinhonha) 5a. subsp. jamacaru

5a. subsp. jamacaru

*Caatinga* element: in stony to sandy soil and on rocks of various kinds, *caatinga-agreste*, rarely entering into *Mata atlântica* in NE Brazil, c. 50–900(–1200) m, widespread in Eastern Brazil, but less frequent west of the Rio São Francisco in south-western Bahia (where replaced by subsp. *calcirupicola* on limestone outcrops) and uncommon within the Chapada Diamantina, southwards to central-northern and north-eastern Minas Gerais (extending as a frequent plant in the Rio Jequitinhonha valley to at least 17°S and beyond in the region of Diamantina, at c. 18°25'S), sometimes occurring further south, as well as within its natural range, ranging north-westwards to Maranhão, northernmost Piauí and Ceará; Northern Brazil (Tocantins & Pará)? Only a few records marking the approximate western, eastern and southern limits of natural range of the subspecies are cited below (Map 19):


CONSERVATION STATUS. Lower Risk (1); PD=1, EI=1, GD=2. Short-list score (1x4) = 4. Sometimes regenerating from stumps and recovering, or intentionally spared, when the forest it inhabits is cut down.

Very important as a source of cattle fodder during times of drought and sometimes planted for hedging purposes. It is also variable in rib number and degree of spine development. A widespread regional variant from western Rio Grande do Norte and adjacent Paraíba differs from 'typical' plants in having more ribs, both as a seedling and subsequently, as well as the stem being less obviously constricted with ± parallel-sided 'segments'. Local variations are common and include specimens with up to 10 ribs and marked differences in number and length of spines.

Apparently very similar to subsp. jamacaru is a plant from Depto Florida (W Santa Cruz), Bolivia, which Ritter (1980: 553) named Piptanthocereus colosseus. Braun & Esteves Pereira (1995) refer this taxon to C. lamprospermus Schumann, but its relationship deserves further investigation.


[C. coerulescens sensu Warming, Lagoa Santa: 150–151, figs 36 & 37 (1908), non Salm-Dyck (1834).]

Caatinga I mata seca Rio São Francisco (Rio das Velhas, MG) element: on ± forest-covered limestone (Bambui) outcrops, where locally co-dominant with other arborescent cacti, more rarely on arenitic rock or sand (at higher elevations only), amongst caatinga, cerradão, cerrado and rarely campo rupestre, c. 450–1200 m, western Bahia to central Minas Gerais (to c. 19°40'S); Central-western Brazil. Map 27A.


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CONSERVATION STATUS. Lower Risk (1); PD=1, EI=2, GD=2. Short-list score (1x5) = 5. Its habitat is declining in some places due to quarrying of limestone.

This subspecies is distinguished from typical subsp. *jamacaru* by relatively minor yet recognizable differences in juvenile stem-morphology and flower shape etc. It ranges to the south-west of the region occupied by subsp. *jamacaru* and is at its eastern limit in the upper drainage of the Rio São Francisco (Rio das Velhas). Tall growing forms with a well-developed trunk and relatively slender branches, from the Serra do Cabral, Minas Gerais (on non-calcareous rock at 900–1200 m), are connected via the type of this subspecies (from Montes Claros) to forms found further west in Goiás and the Distrito Federal on limestone. Some populations on isolated limestone outcrops have developed into distinctive variants, such as that described as var. *pluricostatus* by Ritter (see synonymy above), but such are matched by variations seen in subsp. *jamacaru*.

**6. Cereus hildmannianus** K. Schumann in Martius, Fl. bras. 4(2): 202 (1890). Type: Brazil, Rio de Janeiro (Schumann, l.c.), or Minas Gerais, Queluz [= Conselheiro Lafaiete] (fide Glaziou 1909: 325), Glaziou s.n. (Bt). Lectotype (designated here): Schumann, l.c., t. 41, fig. I (1890) [depicting a 6-ribbed, spineless stem apex bearing a flower].


*Cereus milesimus* E.C. Rost in Desert 4: 43 (1932). Type: Brazil, São Paulo, Ribeirão Preto, living plant assumed not to have been preserved. Lectotype (designated here): Rost, l.c. 42, photo.


[C. *peruvianus* auctt. pro parte, non (L.) Mill.]

Only the following subspecies is found in the area covered here:

**6a. subsp. hildmannianus**

Very similar to *C. jamacaru*, but tree-like or shrubby, to 15 m or more tall, sometimes with a very well developed trunk to > 2 m; stem tissues highly mucilaginous; ribs 5–12, very variable in number, to 50–70 x 10–30 mm, sometimes higher and thinner, juvenile plants 3–5-ribbed; flowers 10–14 cm diam.; fruit 5–12 x 7–12 cm, yellow, orange or reddish depending on exposure, usually splitting open from apex along c. 3 lines to fully expose the white funicular pulp; seeds c. 3 x 2.8 mm, testa with cuticular folds.

Southern humid/subhumid forest element: in rocky places and on dry shallow soils in *mata de planalto*, c. 800–1000 m, southern and western Minas Gerais, from (?) Conselheiro Lafaiete southwards and westwards, but frequently cultivated for ornament outside its natural range in the more humid parts of Eastern Brazil; South-eastern, Southern and Central-western Brazil; central and south-eastern South America (E Paraguay, Uruguay, NE & E Argentina etc., where replaced by the shorter-flowered subsp. *uruguayanus* (Kiesling) N.P. Taylor).


**CONSERVATION STATUS.** Lower Risk (1); PD=1, EI=1, GD=2. Short-list score (1×4) = 4.

This species has not been studied in the field within the core area treated here. However, plants from Rio de Janeiro, south-western Minas Gerais, São Paulo and Paraná have been examined in habitat, though seldom with ripe fruit. The fruits that have been observed in the field and in cultivation generally display the characteristic mode of dehiscence described above and, together with the highly mucilaginous stem tissues, would seem to provide a means for distinguishing *C. hildmannianus* from *C. farnambucensis* subsp. *farnambucensis* and *sericifer*, with whose ranges it slightly overlaps, and from the related but allopatric *C. jamacaru*. All three species exist as spineless forms and when these are cultivated outside their natural range their identification can be very difficult unless ripe fruits are present.

*C. hildmannianus* may be widespread in drier phases of the semi-humid and humid, subtropical and tropical planalto forests north and east of the Chaco in central and south-eastern South America, and has a potentially much more extensive synonymy than that tentatively given above (see Hunt 1992b). For example, the huge plant illustrated by Backeberg (1960, 4: Abb. 2246) from Mato Grosso [do Sul?] probably belongs here. However, the precise identity of such plants will remain uncertain until the *Cereus* species of northern Paraguay and eastern Bolivia are better understood.

Schumann (l.c.) stated that *C. hildmannianus* came from Rio de Janeiro, whereas Glaziou (1909: 325), its collector, later gave a precise locality in southern Minas Gerais as its provenance (see type citation above). There are only the above, poorly documented records of the plant growing wild in the state of Rio de Janeiro, where it is much more commonly cultivated (as elsewhere), but it is assumed to be native in Minas Gerais and is certainly so and not uncommon in the adjacent state of São Paulo. The commonly cultivated form has ± spineless stems, as does that depicted in Schumann's plate, which is here selected as lectotype (in the absence of any extant original herbarium material). This is in contrast to some wild forms, which can have very spiny stems, and it is possible, therefore, that what Schumann received from Glaziou and described was actually a cultivar from Rio de Janeiro and not a wild plant.
The following 3 genera (nos. 17-19) represent a distinct, endemic lineage within the Eastern Brazilian Cereeae, of which the first contains the more basal elements and in future may be shown to be paraphyletic in respect of either of those that follow it.

17. CIPOCEREUS Ritter


Including Floribunda Ritter (1979); Pilosocereus subg. Floribunda (Ritter) P. J. Braun (1988); tantum quod typ.

Shrubby or tree-like, 0.4-3.5 m, branched or not above the ground; vascular cylinder strongly to weakly woody; tissues sometimes stiff, scarcely to extremely mucilaginous; branches showing slight constrictions or ± constant growth, epidermis green, grey or pale waxy blue, smooth; ribs 4-18, acute to rounded, sinuses straight. Areoles with felt and variable spination; spines straight, opaque to translucent. Fertile part of stem not differentiated, random (lateral) and/or subapical. Flowers 1.5-9.0 x 1-7 cm, anthesis commencing at evening or diurnal; flower exterior bluish, covered in wax, sometimes reddish, especially on the distal half, but still waxy, smooth to ridged, glabrous or with areoles, and then hairs and minute spines as well as areolar felt also present; pericarpel oblong, nearly cylindric; flower-tube straight, terete, with some scattered acute bract-scales, more frequent towards its apex; perianth-segments reflexed, outer segments fleshy, inner segments thin, white or cream-coloured; nectar-chamber straight, not protected by the stamens (except in C. pusilliflorus); stamens many, anthers 1-3 mm, verrucose, forming a compact mass; style 9-65 mm, stigma-lobes 8-10, exerted or included in relation to the anthers. Fruit ovoid to globose, indehiscent; floral remnant persistent, blackening, erect, with rounded, deep insertion; pericarp covered in blue wax, dark purplish, brownish, pinkish or green beneath; funicular pulp aquose, translucent, greenish or yellowish. Seeds 1.2-1.8 mm, brown or dark brown-black, cochleariform, hilum-micropylar region differentiated, intercellular depressions present, mainly forming craterae, sometimes only slightly pronounced, testa-cells convex, conic or flat, cuticular folds coarse, very dense.

A genus of 5 very distinct species endemic to the Serra do Espinhaço and Serra do Cabral of Minas Gerais (campo rupestre and sandy phases of the cerrado); see Map 41. The waxy and mostly light bluish, indehiscent, ovoid to globose fruits with translucent pulp are characteristic. Species nos. 1 & 2 may be related on the basis of seed- and stem-morphology (including seedlings); likewise nos. 3-5. However, natural hybridization between nos. 2 and 4 has been observed (Taylor & Zappi 1989).

1. Ribs 4-7, triangular in section; areoles with dense felt and long hairs; central spines larger than radials 2
1. Ribs > 8, rounded in section; areoles with short, brown or white felt, long hairs absent; central and radial spines alike or upper areoles unarm
2. Areoles contiguous; flowers and fruits bearing areoles with spines and long hairs (Serra do Caraça, MG)
  1. laniflorus
  2. crassisepalus
3. Stems 5-8 cm diam., unarmed or bearing very few black spines, transverse folds between adjacent areoles on the same rib well marked, epidermis sky blue, waxy (Serra do Cabral & adjacent W slope of Serra do Espinhaço, MG)
3. Stems 2.5-5.0 cm diam., densely spiny; transverse folds absent; epidermis grey-green or bright green 4
4. Plants highly mucilaginous, to c. 50 cm tall; flowers small, < 2 cm, diurnal; fruits to 1.3 cm diam., pinkish, with a translucent waxy bloom (W slope of Serra Geral, northern Minas Gerais) 5. pusilliflorus
4. Plants not very mucilaginous, to > 50 cm tall; flowers > 4 cm, nocturnal; fruits > 2 cm diam., dark blue-black covered in a pale blue waxy bloom, or whitish 5
5. Flower blue outside, tube smooth, glabrous; perianth-segments patent to reflexed at anthesis; fruits not ridged, smooth (Serra da Bocaina, Grão Mogol southwards to Presidente Kubitschek, Serra do Espinhaço, MG)  

4a. minensis ssp. minensis

5. Distal half of flower brownish, reddish or yellowish, tube ridged, areolate and spiny; perianth-segments erect at anthesis; fruits ridged, with spiny areoles, greenish blue or whitish (Serra do Cipó, Lapinha e Pico de...)  

4b. minensis ssp. pleurocarpus

Holotype: Brazil, Minas Gerais, Mun. Santa Bárbara, Serra do Caraça, c. 1800 m, 11 Sep. 1990, Zappi et al. 240 (SPF; HRCB, BHCB, isos.).

Erect shrub, 0.5–1.5 m, sparsely branched, mainly at ground level; vascular cylinder strongly woody; inner tissues mucilaginous; branches 6–7 cm diam., epidermis olive-green, with strikingly pruinose, bluish wax on the young; growth; ribs 5–7, 2 × 2 cm, triangular in section. Areoles to 6 mm diam., contiguous, felt at first light-brown, becoming black, long hairs white, very dense at apex. Spines opaque, dark brown; central spines 7–9, 1.5–2.0(-3.0) cm, porrect; radials 10–14, to 1 cm, adpressed. Fertile part of stem not differentiated, lateral to subapical. Flower-buds acute 1–2 days before anthesis; flower (May/June) c. 7 × 3.5 cm, exterior dark blue, ridged, with areoles, these bearing 3–5 minute reddish spines and long white hairs; pericarpel 18–20 × 12–15 mm; flower-tube 45 × 24 mm at its widest point, ± parallel-sided, straight, with acute bract-scales at apex; outer perianth-segments 12–14 × 7 mm, dark blue to purplish cream, inner segments 18 × 8 mm, white or pale creamy yellow, spathulate, apiculate; nectar-chamber c. 20 × 6–7 mm; style 40 × 1.6 mm, tapering; stigma-lobes 8, 6 mm, acute at apex; ovary locule c. 7 × 6 mm, quadrangular in longitudinal section. Fruit (in Aug./Sep.) to 2.5 × 2.0 cm, ovoid; seeds (1.5-)1.6-1.7 x 1-1.1 rom, hilum-micropylar region 0.6(-0.7) mm, forming an angle of 30° with long-axis; testa-cells domed, with intercellular depressions and coarse, dense cuticular folds.

South-eastern campo rupestre element: quartzitic outcrops in campo rupestre, c. 1800 m, Serra do Caraça, south-central Minas Gerais. Endemic to the core area within Minas Gerais. Map 39.


CONSERVATION STATUS. Critically Endangered (4) [criterion D]; PD=3, EI=1, GD=1. Short-list score (4x5) = 20. Presently known from only a single, small population (< 15 mature individuals); further field investigations are needed to confirm extent of range and abundance, but it unlikely that it is abundant elsewhere in view of the amount of attention the area concerned has received from botanists. Maintained ex situ at the Royal Botanic Gardens, Kew.

In its flowers and fruits bearing well-developed, woolly and spiny areoles, and in its isolated geographical location, this species seems to be a relict, which has the most plesiomorphic floral characters within tribe Cereeae, with only Cipocereus minensis subsp. pleurocarpus and Cereus subg. Mirabella having comparably primitive floral features.

The strongly glaucous young growth and approximate, darkly spined areoles of this species are strongly convergent with those of Pilosocereus fulvilanatus, q.v.


Erect shrub or treelet, 1–2 m, branched above the ground; root system well developed, roots napsiform; cauline vascular cylinder rather woody; succulent tissues mucilaginous. Young plants slender, stems with 5–8 low ribs, the areoles with dense, white or greyish, long hairs and reddish spines. Mature stems 5–6 cm diam., epidermis olive-green, rather glaucous when young; ribs 4–6, 1.5–2.0 x 2.5–3.0 cm, triangular in section. Areoles to 15 mm diam., 15–30 mm apart, with dense felt and long hairs, at first golden red, later blackish. Spines opaque, yellowish, becoming dark brown or black; central spines 1–2(-3), to 4 cm, porrect; radials 3–8, to 2 mm, adpressed. Fertile part of stem not differentiated, subapical. Flower-buds obtuse before anthesis; flowers c. 7.5–9 x 4–5 cm, dull, dark blue, ridged, glabrous except for scattered apiculate bract-scales; stamens 9–11, with long anther-pedicels; style-beak c. 5 cm, reddish, obtuse; stigma-lobes c. 9, c. 10 mm, ovary c. 13 x 8–9 mm, rectangular in longitudinal section. Fruit to 4.5 x 3.0 cm, narrowly oblong to ovoid; pericarp dark-blue, smooth, naked. Seeds 1.6–1.7 x 1.0–1.2 mm, hilum-micropylar region c. 0.5 mm, forming an angle of 35–40° with long-axis; testa-cells domed, with intercellular depressions and coarse, dense cuticular folds.

South-eastern campo rupestre (cerrado) element: in sandy cerrado/carrasco associated with crystalline rock outcrops, 500–1200 m, north of Diamantina, Serra Negra and east side of Serra do Espinhão, Minas Gerais. Endemic to the core area within Minas Gerais. Map 38A.

MINAS GERAIS: Mun. Itamarandiba, c. 20 km SW of airport, towards Penha de França, 3 Aug. 1988, Eggli 1061 (ZSS); Mun. Diamantina, Horst & Uebelmann 169 (U); c. 25 km along road to Mendanha, E of road towards Rio Jequitinhonha, 31 Oct. 1988, Taylor & Zappi in Harley 25487 (SPF, K) — population including hybrids with sympatric C. minensis; c. between Mendanha and Inhã, 17°59'44"S, 43°26'44"W, M. Machado (obs.); Mun. Rio Vermelho, Serra do Ambroío, 1959, Ritter s.n. (1012) (U), 14 July 1984, Varanda et al. in CFCR 4885 (SP, SPF), 6 Mar. 1988, Zappi & Prado in CFCR 11822 (SPF). Some of the location data used in Map 38A were supplied by M. Machado (pers. commun.), for localities where this species is sympatric with Uebelmannia, but the coordinates are not reproduced here for the protection of the latter.

CONSERVATION STATUS. Vulnerable (2) [criteria B1/2c]; extent of occurrence = 1407 km²; PD=3, EI=1, GD=1. Short-list score (2 x 5) = 10. Habitat destruction by charcoal producers continues to be a problem.

As noted above, this species hybridizes with C. minensis when they come into contact.


VERNACULAR NAME. Quiabo-da-lapa.

Erect shrub or treelet, 1–3.5 m, branched above the ground; vascular cylinder weakly woody; succulent tissues mucilaginous. Seedlings and young plants with 10 low ribs and areoles with dense reddish spination. Mature stems 5–8 cm diam., sometimes slightly constricted, epidermis a striking light blue, covered in thick wax; ribs 8–11, 0.5 x 1.2–1.7 cm, rounded in section, produced below the areoles. Areoles to 3 mm diam., 20–23 mm apart, felt short, at first white, the areoles frequently unarmed, becoming blackish in age. Spines on young areoles 0 or few, if present, black or dark reddish brown, to 15 mm; old areoles with 5–7 spines, to 2.5 cm, porrect. Fertile part of stem not
differentiated, flowers numerous, often from one side of stem and/or subapical region. Flower-buds obtuse before anthesis; flowers c. 6.5–8.0 × 3.5–4.0 cm, exterior dark blue, ridged, glabrous except for scattered bract-scales; pericarpel 15 × 15 mm; tube 50 × 20–25 mm at its widest point, ± parallel-sided, straight, with ovoid to spathulate, apiculate bract-scales at apex; outer perianth-segments 9–12 × 6–8 mm, dark blue to purplish cream, inner segments 18 × 8 mm, white or cream, spathulate, fimbriate and apiculate; nectar-chamber c. 20–23 × 8–10 mm; anthers 2.2–3.0 mm; style 45–50 mm, tapering; stigma-lobes c. 10, c. 9 mm; ovary locule c. 9 × 7 mm, rectangular in longitudinal section. Fruit to 4.5 × 3.5 cm, ovoid; pericarp dark-blue, smooth, naked, but covered in dense, sky blue wax. Seeds 1.6–1.8 × 1.1–1.2 mm, hilum-micropylar region 0.7 mm, forming an angle of 35–40° with long-axis; testa-cells conic, with intercellular depressions and coarse, dense cuticular folds.

South-eastern campo rupestre element: crystalline rocks in campo rupestre, carrasco or cerrado, 500–1200 m, Serra do Cabral and west slope of Serra do Espinhaço, Minas Gerais. Endemic. Map 37A.


CONSERVATION STATUS. Vulnerable (2) [criteria C2a]; extent of occurrence = 1887 km²; PD=3, EI=1, GD=1. Short-list score (2x5) = 10. Of very limited range and not included within any protected area. Subject to commercial seed harvest for the international horticultural trade.

At the second locality cited above C. bradei was found growing with C. minensis and there was evidence of introgression.


VERNACULAR NAMES. Rabo-de-raposa, Quiabo-da-Iapa, Quiabo-do-inferno.

Erect shrub to 2 m, branched above the ground, branches sometimes decumbent; vascular cylinder woody; inner tissues stiff, not mucilaginous. Stems 3–5 cm diam., sometimes constricted, epidermis olive-green; ribs 12–15, 4–5 × 5 mm, rounded in section. Areoles to 2–3 mm diam., 7–8 mm apart, felt short, at first brown, becoming greyish and glabrescent. Spines golden brown to dark reddish brown; central spines 4–6, 5–40 mm, porrect; radials 7–10, 5–10 mm. Fertile part of stem not differentiated, flowers numerous, randomly from lateral and subapical regions. Flower-buds obtuse before anthesis; flowers 4.5–6.0 × 2.5–6.5 cm, ridged or quite terete, glabrous or with spiny areoles; pericarpel 10–18 × 15–18 mm; flower-tube to 50 × 15–30 mm at its widest point, ± parallel-sided, straight, with ovoid, apiculate bract-scales at apex; outer perianth-segments 8–10 × 4–5 mm, inner segments 9 × 8 mm, white or cream, spathulate, fimbriate and apiculate; nectar-chamber c. 15–20 × 8 mm; anthers c. 2.5 mm; style 45–50 mm, tapering; stigma-lobes c. 8, c. 7 mm; ovary locule c. 6–8 × 7–8 mm, rectangular or quadrangular in longitudinal section. Fruit ovoid. Seeds 1.5–1.7 × 1.1–1.2 mm, hilum-micropylar region 0.6–0.8 mm, forming an angle of 30–40° with long-axis; testa-cells domed to conic, with intercellular depressions and coarse, dense cuticular folds.
Two subspecies are recognized:

1. Flowers to 65 mm diam., blue without, outer perianth-segments dark blue or purplish; fruit not ridged, spineless, blue (Grão Mogol and N Serra do Cabral, S to Serras do Caraca and Itabirito)  4a. subsp. minensis

1. Flowers to 25 mm diam., distal half brownish, reddish or yellowish without, outer perianth-segments brownish red or bright yellow; fruit ridged, with spiny areoles, brownish, pale green, whitish or bluish (Serra do Cipó)  4b. subsp. pleurocarpus

4a. subsp. minensis

Spines generally golden brown, central spines not exceeding 15 mm. Flowers to 65 mm diam., blue without; tube smooth, glabrous; outer perianth-segments dark blue or purplish, patent at anthesis. Fruit not ridged, smooth or rarely bearing a few, inconspicuous areoles and minute bristly spines, bright to deep blue-waxy.

Widespread South-eastern campo rupestre element: mostly amongst crystalline rocks in campo rupestre, 500–2020 m, Serra do Espinhaço and northern part of Serra do Cabral, Minas Gerais. Endemic. Map 35C.


CONSERVATION STATUS. Lower Risk (1); PD=3, EI=1, GD=1. Short-list score (1x5) = 5.

Hybridizes with C. crassisepalus and C. bradei, q.v., where they come into contact. Werdermann’s report of this taxon from the Serra do Caraca, which may represent the type collection, needs confirmation, as does the identity of the similarly disjunct, ultimate record cited above. If these are indeed referrable to this subspecies, then it appears that the following taxon interrupts its range, a situation also seen in the case of Arrojadoa dinae.


Spines generally reddish brown to blackish, central spines to 40 mm. Flowers to 2.5 cm diam., distal half brownish, reddish or yellowish without; tube with ridges and areoles with minute spines; perianth-segments brownish or bright yellow, erect at anthesis. Fruit ridged, with spiny areoles, brownish, pale green, whitish or bluish.

South-eastern *campo rupestre* (Serra do Cipó) element: between rocks at c. 1100–1300 m, Serra do Cipó and Lapinha, central-southern Minas Gerais. Endemic to the core area within Minas Gerais. Map 39.


**CONSERVATION STATUS.** Endangered (3) [criteria B1/2c]; PD=3, EI=1, GD=1. Short-list score (3×5) = 15. Endangered from excessive burning of its habitat, which is only partly within the Parque Nacional da Serra do Cipó.


Erect shrub to 50 cm, branched at ground level, branches semi-erect to decumbent; vascular cylinder weakly woody; inner tissues mucilaginous, turning orange when cut. Stems 4–5 cm diam., not constricted, epidermis bright green; ribs 13–18, 2–3 × 3.9–5.5 mm, rounded in section, sinuses straight. Areoles to 2.5 mm diam., to 7 mm apart, felt short, brown, becoming glabrescent. Spines golden brown to dark reddish brown; central spines 2–4, 1–2 cm, procumbent; radials 10–12, 3–6 mm. Fertile part of stem not differentiated, flowers near or below stem apex at one side, buds sometimes developing on the underside of horizontal stems. Flowers c. 1.6 × 1.0 cm, glabrous, ridged; pericarpel 4 × 10 mm, purplish outside; tube parallel-sided, straight, reddish pink, with small bract-scales at apex; perianth-segments erect, whitish, inner segments acute; nectar-chamber c. 2 × 4 mm, closed at apex by the innermost layer of filaments; style 9 mm, tapering. Fruit globose, 6–13 mm diam., reddish, with a blue-waxy bloom. Seeds (1.3–)1.4–1.5 × 1.1 mm, hilum-micropylar region 0.6 mm, forming an angle of 20–30° with long-axis of seed; testa-cells flat, with slight intercellular depressions and coarse, dense, mainly marginal cuticular folds.

Northern *campo rupestre* element: on cliffs and ledges of crystalline rocks, 800–1000 m, west slope of Serra Geral (northern Serra do Espinhaço), east of Monte Azul, central-northern Minas Gerais. Endemic. Map 28A.


**CONSERVATION STATUS.** Critically Endangered (4) [criterion D]; PD=3, EI=1, GD=1. Short-list score (4×5) = 20. Critically Endangered on present knowledge (< 5 individuals seen at the only known locality) and urgently in need of further field studies to determine if its range is more extensive. Maintained in a few *ex situ* collections in Europe, including that at the Royal Botanic Gardens, Kew.

In its stem areoles lacking long trichomes and seed-micromorphology this species is clearly allied with *C. minensis* and *C. bradei* and certainly not directly related to *Arrojadoa bahiensis* (syn. *Floribunda bahiensis*), q.v., with which it is convergent in its floral hummingbird syndrome and habitat details.
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18. STEPHANOCEREUS A. Berger


Columnar-segmented and ± branched, or bottle-shaped and solitary, 0.5-3.5(-6.0) m high. Juvenile plants globose and without long-hairy stem areoles at first. Stems erect, 3-15(-20) cm diam., constricted or not, vascular cylinder very woody; tissues highly mucilaginous; epidermis dull to grey-green; ribs 12-20, sinuses straight. Areoles with felt and abundant, white, long hairs; spines stiff, golden to greyish, central spines porrect to deflexed, longer than the radials; indeterminate growth of basal areoles present. Flower-bearing region of stem differentiated into a slender, elongate chlorophyllous cephalium or a terminal cephalium tuft, this becoming transformed (through continued vegetative growth) into a lateral, ring-like flowering region (cf. *Arrojadoa* spp.) with long bristles, spines and hairs. Flowers nocturnal, white within, 3.5-10.0 × 2.5-5.5 cm; pericarpel and tube ± naked, pericarpel smooth, subglobose to obpyramidal; tube almost terete, with broad, fleshy scales near apex; perianth-segments triangular to lanceolate or spathulate spreading to reflexed, innermost white to slightly pinkish; innermost filaments curved towards the style. Fruit subglobose to ovoid-ellipsoid, impressed or not at apex, indehiscent, naked, flower remnant blackened, pendent to erect, deeply or shallowly inserted in fruit apex; pericarp smooth, greenish or dark purple to blackish, with a blue waxy coating (as in *Cipocereus*), funicular pulp solid. Seeds 1.2-2.2 mm, cochleariform; testa-cells convex; cuticular folds present.

A genus endemic to Bahia, comprising two monotypic subgenera, *Stephanocereus* and *Lagenopsis* (F. Buxbaum) N. P. Taylor & Eggli, the first characteristic of the Bahian caatinga, the second of the campo rupestre of the Chapada Diamantina. They are closely related to *Cipocereus*, but with the apical, flower-bearing part of the stem highly modified and the fruit often with ± pendent floral remnants. From *Arrojadoa* they differ in having a globose juvenile phase and larger, strongly smelling flowers adapted for nocturnal pollination by bats, rather than diurnal for hummingbirds (Taylor & Zappi 1996).

1. Columnar, segmented, at maturity at least 1.75 m, with flowering region terminal and in rings at the articulations of the stem (caatinga surrounding the East Brazilian Highlands of N to S Bahia) 1. leucostele

1. Bottle-shaped, to 1.5 m, rarely more, with subapical flowers on a continuous, elongate, terminal, chlorophyllous cephalium (campo rupestre, Chapada Diamantina, central Bahia) 2. luetzelburgii


Single-stemmed or tree-like, 1.5-3.5(-6.0) m, ± branched, branches arising at the stem-segment joints or more rarely between these. Stems erect, 5-8 cm diam., slightly thickened below the cephalia; vascular cylinder very woody; ribs 13-18, 7-8 × 5 mm; epidermis grey-green; areoles 3-4 mm, to 10 mm apart, with abundant, long white trichomes partly obscuring the stem. Spines golden or whitish, stout; central spines 3-5, 12-20(-30) mm, spreading to deflexed, radials 15-20, to 10 mm. Fertile part of stem apical at first, later forming 5 or more rings on the same branch, flower-bearing areoles with abundant, loose white wool and long, golden or whitish bristles to 40-90 mm. Flowers nocturnal, 9-10 × 5-5.3 cm, smelling strongly of cabbage; pericarpel and tube almost naked, with only a few small, triangular scales, these sometimes slightly woolly in their axis, pericarpel 13-16 × 22 mm, green; tube
50–60 × 22–35 mm, cylindric, somewhat curved, greenish cream, with fleshy, brownish scales at apex; perianth-segments 15–18 × 6–8 mm, spathulate to lanceolate, outer segments reflexed, inner segments spreading to reflexed, pure white; stamens included in relation to the perianth-segments; style to segments 15–18 x 6–8 nun, spathulate to lanceolate, outer segments reflexed, inner segments spreading to reflexed, ovary locale 10 x 10 mm, obtrigangular in longitudinal section. Fruit globose to pyramidal, 4.4–4.7 x 3.5–4.5 cm; pericarp impressed at apex, greenish to dark blue, wall to 8 mm thick, funicular pulp white or red. Seeds 2.2–2.2 mm long, coelhleariform, black, dull; testa-cells convex, with cuticular folds.

Central-southern (Bahian) caatinga element: in caatinga surrounding the Chapada Diamantina, northern Serra do Espinhaco and Serra Geral (BA), 300–1100 m, east of the Rio São Francisco. Endemic. Map 23.


CONSERVATION STATUS. Lower Risk (1); PD=3, E=1, GD=1. Short-list score (1 x 5) = 5. Lower Risk at present, but its habitat is continuing to decline and its status needs to be monitored.

One of the most characteristic cacti of the Bahian caatinga, but absent from north-eastern Bahia, being closely associated with the East Brazilian Highlands, where the following species replaces it in the campos rupestres. This suggests that their common ancestor was a plant of montane origin (cf. Cipocereus).


Solitary, 0.5–1.0(-1.5) m, bottle-shaped, sometimes branched at base, apex unbranched unless damaged; central cylinder very woody at base. Stems erect to decumbent at apex, 12–15(-20) cm diam. at base, 2.5–4 cm diam. at apex, in the flower-bearing region; ribs 12–20, 20 × 18 mm on juvenile stem; epidermis grey-green to dark green. Areoles 5–6 mm, to 1 cm apart, long hairs abundant on the fertile part, white to pale cream. Spines golden or whitish, blackish when old; central spines 4–6, 1.2–2(-3) cm, ascendent to spreading, radials 10–16, to 1.2 cm. Fertile part of stem elongate, with lateral to subapical flower-bearing areoles with abundant, loose white to pale brown hairs and long, golden, whitish or greyish bristles, these 2–4 cm. Flowers 4–6 × 2.5–3.0 cm, smelling strongly of cabbage; pericarpel 10 × 5–6 mm, greenish; tube 2.5 × 1.2–2.0 cm, narrowed above nectar-chamber, slightly curved, greenish cream, with fleshy, brownish bract-scales only at apex; perianth-segments 8–10 × 3–5 mm, spathulate to lanceolate, outer segments reflexed, inner segments spreading to reflexed, white; stamens included in relation to the perianth-segments; style to 28 mm, stigma-lobes 6–8, exserted; ovary locule 4 × 4 mm, obtriangular in transverse section. Fruit obovoid, 2.2–2.5 × 1.5–2 cm; pericarpel smooth, dark blue to blackish, but covered in lighter blue wax, scarcely impressed at apex. Seeds 1.2–1.5 mm, cochleariform, black, dull; testa-cells convex, with cuticular folds.

Northern *campos rupestres* (Chapada Diamantina) element: on and between crystalline and sandstone rocks and gravels, *campos rupestres*, 380–1550 m, Bahia. Endemic. Map 28A.


**Conservation Status.** Lower Risk (1); PD=3, EI=1, GD=2. Short-list score (1×6) = 6.

Unmistakable for its bottle-shaped stem, this species and *Micranthocereus purpureus* are the most characteristic elements of the Chapada Diamantina’s cactus flora. Variable in stem shape and rib number between populations.
19. ARROJADOA Britton & Rose

Cact. 2: 170 (1920). Type: Arrojadoa rhodantha (Giirke) Britton & Rose (Cereus rhodanthus Giirke).


Columnar, shrubby, 0.2-1.5(-3.5) m, branched below, at or above ground, but not forming a definite trunk; vascular cylinder rather woody; tissues very mucilaginous; subterranean stem-tuber system sometimes present. Stems erect or rarely decumbent, 1-7(-12) cm diam, constricted, epidermis dull to bright green; ribs 6-14(-17), low, crenate, sinuses straight. Areoles with felt and long hairs at first; spines stiff, very pungent, central spines porrect to deflexed, longer than the radials; indeterminate growth of areoles near stem base present. Flower-bearing region of stem apical, more or less dilated and forming a cephalium with bristles and wool, or cephalium lacking (A. bahiensis).

Flower-buds coloured bright pink from the earliest stages of their development; flowers diurnal, opening at morning, or late afternoon to evening, and sometimes remaining open through part or all of the night, brightly coloured, 15-42 x 5-20 mm; pericarp smooth, naked, subglobose and clearly delimited from the tube; tube broadened below, cylindric above, reddish, pink or magenta, with broad, fleshy bract-scales only near the apex; innermost filaments curved towards the style, protecting the nectar-chamber; perianth-segments triangular to lanceolate or spatulate, erect to spreading, opening very little, innermost white, yellow, pinkish or purplish. Fruit obovate to turbinate, indehiscent, naked, flower remnant drying black, normally erect, broad at base, forming a deep and often broad point of insertion at apex of fruit; pericarp smooth, variously coloured, funicular pulp white, scarce, ± solid or aqueous. Seeds to 1.5 mm, cochleariform; testa-cells convex; cuticular folds present or nearly absent.

A genus of 4 or 5 very distinct, but rather variable, hummingbird-pollinated species, characteristic of the caatinga-agreste and campos rupestres (and included cerrados). The potential fifth species is a plant discovered in August 2000, in north-eastern Goiás, by biology student Rafaela Forzza (SPF). It appears to be related to A. dinae and A. bahiensis. Prior to this the genus was endemic to Eastern Brazil.

P. J. Braun & E. Esteves Pereira (1995b: 81) have established the Subgenus Albertbuiningia based on the second species treated here, A. dinae Buin. & Brederoo. On present knowledge this should presumably also include the first species treated below (the type of Pierrebraunia E. Esteves Pereira), but a decision may be best deferred until a phylogeny based on gene-sequence data is available for the proposed Cipocereus-Stephanocereus-Arrojadoa clade. The following key does not attempt to distinguish the hybrids that occasionally occur between species nos. 2–4 (2×3, 2×4 & 3×4, see below).

1. Stem 4–8 cm diam., neither strongly constricted nor terminated or interrupted by cephalia, flowers from ± undifferentiated areoles at stem apex (cent. Bahia, campo rupestre, 1000–2000 m) 1. bahiensis

1. Stems constricted, thickened at apex or < 4 cm diam., the flowers developed in cephalia composed of wool and long bristle-spines

2. Stems 10–50 x 2 cm, sometimes arising from a tuberous, rhizomatous rootstock; flowers bicoloured (anthesis p.m.), inner perianth-segments contrasting with flower-tube (Serra do Espinhaço: Caietí BA to Bocaiúva MG, campo rupestre, cerrado & ecotones with caatinga) 2. dinae

2. Stems usually > 50 cm or > 2 cm diam., rootstock fibrous; flowers concolorous

3. Stems to 1.8 cm diam., but expanded and much broader below the cephalia; anthesis p.m., outer perianth-segments expanding (N, E & S Bahia & NE Minas Gerais, caatinga-agreste) 3. penicillata

3. Stems 2–6 cm diam., not as above; anthesis a.m., perianth-segments hardly expanding, erect (widespread, caatinga and ecotones with campo rupestre) 4. rhodantha


Arrojadoa cremnophila Taylor et al. in sched., nom. nud.

Subglobose to elongate plants (depending on exposure), normally to 30 cm, but occasionally to 60 cm or more, unbranched or branched below ground or at base to form clumps of stems; central cylinder not woody. Stems erect or inclined, 4–10 cm diam.; ribs (9–)10–14(–17), 5 × 15(–25) mm, with or without lateral folds; epidermis bright yellow-green to dark green. Areoles 2–3 mm, approximate, with felt and long, white to grey trichomes. Spines brittle, pale pinkish brown or golden, black when old; central spines chamber externally 6 × 8.5 mm, or inclined, with felt and long, white to grey trichomes. Spines narrow, pale pinkish brown or golden, black when old; central spines 1–4, to 30 mm, ascendent, radials 6–8(–10), to 5 mm, spreading; weak indeterminate growth of spines occurring at basal stem areoles. Fertile part of stem apical, flower-bearing areoles scarcely differentiated. Flowers (reported in February and August) few or up to 25 developing together, opening first at night and closing around noon the following day (timing and degree of perianth expansion apparently linked to light and low temperatures), c. 29–39(–42) × 11 mm at apex of tube, the inner perianth-segments expanding to give an opening 8–13 mm in diam., pericarpel and tube together to c. 30 mm, naked or the latter with a few minute bract-scales in distal half, magenta-pink outside, pericarpel c. 5 × 7 mm, nectar-chamber externally 6 × 8.5 mm, tube constricted above and below; outer perianth-segments short and fleshy, magenta-pink, inner thin and delicate, white, 3.9–4.7 × 2.3–2.8 mm; stamens 3–14 mm, the lowermost with thickened filament bases protecting the nectar-chamber, anthers c. 0.8–1.1 mm, pale yellow, with abundant pollen; style to 28 × 0.8–0.4 mm, white; stigma-lobes 5–6, white, pointed, partly exserted in relation to the anthers or hidden amongst them, c. 4 × 1 mm. Fruit c. 17 × 15 × 12 mm, broadly ovoid, somewhat compressed, ridged and contracted or beaked at apex, deep shocking pink, with a paler waxy bloom, funicular pulp liquid, translucent, floral remnants ± blackened. Seeds to 1.3 mm, cochleariform, black, dull; testa-cells convex, cuticular folds present.

Northern campo rupestre (Chapada Diamantina) element: on cliffs and rock ledges in sun or deep shade, campo rupestre, c. 1000–2000 m, central Bahia. Endemic. Map 28B.


Conservation Status. Vulnerable (2) [criteria D2]; extent of occurrence = 1614 km²; area of occupancy estimated to be < 100 km²; PD=3, EI=1, GD=2. Short-list score (2×6) = 12. Known from only 4 populations (one within the Parque Nacional da Chapada Diamantina) and at risk from collection of plants and seeds. However, many individuals are protected by the plant’s preference for steep slopes and cliffs inaccessible to the collector.

This unique and remarkable Bahian endemic was first collected by scientists only in 1981, but could prove to be quite widespread in the Chapada Diamantina when the inaccessible cliff habitats it occupies have been further investigated. Its flowers (!), fruit and seed clearly ally it with the following allopatric-vicariant species. However, small, sterile individuals strongly resemble juvenile plants of the sympatric Stephanocereus luetzelburgii and in morphology (but not size and colour) their flowers are also very similar. It is presently unclear whether the absence of a cephalium in A. bahiensis should be considered as a primitive or derived character state within the Arrojadoa-Stephanocereus alliance. It is superficially similar and convergent
with *Cipocereus (Floribunda) pusilliflorus*, but has rather different, woolly adult areoles, mature fruits and seeds, and its perianth is clearly and abruptly differentiated into coloured fleshy outer segments and white thinner inner segments, as in *A. dinae*.


VERNACULAR NAME. Rabo-de-raposa.

Subshrub, sometimes creeping/suckering or semidecumbent, 10–60 cm, poorly branched above ground; vascular cylinder moderately woody; subterranean stems not or slightly thickened, or strongly tuberous, sprouting when above-ground parts are damaged. Aerial stems erect, 1-2 cm diam., slightly to strongly thickened below the flower-bearing apical cephalium and sometimes to 3.5 cm diam. near rootstock; ribs 6–11, 3–4 × 2–4 mm; epidermis olive-green. Areoles 2 mm, to 5 mm apart, with few to many, long, white to grey trichomes, conspicuously hairy in some forms. Spines reddish at first, paler to off-white in age, delicate, needle-like; central spines 1–2, to 10 mm, radials 8–10, 3–5 mm. Cephalium with much loose wool and long reddish bristle-spines to 20 mm, up to 6 cephalia per stem. Flowers 14–29 × 4–9 mm, opening late in the afternoon; pericarpel 4 × 3.5 mm; tube to 10 × 4–5 mm, cylindrical, coral-red, orange-red or magenta, with fleshy bract-scales only at apex; perianth-segments 2–3 × 2 mm, triangular to lanceolate, outer segments erect, coral-red to reddish pink, inner segments opening very slightly, rather variable in colour, pale creamy yellow, white or lilac-pink to purplish; stamens included in relation to the perianth; style 8–9 mm, stigma-lobes 7–8, included; ovary locule 1.8–2.0 × 2 mm, hemicircular in longitudinal section. Fruit obovoid, broadly beaked to truncate at apex, to 7–21 × 5–18 mm, pericarp smooth, greenish, pink, reddish or purplish brown at apex. Seeds 0.9–1.8 × 0.8–1.4 mm, cochleariform, black, dull; testa-cells convex, with cuticular folds.

The following subspecies are recognized — both are rather variable in flower and fruit colour:

1. Well-developed subterranean stem-tubers present; stem areoles very woolly, giving the stem a felted appearance
   a. subsp. eriocaulis
   b. subsp. dinae

1. Subterranean part of stem sometimes thickened, but well-developed tubers lacking; above-ground vegetative part of stem not as above
   a. subsp. dinae

2a. subsp. dinae

Northern campo rupestre element: sandy cerrado, campo rupestre (sometimes on rocks), gerais and in the caatinga / campo rupestre ecotone, 550–1400 m, central-southern Bahia (from c. 13°55'S southwards) and northern Minas Gerais (south to Bocaiuva) in the Serra do Espinhaço (and Serra Geral). Endemic to the core area within Eastern Brazil. Map 28B.

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CONSERVATION STATUS. Vulnerable (2) [criteria B1/2c]; extent of occurrence = 17513 km²; PD=3, EI=1, GD=2. Short-list score (2×6) = 12. Vulnerable from habitat destruction by charcoal producers and forestry.

Very variable in stem morphology and flower colour. On present knowledge, the typical northern populations and the southern forms (described as A. beateae and A. heimenii) appear to be disjunct, being interrupted by the following subspecies. The plant recently discovered in northeastern Goiás by Rafaela Forzza (SPF) is vegetatively almost indistinguishable from subsp. dinae, but appears to have flowers more similar to those of A. bahiensis.


A. eriocaulis var. rosenbergeriana van Heek & Strecker in ibid. 44: 258–262 (1993). Type: Brazil, Minas Gerais, SE of Mato Verde, W. van Heek & W. Strecer 85/216 (KOELN, hol., n.v.). Synon. nov.

Northern campo rupestre element: in sandy cerrado, 700–950 m, eastern drainage of Serra do Espinhaco, northern Minas Gerais. Endemic to the core area within Minas Gerais. Map 28B.


CONSERVATION STATUS. Endangered (3) [criteria B1/2c]; extent of occurrence = 1007 km²; PD=3, EI=1, GD=2. Short-list score (3×6) = 18. Endangered from habitat destruction by charcoal producers; needs regular monitoring in view of this and its restricted range.

Variable in flower colour. The plant described and illustrated as A. eriocaulis var. rosenbergeriana by van Heek & Strecker, l.c., appears to be somewhat intermediate between the two subspecies recognized.

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**VERNACULAR NAME.** Rabo-de-raposa.

Shrubby or semi-scandent to decumbent (especially when growing in sand-dunes), to 4 m, ± branched; rootstock fibrous. Stems erect or rarely (?) decumbent, 1–1.8 cm diam., not very fleshy, expanded to 2.5–(3.0) cm diam. below the cephalia, vascular cylinder very woody; ribs 7–12, 2–4 × 3 mm; epidermis olive-green. Areoles 2 mm, to 7 mm apart, long trichomes present but soon falling. Spines reddish brown, delicate; central spines 2–4, 4–30 mm, ± deflected, radials 6–10, 3–5 mm. Cephalia sometimes forming 3 or 4 rings on the same axis, with abundant, loose wool and long red to brownish bristle-spines to 20–30 mm. Flowers to 30 × 20 mm, opening shortly before dusk, pinkish magenta or reddish pink; pericarpel 7–8 × 5 mm; tube to 12 × 4–7 mm, cylindrical, with fleshy bract-scales only at apex; perianth-segments bright pink with a very fine darker line around the margin, outer segments to 7 × 2.8 mm, triangular to lanceolate, patent (well-expanded), innermost segments remaining erect and forming a tube which encloses the stamens etc., its opening 3–4 mm in diam.; stamens included in relation to the perianth-segments; style 10 mm, stigma-lobes 6–8, included; ovary locule 2.2–3.5 × 2 mm, obtriangular in longitudinal section. Fruit obovate to globose, sometimes laterally compressed, 12–25 × 12 mm; pericarp smooth, greenish to dull red, olive-brownish or whitish. Seeds c. 1.2 mm, cochl eariform, black, dull; testa-cells convex, with or without cuticular folds.

Central-southern *caatinga* element: on granite/gneiss inselbergs or *lajedos*, sand-dunes and stony ground (rarely on limestone), growing under or through shrubs in the *caatinga-agreste* and *caatinga / campo rupestre* ecotone, c. 200–850 m, north-western Bahia (Pilão Arcado & Barra), northern to southern Bahia east of the Chapada Diamantina, and north-eastern Minas Gerais (Rio Jequitinhonha valley). Endemic to core area of Eastern Brazil. Map 22B.


MINAS GERAIS: NE Minas Gerais, Mun. Iaobim, 1 km W of town, 0.5 km N of the Rio Jequitinhonha, 16°34'S, 41°31'W, 18 Nov. 1988, Taylor & Zappi in Harley 25529 (K, SPF); l.c., 8 km W of town on road BR 357 towards Itinga, 14 Dec. 1990, Taylor & Zappi 761 (K, HRCB, ZSS, BHCB), 9 Apr. 1983, Martinelli & Leuenberger 9224 (K); Mun. Itinga, 2 km E of town on road BR 357, 14 Dec. 1990, Taylor & Zappi (obs.).

Conservation Status. Lower Risk (1); PD=3, EI=1, GD=2. Short-list score (1x6) = 6. Lower Risk, but its habitat continues to decline.

This species has a more restricted range than the following, but is not nearly as common, nor as variable. The record by Uebelmann (1996) from western Pernambuco seems to be a misidentification of the following species, which is abundant in the region. Their different habitat preferences deserve further analysis—they are rarely sympatric despite the considerable overlap in distribution.

4. Arrojadoa rhodantha (Gürke) Britton & Rose, Cact. 2: 171–172 (1920). Type: Brazil, Piauí, Caatinga de São Raimundo [Nonato], 1907, Ule 11 (B, holo.; K [photo ex B]).


A. rhodantha subsp. reflexa P.J. Braun in Kakt. and. Sukk. 35: 34–38 (1984). Holotype: Brazil, Bahia, 1000 m, Braun 68 (KOELN, n.v.).


VERNACULAR NAMES. Rabo-de-raposa, Rabo-de-onça.

Shrubby, to 2 m, rarely reaching 3.5 m, ± branched. Stems erect or semi-decumbent, 1.7–6 cm diam., not or scarcely expanded below the cephalia, vascular cylinder very woody; ribs 8–14, 4–5 × 5 mm, epidermis olive-green. Areoles 2–3 mm, to 10 mm apart, long hairs apparently absent. Spines reddish, golden, greyish or brown, stiff, very sharp; central spines 4–5, 1.5–4.0–(5.0) cm, ascendent to spreading, radials 6–10, to 1 cm. Fertile part of stem apical, later forming up to 4 and sometimes many more rings on the same axis, cephalium areoles with abundant, loose white hairs and long red, golden or brownish bristles, these 2–3 cm. Flowers 20–35 × 8–10 mm (at apex), opening at morning, pinkish magenta or reddish pink; pericarpel 6–7 × 4–5 mm; tube to 20 × 10–14 mm, cylindrical or constricted above the nectar-chamber, with fleshy bract-scales only at apex; perianth-segments 5–6 × 5 mm, obovate, outer segments erect, inner segments opening only partially to give an aperture of only a few mm; stamens included in relation to the perianth-segments; style 20 mm, stigma-lobes 6–8, included; ovary locule 2–3 × 2 mm, obovate in longitudinal section. Fruit globose, 20–25 × 10–18 mm, often somewhat laterally compressed; pericarp smooth, dark red. Seeds c. 1.2 mm, cochleariform, black, dull; testa-cells convex, with or without cuticular folds.

Central-southern caatinga element: found on various substrates (including in dense caatinga forest and inselbergs) and entering the caatinga / campo rupestre ecotone, 220–1330 m, south-western Piauí and western Pernambuco to central-northern Minas Gerais. Endemic to the core area of Eastern Brazil. Map 22C.


This extremely variable species comprises many locally distinct forms but cannot be conveniently divided into a manageable and meaningful number of infraspecific taxa. A part of this variation can be attributed to gene exchange with species nos. 2 and 3 (see below), but much of it is probably inherent and independent of such influence, occurring in areas remote from the known ranges of its congeners. *A. rhodantha* is one of the most characteristic cactus species of the central and southern caatingas, but is absent from north-eastern Minas Gerais (Rio Jequitinhonha drainage), where *A. penicillata* occurs.

**2 x 3**: *Arrojadoa dinae* subsp. *dinae × Arrojadoa penicillata*

Vegetatively intermediate between the presumed parents, the ends of some stems strongly expanded beneath the cephalium. Flowers described as pink, green within.


Although *A. penicillata* is not otherwise recorded west of the Serra do Espinhaço in southern Bahia, the above-cited collection seems to confirm its presence. The characters displayed by this presumed hybrid can only have come from *A. penicillata* and *A. dinae*. 

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2 × 4: *Arrojadoa dinae* subsp. *dinae × Arrojadoa rhodantha*


Intermediate between the parents, but variable in flower colour. See Ritter (1979: Abb. 61) for a good illustration.


Probably to be found at other sites where the species are almost or quite sympatric, eg. east of Monte Azul (MG).

3 × 4: *Arrojadoa penicillata × Arrojadoa rhodantha*

Sometimes forming a complete range of intermediates between the parents in places within the areas of sympathy cited below.

_Caatinga_ in the drainage of the Rio Paraguaçu and Rio Brumado / Rio de Contas, 300–450 m, southern Bahia.

20. PILOSOCEREUS Byles & Rowley


Including Pseudopilocereus F. Buxbaum (1968).


Shrubby or tree-like, rarely epiphytic (on carnaúba palm trunks), 0.3–10.0 m; branched or not above ground; vascular cylinder strongly to weakly woody; tissues mostly extremely mucilaginous; branches showing more or less constant growth, rarely constricted; ribs triangular, (3–)4–28. Areoles with felt and generally with long trichomes, spination diverse; spines straight, rarely curved at base, opaque to translucent. Fertile part of stem not or various differentiated, when strongly so flower-bearing areoles with long hairs and/or bristly spines, lateral cephalium rarely even sunken into the branch. Flowers 2.5–9.0 × 2–7 cm, anthesis starting at evening; flowers dull or sometimes reddish outside, smooth to slightly striate, glabrous, without areoles; pericarpel with few and minute bract-scales; symmetry of flowers dependent on shape of flower-tube, which can be straight or curved, terete or infundibuliform, distal half or third with broad bract-scales; outer perianth-segments thick, inner segments thin, white or rarely pinkish; nectar-chamber broad, ± protected by the innermost filaments; stamens many, anthers 1.2–2.5 mm, forming a compact mass; style 25–65 mm, stigma-lobes 8–12, exserted or included in relation to the anthers. Fruit depressed-globose, very rarely globose, always dehiscent by lateral, abaxial, adaxial or central slit, floral remnants persistent, blackening, pendent or rarely erect; pericarp green, purplish, brownish, magenta, deep red or wine-coloured, smooth, striate or rugose; funicular pulp solid, white, red or magenta. Seeds 1.2–2.5 mm, dark-brown· or black, cochleariform, rarely hat-shaped, hilum-micropylar region differentiated, intercellular depressions present to absent, testa-cells flat, convex or conic, cuticular folds fine, coarse or absent.

A genus of some 35 species in Mexico, the Caribbean (incl. Florida Keys), Venezuela, Suriname, Guyana, Peru, Ecuador, Brazil and Paraguay. Its range in Brazil includes Roraima, Pará, Maranhão, Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, Bahia, Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Tocantins, Goiás, Mato Grosso and Mato Grosso do Sul. This is the largest and most important genus of Cactaceae in Eastern Brazil, represented by some 20 species, plus various heterotypic subspecies, and occurring in a wide variety of vegetation types, though sometimes restricted to rock outcrops within habitats such as cerrado and Mata atlântica. On occasions certain species may even dominate the vegetation in which they occur, e.g. P. gounellei, P. catingicola and P. pachycladus. The Brazilian species are classified into two subgenera and various species-groups.

1. Branching candelabrom form, the new branches arising near the apex of the subtending stems; floral remnants erect to pendent, not deeply immersed in apex of fruit, forming a circular insertion point (Subg. Gounellea) 2
2. Treelike, with a well-defined trunk, not branching near base; ribs 4–7; flower-bearing areoles without long trichomes 1. tuberculatus
3. Shrubby, without a well-defined trunk, branching near base; ribs (8–)10–15; flower-bearing areoles with abundant, silky, long trichomes enveloping the flowers 2. gounellei
4. Apical, subapical and flower-bearing areoles without long hairs (at least in habitat) 4
5. Epidermis blue, covered in wax 8. pentaedrophorus
5. Epidermis greyish, pale or olive-green, not strongly waxy

6. Spines brown to greyish, opaque; flower-buds acute; flower opening wide, 6–7 × 4–5 cm, tube straight (restinga, SE Brazil & S Bahia)

5. arrabidae

6. Spines golden to greenish yellow; flower-buds obtuse; flower narrow, 5.8–6.0 × 3.5–3.7 cm, tube curved (caatinga and littoral zone, Ceará, Piauí and S Maranhão)

7. Epidermis rough, green to grey-green, not covered in wax

10. floccosus

7. Epidermis smooth, frequently bluish or covered in wax

8. Areoles continuous, difficult to isolate from one another

10. arrabidae

8. Areoles > 2 mm apart, distinct

9. Flower-bearing areoles with scarce, white long hairs; young spines golden, flexible

13. P. magnificus

9. Flower-bearing areoles with abundant dark yellow to reddish brown long hairs; spines dark brown to blackish

11. fulvilanatus

10. Spines golden, translucent

10. Spines brownish, reddish or blackish, opaque

11. Long hairs not more abundant on flower-bearing areoles than on the vegetative areoles; flower-tube narrow, curved, pinkish or reddish without

11. F. pachycladus

11. Long hairs more abundant on the flower-bearing areoles; tube ± straight, broad at apex, greenish, brownish or dark purplish brown

12. F. pachycladus ssp. pachycladus

12. Ribs > 12; central spines delicate, nearly indistinguishable from the radials, stem epidermis green or bluish

12. Ribs ≥ 12; central spines thicker and longer than the radials; stem epidermis blue

12a. pachycladus ssp. pachycladus

13. Fertile part of stem with golden bristles to 3–4 cm and few long hairs; ribs (15–)18–26

19. multicostatus

13. Fertile part of stem without or with few bristles, long hairs white, silky; ribs 13–19

14. Spines golden; ribs wider than high; fertile part of the stem apical or subapical, not strongly modified (caatinga, N Bahia and Pernambuco)

19. F. pachycladus ssp. pernambucensis

14. Spines pinkish yellow to brownish; ribs higher than wide; fertile part of stem lateral, true, sunken cephalium sometimes present (Bambui limestone outcrops, W Minas Gerais and SW Bahia)

20. densiareolatus

15. All stems with 7 or more ribs (seedlings excepted), or flowers > 4 cm in diameter at full anthesis

16. Ribs 4–6, or some stems with up to 7 ribs

17. Treelike or shrubby, primary branches 4–6-verticillate; flower-buds acute, with triangular bract-scales, flowers ± solitary, 4.7–7.0 cm in diameter, tube straight, wide (NE Brazil)

3. cateingicola

17. Shrubby, sparsely branched; flower-buds obtuse, with obovate to truncate bract-scales, flowers aggregated, 2.5–3.0 cm in diameter, tube curved, narrow (SE Brazil)

3. cateingicola

18. Ribs (5–)6–8, transverse folds visible; flower-bearing areoles not differentiated; spines opaque, brown to grey, central spines well differentiated from the radials (restinga)

5. arrabidae

18. Ribs 8–23, transverse folds not visible; areoles hairy; spines red, dark brown or golden, translucent, central spines not very different from the radials (cerrado, caatinga and campo rupestre)

19. F. pachycladus

19. F. pachycladus

19. Flower exterior reddish or pinkish brown; flower-tube infundibuliform; ribs 8–17

20. F. pachycladus

19. Flower exterior green to brownish; flower-tube cylindrical, straight to curved; ribs 12–27

21. F. pachycladus

20. Fruit dehiscent by central slit; pericarp rugose, red to wine-coloured when ripe; seeds with flat testa-cells (Serra do Espinhaço, Minas Gerais)

15. aurisetus

20. Fruit dehiscent by lateral slit, pericarp smooth, dark purple to bluish; seeds mostly with domed to highly conical testa-cells (W Bahia)

14. machrisii

21. Flower-bearing areoles strongly differentiated, forming a lateral cephalium sunken into the branch, with abundant wool and bristles to 3–6 cm; stem epidermis bright green

19. chrysostele

21. Flower-bearing areoles not strongly differentiated, appearing randomly or at apex of branches, sometimes with bristles and some hairs

22. Vegetative areoles with long hairs; fruit pulp of white; seeds dull, testa-cells domed to conic (SEM: cuticular folds coarse, dense); flowers < 2.5 cm wide (Bahia, near the Rio São Francisco)

16. aureispinus

22. Vegetative areoles without long hairs; fruit pulp magenta; seeds shiny, testa-cells slightly domed to flat (SEM: cuticular folds scarce to absent); flowers c. 3 cm wide or more

22. F. pachycladus

23. Flowers curved, > 5 cm, flower-buds obtuse before anthesis (SE Piauí northwards)

18. piauhyensis
23. Flowers straight, < 5 cm, flower-buds acute before anthesis (NE Minas Gerais) 17. multicostatus

Subg. Gounellea Zappi (nrs 1 & 2). Endemic to the caatingas of NE Brazil.


VERNACULAR NAMES. Caxacubri, Mandacaru-de-Iayo.

Tree, 2–5(–6) m, with a spread of up to 6 m diam., trunk to c. 20 cm diam.; vascular cylinder strongly woody up to the apex of mature branches; branches 3–6 cm diam., apex erect to inclined, older parts ± horizontal, new branches arising subapically, epidermis olive-green, with pruinose wax on the tips when young; ribs 4–7(–8–12, in seedlings), 1–2 x 0.5–2.0 cm, with sinuate sinuses and pronounced, oblique, transverse folds above the areoles. Areoles 8–10 x 6–7 mm, 2–3.3 cm apart, situated upon prismatic stem-projections (podaria), felt at its widest point, ± parallel-sided, straight, nearly terete, olive-green, striate, distal third with a few acute bract-scales; style 30–65 mm, lowermost generally longest, often decurved near base, radials 10–12, 4–7(–10) mm, adpressed, decurved. Fertile part of stem not differentiated, subapical. Flower-buds acute 1–2 days before anthesis; flowers 6-6.7 x 3 cm; pericarpel obconical, tube 45 x 20–23 mm at its widest point, ± parallel-sided, straight, nearly terete, olive-green, striate, distal third with a few acute bract-scales; style 40–42 x 3–2 mm, tapering; stigma-lobes c. 8, 6 x 0.7 mm; ovary locule obtriangular in longitudinal section. Fruit to 4 cm diam., globose to slightly depressed, dehiscent by a lateral slit, intercellular depressions and fine cuticular folds.

Central-southern caatinga element: in dense or sparse caatinga vegetation, on fine, white or reddish, sandy soil (especially of the Cipó series), c. 200-790 m, northern Bahia and Pernambuco. Endemic to the core area within North-eastern Brazil. Map 22D.


CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=1. Short-list score (1x4) = 4. Lower Risk, but its habitat continues to decline.
This species shares unique apomorphic characters with P. gounellei, such as the sub-apical branching-pattern and the morphology of the fruits, lacking a deeply sunken floral remnant. This pair of species are the only representatives of subg. Gounellea and are endemic to Eastern Brazil.

P. tuberculatus is characteristic of the region of sand-dunes west and north of the São Francisco River, but is also known from NE Bahia, between Araci and Glória, including the Raso da Catarina. A collection by Lützelburg (no. 19, M!), bearing a label indicating southern Paraiba (Monteiro), is clearly a labelling error, since the vernacular name given on the label, 'Rabo de Raposa', was applied to Harrisia adscendens by Lützelburg, which is common about Monteiro, where P. tuberculatus is absent. Andrade-Lima (1981: 159) lists this species as one of those characteristic of his caatinga type no. 5, which is found on the ‘Cipó’ soil series.

The biology of P. tuberculatus is interesting in that it is able to secrete nectar from the outer bract-scales of the flower-buds, tube and fruit, which attracts ants. In large specimens, these insects inhabit the hollow pith of old, dead branches, suggesting a symbiotic relationship of attraction/defense. The slight damage or sudden movement of a branch of this plant is immediately followed by a quick defense reaction by the ants, which run out from inside the dead branches to attack the supposed agressor.


Shrub, more rarely treelike, 0.5-4.0 m, with many branches arising from the main stem; vascular cylinder moderately woody; branches with apex erect to inclined, older parts horizontal, new branches arising sub-apically, epidermis olive-green, or strongly glaucous, especially when young; ribs 8–15, with sinuate sinuses and transverse folds above the areoles. Areoles ovate, felt cream, grey or brownish, with white long hairs to 35 mm, growth indeterminate near base of plant. [Spination: see subspecies.] Flower-buds completely encircled by silky long hairs, obtuse 2 days before anthesis; flower 4–9 × 2.5–6.0 cm; pericarpel obconic; tube 32–60 × 16.5–17.0 mm at base, widening towards apex to 20–25 mm, curved, greenish brown to pinkish, slightly striated, with decurrent triangular bract-scales, these more frequent and larger towards tube apex; style 2.6–3.5 × 2.5–1.2 mm, tapering, stigma-lobes c. 10, 4 mm long; ovary locule obtriangular in longitudinal section. Fruit 3.5–4.5 × 4.5–6.0 cm, globose to depressed, dehiscing by adaxial or abaxial slit, floral remnant erect or pendent, with rounded, shallow insertion; pericarp pinkish red, smooth or striate. Seeds (1.6–)1.7–1.8 × 1.4–1.6 mm, hat-shaped, symmetric, hilum-micropylar region expanded, forming an angle of 70–80° with long axis of seed, testa-cells flat, without intercellular depressions or cuticular folds.

The neotype chosen (Zappi 1994) was collected by Lützelburg in the state of Paraiba (Lützelburg 26921), and is a form which agrees with Weber's description, where the spines are given as relatively short (1 cm long), this being somewhat atypical for the species as a whole. P. gounellei is the type of subg. Gounellea, including its sister species, P. tuberculatus, from which it differs in its mostly shrubby, not treelike habit, mature branches with a higher
number of ribs (8–)9–15, only moderately woody vascular cylinder, flowering areoles with white silky hairs and very distinct seeds, which may be adapted for dispersal by water (Zappi 1994). In the Brazilian Nordeste it is commonly known by the vernacular name of xique-xique, and represents one of the most characteristic plants of the caatinga, and, together with Cereus jamacaru DC. (vernacular: manacaru) and Tacinga inamoena (K. Schum.) Stuppy & N. P. Taylor (quipá), is one of the most common and widespread cacti of Eastern Brazil.

This species is divided in two subspecies:

1. Spines stout, strong, brownish to greyish, opaque, (0.9–)1.0–1.9 mm diam. near base, centrals distinctly longer than the radials (NE Brazil)

1. Spines slender, fragile, golden to reddish, translucent, 0.25–0.6(–0.8) mm diam. near base, centrals and radials ± equal (N Minas Gerais to N Bahia)

2a. subsp. gounellei

VERNACULAR NAMES. Xique-xique, Alastrado.

Shrub; branches 5–9 cm diam.; ribs (8–)9–13, 7–12 × 12–20 mm. Spines 0.25–0.6(–0.8) mm diam. at base, brown to greyish, opaque; centrals 1–5(–6), 1–13(–15) cm, ascending to porrect, the lowermost porrect to reflexed, radials 12–15, 6–30 mm, adpressed. Flower-bearing areoles occupying the subapical region of 1–2 ribs, with silky long hairs covering the flower-buds only. Fruit with magenta (rarely white) funicular pulp.

Caatinga element: widely distributed, common and locally dominant in low, sparse caatinga and along road sides, on shallow, rocky or sandy soils and granitic outcrops/inselbergs, including those surrounded by more humid forest, rarely as epiphyte in seasonally flooded carnaúba (Copernicia prunifera) forest, near sea level to c. 1200 m, E Maranhão, Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe and Bahia (N of 15°S). Endemic to North-eastern Brazil. Map 19.


RIO GRANDE DO NORTE: Chapada do Apodi, Pedra das Abelhas, 11 July 1960, Castellanos 22895 (RB); Mun. Natal, 5 km S of Ponta Negra, 2 Sep. 1946, Wurdack B-136 (US); Mun. Pau dos Ferros, 2 April 2000, E.A. Rocha et al. (obs); Mun. Tangará, W of town on road BR 226 to Currais Novos, 6°14'S, 35°51'W, 1 April 2000, E.A. Rocha et al. (photo); Mun. Jardim do Seridó, 1 April 2000, E.A. Rocha et al. (obs).


CONSERVATION STATUS. Lower Risk (1); PD=1, EI=2, GD=2. Short-list score (1×5) = 5.

Subspecies gounellei is characterized by stout and sometimes very long spines, to 2 mm diam. and to 15 cm long. It received the nickname of ‘tyre-killer’ from Wedermann (1933, 1942) and is typical of low, very dry caatinga on sandy or stony soil and common on gneiss/granite outcrops. It can also be seen as an epiphyte on Copernicia palms in the northern caatinga vegetation type defined in Andrade-Lima (1981: 160).


Shrub or treelike, with a definite trunk to 1 m or more, branches 3.7–7.0 cm diam.; ribs 9–15, 3–8 × 6–13 mm. Spines (0.9–)1.0–1.9 mm diam. at base, whitish or golden to reddish, translucent, centrals 4–10, 10–20 mm, porrect to reflexed, radials 10–20, 7–10(–20) mm, adpressed. Flower-bearing areoles slightly to strongly modified, apical and subapical, on 1–3 ribs, often forming a true lateral cephalium sunken into the branch, with greyish white long hairs to 4 cm. Fruit with white or magenta funicular pulp.

Rio São Francisco caatinga element: rupicolous, on outcrops of Bambuí limestone (or sandstone in northern part of range), c. 450–1000 m, northern Minas Gerais and central-western and northern Bahia. Endemic to the core area of Eastern Brazil. Map 25A.


CONSERVATION STATUS. Lower Risk (1); PD=1, EI=1, GD=2. Short-list score (1×4) = 4. Lower Risk, but since many populations are found on limestone it may decline due to quarrying activities.

Ritter (1979), having visited Montes Claros (MG) and Bom Jesus da Lapa (BA), recognized P. zehntneri as a good species and combined it under Pilosocereus. Not taking account of this, E. Esteves Pereira (1987) described the populations from Santana and Bom Jesus da Lapa (BA) as a new species, P. braunii, based on the presence of a true cephalium and glaucous epidermis. Study of diverse populations of P. zehntneri and P. braunii suggests that there is a clinal variation in these characters, which become less obvious towards the eastern limits of its distribution, the floriferous areoles being much less hairy and modified in populations from Montes Claros (MG) and west of Morro do Chapéu, América Dourada (BA). It is clear that P. braunii is represented by populations of extreme plants that belong to a more wide-ranging and variable taxon, recognized by Ritter (1979) as P. zehntneri, and treated by Zappi (1994) as a subspecies of P. gounellei.

The recognition of two subspecies for P. gounellei is based in the absence of absolute discontinuities between the taxa concerned. The incomplete geographical isolation of these taxa in regions such as west of Morro do Chapéu (BA) explains the difficulties of delimitation between them.
In localities such as those near Montes Claros, Varzelândia, Cocos, Santana and Bom Jesus da Lapa, *P. gounellei* subsp. *zehntneri* is sympatric with *P. densiareolatus* (see notes under this species), and has been confused with it. *P. superfloccosus* was described on the basis of a mixture of material of *P. gounellei* subsp. *zehntneri* and *P. densiareolatus*, and this name has been used by some authors in error for the latter species.

Subg. *Pilosocereus* (nos. 3–20):

PILOSOCEREUS ARRABIDAE GROUP (nos. 3–5)

This group ranges from the coastal restinga into the caatinga via the agreste.


Tree-like or shrubby, branched above base, branching pattern 3–6-verticillate; central vascular cylinder somewhat to strongly woody; cortex only moderately mucilaginous; epidermis olive-green to glaucous, smooth; ribs (3–)4–12, sinuses straight, sometimes with pronounced transverse folds above the areoles. Areoles brownish to greyish, with long hairs, presenting weak indeterminate growth. Spines yellowish brown when young, opaque. Fertile region of stem not or slightly modified, on the apical and subapical areoles of 1–2(–3) ribs; flower-bearing areoles with white to greyish long hairs to 30 mm. Flower-buds acute 3 days before anthesis; flowers 5.5–6.7 × 4.7–7.0 cm, opening widely, somewhat compressed; pericarpel hemiglobose, tube 38–40 × 15–22 mm at base, to 30–45 mm wide at apex, pale green, glaucous, smooth, straight, distal half with some broad bract-scales; style 48–53 × 2–5 mm tapering to 1.8–3.5 mm, stigma-lobes 9–12, 5 mm, exserted; ovary locale quadrangular, triangular or depressed in longitudinal section. Fruit to 4.2–6.0 cm diam., depressed-globose, dehiscent by lateral slits, floral remnant erect, deeply inserted; pericarp smooth, purple; funicular pulp magenta. Seeds 2–2.3 mm, with intercellular depressions.

This species is divided in two subspecies:

1. Branches (6–)8–12 cm diam., ribs 4–6, spines stout, 10–40 mm (Bahia) 3a. subsp. *catingicola*
1. Branches 3.5–6.0(–8.0) cm diam., ribs (5–)6–12, spines slender, 2–10 mm (Bahia northwards from Salvador to Rio Grande do Norte and inland as far as cent.-S Pernambuco) 3b. subsp. *salvadorensis*

3a. subsp. *catingicola*

VERNACULAR NAME. Facheiro.
Eastern caatinga element: locally co-dominant with other arborescent plants in caatinga-agreste, c. 200–850 m, eastwards from the Chapada Diamantina, northern, north-eastern, central-eastern and southern Bahia. Endemic. Map 31B.


Besides the examined specimens cited above, this taxon has been observed in the following municipios of Bahia: Itapicuru, Olindina, Aporó, Inhambupe, Euclides da Cunha, Fílhedilha, Itiuba, Ponto Novo, Várzea Nova, Capim Grosso, Miguel Calmon, São José do Jacuibe, Gavião, Baixa Grande, Candeal, Serra Preta, Iaçu, Maracás, Barra da Estiva, Contendas do Sincoré, Jequié, Planalto.

CONSERVATION STATUS. Lower Risk (1); PD=1, EF=2, GD=2. Short-list score (1×5) = 5. Lower Risk, but its habitat continues to decline and its status needs to be monitored.

Subspecies catingicola is represented by populations of arborescent plants that occur inland in the caatinga-agreste zone of Bahia, presenting branches with 4–6 ribs and strong spination. This subspecies provisionally includes P. arenicola, which was probably based on marginal populations intermediate with subsp. salvadorensis, and thus could not be safely neotypified.


VERNACULAR NAMES. Facheiro, Facheiro-da-praia.

Shrubs or trees 2--10 m, with or without a definite trunk, branching at ground level and upwards; vascular cylinder slightly woody; branches 3.5--6.0(--8.0) cm diam., erect; ribs (5--)6--12, 10--20 × 16--20 mm; areoles 4 mm diam., 8--10 mm apart, rounded, reddish brown to grey, slightly hairy when young. Spines 0.3--0.7(--1.0) mm diam. at base, central(s) 1--11, 5--12 mm, ascending to porrect, radials 8--12, 3--4(--5) mm, adpressed. Flowers 5.5 × 4.7 cm, inner perianth-segments white; style 48 × 2--1.8 mm, tapering, stigma-lobes c. 9, exserted. Fruit to 4.2 cm diam. Seeds black, shiny, 2--2.1 × 1.1--1.3 mm, hilum-micropylar region 6--8 mm, forming an angle of 40° with long axis of seed, testa-cells domed to flat, with intercellular depressions and coarse, sparse cuticular folds.

Widespread caatinga / humid forest (restinga) element: in dense or sparse restinga on sand-dunes north of Salvador (BA) to Rio Grande do Norte, extending up the São Francisco River valley and westwards to the caatinga region around the borders of Bahia (Raso da Catarina), Alagoas, Sergipe and Pernambuco, where locally co-dominant with other arborescent vegetation, near sea level to 550 m. Endemic to North-eastern Brazil. Map 13.


CONSERVATION STATUS. Lower Risk (1); PD=1, EI=2, GD=2. Short-list score (1x5) = 5. Lower Risk, but its habitat continues to decline, especially near the coast, and so its status needs to be monitored.

The pollination of this subspecies by the phyllostomid bat, Glossophaga soricina Pallas, and by hawkmoths, has been documented and photographed by Locatelli et al. (1997).

The author has been shown photographs of what is assumed to be dense stands of this taxon growing on the rocky banks of the lower reaches of the Rio São Francisco, where it apparently develops into exceptionally tall specimens with many erect branches.


Treelike, c. 4 m, branched above the ground, with a well-defined trunk; vascular cylinder weakly woody; branches 8-9.5 cm diam., erect, epidermis dark green, slightly rough; ribs 8-10, 10-15 x 15 mm sinuses straight, and without visible transverse folds. Areoles 3-4 mm diam., 5-7 mm apart, felt greyish with brown long hairs to 3-5 mm. Spines 0.3-0.5 mm diam. at base, opaque, brown to blackish, centrals 1-4, 10-15 mm, ascending, radials 10-14, 2-8 mm, adpressed. Fertile part of stem slightly differentiated, with few apical or sub-apical flower-bearing areoles with bristly, black spines to 20 mm and white tufts of hair to 10 mm. Flowers not seen. Fruits (dried) depressed-globose, floral remnant pendent, deeply inserted. Seeds 1.5-1.6 x 1.0 mm, black, shiny, cochleariform, hilum-micropylar region 0.6-0.7 mm, forming an angle of 25-35° with long axis of seed, testa-cells domed, with inconspicuous intercellular depressions and hardly any cuticular folds.

South-eastern caatinga (inselberg) element: associated with gneissic inselbergs in caatinga-agreste; known only from the region of Pedra Azul, Minas Gerais (and from perhaps the same area recorded as a vaguely localized collection from south of Vitória da Conquista, Bahia). Endemic to the core area within Eastern Brazil. Map 33B.


Unlocalized: Bahia / Minas Gerais (?), S of Vitória da Conquista, 10 Apr. 1968, Castellanos 27073 (HB).

CONSERVATION STATUS. Critically Endangered (4) [criteria C2]; PD=2, EI=1, GD=1. Short-list score (4x4) = 16 This species is currently known from only a small area of dry forest vegetation, which is being cleared for agriculture and charcoal production.

A single living specimen of this taxon has been observed in semi-shade of dry forest (agreste), sympatric with Pilosocereus floccosus subsp. quadricostatus. The shape of the ribs and spination, as well as the only slightly differentiated flowering region are reminiscent of the P. ARABIDAE Group, especially of some populations of P. catingicola subsp. salvadorensis.
Although flowering material has yet to be examined, vegetative morphology and seeds suggest that this species belongs to the P. ARRABIDAE Group, which is otherwise unrepresented in the region of the Rio Jequitinhonha drainage, where all other Groups in Subg. Pilosocereus are present. The alternative explanation, that it is a hybrid involving P. catingicola and one of the other Pilosocereus from the area (eg. P. multicostatus, P. pachycladus), does not seem plausible given the characters it displays.


Cephalocereus arrabidae (Lemaire) Britton & Rose, Cact. 2: 42 (1920).


Cereus warmingii K. Schum. in Martius, Fl. bras. 4(2): 204 (1890), quoad typo. Type: Brazil, Rio de Janeiro, restingas de Copacabana, Warming s.n. (Bt).


Cactus hexagonus sensu Vellozo, Fl. flum.: 205 (1825 publ. 1829), non Linnaeus (1753).

Cactus heptagonus sensu Vellozo, Fl. flum.: 205 (1825 publ. 1829), non Linnaeus (1753).

Cereus macrogonus sensu K. Schum. in Martius, Fl. bras. 4(2): 202, t. 40 (1890), non Salm-Dyck (1850).


VERNACULAR NAME. Facheiro-da-praia.

Shrub, 0.1–3.0(–4.0) m, or rarely with a short trunk, branching near base or above, sometimes 3–5-verticillate; vascular cylinder weakly woody; stems 4.5–9.5 cm diam., straight, slightly upcurved, epidermis yellow-green to dark green, sometimes slightly greyish; ribs (5-)6-8, 13–15 x 12–20 mm, sinuses straight, with oblique transverse folds above the areoles. Areoles (5-)6-8 mm diam., (7-)15–32 mm apart, situated upon more or less conspicuous stem-projections (podaria), felt whitish to brownish or greyish. Spines 0.6–1.1 mm diam. at base, translucent only when young, brown to greyish, centrals (0--)2-4(-8), 15–40 mm, sometimes decurved near base, often 1 ascending and two pectinate, radials 7–10, 2–20 mm, adpressed. Fertile part of stem not differentiated, flowers distributed along the branches. Flower-buds acute 2–3 days before anthesis; flowers 6–7 x 4–5 cm; pericarpel subglobose, tube flared from 11 to 30–32 mm wide, infundibuliform, straight, creamy green, smooth, distal half with wide, broadly triangular bract-scales; style 45–48 x 3–2 mm, tapering, stigma-lobes c. 9, 6–7 mm, exserted; ovary locule obovate, compressed in longitudinal section. Fruit 3–5 x 5–5.8 cm, depressed-globose, dehiscent by a lateral or abaxial slit, floral remnant pendent, deeply inserted; pericarp green to deep reddish pink, slightly rugose; funicular pulp magenta. Seeds (1.4–)1.5–1.7(–1.8) x 1–1.2 mm, testa-cells domed, with intercellular depressions and dense, coarse cuticular folds.

Southern humid forest (restinga) element: in dense or sparse, sandy restinga, near sea level, southern Bahia and Espírito Santo to Rio de Janeiro. Map 17D.


RIO DE JANEIRO: Mun. São João da Barra, c. 10 km from town by the crossing towards Gruçai, 23 Mar. 1982, Rocha et al. 893 (RB); Mun. Quiçamã (Quissamã), road to Barra do Furado, 22°6'5"S, 41°26'W, 23 Nov. 1999, Zappi et al. 397 (K, UEC).
Inhabiting a long stretch of restinga vegetation, from between Santa Cruz Cabrália and Porto Seguro, Bahia, to west of the city of Rio de Janeiro, *P. arrabidae* has been rather frequently confused with *P. brasiliensis* subsp. *brasiliensis*, with which it is sympatric, at least along the coast of Espírito Santo (cf. Pereira 2119). There are some superficial similarities, such as the undifferentiated flower-bearing areoles and green epidermis, but *P. arrabidae* presents (5–)6–8 ribs, thicker branches, acute, straight flower-buds, large flowers, 4–5 cm diam. at anthesis, whereas *P. brasiliensis* subsp. *brasiliensis* has 4–5 ribs, thinner branches, 4.5–5.5 cm diam. and obtuse, curved flower-buds, with narrow flowers up to 3 cm diam. at anthesis. Their seeds also differ considerably.

PILOSOCEREUS PENTAEDROPHORUS Group (nos. 6–10). Found in *Mata atlântica* through to *caatinga de altitude* and in the *caatinga-cerrado* ecotone, but avoiding the driest areas and completely absent from the caatingas of the Rio São Francisco valley.


Erect or semi-scandent shrub, 2–4 m, without a well-defined trunk, main stem little branched; vascular cylinder moderately woody, branches 4.5–5.5 cm diam., semi-decumbent to prostrate when shaded, erect when in full light; ribs 4–6–(–7), 15–17 × 8–18 mm, sinuses straight, transverse folds above the areoles oblique. Areoles 4–7 mm diam., 6–8 mm apart, situated upon stem-projections (podaria), felt white, brown to blackish, with white, greyish or brown long hairs to 15 mm, indeterminate growth not observed. Spines opaque, at first reddish or yellowish brown, later greyish. Fertile part of stem not or only slightly differentiated, flowers appearing randomly over the stem. Flower-buds obtuse 1–2 days before anthesis; flowers 4.5 × 2.5–3.0 cm; pericarpel subglobose, tube 20–40 × 10–12 at base, flared to 23 mm at apex, constricted beneath and above nectar-chamber, curved, nearly cylindric, pale green, smooth, apex with few, thick, rounded bract-scales; style 26–32 × 1.5–1.0 mm, tapering; stigma-lobes 7–8, 8 mm; ovary locule hemicircular in longitudinal section. Fruit 2 × 3–3.5 cm, depressed-globose, dehiscent by a lateral slit, floral remnant pendent, deeply inserted; pericarp wine-coloured, smooth; funicular pulp magenta. Seeds (1.4–)1.6–1.7(–1.8) × 1.1–1.2 mm, testa-cells domed, with intercellular depressions and dense, coarse cuticular folds.

Two subspecies are recognized as follows:

1. Branches dark green; ribs 4–5
1. Branches greyish green to glaucous; ribs (4–)5–7

6a. subsp. *brasiliensis*
Branches 4.5–5.5 cm diam., semi-decumbent to prostrate when shaded, erect in exposed habitats, epidermis shiny dark green, sometimes slightly greyish; ribs 4–5; areoles usually hairy only at the stem apex (except in cultivation under glass), long hairs pale brown, to 10 mm, later glabrescent, brown to black. Spines 0.8–1.0 mm diam. at base, centrals (0–1)–3, 10–30 mm, ascending to prorect; radials 4–8, 3–16 mm, adpressed. Fertile part of stem not or only slightly differentiated, flowers solitary or in groups of 2–3; anthers 1.5–1.8 mm; stigma-lobes c. 7, not exserted much beyond anthers.

Southern humid forest (restinga) element: in restinga and gneissic inselbergs of the coast, to 100 m, Espírito Santo; Rio de Janeiro. Endemic to South-eastern Brazil.


CONSERVATION STATUS. Vulnerable (2) [criteria A2c]; PD=1, EI=1, GD=2. Short-list score (2×4) = 8. Has apparently declined in the southern part of its range (around the city of Rio de Janeiro) and may be affected by ongoing touristic developments along the length of its coastal habitat.

Variable in the degree of areolar wool developed in some populations.


Branches 4.5–6.5 cm diam., erect or procumbent, epidermis grey-green, slightly glaucous at apex; ribs (4-)5-7, variable in number between populations; areoles with white to greyish long hairs, mainly at the apex of stems.

Southern humid/subhumid forest (inselberg) element: on gneissic inselbergs associated with agreste and mata seca, c. 80–700 m, southern Bahia, Espírito Santo and eastern Minas Gerais. Endemic to the core area within Eastern Brazil. Map 16A.


Variable in rib number between populations.


Slender, sparsely branched tree, 2–5(-8) m, with a well-defined trunk; vascular cylinder strongly woody; branches 3–12(-15) cm diam., closely grouped and erect or sometimes semi-decumbent, epidermis olive-green, glaucous at apex when young; ribs 6–12, 8–17 × 9–15 cm, sinuses straight, with oblique transverse folds above the areoles. Areoles 5–10 mm, 10–15 mm apart, situated upon rounded stem projections, felt yellowish white, long hairs pale brown to grey, apical areoles sometimes unarmed. Spines medium, ascending when young, later greyish; centrals 3–5(-7), 15–70 mm, porrect, lowermost largest; radials 12–15, 5–14 mm, adpressed. Fertile part of stem not differentiated, subapical, on 2–4 ribs. Flower-buds acute 2 days before anthesis; flowers 5.8–6.0 × 3.5–3.7 cm, pericarpel subglobose, tube 40 × 13 mm at base to 25 mm at apex, constricted above and below the nectar-chamber, strongly curved, slightly compressed, pale green, glaucous, smooth, distal half with acute bract-scales; style 42–46 × 2.5–2.0 mm, tapering, stigma-lobes c. 9, 5 mm, exerted in relation to the stamens; ovary locule hemicircular in longitudinal section. Fruit to 2–2.5 × 3–3.5 cm, depressed-globose, dehiscent by a lateral slit, floral remnant pendent, deeply inserted; pericarp pale green, slightly rugose; funicular pulp magenta. Seeds (1.6–)1.7–1.8(-1.9) × 1.1–1.2 mm, testa-cells domed to flat, with intercellular depressions and coarse, sparse cuticular folds.

Northern caatinga element: in the caatinga/cerrado ecotone, dense, high and low shrubby caatinga, open, seasonally flooded carnauba (Copernicia prunifera) forest (often as epiphyte) and caatinga-mangrove ecotone, in northern draining river valleys and at the coast, sea level to c. 350 m, northern and eastern-central Ceará, northern to central-south-eastern Piauí and along the border regions between Piauí and Maranhão; (?) to northern Tocantins. Endemic to North-eastern Brazil? Map 20.


CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1x5) = 5. Lower Risk at present, but needs to be monitored in view of increasing habitat destruction in the areas of higher rainfall that it inhabits.

This species ranges through the northern part of the caatinga, reaching that vegetation’s north-western limits, and occupying the ecotones with the cerrado and forests transitional to those of Amazônia. It is the only Pilosocereus that enters the coastal mangrove-caatinga ecotone (NW Ceará) and is also frequently epiphytic on the trunks of carnaúba palms in seasonally flooded palm forest at its northern limit (caatinga type no. 12 of Andrade-Lima 1981: 160). Its stems vary considerably in thickness, those of plants from the drier vegetation of central-southern Piauí and adjacent parts of Maranhão being much more slender than those from further north.


VERNACULAR NAMES. Facheiro, Facheiro-fino, Mandacaru-de-veado.

Shrub or treelike to 6 m; vascular cylinder woody; branches blue-green, glaucous; ribs 4–8(-10), sinuses sinuate and pronounced, horizontal transverse folds above the areoles. Areoles 3–7(–8) mm, 12–22 mm apart, felt white to greyish black, apical young areoles frequently unarmed, growth indeterminate, strong, near base of plant. Spines 0.5–1.0 mm diam. at base, translucent, yellowish brown. Fertile part of stem not differentiated, subapical, occupying several consecutive areoles of more than one rib. Flower-buds curved and obtuse, constricted in the region of the nectar-chamber, varying markedly in colour in different populations between green, reddish or purplish blue; flower 3.5–5.5 × 2.8 cm; tube 35–45 × 11 mm at base to 20–21 mm diam. at apex, constricted below and above the nectar-chamber region, strongly curved, smooth, terete or nearly so, apex with few ovoid to spathulate bract-scales; style 35 × 2–1.5 mm, tapering, stigma-lobes c. 10; ovary locule hemispheric to depressed in longitudinal section. Fruit 1.5–2.0 × 2–3 cm, depressed-globose, dehiscent by a lateral slit, with pentagonal to hexagonal outline, floral remnant pendent, deeply inserted; pericarp pale green to wine-coloured; funicular pulp purplish or magenta. Seeds (1.6)–1.7–1.9(–2.0) × (1)–1.1–1.3(–1.4) mm, testa-cells flat, with intercellular depressions nearly absent and fine, sparse cuticular folds.

Two subspecies are recognized within this taxon, the typical one inhabiting forest vegetation east of the Chapada Diamantina (Bahia) and northwards, reaching Pernambuco, and subsp. robustus, distributed towards the southern limit of the species, in southern Bahia and north-eastern Minas Gerais. These are distinguished as follows:
1. Branches slender, long and leaning, to 4.5(-6.0) cm diam., ribs 4-6(-7), obtuse (Bahia to Pernambuco)

8a. subsp. pentaedrophorus

1. Branches stout, never leaning, to 7.5 cm diam., ribs (5–)6-10, acute (S Bahia & NE Minas Gerais)

8b. subsp. robustus

8a. subsp. pentaedrophorus

Tree-like, sparsely branched; branches sometimes leaning on other vegetation for support, 3-4.5(-6.0) cm diam.; ribs 4-6(-7), 9-18 x 8-20 mm, obtuse. Central spines 1-3, 10-25 mm, proper to deflexed, radials 3-12, 4-12 mm, adpressed, all deflexed.

Eastern caatinga element: in agreste and dense caatinga, on rocky substrates, rarely reaching into restinga sand-dunes (N of Salvador, BA), c. 5–1000 m, north-eastern Pernambuco, western Sergipe, and north-eastern and eastern Bahia. Endemic to the core area within North-eastern Brazil. Map 30B.


Besides the examined specimens cited above, this taxon has been observed in the following municípios in Bahia: Andarai, Oindina, Rui Barbosa, Ibatiba.

Shrubby or treelike, densely branched; branches erect, to 7.5 cm diam.; ribs (5-)6-10, 15-21 × 8-19 mm, acute. Central spines 0–2(-3), 20-26 IllIl1, 1-2 ascending and sometimes 1 porrect; radials 3-8, 4-20 IllIl1, well-developed, adpressed.

Eastern *caatinga* element: in dense *caatinga-agreste* of the Rio de Contas (Rio Gaviao) and Rio Pardo drainage systems, c. 400-900 m, southern and south-eastern Bahia and north-eastern Minas Gerais. Endemic to the core area of Eastern Brazil. Map 32B.


Besides the examined specimens cited above, this taxon has been observed in the following municípios of Bahia: Iramaia, Itaeté, Barra da Estiva, Contendas do Sincora, Jequié.

**CONSERVATION STATUS.** Lower Risk (1); PD=1, EI=1, GD=2. Short-list score (1×4) = 4. Lower Risk at present, but its habitat continues to decline.

Variable in rib number and stem thickness.

Intergeneric hybrids between *P. pentaedrophorns* and *Micranthocereus purpureus*, cited by Ritter (1979), have been observed in the region of Andaraí and Ituacu, Bahia. At the southern limit of distribution of *P. pentaedrophorns*, in the drainage of the Rio Pardo (*Taylor et al.* 1515D), *P. p. subsp. robustus* can be found sympatric with *P. floccosus* subsp. *quadricostatus*.


Treelike, to 3–5 m, sparsely branched, with a well-defined trunk; vascular cylinder woody; branches 3–6.5(–7.0) cm diam., inclined, epidermis bluish or greyish green, glaucous; ribs (3–4[seedlings/juveniles]–)5–10, 7–12 × 7–18 mm, sinuses straight, transverse folds above the areoles straight. Areoles 4–6 mm, 6–10 mm apart, situated upon rounded, low projections (podaria), with blackish felt and white long hairs to 20 mm, mainly on the apical region of branches. Spines 0.5–1.0 mm diam. at base, translucent when young, golden yellow to greyish, centrals 2–4(–5), ascending to porrect, 20–35(–40) mm, radials 7–14, adpressed, mainly horizontal, 8–15 mm. Fertile part of stem not or slightly differentiated, apical to subapical, on many consecutive areoles of 2–5 ribs. Flower-buds obtuse 2 days before anthesis; flowers 4–5.2 × 2.5 cm; pericarpel subglobose, tube 34–38 × 10–12 mm at base, flared to 15–19
diam. mm at apex, curved, cylindrical, constricted above and below the nectar-chamber, pink to orange-red, smooth, glaucous, distal third with ovate, wine-coloured bract-scales; style 24–29 × 1.7–1.2 mm, tapering, stigma-lobes 7–8, included in relation to the stamens; ovary locule hemicircular to depressed in longitudinal section. Fruit depressed-globose, dehiscent by a lateral slit, floral remnant pendent, deeply inserted; pericarp olive-green to purplish, smooth; funicular pulp purplish. Seeds 1.6–1.9 × 1.1–1.2 mm, testa-cells flat with inconspicuous intercellular depressions and fine, sparse cuticular folds.

Caatinga / Northern campos rupestres (Chapada Diamantina) element: in 'caatinga de altitude', c. 740–950 m, on calcareous substrates, Chapada Diamantina, central Bahia. Endemic. Map 28C.


CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1×5) = 5. Lower Risk at present, but its habitat continues to decline.

The brightly coloured tube of the flower of this species is unusual in the genus, otherwise occurring only in *P. machrisii* and *P. aurisetus*. The nocturnal flowers of *P. glaucochrous* remain open for part of the following morning and, therefore, may be adapted for pollination by both bats and hummingbirds. Variable in rib number between populations.


*[Cereus macrogonus* sensu Warming (1892), cf. Warming (1908: 151, footnote, 254), non Salm-Dyck (1850).]*

Shrub, not branched above base, or treelike, 1–4(-5) m, with or without a well-defined trunk, sparsely or much branched; vascular cylinder weakly woody; branches erect, epidermis verrucose, greyish green; ribs with straight sinuses and without visible transverse folds. Areoles 3–10 mm, (2-)4–10 mm apart, with white to brownish grey felt and white or brownish long hairs to 10 mm, growth indeterminate near base of plant. Spines 0.3–1.1 mm diam. at base, opaque, yellowish brown or reddish, becoming greyish. Fertile part of stem strongly differentiated, flower-bearing areoles with pale brown or grey, woolly, long hairs to 15–20 mm and dark bristly spines to 35 mm, forming a ring around the subapical region of the stem. Flower-buds obtuse 2–3 days before anthesis; flowers 4–5 × 3 cm; pericarpel subglobose, tube to 40 × 12 mm at base, flared to 25 mm diam. at apex, curved, constricted above and below nectar-chamber, green, glaucous, smooth, distal third with broad ovate bract-scales; style 30 × 1.7–1.5 mm, tapering, stigma-lobes 9–10, exserted or included in relation to the stamens; ovary locule obovateangular in longitudinal section. Fruit dehiscent by a lateral, abaxial or adaxial slit; pericarp wine-coloured, smooth to somewhat rugose; funicular pulp bright red. [Seeds: see subspecies.]

When first described by Backeberg & Voll, l.c., this species was placed in the genus *Pilocereus*, as *P. floccosus* Backeb. However, this name is illegitimate because of the prior-published *Pilocereus floccosus* Lemaire, which relates to a Caribbean taxon (nowadays a synonym of
Pilosocereus royenii (L.) Byles & Rowley. The legitimate name is, therefore, to be attributed to Byles & Rowley (1957), who published Pilosocereus floccosus Byles & Rowley based on Backeberg’s illegitimate name.

Easy to distinguish from all the other species of the genus by its rough, verrucose epidermis, *P. floccosus* differs by its long-hairy flower-bearing areoles, forming a crown or zone at the apical or subapical region of the branches. Although, as circumscribed here, this species is endemic to the core area of Eastern Brazil, a potentially closely related taxon occurs in northwestern Minas Gerais — *P. albisummus* P. J. Braun & E. Esteves Pereira in Kakt. and. Sukk. 38: 126–131 (1987). It has not been possible to study this plant at close quarters in the field, but living and herbarium material at Zürich (ZSS), photographs of the plant, flower-buds and seeds (SEM), and its known ecological preference for Bambuí limestone outcrops are strongly indicative of an affinity to *P. floccosus* subsp. *floccosus*.

The typical subspecies occurs only on limestone rock outcrops of the Bambuí formation, in central Minas Gerais, where it does not normally become very tall, unless growing in very dense forest. North-east of the distribution of subsp. *floccosus*, *P. f. subsp. quadricostatus* lives in the caatinga associated with gneissic outcrops of the semi-arid region of the Rio Jequitinhonha valley (Taylor & Zappi 1992a). This species is subdivided as follows:

1. Branches 5–9 cm diam.; ribs 5–8; seeds shiny, testa-cells without cuticular folds (SEM)  
10a. subsp. *floccosus*

1. Branches branches 8–11 cm diam.; ribs 4–5; seeds dull, testa-cells with dense cuticular folds (SEM)  
10b. subsp. *quadricostatus*

**10a. subsp. *floccosus***

Shrub, branching near base or above ground, rarely treelike, with or without a well-defined trunk; branches 5–8 cm diam., ribs 5–8, 12–30 × 20–30 mm. Central spines 3–6, 8–25 mm, ascending to prorect, radials 5–16, 2–25 mm, ascending or adpressed. Fruit 2.5–3.0 × 3–3.5 cm, depressed-globose. Seeds (1.8–)1.9–2.2 × (1.2–)1.3–1.4(–1.5) mm, hilum-micropylar region forming an angle of 50° with long-axis of seed, testa-cells flat with inconspicuous intercellular depressions and lacking cuticular folds.

Rio São Francisco (Rio das Velhas) caatinga / mata seca element: mostly on Bambuí limestone outcrops west of the Serra do Espinhaço, c. 600–800 m, Minas Gerais. Endemic to the core area within Minas Gerais. Map 27B.


**CONSERVATION STATUS.** Lower Risk (1); PD=1, EI=1, GD=1. Short-list score (1×3) = 3. Lower Risk, but its habitat on limestone outcrops is at risk from quarrying operations. Forest surrounding outcrops may also be cleared affecting local climate.


Shrubby or treelike, branched above ground, with a well-defined trunk; branches 8–11 cm diam., ribs 4–5 (3–7 in young plants and seedlings *fide* Ritter), 26–30 x 15–40 mm. Areoles either with very short spines or central-spines 1–3, 2–50 mm, ascending to porrect, and radials 6–8, c. 2–10 mm, ascending to adpressed. Fruit to 6 x 5 cm, depressed but often compressed due to the presence of many fruits close together on the same rib. Seeds 1.7–1.8 x 1.1–1.3 mm, hilum-micropylar region forming an angle of 40° with the long-axis of seed, testa-cells domed to flat with inconspicuous intercellular depressions and dense, coarse cuticular folds.

South-eastern *caatinga* element: in *caatinga* and on associated gneissic inselbergs within the drainage of the Rio Jequitinhonha and high ground separating it from the Rio Pardo, c. 250–800 m, north-eastern Minas Gerais. Endemic to the core area within Minas Gerais. Map 33B.


CONSERVATION STATUS. Vulnerable (2) [criteria B1/2c]; PD=1, EI=1, GD=1. Short-list score (2x3) = 6. Vulnerable from clearance of its *caatinga* habitat.

10b × 13: *Pilosocereus floccosus* subsp. *quadricostatus* × *Pilosocereus magnificus*


Treelike or shrubby, 2–5 m, usually with a ± well-defined trunk, sparsely branched above ground; vascular cylinder weakly woody; branches 7–10 cm diam., erect, epidermis dark green to olive-green, more or less glaucous, slightly rough; ribs 4–7, 17–30 x 20–35 mm, sinuses straight, transverse folds not visible. Areoles 4–6 mm diam., 2–5 mm apart, felt greyish, with white to brownish, long hairs 6–10 mm. Spines 0.3–0.5 mm diam. at base, translucent when young, yellowish, pale brown or reddish, centrals 4–5, 7–15 mm, ascending to porrect, radials 10–14, 6–10 mm, ascending to porrect or deflexed. Fruit to 6 x 5 cm, depressed but often compressed due to the presence of many fruits close together on the same rib. Seeds 1.5–1.6 x 1.1 (1–1.2) mm, hilum-micropylar region forming an angle of 40° with the long-axis of seed, testa-cells domed to flat, with inconspicuous intercellular depressions nearly inconspicuous, and coarse, sparse cuticular folds.

On gneissic inselbergs and in associated *caatinga-agreste*, c. 250–600 m, north-eastern Minas Gerais.


CONSERVATION STATUS. Vulnerable from clearance of its *caatinga* habitat.
PILOSOCEREUS ULEI Group (nos. 11–13).
Found in caatinga-agreste, caatinga and campo rupestre.

Holotype: Brazil, Minas Gerais, N Serra do Espinhaço, [Grão Mogol], 800–1000 m, 1968, Horst 277 (U).


VERNACULAR NAME. Quiabo-da-Iapa.

Shrubby to tree-like, 2–3(-4) m, branching above the ground; vascular cylinder weakly woody; branches 5–12 cm diam., erect, epidermis greyish green, coated with intense sky blue wax near apex; ribs 4–8, sinuses straight, transverse folds absent. Areoles almost contiguous, felt dark brown or black with dark long hairs, paler to glabrescent with age. Spines opaque, yellowish brown to blackish, thickened at base. Fertile part of stem strongly differentiated, flower-bearing areoles subapical, on one or several ribs, with abundant reddish brown and golden brown long hairs to 20–40 mm. Flowers 3.6–6.0 \times 3–4 cm; pericarpel subglobose, greenish; tube straight, infundibuliform, distal third with thick acute bract-scales; nectar-chamber swollen; ovary locule hemicircular to triangular in longitudinal section. Fruit depressed-globose, frequently compressed, deliscent by lateral slit, floral remnant pendent, deeply inserted; pericarp greenish, pink or dark purplish; funicular pulp magenta. Seeds with flat testa-cells, intercellular depressions nearly absent, cuticular folds absent.

This distinctive species can be easily differentiated from the rest of the genus by the unusual combination of intensely blue epidermis and dark reddish brown areolar hairs, which are more abundant when the plants are flowering. The areoles with short dark spines are so closely arranged that it is sometimes difficult to isolate one from the next. It is the sister species of P. ulei, from the region of Cabo Frio, Rio de Janeiro.

This taxon is divided into two subspecies, found on crystalline rock outcrops associated with the campos rupestres, on both sides of the Serra do Espinhaço, Minas Gerais, where the species is endemic. The subspecies are differentiated as follows:

1. Branches 8–12 cm diam.; ribs 4–7; fruit dark pink to dark purple
11a. subsp. fulvilanatus

1. Branches to 5.5 cm diam.; ribs (5-)6–8; fruit green to brownish red
11b. subsp. rosae

11a. subsp. fulvilanatus

Treelike or shrubby, 2–3(-4) m, branching above the ground; branches 8–12 cm diam.; ribs 4–7, 30–40 × 30–40(–45) mm. Areoles 3–7 × 2–5 mm, 1–3 mm apart, very congested. Spines 0.6–0.9 mm diam. at base, centrals 1–7, 15–30(–45) mm, ascending to porrect, radials 8–10, 8–15 mm, adpressed. Flower-bearing areoles extremely hairy. Flowers 3.6–5.2 × 3 cm; tube 21 × 11 mm at base, flared to 20 mm diam. at apex, greenish; style 20 mm, stigma-lobes c. 12. Fruit 3 × 3.5–4.0 cm; pericarp dark pink to dark purple, rugose. Seeds 1.5–1.6 × 1–1.1 mm.

South-eastern campo rupestre (Grão Mogol region) element: locally co-dominant with other woody vegetation on quartzitic rock outcrops, campo rupestre, Serra do Espinhaço, in the drainage of the Rio Jequitinhonha, c. 720–1000 m, northern Minas Gerais. Endemic to the core area within Minas Gerais. Map 36A.

MINAS GERAIS: Mun. Grão Mogol, Serra da Bocaina, 28 km E of Caveira and 48.5 km W of Rio Vacaria on road BR 251, 31 Jan. 1991, Taylor et al. 1513 (K, HRCB, ZSS, BHCB); Serra de Grão Mogol, 1968, Horst 277 (U); l.c., 18 km W of town, 21 Feb. 1969, Irwin et al. 23676 & 23684 p.p. (NY); l.c., campo rupestre NE of the town, 22 May 1982, M.C.H. Mamede et al. in CFCR 3475 (SPF); Mun. Cristália, slopes of the Serra das Cabras, 28 May 1988, Zappi et al. in CFCR 12046 (SPF); l.c., margins of the Rio Itacambiruçu, 16°37'S, 42°56'W,
130


**Conservation Status.** Vulnerable (2) [criteria B1/2c]; extent of occurrence = 724 km$^2$; PD=1, EI=2, GD=1. Short-list score (2×4) = 8. Vulnerable from disturbance and destruction of its habitat for charcoal production.

Known from only three populations between Grão Mogol and Botumirim (MG), subsp. *fulvilanatus* presents a rather restricted distribution, but it has to be said that this region is still rather under-explored.


Shrubby, to 3 m, sparsely branched above ground, without a well-defined trunk; branches c. 5.5 cm diam.; ribs (5-)6-8, 15-20 × 15-25 mm. Areoles 3-4 × 3-4 mm, 2-4 mm apart. Spines 0.4-0.6 mm diam. at base; centrals 3-4, 10-20 mm; radials 8-10, to 12 mm, adpressed. Fertile part of stem differentiated, with long hairs to 3-4 cm, and black bristly spines to 2-3 cm. Flowers 3.8-6.0 × 3-4 cm; tube 30-45 × 11 mm at base, flared to 25 mm diam. at apex, straight, greenish brown to pinkish; style 25-30 mm, stigma-lobes c. 10. Fruit to 6.5 cm diam.; pericarp green to brownish red, striate. Seeds 1.6-1.8 × 1-1.2 mm. [Description based on dried material and protologue.]

South-eastern *campo rupestre* (Rio São Francisco drainage) element: on quartzitic rock outcrops, *campo rupestre*, c. 800 m, Serra do Espinhaço, in the drainage of the Rio das Velhas, central-northern Minas Gerais. Endemic to the core area within Minas Gerais. Map 37B.

**Conservation Status.** Endangered (3) [criteria C2b]; PD=1, EI=1, GD=1. Short-list score (3×3) = 9. Endangered from habitat disturbance caused by local industry at its only known location, the extent of which needs to be determined in case it proves to be a Critically Endangered taxon.

Although it has not been possible to study populations of subsp. *rosae* in the field, its striking morphological and ecological similarities with *P. fulvilanatus*, sens. str. have led to its present position (Zappi 1994). It has a less robust habit, with branches less than 6 cm in diameter, and a tendency to develop a higher number of ribs (6-8) than in mature stems of subsp. *fulvilanatus* (4-6). Otherwise, the remaining characteristics of both taxa are very similar, and only the geographical separation on either side of the Serra do Espinhaço — the two taxa being found c. 170 km apart — justifies the acceptance of *P. rosae* as a very restricted western subspecies, which is so far known from only a single population, found near the village of Santa Bárbara, in the Municipio of Augusto de Lima, Minas Gerais. Its extent of occurrence remains uncertain.


Pilosocereus atrojlavispinus
Pilosocereus azureus
P. Treelike or shrubby, bract-scales; inner perianth-segments white to pink; style
P. Pilosocereus cenepequei
Pilosocereus superbus
Pilosocereus splendidus
Pilosocereus pernambucoensis
Pilosocereus oreus
differentiated. Flower-buds acute or obtuse 1-2 days before anthesis; flowers very variable, 4-7 x 2.2-4.5 cm,
diam., erect, epidermis glaucous, grey-green to blue, smooth; ribs 5-19, sinuses straight, transverse folds above the
whose chosen epithet is blocked within Pilosocereus. One of the earlier names associated with this
taxon, Pilocereus glaucescens A. Linke 1858, is of doubtful application, having been based on sterile living material
collected in Brazil, without precise locality (see ‘Insufficiently known taxa’, pages 139-140). Ritter (1979) argues that the
description is very ambiguous and is impossible to attribute to a single taxon with certainty. From this
description, in fact, one cannot

Vernacular names. Facheiro, Facheiro-azul, Mandacaru-de-facho.
Treelike or shrubby, 2-10 m or more; vascular cylinder weakly to moderately woody; branches 5.5–10.0(-15.0) cm
diam., erect, epidermis glaucous, grey-green to blue, smooth; ribs 5–19, sinuses straight, transverse folds above the
areoles visible at apex of young branches. Areoles 3–10 mm diam., 2–10 mm apart, felt white to greyish, long,
white long hairs. Spines transverse, golden-yellow, greyish with age. Fertile part of stem slightly to strongly
differentiated. Flower-buds acute or obtuse 1–2 days before anthesis; flowers very variable, 4–7 x 2.2–4.5 cm,
sometimes compressed; pericarpel subglobose; tube 25–50 x (8–)12–25 mm at base, flared to 24–35 mm diam. at
apex, constricted below nectar-chamber, slightly to strongly curved, pale green to dark brown, distal third with broad
bract-scales; inner perianth-segments white to pink; style 20–58 x 3–1.2 mm, tapering; stigma-lobes 9–13, exserted
in relation to the anthers; ovary locule broadly hemispherical to triangular in longitudinal section. Fruit depressed-
globose, dehiscent by a lateral slit, floral remnant pendent, deeply inserted; pericarp purplish; funicular pulp
magenta. [Seed morphology: see subspecies].

Although *P. pachycladus* is one of the most conspicuous species in North-eastern Brazil, being both
common and widely distributed, it has an involved history of taxonomic confusion and was
first unequivocally named only two and a half decades ago by Buining & Brederoo (1975),
whose chosen epithet is blocked within *Pilosocereus*. One of the earlier names associated with this
taxon, *Pilocereus glaucescens* A. Linke 1858, is of doubtful application, having been based on sterile living material
collected in Brazil, without precise locality (see ‘Insufficiently known taxa’, pages 139–140). Ritter (1979) argues that the
description is very ambiguous and is impossible to attribute to a single taxon with certainty. From this
description, in fact, one cannot
exclude *P. glaucochrous* (Werdermann) Byles & Rowley, some of the forms of *P. pachycladus*, or even the possibility of the original plant being a specimen from another country. Werdermann (1933, 1942) used the name *Pilocereus glaucescens* for populations here included within *Pilosocereus pachycladus* subsp. *pachycladus*. A second name incorrectly used for this species in the broad sense was *Cereus ulei* by Lützelburg (1926, 3: 69), while a third once applied to *P. pachycladus* is *P. piauhyensis* (see *P. pachycladus* subsp. *pernambucoensis* and *P. piauhyensis*).

This very variable species comprises a number of heterotypic synonyms described by Ritter, Buining & Brederoo, and Braun (see above). The species concepts utilized by these authors have proved to be too narrow and, if applied to all the forms now known, would lead to a new species name for each slightly different population of this complex.

*P. pachycladus* presents a broad range of forms, including tree-like populations, widely distributed in the dense or sparse *caatinga* forests of the Nordeste, and more shrubby forms in rupicolous populations near its southern limit, in northern Minas Gerais. To the south of Pedra Azul, is the endemic *P. magnificus*, which has probably arisen by a process of allopatric speciation following isolation from a population of common ancestry with *P. pachycladus*, of which it is assumed to be the sister species.

Two subspecies are recognized:

1. Ribs 5–12, high and broad; central spines long, well differentiated from radials; flower-bearing areoles densely hairy (S of 10°S)
   a. subsp. *pachycladus*

1. Ribs (10–)13–19, low and close together; central spines poorly differentiated from radials, equalling them or slightly longer; flower-bearing areoles scarcely hairy (N of 10°S)
   b. subsp. *pernambucoensis*

12a. subsp. *pachycladus*

Treelike or shrubby, 1–5(–8) m, branched only at base or forming a well-defined trunk; branches 5.5–10.0(–11.0) cm diam., epidermis pale-blue; ribs 5–12, 15–35 × 12–24 mm. Areoles 3–10 mm diam., 2–12 mm apart, woolly. Spines 0.4–1.2 mm diam. at base; golden yellow to brownish or greyish, centrals 1–8, (5–)15–30(–45) mm, ascending to pro erect, radials 8–18, (3–)5–15 mm, adpressed. Fertile part of stem differentiated, with 1–4 subapical flower-bearing areoles on more than one rib, with white long hairs and sometimes bristly spines to 30 mm. Flower-tube pale green to very dark brown, slightly to strongly curved; inner perianth-segments white. Seeds 1.5–2.0 x 1–1.3 mm, testa-cells domed to flat, with intercellular depressions and coarse, dense to sparse cuticular folds.

Central-southern *caatinga* / Northern *campo rupestre* element: on quartzitic outcrops and scrub associated with the *campos rupestres*, and locally co-dominant with other woody vegetation in *caatinga*, on stony ground within and on either side of the Chapada Diamantina, central Bahia, south of 10°S, on limestone outcrops of W Minas Gerais and W Bahia, in N part of the Serra do Espinhaço, Minas Gerais and eastwards on gneissic in selbergs, and disjunctly in *campo rupestre*, northern part of the Serra do Cabral, Minas Gerais, c. 400–1550 m. Endemic to the core area within Eastern Brazil. Map 21B.

Further field study of this complex, geographically variable taxon may justify its division into additional subspecies, especially for the distinctive regional forms from the Rio São Francisco valley (BA/MG), Rio de Contas drainage (BA) and north-eastern Minas Gerais.

Pilocereus pernambucoensis

P.V. Heath in Calyx 4: 140 (1994) ("pernambucoensis").


[Cephalocereus piauhyensis sensu (Gürke) Britton & Rose, Cact. 2: 49 (1920), fig. 72 tantum, typ. excl.]

[Pilocereus piauhyensis sensu (Gürke) Werderm., Bras. Säulenkakt.: 111 (1933), fig. p. 107 tantum, typ. excl.]

VERNACULAR NAME. Calumbi.

Treelike, 2–10 m, with a well-defined trunk; branches 7–15 cm diam., epidermis grey-green to glaucous, smooth; ribs (10–)13–19, 8–12 × 7–10 mm. Areoles 3–10 mm diam., 5–8 mm apart. Spines 0.3–0.8 mm diam. at base, golden yellow, centrals 8–12, 12–18 mm, ascending to perrect, radials 16–18, 5–8 mm, adpressed. Fertile part of stem slightly differentiated, with 1–3 subapical flower-bearing areoles on 1 or more ribs, with few white long hairs and sometimes also 15–20 mm, bristly spines. Tube pale green to brownish, curved; inner perianth-segments white to pink. Seeds (1.3–)1.4–1.6–(1.8) × (0.9–)1.0–1.1 mm, testa-cells flat, with intercellular depressions, cuticular folds coarse, few or absent.

Northern caatinga element: locally co-dominant with other woody vegetation in dense or sparse caatinga and agrestic, on sandy or rocky substrates (including sandstones and gneissic inselbergs), c. 50–750 m, northern Bahia (north of 10°S), Alagoas, Pernambuco, Paraíba, Rio Grande do Norte, south-easternmost Piauí and southern and north-western Ceará (E, W & S sides of Chapada do Araripe, Chapada da Borborema & plateau of the Serra do Ibiapaba). Endemic to North-eastern Brazil. Map 20.

PIAÚ: SE Piauí, Mun. Jaciós, near the town, 7°13'S, 41°17'W, 6 April 2000, E.A. Rocha et al. (K, photo); Mun. Padre Marcos, 2 km along road to Simões from Marcolândia, 7°28'S, 40°41'W, 5 April 2000, E.A. Rocha et al. (K, photos); Mun. Simões, road to town from Marcolândia, W escarpment of Chapada do Araripe, 7°36'S, 40°45'W, 5 April 2000, E.A. Rocha et al. (K, photos); Mun. Paulistana, 54 km N and 24 km S of town on road BR 407, 6 April 2000, E.A. Rocha et al. (obs).

CEARÁ: NW Ceará, Mun. Tianguá, road BR 222, 10.5 km W of access road to Tianguá, 20 Feb. 1995, J.B. Fernandes da Silva 366 (MG), Taylor (K, photos); S Ceará, Mun. Jardim, SE escarpment of Chapada do Araripe, 7°34'S, 39°19'W, 4 April 2000, E.A. Rocha et al. (K, photos) — glaucous form with only 10–12 ribs.

RIO GRANDE DO NORTE: 'Sebastianópolis' – Chapada do Apodi, 11 July 1960, Castellanos 22894 (R); Mun. Mossoró, 11 July 1960, Castellanos 22877 (R); Mun. Tangará, W of town on road BR 226 to Currais Novos, 6°14'S, 35°51'W, 1 April 2000, E.A. Rocha et al. (obs); l.c., 7 km S of town on road to Guarabira (PB), 1 April 2000, E.A. Rocha et al. (obs).


Besides the examined specimens cited above, this taxon has also been observed in the following municípios of Pernambuco: Lagoa Grande, Santa Maria da Boa Vista, Oroco, Floresta, Airi, Cruzeiro do Nordeste, Arcoverde, Sertãnia, Garanhuns, Caetés, Terezinha, Bom Conselho; and Bahia: Remanso.

**CONSERVATION STATUS.** Lower Risk (1); PD=1, EI=2, GD=2. Short-list score (1 × 5) = 5. Lower Risk, but habitat continues to decline and has already declined very considerably.

This subspecies includes populations found from the Rio São Francisco valley region northwards (Bahia, N of 10°S), that comprise distinctly treelike, sometimes massive plants, with usually high numbers of ribs (13–19) and fine, golden spination, which were described by *Ritter* (1979) as *Pilosocereus pernambucoensis*. The treatment of this taxon at subspecific level is justified by the existence of morphologically intermediate populations in the region of Juazeiro and Sento Sé (*Taylor* 1375, 1394), presenting 10–15 ribs and relatively fine spination. A 10-ribbed form has also been observed in southern Ceará (Mun. Jardim).

*P. pachycladus* subsp. *pernambucoensis* may present either coerulescent blue (eg. *Zappi* 225) or greyish green epidermis (*Taylor & Zappi* 1630), the greenish plants predominating in the eastern part of its range, glaucous forms being the norm to the west. There is no reason to maintain *Ritter's variety caesius* (*Ritter* 1979), proposed on the basis of its glaucous epidermis. However, stem thickness does differ and is somewhat correlated with stem colour, the eastern populations, from central-eastern Pernambuco northwards to Rio Grande do Norte, being uniformly narrow-stemmed and greenish, suggesting that these could be recognised as a further subspecies, for which there is currently no name at any rank. This slender, greenish form obeys the distribution pattern of other taxa characteristic of the Eastern caatinga-agrestes, eg. *Tacinga palmadora*.

The collection cited above for north-western Ceará seems rather disjunct on present knowledge and underlines the need for field studies in the intervening areas of south-western Ceará.

Britton & Rose and Werdermann confused populations of *P. pachycladus* subsp. *pernambucoensis* with *Cereus piauhyensis* Güérke (1907), which they combined as *Cephalocereus piauhyensis* (Güérke) Britton & Rose (1920) and *Pilocereus piauhyensis* (Güérke) Werdermann (1933). The type material of *Cereus piauhyensis* Güérke was collected by Ule in the Serra Branca, north of São Raimundo Nonato, Piauí. It is clear that this name belongs to another species (see discussion under *P. piauhyensis*) and, to date, *P. pachycladus* has not been encountered further west than Mun. Paulistana in the south-easternmost corner of Piauí. This confused nomenclature also appears in Andrade-Lima (1989), where he follows the concept of Britton & Rose (1920) and Werdermann (1933), and illustrates and describes *P. pachycladus* subsp. *pernambucoensis* as *P. piauhyensis*. However, in the same work Andrade-Lima places the
southern forms of \textit{P. pachycladus} (ie. subsp. \textit{pachycladus}) under \textit{Pilosocereus glaucescens} (A. Linke) Byles & Rowley, a name of uncertain application (see notes at end of genus).

Egler (1951: 587, fig. 6) confuses this widespread northern subspecies with \textit{Facheiroa squamosa}, which in Pernambuco is restricted to the south-westernmost part of the state.


\textbf{VERNACULAR NAME.} Facheiro.

Shrubby to treelike, 1.5–5.0 m, with or without a well-defined trunk; vascular cylinder weakly woody; branches 4–6(–7.5) cm diam., erect, epidermis pale blue, waxy, smooth; ribs (4–)5–12(–15), 15 × 18 mm, sinuses straight, transverse folds above the areoles only visible at apex of branches. Areoles 4 mm diam., 2 mm apart, felt white or brownish, with white long hairs white. Spines 0.2–0.4 mm diam. at base, translucent, bristly, golden-yellow to brownish; centrals 8, to 15 mm, porrect; radials c. 16, to 10 mm, ascending. Fertile part of stem slightly modified, flower-bearing areoles in groups of 3–6, randomly distributed along the whole length of the branches, especially at the mid to basal part of the stems, bearing white long hairs. Flower-buds obtuse 2–3 days before anthesis; flowers to 6 × 2.3 cm; pericarpel subglobose, pale green; tube 35 × 10 mm at base, flared to 16 mm diam. at apex, constricted above and below the nectar-chamber, straight to slightly curved, greenish with purplish patches, smooth, apical region with acute; style 41 × 2.0–1.3 mm, tapering; stigma-lobes c. 10, exserted in relation to the anthers; ovary locule hemicircular to depressed in longitudinal section. Fruit 1.5–2.5 × 2.5–3.0 cm, depressed-globose, dehiscent by lateral, abaxial of adaxial slit, floral remnant erect to pendent, deeply inserted; pericarp thick, wine-coloured to purple, smooth; funicular pulp magenta. Seeds 1.3–1.5 × 0.8–1.2 mm, testa-cells domed, with intercellular depressions, cuticular folds lacking.

South-eastern caatinga (inselberg) element: locally co-dominant with other arborescent cacti on gneissic inselbergs in caatinga-agreste, c. 250–700 m, in the drainage of the Rio Jequitinhonha, north-eastern Minas Gerais. Endemic to the core area within Minas Gerais. Map 33C.


\textbf{CONSERVATION STATUS.} Lower Risk (1); PD=2, EI=2, GD=2. Short-list score \((1\times6) = 6.\) Lower Risk, but range limited and needs monitoring for habitat change.

Distinct within the genus for its approximate areoles bearing golden, bristly spines, which contrast with its strikingly pale blue, wax-covered epidermis. \textit{P. magnificus} can also be distinguished by its small, narrow flowers, that appear randomly along the branches. Rather variable in rib number between populations.

\textbf{PILOSOCEREUS AURISETUS Group (nos. 14–16)}
Stems branching only at base. Found on or amongst rocks in *cerrado* and in *campo rupestre*.

14. **Pilosocereus machrisii** (Y. Dawson) Backeb., *Die Cactaceae* 4: 2419 (1960). Holotype: Brazil, Goiás, E from Ceres, road S from Uruaçu, 3 km from the town, 26 May 1956, Dawson 15110 (R; RSA, iso.).


Shrubby, 0.4–3.2 (–3.5) m, not normally branched above base; vascular cylinder weakly woody; branches 3.2–9.0 cm diam., erect, epidermis not distinctly green, slightly greyish to glaucous, smooth; ribs 8–15, 7–15 × 13–20 mm, sinuses straight, transverse folds not visible; areoles 2–5 mm diam., 3–5 mm apart, felt white to greyish with white to brownish long hairs to 5–10 mm. Spines 0.25–0.60 mm diam. at base, translucent when young, reddish, pale brown or golden, centrals 3–8, 15–30 (–40) mm, porect or ascending, the largest deflexed on old areoles, radials 9–24, 3–25 mm, adpressed, the lowermost longer. Fertile part of stem strongly differentiated on 3 or more ribs of each branch, with yellowish to greyish long hairs to 20–30 mm, without bristles or these to 47 mm. Flower-buds acute 2 days before anthesis; flowers 3–7 (–8) × 3–5 (–6) cm; pericarpel subglobose to ovoid; tube 35–50 × 9–12 mm at base, flared to 21–30 mm diam. at apex, infundibuliform, straight, pinkish to brownish red, slightly striate, distal half with triangular, pinkish bract-scales; style 32–50 × 3–11 mm, tapering, stigma-lobes 8–12, exserted or equal to anthers; ovary locule clear to compressed in longitudinal section. Fruit 1.5–2.5 × 2–3.5 cm, depressed-globose, dehiscent by a lateral slit, floral remnant suberect to pendent, deeply inserted; pericarp exterior yellowish, red or purplish, interior yellow, smooth; funicular pulp white or pinkish magenta. Seeds (1.3–) 1.6–1.7 (–1.8) × 1–1.3 mm, testa-cells domed flat, with intercellular depressions, cuticular folds coarse, dense, sparse or absent.
Western cerrado element: on quartzitic, arenitic or limestone rock outcrops associated with cerrado, cerrado de altitude or campo rupestre, c. 500–800 m, southern Piauí and western Bahia; southern Pará (Araguatins), Goiás, Mato Grosso, Mato Grosso do Sul, western Minas Gerais (Serra da Canastra) and São Paulo (Altinópolis & Brotas); north-eastern Paraguay. Map 35A.


Material tentatively referred here (see tentative synonymy above):

BAHIA: W Bahia, Mun. São Desiderio, Sitio Grande, road to Barreiras, s.d., Horst & Uebelmann HU 203, cult. (ZSS) — P. parvus; Mun. (?), Serra do Moquém/Muquém, 550–600 m, — P. estevesii.

CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1×5) = 5.

The inclusion of the poorly known P. parvus is based on the lack of other distinctive characteristics apart from its dwarf habit (Zappi 1994). It may be sympatric with P. machrisii in western Bahia (cf. Horst & Uebelmann 203 and Taylor et al. 1440, see above).

The recently described P. estevesii P. J. Braun is also tentatively referred here. Its supposed distinctive characteristics seem no more unusual than those of other synonyms listed above and, given the extensive range of P. machrisii and its pronounced variability throughout this range, it would be unwise to assume that this western Bahian plant (now said to be extinct at its only known locality) is worthy of specific status. As Braun, l.c., comments, it is somewhat reminiscent of the geographically proximal P. flexibilispinus P. J. Braun & E. Esteves Pereira, from the adjacent state of Tocantins, but the flowers of the latter confirm its proposed relationship with the P. PENTAEVROPHORUS Group (Zappi 1994), whereas those of P. estevesii offer no differences with those of P. machrisii and its allies. P. estevesii has fruit with magenta funicular pulp, whereas previously known populations of P. machrisii are reported to have white fruit pulp. However, variation in this character is common in the genus and is particularly so in the closely related P. aurisetus.


Pilosocereus saxatilis Ritter, Kakt. Südamer. 1: 77 (1979), nom. inval. (Art. 34(c)). Based on: Brazil, Minas Gerais, Conceição [do Mato Dentro], 1964, Ritter 960A (U).


Pilocereus supthutianus

- Base, white to golden yellow, centrals 5-7, 8-25(-30) mm, ascending to porrect, radials 12-16, 7-11 mm, cuticular folds lacking.
- To the anthers; ovary locule hemicircular to compressed in longitudinal section. Fruit depressed-globose, dehiscent to tomentose, with white long hairs to bristles to
- Spines 3.2-5.0 x 3-4 cm; pericarpel subglobose, greenish to brownish; tube 25-30 x 10-12 mm at base, flared to 20-28 mm diam. at apex, infundibuliform, straight, pinkish to brownish red, slightly striate, distal half with pinkish bract-scales; style 22-25 x 1.5-0.8 mm, tapering, stigma exserted in relation to the anthers; ovary locule hemicircular to compressed in longitudinal section. Fruit depressed-globose, dehiscent by central slit beneath the floral remnant, which is pendent, deeply inserted; pericarp thick, folded and rugose; funicular pulp white, pink or magenta. Seeds with flat testa-cells, intercellular depressions visible to inconspicuous, cuticular folds lacking.

One of the specific features of P. aurisetus is found in its fruit, which characteristically splits across the apex, breaking the floral remnant. It also has very smooth seeds.

Two subspecies are distinguished as follows:

1. Plants to 2 m; branches 2.8-5.5 cm diam.; ribs 11-13; flower-bearing areoles with white hairs (Serra do Espinhoço)
2. Plants to 2 m; branches 4.5-7.0 cm diam., ribs 10-17; flower-bearing areoles with golden hairs (Serra do Cabral)

15a. subsp. aurisetus

VERNACULAR NAMES. Rabo-de-raposa, Quiabo-da-lapa, Quiabo-do-inferno, Cabeça-de-velho.

Shrub, 1-2 m; branches 2.8-5.5 cm diam., epidermis bluish to green; ribs 11-13, 5-6 x 9-11 mm. Areoles 2-4 mm diam., 4-6 mm apart, brown to blackish, slightly to densely hairy, hairs white. Spines 0.1-0.3(-0.35) mm diam. at base, white to golden yellow, centrals 5-7, 8-25(-30) mm, ascending to porrect, radials 12-16, 7-11 mm, adpressed. Fertile part of stem slightly differentiated, lateral or subapical, flower-bearing areoles with white hairs to

Widespread South-eastern campo rupestre element: quartzitic rock outcrops associated with campo rupestre, c. 650-1300 m, Serra do Espinhoço, central Minas Gerais. Endemic to the core area within Minas Gerais. Map 35C.


CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1x5) = 5.

The easternmost populations from Itamarandiba and Rio Vermelho (subsp. densilanatus (Ritter) P.J. Braun & E. Esteves Pereira) have densely woolly stems and at first seem rather distinctive, but on close examination do not differ sufficiently to merit recognition as an additional subspecies.


VERNACULAR NAME. Rabo-de-raposa.

Shrub, 1.5-3.0 m; branches 4–6 cm diam., epidermis olive-green, greyish, light blue waxy only at apex of branches; ribs 10–17, 4.5–7.0 x 9–10 mm. Areoles 3–6 mm diam., 4–6 mm apart, felt brownish, with white or yellowish long hairs to c. 5 mm, glabrescent when old. Spines 0.3–0.4 mm diam. at base, golden yellow, centrals 8–9, 10–25 mm, ascending to porrect, radials 14–16, adpressed, somewhat pectinate. Fertile part of stem lateral, with yellow to ferrugineous long hairs to 30 mm and golden bristles to 50 mm. Stigma-lobes c. 12, 5–12 mm. Fruit 3.5 x 3–4.3 cm; pericarp olive-green to wine-coloured; funicular pulp magenta. Seeds 1.8–2.0 x (1.3–)1.4–1.5 mm.

South-eastern campo rupestre (Serra do Cabral) element: locally co-dominant with other cacti on quartzitic rock outcrops, campo rupestre, 800–900 m, Serra do Cabral, Minas Gerais. Endemic to the core area within Minas Gerais. Map 37B.


CONSERVATION STATUS. Endangered (3) [criteria B1/2c]; area of occupancy estimated to be < 500 km²; PD=1, EI=2, GD=1. Short-list score (3x4) = 12. Known only from a small region without protected areas, the surrounding habitats being at risk from charcoal production activities.

Although it has a very restricted distribution and somewhat different habit, this taxon described by Ritter (1979) from the Serra do Cabral, a disjunct mountain range west of the Serra do Espinhaço, is not considered worthy of more than subspecific rank (Zappi 1994). It is linked to subsp. auriisetus via the form of the latter described under the synonym, P. supthutianus. The most striking feature of subsp. aurilanatus is its stouter, taller stems with dense, golden hairs on the flower-bearing areoles.


Shrubby, to 2 m, branched only at base; vascular cylinder weakly woody; branches 5–9 cm diam., erect, epidermis dark green, smooth; ribs (18–)20–24, 3–5 × 5–7 mm, sinuses straight, transverse folds not visible. Areoles 5 mm diam., 4–5 mm apart, felt white, with white long hairs to 10 mm, showing indeterminate growth near base of plant. Spines 0.3–0.4 mm diam. at base, translucent, golden to ferrugineous, sometimes bristly, centrals 8–16, 4–12–(18) mm, ascending to porrect, radials 14–16, 4–7–(12) mm, adpressed. Fertile part of stem weakly differentiated, flower-bearing areoles either lateral or forming rings around the branches, with sparse white long hairs and golden bristles to 50 mm. Flower-buds acute 5 days before anthesis; flowers 5 × 2–2.2 cm; pericarpel hemiglobose; tube 35 × 13 mm at base, flared to 15 mm diam. at apex, straight, terete, narrow, brownish, smooth; style 35 mm; stigmalobes c. 10, exserted in relation to the anthers; ovary locule hemicircular in longitudinal section. Fruit 20–26 × 20–28 mm, globose to depressed-globose, dehiscent by a lateral slit, floral remnant erect to pendent, deeply inserted; pericarp reddish to deep purple, smooth, shiny, with folds around base of floral remnant; funicular pulp white. Seeds 1.4–1.5 × 1–1.2 mm, hilum-micropylar region narrow, forming an angle of 60° with long axis of seed, testa-cells conic, periclinal walls much elongated, with intercellular depressions and coarse, dense cuticular folds.

Western cerrado element: amongst arenitic rocks in cerrado, c. 450–550 m, central Bahia, east bank of the Rio São Francisco. Endemic to Bahia. Map 35A.


**CONSERVATION STATUS.** Vulnerable (2) [criteria B1/2c]; area of occupancy estimated to be < 2000 km²; PD=2, EI=1, GD=1. Short-list score (2x4) = 8. Range poorly understood, but assumed to be more extensive than currently known habitat; if not, this taxon may merit a conservation category of Endangered in view of its small population size.

Characteristic of this species is its small, narrow, dark-brown flower and unusual seeds, with remarkably conic testa-cells and narrow hilum-micropylar region. The only other species of this group whose seeds show any similarity to those of *P. aureispinus* is *Pilosocereus vilaboensis* from Goiás. Furthermore, the seeds of a probable synonym of the latter, *P. rizzoanus* P. J. Braun & E. Esteves-Pereira (1992), seem to present intermediate characteristics. The population described as *P. rizzoanus* is also geographically intermediate, occurring half way between those of *P. vilaboensis* and *P. aureispinus*.

The peculiar testa of the seeds of *P. aureispinus* may be related to dispersal by ants, that are especially abundant in the cerrado where this plant occurs, the conic testa-cells perhaps representing an adaptation related to the transport of the seed. Indeed, some of the plants were actually seen growing on top of anthills.

Known only from east of the Rio São Francisco, near Ibotirama, this species inhabits arenitic rock outcrops in a phase of the cerrado and is sympatric with *Facheiroa squamosa* (Gürke) P. J. Braun & E. Esteves Pereira. However, it may be expected to occur elsewhere to the north and south in this little-botanized region.

**PILOSOCEREUS PIAUHYENSIS** Group (nos. 17–20)
Stems branched at base and above. Found on or amongst rocks in caatinga.


*Pseudopilocereus multicostatus* (Ritter) P.V. Heath in Calyx 4: 140 (1994).

Shrubby, 1.5–3.5 m, branched at base or above, without a well-defined trunk; vascular cylinder weakly woody; branches 3.8–7.5 cm diam., erect, epidermis dark green, shiny, smooth; ribs (15–)18–25(–26), 3–6 × 6–9 mm, sinuses straight, transverse folds not visible. Areoles 2–3 mm diam., 4–7 mm apart, felt white to greyish, without long hairs. Spines 0.15–0.40 mm diam. at base, translucent, golden yellow to brownish, centrals 3–7, 10–20 mm, ascending to porrect, radials 15–18, 5–10 mm, adpressed. Fertile part of stem not to slightly differentiated, flower-bearing areoles randomly distributed along the branches, mostly sub-apical, with long, flexible, golden, to 40 mm bristles, and sparse white to grey, long hairs. Flower-buds acute 1–3 days before anthesis; flowers 4.7 x 2.9–3.0 cm; pericarpel nearly globose; tube 25 x 8.5 mm at base, flared to 18 mm diam. at apex, straight, terete, pale green, smooth, apex with triangular bract-scales; style 24–26 x 1.5–1.0 mm, tapering; stigma-lobes c. 10, not extending beyond the anthers; ovary locule circular to hemicircular in longitudinal section. Fruit 2.2–2.5 x 2.5–3.0 cm, depressed-globose, dehiscent by an adaxial or abaxial slit, floral remnant pendent, deeply inserted; pericarp bright green tinged purplish, opaque, smooth; funicular pulp magenta. Seeds 1.5 x 1.2 mm, testa-cells domed, with intercellular depressions and coarse, sparse cuticular folds.

South-eastern caatinga (inselberg) element: on gneissic inselbergs amongst caatinga-agreste in the drainage of the Rio Lequitinhonha, c. 670–900 m, north-eastern Minas Gerais. Endemic to the core area within Minas Gerais. Map 33C.

**CONSERVATION STATUS.** Vulnerable (2) [criteria B1/2c]; extent of occurrence = 1703 km²; PD=2, EI=1, GD=1. Short-list score (2x4) = 8. Needs to be monitored in view of its restricted distribution and the destruction of natural vegetation surrounding its rocky habitat.

*Pilosocereus multicostatus* is characterized by the high number of ribs and golden, flexible spines, together with the slender and delicate flowers. The bristly flower-bearing areoles and its habit and ecology, on inselbergs in caatinga, recalls *P. chrysostele*, which presents strongly differentiated flowering-bearing areoles with abundant white hairs, and inhabits similar rock outcrops in Pernambuco, Paraíba, Rio Grande do Norte and Ceará.


Pilosocereus gaturianensis


CEARÁ: N Ceará, Serra de Mucóca, between Coreaú and Alicantaras, 20 Feb. 1995, Taylor (K, photos); Cent. & S Ceará, unlocalized, see synonym cited above.


CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1 x 5) = 5. Lower Risk, since most plants are inaccessible on steep rocky slopes.

Described by Gürke (1908) as Cereus piauhyensis, on the basis of material collected by Ule (Ule 09) at the Serra Branca, Piauí, its specific name was long misapplied to P. pachycladus, first by Britton & Rose (1920), who published Cephalocereus piauhyensis (Gürke) Britton & Rose, and later by Werdermann (1933), as Pilocereus piauhyensis (Gürke) Werdermann. Both authors had not seen true material of P. piauhyensis and confused it with what is now known as P. pachycladus Ritter subsp. pernambucoensis (Ritter) Zappi, a very widespread taxon from North-eastern Brazil. The same mistake is made in the illustrated work of Andrade-Lima (1989).

The recently described, but poorly localized, P. chrysostele subsp. cearensis, is surely a northern smaller-flowered form of this species rather than that to which it is referred by its authors. The critical characters, which place it within P. piauhyensis rather than P. chrysostele, are the lack of a cephalium, the slender flower-tube and the morphology of the dehiscent fruit.


**VERNACULAR NAMES.** Facheiro, Facheiro-de-serra, Rabo-de-raposa.

Shrubby, branching from the base upwards or only above and treelike with a trunk to 1.5 m or more, 1.5–60 m.; vascular cylinder weakly woody; branches 4–7 cm diam., erect, epidermis pale green, smooth; ribs 19–27, 5 × 5 mm, sinuses straight, transverse folds not visible. Areoles 2–3 mm diam., 4–5 mm apart, felt white to blackish, with part of stem weakly to strongly differentiated, the flower-bearing areoles occupying the lateral and subapical region 4 days before anthesis; flowers 4.5–6.0 × 3.7 cm; pericarpel hemiglobose; tube 33–35 × 17 mm at base, flared to 22 translucent, pale yellow, centrals 6–8, 5–12 mm, ascending to porrect, radials 9–12, 4–10 mm, adpressed. Fertile mm diam. at apex, constricted above and below the nectar-chamber, straight, slightly compressed, brownish green to white long hairs to 8 mm, growth indeterminate near base of branches.

Variable in stem thickness and rib number.


**RIO GRANDE DO NORTE:** ‘Sebastião-pólis’–Apodi, 11 July 1960, *Castellanos* 22633 (GUA); Mun. (?), between Lajes and Fernando Pedroso, reported by Braun & Esteves Pereira (1999a: 21); Mun. Currais Novos / Acari, beside road BR 427, S of Currais Novos, 6°23’S, 36°38’W, 1 April 2000, *E.A. Rocha et al.* (K, photo).


**CONSERVATION STATUS.** Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1×5) = 5. Lower Risk, since often occurring on steep, dry rocky hillsides where destruction of vegetation is less likely.
Pseudopilocereus densiareolatus (Ritter) P.V. Heath in Calyx 4: 140 (1994).

Pilocereus superfloccosus auctt. pro parte, non (Buin. & Brederoo) Ritter.]


VERNACULAR NAMES. Cabe9a-de-velho, Facheiro-da-Iapa.

Treelike, 2–5(–6.5) m, with a well-defined trunk; vascular cylinder weakly woody, pith wide; branches 3–7 cm diam., erect, epidermis olive-green to bluish, glaucous, smooth; ribs 13–22, 5–10 × 4–10 mm, sinuses straight, transverse folds not visible. Areoles 2.5–5.0(–6.0) mm diam., 2–6 mm apart, felt white to greyish with white long woolly plants on Bambui limestone outcrops in Minas Gerais. Endemic to the core area within Eastern Brazil. Map 26D.

Southern Rio São Francisco caatinga element: sometimes locally co-dominant with other arborescent cacti and other woody plants on Bambuí limestone outcrops in caatinga, c. 450–800 m, central northern Minas Gerais and western Bahia. Endemic to the core area within Eastern Brazil. Map 26D.


CONSERVATION STATUS. Lower Risk (1); PD=2, EI=2, GD=2. Short-list score (1×6) = 6. Lower Risk, but habitat liable to decline through limestone quarrying, so monitoring is desirable.

Variable in stature and extent of cephalium wool developed.

Probable hybrids with P. pachycladus subsp. pachycladus:
Shrubby to treelike; branches to 8 cm diam., epidermis bluish green; ribs 8–11, 10 × 8 mm. Areoles c. 5 mm diam., 3 mm apart. Spines 0.3–0.7 mm diam. at base, centrals 10(–35) mm. Fertile part of stem with brownish hairs to 8 cm.

BAHIA, Mun. Santana, 8 km from Porto Novo, 460 m, 16 Jan. 1991, Taylor et al. 1434 (K, HRCB, ZSS, CEPEC); 28 km S from Santana towards Santa Maria da Vitória, 530 m, 15 Jan. 1991, Taylor et al. 1427 (K, HRCB, ZSS, CEPEC).

MINAS GERAIS: unlocalized (W of Rio São Francisco), E. Esteves Pereira 223 (see synonym tentatively cited above); Mun. Varzelândia, 10 km N from the town, on road to Jaíba, 12 Aug. 1988, Eggli 1150 (ZSS).

**Conservation Status.** Not evaluated.

Braun & Esteves Pereira’s recently described species is referred as a putative, above, with little hesitation, since it characters are strongly suggestive of hybrid origin (NB. stem morphology, cephalium, flower form, fruit, seed size etc.), involving *P. pachycladus* and *P. densiareolatus*, the latter being reported as sympatric by the authors. *P. pachycladus* certainly also occurs in this region (see above).

*Pilosocereus densiareolatus* Ritter (1979) was described on the basis of populations inhabiting Bambuí limestone outcrops in central-northern Minas Gerais, which have flower-bearing areoles only moderately differentiated.

Northwards from Minas Gerais, the same species presents an increasingly well-developed lateral cephalium, with flower-bearing areoles immersed in the branches, and those populations have become known as *Pilosocereus superfloccosus* (Buin. & Brederoo) Ritter, described from W Bahia. This is, in fact, a misapplied name, since its protologue (cf. *Pseudopilocereus superfloccosus* Buining & Brederoo 1974a) clearly illustrates reproductive parts of *Pilosocereus gounellei* subsp. *zehntneri*, and the positively identifiable elements amongst its type material (U, holo.) consist of fragments of flower and fruit of *Pilosocereus gounellei* subsp. *zehntneri*, and none of *P. superfloccosus* as interpreted by most authors.

The problem of confusion between *P. densiareolatus* and *P. gounellei* subsp. *zehntneri*, is not an unusual one. Most material examined from these species was found to be mixed (Zappi 1994). Field study of such sympatric populations indicates that the arborescent *P. densiareolatus* only flowers when the branches are far away from the ground, ie. 2.5–4.0 metres high and, furthermore, the flowers are hidden in a hairy lateral cephalium. *P. gounellei* subsp. *zehntneri* has a shrubby to treelike habit, but produces flowers when less than 1 metre tall, its reproductive parts being much more accessible and obvious to collectors. Young plants of *P. densiareolatus* frequently look like *P. gounellei* subsp. *zehntneri*, but the branching pattern is completely different, being candelabrum for *P. gounellei* subsp. *zehntneri* and erect for *P. densiareolatus*, whose spination is also denser and finer. The examination of the apex of the fruits has proved to be the best character to differentiate them: *P. densiareolatus* has a deeply sunken, pendent floral remnant, typical of subgenus *Pilosocereus*, while *P. gounellei* subsp. *zehntneri* has fruits with rounded and superficially inserted floral remnants, characteristic of subgenus *Gounellea*. **
Insufficiently known taxa

1) The following names refer to a taxon treated as *incertae sedis* here (cf. Zappi 1994: 103; Ritter 1979: 64–65): *Pilocereus glaucescens* A. Linke (1858); *Cephalocereus glaucescens* (A. Linke) Borg; *Pilosocereus glaucescens* (A. Linke) Byles & Rowley; *Pseudopilocereus glaucescens* (A. Linke) F. Buxbaum; ‘Cereastreæ glaucescens’ Labouret (1853), nom. inval. (Art. 43.1); *Pilocereus coerulescens* Lemaire (1862), nom. illeg. (type as for above); *Pilosocereus coerulescens* (Lemaire) Ritter, nom. illeg. (The plant described by Lemaire under this illegitimate name originated from the Serra do Cipó, MG and is identifiable as *P. aurisetus*, q.v.) Being guided only by Labouret’s original description it is clear that the small plant he had before him could have represented any one of at least 3 Brazilian species, even assuming that his statement that it came from Brazil was correct. This plant was not preserved and it is futile to speculate further on its identity in the absence of a definite locality.

2) The recently described *Pierrebraunia brauniorum* E. Esteves Pereira in Kakt. and. Sukk. 50: 311–314 (1999) will likely remain a botanical mystery until the extreme secrecy displayed by its author (and his collaborator, Braun) about its geographical origin is overcome. Esteves Pereira gives away no more than to say that it emanates from high mountains in the Serra do Espinhaço of Minas Gerais (a mountain range more than 1000 km in extent) and inhabits an area where a decidedly improbable list of other cactus genera are said to grow (improbable in the sense that more than ten years of study of the cacti of Eastern Brazil by the present author has so far failed to reveal any instance where the genera *Facheiroa* and *Cipocereus* occur in proximity, especially since in Minas Gerais the former genus is restricted to limestone outcrops close to the Rio São Francisco, very far from the Serra do Espinhaço, where *Cipocereus* is found). The plant’s extraordinary combination of characters is unequaled and its stated rarity lends support to the idea, ventured here, that this is some sort of bizarre intergeneric hybrid, the likes of which are not unknown elsewhere in the family, eg. *Bergerocactus* with *Pachycereus* (*x*Pachgerocactus) and, separately, with *Myrtillocactus* (*x*Myrtgerocactus), from northern Baja California, Mexico. In the case of the vaingloriously named *Pierrebraunia brauniorum*, its combination of few-ribbed stems covered by a visibly roughened epidermis and small, deep pink, hummingbird syndrome, laterally-borne flowers tempts the suggestion that this is a hybrid between two genera of Cereeæ, the most plausible being a *Pilosocereus* (eg. *P. floccosus* subsp. *quadricostatus*) and either an *Arrojadoa* or a *Micranthocereus*, both of which are said to occur in the vicinity. However, until more is known, or revealed, about this plant, such comments amount to little more than idle speculation. Did it really emanate from a natural habitat, or is it a garden hybrid?
21. MICRANTHOCEREUS Backeberg


Columnar, erect, unbranched or more commonly shrublike but branched only at base; vascular cylinder rather to scarcely woody, cortical tissues mostly very mucilaginous; seedlings frequently densely hairy and juvenile to adult stages also with long, flexible, bristly hypotrophic spines at stem base (except in species nos. 1–3). Branches erect or decumbent, 3–10 cm diam. or more, not constricted, epidermis dull to bright green or glaucous; ribs 14–33, low, crenate, sinuses straight. Areoles with felt and long hairs; spines weak, flexible to brittle, not very pungent, central spines porrect to deflexed, longer than the numerous radials; indeterminate growth at basal areoles present, sometimes forming long curled bristles. Flower-bearing region of stem lateral or subapical, differentiated and sometimes forming a cephalium modifying the stem’s morphology. Flowers nocturnal or diurnal, when nocturnal strongly odoriferous, 15–42 x 5–32 mm; pericarpel smooth, naked, hemiglobose and often very clearly delimitated from the tube; tube broadened below, then cylindrical, white, greenish, yellowish, orange-red, pink or magenta, with broad bract-scales only near the apex; innermost filaments curved towards the style; perianth-segments triangular to lanceolate or spathulate, innermost white, yellowish, pinkish or purplish. Fruit obovate to turbinate, indehiscent, flower remnant drying brownish or black, erect, sometimes tardily deciduous, forming a broad scar at the fruit apex, but ± superficial; pericarp smooth, funicular pulp white or pinkish, solid. Seeds 1–1.7 mm, cochleariform or elongate; testa-cells flat or convex; cuticular folds present or absent.

The relationships of this endemic Brazilian genus within tribe Cereae are unclear, but fruits with non-impressed apex, ± superficial floral remnants and stems bearing lateral cephalia are found in *Pilosocereus* subg. *Gounellea* (cf. *P. gounellei* subsp. *zechntneri*) and *Coleocephalocereus*. Some species in the latter genus display hypertrophic spine growth at the base of stems as in the majority of *Micranthocereus* species, but their seeds differ in shape and in the position of the hilum region. A hybrid between *Pilosocereus* (subg. *Pilosocereus*) *pentaedrophorus* and *M. purpureus* has been recorded from two distant sites at the eastern margins of the Chapada Diamantina, Bahia and implies that these two genera may be closely related.

The 8 species treated here are all very distinct, though nos. 2 & 3, 4 & 5, and 6 & 7 may represent vicariant species-pairs. Nos. 1–7 are *campo rupestre* taxa (see Map 41), while no. 8 is found amidst caatinga forest on limestone outcrops. A ninth species closely related to no. 8 occurs on Bambuí limestone outcrops around the Serra Geral de Goiás, from southern Tocantins and Goiás to north-western Minas Gerais (*M. estevesii* (Buin. & Brederoo) Ritter). Two of the species are single-site endemics (nos. 4 & 5) and three more are known from very small areas (nos. 1, 6 & 8) and thus their conservation status needs to be carefully monitored.

1. Plants 0.3–2.5(-3.0) m, suffrutescent or with solitary inclined stems, vascular cylinder not woody, or, if woody, ribs 14–17; seeds cochleariform (crystalline rocks and sandstones, *campo rupestres*, Serra do Espinhaço and Chapada Diamantina)
2. Plants to > 3 m, maturing when > 1.2 m, solitary, erect with very woody vascular cylinder; ribs 21–30 or more; fruits drying inside the cephalium; seeds with the hilum border expanded into a wing (Bambuí limestone, SW Bahia) 8. dolichospermaticus
1. Flowers > 30 x 20 mm, anthesis predominantly nocturnal 3
2. Flowers slender, < 25 x 11 mm, anthesis diurnal 4
3. Ribs 23–29(-32); cephalium wool white to yellowish; epidermis bright green; flowers greenish or pinkish white outside (Serra do Espinhaço, N Minas Gerais and southernmost Bahia) 2. albicephalus

3. Ribs 10–26; cephalium wool pale brown, with pinkish or grey shades; epidermis grey-green or glaucous; flowers deep magenta outside (Chapada Diamantina, Bahia) 3. purpureus

4. Stem solitary; floral remnants strongly blackened; central spines and bristles of flower-bearing areoles dark red to brown; ripe fruits green; vascular axis of stem woody; seeds black (N Minas Gerais: Serra da Bocaina & Serranópolis) 1. violaciflorus

4. Stems branched at base; floral remnants pale brown, not blackened; spines and bristles of flower-bearing areoles mostly golden or pale yellow; ripe fruits red or pinkish; vascular cylinder of stem not woody; seeds brownish 5

5. Flowers 15–18 mm, outer and inner perianth-segments of contrasting colours; stems 3–5.5 cm diam., erect to ± inclined or decumbent 6

5. Flowers 20–25 mm, perianth-segments ± concolorous or innermost paler; stems 5.5–7.0 cm diam., erect 7


6. Flowers pale purplish with pale cream or white inner perianth-segments (S Bahia: Mun. Caitité) 6. polyanthus

7. Fertile part of stem not sunken, wool white or greyish (near Grão Mogol, Minas Gerais) 4. auriazureus

7. Cephalium sunken, wool golden or brownish (W of Seabra, Bahia) 5. streckeri

Subg. Austrocephalocereus (Backeb.) P. J. Braun & E. Esteves Pereira (nos. 1–3): Stems woody or lacking well-developed wood, erect and branched at base or solitary and then often inclined, 0.7–2.0(-3.0) m high, with a ± sunken, and sometimes discontinuous cephalium; lacking hypertrophic spine development at stem base; flowers diurnal and/or nocturnal; fruit with persistent, blackened perianth remains; seeds black, testa-cells with ± convex periclinal walls and cuticular sculpturing. Endemic to the core area within Eastern Brazil and characteristic of the Northern campos rupestres.


Solitary, rarely branched at base, to 1 m high; vascular cylinder very woody. Stems erect to inclined, 3.5–4.0 cm diam.; ribs 14–17, 2 × 3–5 mm; epidermis green. Areoles 2 mm, to 3 mm apart, long hairs white to grey. Spines flexible, pale golden to golden brown, reddish or dark brown, central spines 6–8, longest one to 25 mm, radials 25–30, 5–15 mm. Fertile part of stem lateral, sunken, flower-bearing areoles with abundant, loose white hairs and long reddish or dark brown bristles to 3 cm. Flowers poorly known, 23 × 7 mm, diurnal, tube violet or pinkish red, perianth-segments deep pink, spreading to erect. Fruit obovate, truncate at apex, 11 × 9 mm, flower remnants black, pericarp smooth, dull, green. Seeds c. 1 mm, cochleariform, black; testa-cells weakly convex, with cuticular folds.

Northern campo rupestre (N Serra do Espinhaço) element: amongst rocks at c. 900–1100 m, Serra da Bocaina and Serranópolis, northern Minas Gerais. Endemic to the core area within Minas Gerais. Map 29.


CONSERVATION STATUS. Critically Endangered (4) [criteria B1/2c]; PD=2, EI=1, GD=1. Short-list score (4×4) = 16. Will be under increased threat if charcoal producers move into the very restricted area where it occurs. Needs regular monitoring.
This rare species is characterized by a suite of presumably plesiomorphic character states (a rather woody vascular axis, only moderately mucilaginous stem tissue, absence of hypotrophic spines at stem base, green pericarpel, strongly blackening, persistent perianth remnants and black seeds with intercellular pits), which suggest that its phylogenetic position within *Micranthocereus* is basal. It has most characters in common with Subg. *Austrocephalocereus*, but its small seeds are closer to those of Subg. *Micranthocereus*. It seems to be a relictual species, occupying a restricted habitat in a small area in the northern half of the Serra do Espinhaço (MG).


Shrubby, to 0.5–2.5(-3.0) m, branched mainly at base; vascular cylinder not woody. Stems erect, 6–8.5 cm diam.; ribs 23–29(-32), 5 × 6.5 mm; epidermis bright green. Areoles 3–4 mm apart, long hairs white to grey. Spines flexible to brittle, golden, showing only weak indeterminate growth at basal areoles, central spines to 12, to 10 mm, radials 15–18, 5–15 mm, the lowermost slightly longer. Fertile part of stem lateral, sunken into the stem, flower-bearing areoles with abundant, white, compact hairs and long golden bristles to 6.5 cm. Flowers 45–50 × 26 mm, nocturnal; pericarpel 4–5 × 9 mm, whitish to cream; tube 27–30 × 10–25 mm, broadened at base, constricted at the middle, white or pale green with pink shades, with broad bract-scales only at apex; perianth-segments 10 × 3.5–5.5 mm, triangular to lanceolate, outer segments spreading to recurved, white, brown to magenta-pink at tips, inner segments spreading, white, pinkish to reddish brown at tips; stamens included in relation to the perianth-segments; nectar-chamber 7 × 8 mm; style 32 mm, stigma-lobes c. 8, exserted; ovary locule 3–4 × 4–5 mm, obtriangular in longitudinal section. Fruit broadly turbinate, 3.5 cm diam., flower remnants strongly blackened; pericarp smooth, shiny, dark green to wine-coloured. Seeds 1.5–1.7 mm, cochléariform, black; testa-cells convex, with cuticular folds.

Northern campo rupestre element: between crystalline rocks and on cliffs in campo rupestre, c. 800–1000 m, Serra do Espinhaço (Serra Geral) northern Minas Gerais and adjacent southernmost Bahia. Endemic to the core area of Eastern Brazil. Map 29.

**CONSERVATION STATUS.** Vulnerable (2) [criteria B1/i2e]; area of occupancy estimated to be < 2000 km²; PD=2, EI=1, GD=3. Short-list score (2×4) = 8. Vulnerable due to its limited range and generally small population size.

This is the southern sister species of the following.
Shrubby, 0.6–2.5(–3.0) m, branched at base; vascular cylinder not woody. Stems erect, 4.5–10.0 cm diam.; ribs 12–26, rarely only 10 when immature, 4–5 × 8–9 mm; epidermis blue-green to strongly glaucous. Areoles 3–4 mm, to 6–8 mm apart, long hairs pale brown to grey. Spines flexible to brittle, golden or reddish, brown when old, showing only weak indeterminate growth at basal areoles, central spines 4–7, to 20(–25) mm, radials 20–25, to 10 mm. Fertile part of stem lateral, sunken into the stem, flower-bearing areoles with pale brown, pinkish or greyish, abundant, loose or compact hairs and few long golden or brownish bristles to 4 cm. Flowers 42 × 30–32 mm, partially opening at late afternoon, fully expanded at night; pericarpel 8 × 12 mm, whitish to pale pink; tube 20–25 × 20–25 mm, broadened at base, slightly constricted at the middle, deep pink-magenta, with broad bract-scales only at apex; perianth-segments 9–11 × 6–9 mm, triangular to lanceolate, outer segments recurved, deep pink to reddish, inner segments spreading to recurved, white; stamens included in relation to the perianth-segments; nectar-chamber 7 × 8 mm; style 25–28 mm, stigmas lobes c. 10, exserted; ovary locale 4–6 × 5–6 mm, obtriangular in longitudinal section. Fruit broadly turbinate, 1.7–2.0 cm diam., flower remnants brown, not blackened, pericarp smooth, shiny, purplish pink. Seeds 1.5–1.7 mm, ellipsoid, black; testa cells convex, with cuticular folds.

Northern campo rupestre (Chapada Diamantina) element: on crystalline rocks in campo rupestre and its ecotones with caatinga and cerrado, c. 350–1900 m, eastern flanks and highest peaks of the Chapada Diamantina. Endemic to Bahia. Map 29.


CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1×5) = 5.
The name *Cephalocereus purpureus* was misapplied to what is now known as *Coleocephalocereus goebelianus* by Britton & Rose (1920) and Werdermann (1933), the latter redescribing the true *C. purpureus* as *C. lehmannianus*. Lützélburg (1925, 1: fig. 38) illustrated the true *M. purpureus* as 'Pilocereus na caatinga' and commented in the caption that it was always accompanied by *Cereus leucostele* (= *Stephanocereus leucostele*), which is not the case. He was evidently confusing it with *C. goebelianus* at this stage (however, cf. Lützélburg 1926, 3: 69). The true identity of *M. (Austrocephalocereus) purpureus* was recognized by Ritter (1968) and Buining (1975).

*M. purpureus* is the most wide-ranging and variable species in the genus and a characteristic element of the campo rupestre flora in the higher and eastern parts of the Chapada Diamantina, where it is constantly associated with *Stephanocereus luetzelburgii*. It hybridizes with *Pilosocereus pentaedrophorus* near Andarai and Ituçu.

Subg. *Micranthocereus* (nos. 4–7): Stems never woody, branched at base, erect or semi-sprawling, 0.3–1.2 m high, with a superficial to sunken, and sometimes discontinuous cephalium and hypertrophic spine development at stem base; flowers diurnal; fruit with tardily deciduous, non-blackening perianth remains; seeds brown to brown-black, testa-cells with nearly flat periclinal walls lacking cuticular sculpturing. Endemic to the core area within Eastern Brazil and characteristic of the Northern and South-eastern campos rupestres.


**VERNACULAR NAME.** Rabo-de-raposa.

Shrubby, to 1.2 m, much branched at base; vascular cylinder not woody. Stems erect, 6–7 cm diam.; ribs 15–19, 5 × 8–9 mm; epidermis blue-green, glaucous. Areoles 3–7 mm, to 4 mm apart, long hairs white to grey. Spines flexible to brittle, golden, showing indeterminate hypertrophic growth at basal areoles, forming long curled bristles, central spines to 6, 2–3(–8) cm, radials 25–30, 5–15 mm. Fertile part of stem lateral, superficial, flower-bearing areoles with white hairs and long bristles to 4(–8) cm. Flowers 20–25 × 10–11 mm, diurnal; pericarpel 2.5 × 5 mm, brownish to pale pink; tube to 16 × 7–9 mm, broadened at base, constricted at the middle, deep magenta pink, with broad bract-scales only at apex; perianth-segments 4–7 × 2.5–3.5 mm, triangular to lanceolate, outer segments spreading, magenta-pink, inner segments erect to spreading, lilac-pink; stamens included in relation to the perianth-segments; nectar-chamber 8 × 5–6 mm; style 15–19 mm, stigma-lobes c. 8, exserted; ovary locule 3–4 × 2–3 mm, obtriangular in longitudinal section. Fruit obovate, truncate at apex, 1.8 × 1.4–1.6 cm, flower remnants pale brown, deciduous when fruit ripe, pericarp smooth, dull, pale pink to reddish. Seeds c. 1.5 mm, cochleariform, brown, shiny; testa-cells flat to convex, without cuticular folds.

South-eastern campo rupestre (Grão Mogol) element: between crystalline rocks and in quartz sand, c. 750–1000 m, Serra do Barão and vicinity, northern Minas Gerais. Endemic to the core area within Minas Gerais. Map 36C.


**CONSERVATION STATUS.** Vulnerable (2) [criteria D2]; area of occupancy estimated to be < 100 km²; PD=2, EI=1, GD=1. Short-list score (2x4) = 8. Vulnerable due to its very restricted distribution, but part of this is inside a recently created reserve.
According to the list in Uebelmann (1984) and the label on the type specimen at Utrecht, the type collection of *M. auriazureus* is HU 346, and the name should be considered legitimate, since it is clear that HU 348 was cited erroneously as its holotype in the protologue (HU 348 is the type number for the prior-published *M. albicephalus*, q.v.).


Shrubby, to 0.8 m, densely branched at base. Stems erect, 3–5(-5.5) cm diam., vascular cylinder not woody; ribs 17–24(-25), 2–3 x 6–8 mm; epidermis grey-green, slightly glaucous. Areoles 2–3 mm, to 5 mm apart, with white to grey trichomes. Spines flexible, pale golden, hypotrophic growth of spines at basal areoles present, central spines 6–8, spreading, lowermost longest, to 25 mm, radials 20–30, 5–10 mm. Fertile part of stem lateral, superficial to sunken, flower-bearing areoles with compact white to brownish hairs and long pale golden to reddish brown bristles to 30 mm. Flowers 40–50 x 22 mm, diurnal; pericarpel 3.5 x 3.5 mm, pale pink; tube to 18 x 3–5 mm, broadened at base, cylindric above, deep pink, with bract-scales only at apex; perianth-segments 4–5 x 2.5 mm, triangular to lanceolate, outer segments spreading, deep pink, inner segments erect, purplish pink; stamens included in relation to the perianth; style 13–15 mm, stigma-lobes 5–6, included; ovary locule 2 x 2.5 mm, obtriangular in longitudinal section. Fruit obovoid, 11 x 10 mm, floral remnants pale brown, deciduous; pericarp smooth, dull, purplish. Seeds c. 1.2 mm, cochlleariform, blackish, shiny; testa-cells flat to convex, without cuticular folds.

Northern *campo rupestre* (Chapada Diamantina) element: in the *campo rupestre / cerrado de altitude* ecotone, c. 1100 m, west of Seabra, central Bahia. Endemic. Map 29.

**CONSERVATION STATUS.** Critically Endangered (4) [criteria B1/I2c]; PD=2, EI=1, GD=1. Short-list score (4x4) = 16. Critical due to its very restricted distribution, small population size (< 50 individuals seen) and potential for alteration of its habitat.

This species is poorly understood, being known from only the locality cited above where it appears to be undergoing introgression with the sympatric *M. purpureus*, making assessment of its typical morphological state rather difficult. Specimens which the author interprets to be least influenced by this introgression show a certain resemblance to the geographically distant *M. auriazureus* (Grão Mogol, MG), but have sunken cephalia and darker seeds.


Shrubby, to 1.2 m, much branched at base; vascular cylinder not woody. Seedlings with abundant white hairs and long curled, hypertrophic bristles at base. Stems erect, 3.5–5.0 cm diam.; ribs 15–20, 4–5 x 3–6 mm; epidermis grey-green, glaucous. Areoles 2–4 mm, to 10 mm apart, long hairs white to grey. Spines flexible, pale golden, showing indeterminate growth at basal areoles, forming long curled bristles, central spines 4–8, to 15 mm, radials
20–28, 5–10 mm. Fertile part of stem lateral, superficial to slightly sunken, flower-bearing areoles with abundant, loose white hairs and long, pale golden bristles to 20 mm. Flowers 18 × 7–8 mm, diurnal; pericarpel 2 × 3 mm, pale pink; tube to 16 × 5–6 mm, broadened at base, constricted at the middle, coral red to pale pink, with broad bract-scales only at apex; perianth-segments 4–5 × 1–2 mm, triangular to lanceolate, outer segments spreading to erect, coral red to reddish pink, inner segments opening very slightly, pale cream to white; stamens included in relation to the perianth-segments; style 13–15 mm, stigma-lobes c. 8, included; ovary locule 1–2 × 1.5–2.0 mm, obtriangular in longitudinal section. Fruit obovate, truncate at apex, 5–7 × 5 mm, flower remnants pale brown; pericarp smooth, dull, pale pink. Seeds c. 1 mm, cochleariform, dark brown, shiny; testa cells flat to convex, without cuticular folds.


**CONSERVATION STATUS.** Vulnerable (2) [criteria D2]; area of occupancy estimated to be < 100 km²; PD=2, EI=1, GD=1. Short-list score (2×4) = 8. Vulnerable, due to its restricted distribution and mining activities.

In its overall appearance, but especially in habit, soft stems, superficial cephalium and bicoloured flowers, it may be the southern sister species of the following.


Shrubby, 30–100 cm, much branched at base; vascular cylinder not woody. Stems partly decumbent, 4–5 cm diam.; ribs 12–16, 3–5 × 5–7 mm; epidermis grey-green, glaucous. Areoles 2–3.5 mm, to 3 mm apart, long hairs white or cream to grey. Spines flexible, golden, sometimes reddish, showing indeterminate hypertrophic growth at basal areoles, forming long curled bristles, central spines 4–8, 10–25 mm, radials 20–25, 10–12 mm. Fertile part of stem lateral to apical, superficial, flower-bearing areoles with loose white to yellowish hairs and long pale to brownish golden bristles to 2.5 cm. Flowers 14–18 × 5–8 mm, diurnal; pericarpel 2 × 2.5–3.0 mm, pale pink; tube to 12 × 4–6 mm, broadened at base, constricted at the middle, orange-red, with bract-scales only at apex; perianth-segments 2–4 × 1–3 mm, triangular to lanceolate, outer segments spreading to erect, orange-red to reddish pink; inner segments opening very slightly, yellow to pale cream; stamens included in relation to the perianth-segments; style 10–12 mm, stigma-lobes 4–6, included; ovary locule 1.5 × 1.8–2.0 mm, obtriangular in longitudinal section. Fruit obovoid to globose, truncate at apex, 5–8 × 5–8 mm, flower remnants pale brown, deciduous; pericarp smooth, dull, red to reddish pink. Seeds c. 1–1.5 mm, cochleariform, blackish, shiny; testa-cells flat to convex, without cuticular folds.

Northern *campo rupestrae* (Chapada Diamantina) element: in the *campo rupestrae* / *caatinga* ecotone on sandstone, c. 700–1130 m, northern and western flanks of the Chapada Diamantina (northwards from the region west of Morro do Chapéu), northern Bahia. Endemic. Map 29.


Conservation Status. Vulnerable (2) [criteria BI/2c]; extent of occurrence = 1024 km²; PD=2, EI=1, GD=2. Short-list score (2×5) = 10. Area of occupancy unknown, but assumed to be <30% of extent of occurrence.

The distribution of this species seems somewhat disjunct, but the region between its northern and southern sites has been little explored. However, this includes extensive areas of limestone and derived calcareous soils, which would not suit it and thus it is almost certain that its distribution is highly fragmented, justifying the 'Vulnerable' conservation status accorded here. It is variable between populations, as the above synonymy indicates.

Subg. Siccobaccatus (P. J. Braun & E. Esteves Pereira) N. P. Taylor (no. 8): Stems normally unbranched above ground unless damaged, forming erect, very woody columns to 5 m or more, with hypertrophic spine development at base when young; cephalium deeply sunken, continuous; flowers nocturnal; seeds slender elongate (for wind dispersal) or with many, small testa-cells. Limestone outcrops west of the Rio São Francisco.


Solitary, fertile from c. 1.2 m, reaching more than 3 m, unbranched above ground, but sometimes sprouting at the base (when damaged?) and forming a compact group of erect stems; vascular cylinder very woody. Seedlings with spines curved upwards and long, curled, hypertrophic bristles at base. Stems erect, 8–12 cm diam.; ribs 21–30(-32), 10–20 x 10–22 mm, in cephalium region 12 x 13 mm; epidermis blue-green, glaucous. Areoles 3–5 mm, to 2–6 mm apart, long hairs white to grey, to 3 cm. Spines hard, brittle, golden to brown and black when old, indeterminate growth at basal areoles present, central spines 4–7, to 15 mm, radials 8–12, to 5 mm. Fertile part of stem lateral, sunken into the stem, flower-bearing areoles with white to pale yellow, abundant, compact hairs and long brownish or reddish bristles to 4 cm. Flowers 4 x 2.5 cm, nocturnal, all white or cream-coloured; pericarpel 5 x 11–12 mm; tube 35–38 x 12–18 mm, slightly constricted at the middle, with broad bract-scales only at apex; perianth-segments 9–11 x 6–9 mm, triangular to lanceolate, outer segments recurved, inner segments spreading; stamens included in relation to the perianth-segments; nectar-chamber 10 x 9–10 mm; style 32–36 mm, stigma-lobes 8–9, exserted; ovary locule 4–5 x 2 mm, depressed in longitudinal section. Fruit broadly turbinate, 9–10 mm diam., flower remnants pale brown; pericarp dry, brownish, wrinkled. Seeds 2 mm, elongate, brownish; testa-cells flat, hilum depressed.

Southern Rio São Francisco caatinga element: on Bambui limestone outcrops surrounded by caatinga or forest with caatinga elements, c. 450–650 m, west of the Rio São Francisco, south-western Bahia. Endemic to Bahia. Map 27B.

CONSERVATION STATUS. Vulnerable (2) [criteria B1/2b–c]; area of occupancy estimated to be < 2000 km²; PD=2, EI=1, GD=1. Short-list score (2×4) = 8. Vulnerable from the destructive collection of seeds and also potentially from the quarrying of limestone.

The peculiar, slender-elongate seeds of this species are assumed to be an adaptation for wind dispersal (W. Barthlott, pers. comm.).

This species, whose geographical range is poorly understood, may be more threatened than the 'Vulnerable' category assigned here due to the destructive felling of mature individuals by seed-collectors operating to satisfy the demand for the production of the attractive seedlings in Europe, North America and elsewhere.

It is closely related to *M. estevesii* (Buining & Brederoo) Ritter, the only member of this genus occurring outside the geographical area treated here (NW Minas Gerais to S Tocantins).
A genus of 6 well-defined species (plus 2 heterotypic subspecies), all native to Eastern Brazil (5 endemic to the core area) and ranging between the caatinga (3 taxa) and Mata atlântica (5 taxa) regions (cf. Porembski et al. 1998: 116), almost exclusively on or closely associated with gneiss/granite inselbergs (C. goebelianus rarely on other substrates). The genus, though small, is divisible into 3 allopatric subgenera, recognized on the basis of seed-morphology, presence/absence of stem mucilage, spination and floral pollination syndrome.

Although there is currently little disagreement over the circumscription of the genus, Coleocephalocereus names have also been published for species here referred to Cipocereus, Stephanocereus, Pilosocereus, Micranthocereus and Espostoopsis.

1. Flowers nocturnal, expanding fully, white within; seeds verrucose, testa-cells domed; ribs with (rarely without) transverse folds above the areoles
  2. Spines > 16 per areole, some strongly hooked in seedlings, lacking hypertrophic spination at ground level; stem tissues non-mucilaginous (cent.-N Minas Gerais & S Bahia) 4. goebelianus
  3. Stems with long, hypertrophic spines near base, vascular cylinder rather woody; cephalium bristles golden yellow at least when young, more conspicuous than the wool 1. buxbaumianus
  3. Stems lacking hypertrophic spines near base, vascular cylinder scarcely woody; cephalium bristles brownish, or yellow but less conspicuous than the abundant white wool
  4. Flowers c. 30–60 mm; cephalium bristles mostly yellowish or porrect, intermixed with abundant whitish wool; stem 6–19-ribbed 2. fluminensis
  4. Flowers c. 19–35 mm; cephalium bristles dark brown and adpressed, not intermixed with wool; stem 12–34-ribbed 3. pluricostatus
  5. Flowers yellow-green; seeds c. 1.35 mm; spines yellowish 5. aureus
  5. Flowers magenta; seeds c. 1.75 mm; spines reddish brown 6. purpureus
Subg. Coleocephalocereus (nos. 1–3): stems short to tall (0.5–5.0 m), branched at or above base or solitary, tissues mucilaginous; ribs often with transverse epidermal folds above the areoles; spines finely needle-like; flowers nocturnal, whitish at least within; seeds with strongly convex testa-cells, these ornamented with characteristic, crown-like, cuticular folds encircling each convex periclinal wall (SEM), hilum ± broad. E & S Minas Gerais and adjacent Espírito Santo (drainage of Rios Mucuri and Doce southwards); Rio de Janeiro and off-shore islands of São Paulo.


VERNACULAR NAMES. Mandacaru-de-topete, Facheiro-das-pedras.

Stems solitary or branched at or near base, erect from the rootstock or the basal parts decumbent on the rock surface and the apical parts slightly inclined, to 220 × 5–13 cm. Ribs 14–36, 5–10 mm high and 10–15 mm wide, ± tuberculare, with prominent folds above the areoles, epidermis dark green, shiny. Areoles 1.5–7.0 × 1.5–5.0 mm, 6–13 mm apart, with pale yellowish to brownish, later greyish felt, displaying very strong indeterminate growth on basal half of stem. Spines finely needle-like, yellow, golden or partly brownish at first, later pale greyish to black, c. 10–25 per areole above the stem base, central and radial spines weakly differentiated, centrals (0–)3–6(–9), 8–40 mm, radials 7–18, to 28 mm, basal areoles with abundant, sinuate, hypertrophic spines to 400 mm or more. Cephalium rather broad, sometimes as wide as the stem, with dense, golden bristle-spines to 60 mm, wool inconspicuous except near stem apex, bristle-spines blackish when old. Flowers (25–)30–75 × 23–40 mm, brownish to greenish white when in bud; pericarpel 3–6 × 5–9 mm, with or without small bract-scales, tube 20–50 × 10–13 mm at apex, bearing few, 2–11 × 0.2–2.0 mm bract-scales; nectar-chamber c. 7–12 × 6–7 mm; outer perianth-segments 7–17 × 3.5–6.0 mm, whitish with reddish, brownish or greenish apex and mid-stripe, inner segments 8–20 × 3.5–6.0 mm, acuminate, white; stamens 8–20 mm, white; style 18–60 mm, stigma-lobes c. 8–10, to 5 mm, pale yellow to whitish; ovary locule 1–5 × 2–6 mm. Fruit 18–35 × 10–22 mm, often somewhat laterally compressed or channelled, blood-red to shocking pink at apex, deep or paler pink below, whitish near the basal pore, floral remnants whitish near base, darker to blackish above. Seed c. 1.3–1.8 × 1–1.4 mm.

Two subspecies are recognized, subsp. buxbaumianus replacing subsp. flavisetus at the eastern edge of the species’ range, which is poorly recorded due to the inaccessibility of many of its inselberg habitats:

1. Stems 5–8 cm diam., branching freely from the decumbent bases, forming loose, sprawling clumps; flowers c. 25–42 × 25 mm (NE/E Minas Gerais and Espírito Santo, E of 42°W) 1a. subsp. buxbaumianus

1. Stems 7–13 cm diam., solitary and erect or forming small compact clusters; flowers c. 50–75 × 30–40 mm (SE & SW Minas Gerais, W from 42°W) 1b. subsp. flavisetus

1a. subsp. buxbaumianus

Southern humid/subhumid forest (inselberg) element: locally co-dominant with other cacti on gneissic inselbergs / lajedos, 100–700 m, eastern Minas Gerais and western Espírito Santo (Rio Doce drainage). Endemic to the core area within South-eastern Brazil. Map 16D.


CONSERVATION STATUS. Lower Risk (1); PD=1, EI=2, GD=2. Short-list score (1×5) = 5. Although the vegetation around the inselbergs where this taxon occurs has largely been destroyed, the actual habitat of the plant is less affected. However, disturbance is likely to increase and so monitoring of its status is essential.

The presence of abundant, long, basal hypertrophic spines in this taxon may have a moderating influence on the plant’s temperature near to the sun-baked rock surface (Porembski et al. 1998: 115, fig. 6). It is quite variable in stature and spination.


Ribs 18–36. Cephalium to 13 cm wide. Fruit bearing minute bract-scales.

Southern humid/subhumid forest (inselberg) element: on gneissic inselbergs / lajedos, 100–1000 m, south-eastern and south-western Minas Gerais (disjunct). Endemic to the core area within Minas Gerais. Map 16D.


CONSERVATION STATUS. Vulnerable (2) [criteria B1/2c]; area of occupancy estimated to be < 2000 km²; PD=1, EI=1, GD=2. Short-list score (2×4) = 8. More secure in the eastern sector of its range, especially where it occurs on larger, steep-sided inselbergs, but probably endangered in the west, where mining operations have destroyed much of its habitat. By no means a common plant.

The eastern part of the range of this species is mostly within the drainage of the Rio Doce in a region of relatively low rainfall (< 1000–1250 mm/yr, cf. map ‘isoietas anuais 1914–1938’ in Azevedo 1972; Nimer 1973: 40, fig. 18), where there is a mixture of Mata Atlântica and caatinga-like vegetation (Lützelburg 1926, 2: 112–115). The following two species are also found in this region, but range further south into wetter areas. They have not yet been found truly sympatric with C. buxbaumianus, but occur in very close proximity.


Stems solitary or more commonly branched from the decumbent basal parts, erect above or inclined towards the rock surface, to 2 m high and > 300 × (3.5–)4.0–12.0 cm; ribs (5–)6–16(–19), ± triangular in cross-section, to 16 mm high and 10–30 mm wide, with ± well-defined folds above the areoles, epidermis light to dark, shiny green or greyish green. Areoles 1–4 mm, to c. 8 mm apart, with white to greyish felt at first, indeterminate growth weak. Spines mostly few, 1–6, to 40 mm, finely needle-like, rarely stouter, whitish, yellowish or darker, central and radial spines poorly differentiated, the former 0–3, the latter 0–13. Cephalium mostly no more than half the stem's diameter, composed of abundant white wool interspersed with yellow or more rarely brownish bristle-spines, these straight or curved, to 30 mm. Flowers 30–60 × 20–40 mm; pericarpel c. 4 × 5–7 mm, tube 25–40 × 8–15 mm, with few narrow bract-scales, the uppermost to 7 × 2.5 mm; nectar-chamber 8–17 × 4–7.5 mm; outer perianth-segments c. 12–20 × 3.5–6.0 mm, greenish brown, purplish pink or creamy yellow, inner segments to 15 × 2.5–6.0 mm, white; stamens to 25 mm; style to 53 mm; stigma-lobes 8–15, to 6 mm, pale yellow. Fruit 15–26 × 13–20 mm, red, paler towards base. Seed 1.25–1.50 × 1.0 mm.

The following subspecies are distinguished:

1. Stem erect except near base, to 12 cm diam. (southwards from border region between E Minas Gerais and SE Bahia)  

2a. subsp. *fluminensis*  
2b. subsp. *decumbens*

2a. subsp. *fluminensis*

Ribs to 16(–19), epidermis light to dark shiny green. Spines all finely needle-like, mostly pale yellow to greyish white, rarely partly brownish. Cephalium bristle-spines slender hairlike, mostly pale.

Southern humic/subhumid forest (inselberg) element: locally dominant on gneissic inselbergs or *lajedos* within the *Mata atlântica* and restinga zones, near sea level to c. 900 m, north-eastern (MG/BA border region) to south-eastern Minas Gerais (border region between MG and ES/RJ) and Espirito Santo; Rio de Janeiro and off-shore islands of São Paulo (to Ilha Queimada Grande). Map 16C.

MINAS GERAIS: Mun. Nanaque, 1994, S. Porembski et al. (K, photos); Mun. Serra dos Aimorés, c. 8 km E of Nanaque on road to state border (BA), 1994, S. Porembski et al. (K, photo); (?) Mun. Mantena, near frontier.


RIO DE JANEIRO: Mun. (?), between Muriaé (MG) and Itaperuna, Uebelmann (mss.).

CONSERVATION STATUS. Lower Risk (1); PD=1, EI=2, GD=2. Short-list score (1x5) = 5.

This subspecies is very variable in size, habit, rib number, cephalium colour etc., and especially so near the northern limits of its range, but apart from this the variation does not seem to show any obvious geographical pattern that would allow its division into additional subspecies, nor does there seem to be any point in naming every local form. It is sometimes sympatric with C. pluricostatus.


Stem to c. 6 cm diam.; ribs to 13, epidermis dark or grey-green. Spines stout, stiff, dark brownish at first. Cephalium bristle-spines stiff, dark brown.

Southern humid/subhumid forest (inselberg) element: locally dominant on gneissic inselbergs/lajedos, in the agreste / Mata atlântica transition, c. 650 m, north-eastern Minas Gerais. Endemic to the core area within Minas Gerais. Map 16C.


CONSERVATION STATUS. Endangered (3) [criteria B1/2c]; extent of occurrence = 91 km²; PD=1, EI=2, GD=1. Short-list score (3x4) = 12. Endangered from urban expansion at its extensive type locality, but range probably under-recorded.

The range of this taxon in north-eastern Minas Gerais is not well understood and more field studies are needed in the area between Padre Paraíso (MG) and the Rio Doce in Espírito Santo (eg. municípios Nova Venécia and Pancas), where plants intermediate with subsp. fluminensis have been observed and collected. At the type locality it is represented by a relatively uniform
population occupying an area some kilometres in extent. It appears sufficiently distinct to warrant subspecific status at present, but may well prove to be of lesser significance once the variation of the species as a whole is better known.


Stem an unbranched, erect, solitary column or branched from the decumbent base, 100–500 × 7.5–11.0 cm; ribs (in seedlings 9-)12–34, 8–18 mm high and 12–26 mm wide, epidermis dark green. Areoles to 2.5 mm, to C. 9 mm apart, at first with whitish to pale grey felt, soon almost naked, indeterminate growth almost lacking. Spines (0-)4–8, to 11 mm, brownish, not very conspicuous, sometimes lacking on older stems, central spine 0–1, radials to 8, slender. Cephalium becoming nearly as broad as the stem, composed of densely packed, dark, shiny brown, curved-adpressed bristle-spines, wool sparse, inconspicuous. Flowers c. 19–35 × 10–22 mm; pericarpel to 2.5–3.0 × 4.5–6.0 mm; tube to C. 24 × 12 mm, bearing few, greenish, to 1.5 mm bract-scales; nectar-chamber to 9 × 12 mm; outer perianth-segments 6–7 × 2.5 mm, pale green, inner segments C. 7 × 2–2.5 mm, white; stamens to 12 mm, bearing pale yellow anthers; style 15–19 mm, stigma-lobes 6–10, 2–3 mm, greenish white; ovary locale 1–1.5 × 3 mm. Fruit 14–25 × 8–13 mm, red, shining. Seed 1–1.2 × 0.8–1.1 mm, testa-cells strongly convex.

Southern humid/subhumid forest (inselberg) element: on gneissic inselbergs within the Mata atlântica zone, 100–300 m, near the eastern border of Minas Gerais and in adjacent Espírito Santo, from the region of Barra de São Francisco southwards for some 250 km. Endemic to the core area within South-eastern Brazil. Map 16D.


Unlocalized (MG/ES): [probably near the Rio Doce, c. 1917], Lützelburg ‘32’ (M).


CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1x5) = 5. Lower Risk, since its habitats are mostly inaccessible, steep slopes. Range and frequency of occurrence probably under-recorded.

The caespitose, southern form described by Braun & Esteves Pereira as subsp. uebelmanniorum, and published without precise locality information (based on an illegal collection of Uebelmann), is neither so geographically remote as its authors claim, nor the first collection from Espírito Santo, since Brade collected the species in the intervening area of the state in May 1946 (see above). Their use of subspecific status needs to be evaluated in the light of studies of such intervening populations. The first collection of the species is even earlier, dating from around 1917, by Lützelburg, who is known to have visited the border region between Minas Gerais and Espírito Santo while travelling up the Rio Doce (Lützelburg 1925–26). It should also be noted that the phrase 'Holotypus: Brasilia, Espírito Santo, in regione septentrionali ...' following the Latin diagnosis published by Braun & Esteves Pereira (l.c., 152) is evidently an error, since from elsewhere in the German text it is clear that Uebelmann 1502 must be from the southern part of this state (in any case 250 km northwards from the type locality of the species would be localized in Bahia or NE Minas Gerais).
Subg. *Simplex* N. P. Taylor (no. 4): stem tall (to 6.5 m), normally solitary unless damaged, tissues non-mucilaginous; ribs with transverse epidermal folds above the areoles; spines stout, hooked in seedlings; flowers nocturnal, white; seeds with strongly convex testa-cells, hilum narrow, sunken. S Bahia & cent.-N Minas Gerais. Type and only species:


[Cephalocereus purpureus* Britton & Rose, Cact. 2: figs 25, 27 & 28 (1920); Werdern., Bras. Säulenkakt.: 58, 117 (1933), non Gurke (1908).]

[Austrocephalocereus purpureus* sensu (Gurke) Backeb. in Blät. Kakteenforsch. 1938(6): [22] (1938) non Cephalocereus purpureus* Gurke (1908).]

[C. lehmannianus* sensu Werdern., quoad sem., ibid., 120, fig. 6 (1933), non Werdern. (1932).]

Stem solitary branching only if damaged, columnar-erect, 150–500–(650) × 7–12 cm, tissues non-mucilaginous; ribs c. 10 in seedlings, 14–30 or more in mature individuals, to 10 mm high, to 15 mm wide, somewhat tuberculate, with transverse folds above the areoles, epidermis mid- to dark green. Areoles to 5 mm diam., 6–12 mm apart, with sparse whitish felt. Spination variable depending on age and maturity, spines mostly curved, pale with dark tips and bases, mostly rather stiff, not flexible: seedlings with strongly recurved to hooked central spines to 10–30 mm, juvenile plants with straight central spines to 60–100 mm, adult stems with shorter and finer spination of c. 4–8 central spines to 60 mm and 12–18 radial spines to 15 mm. Cephalium developed when immature stem overtops surrounding vegetation (ie. when the plant is between 0.4 and 6.0 m high), becoming as broad as the stem, comprising creamy white wool interspersed with abundant dark, curved bristle-spines to 25–50 mm. Flower c. 40–55 × 25–28 mm; pericarpel white, c. 3–6 × 6–7 mm; tube c. 35–45, with few, 1 mm, pinkish bract-scales; nectar-chamber to 18 × 10 mm; perianth-segments c. 10–12 × 4–5 mm, the outermost red-brown to greenish, the remainder white; stamens to 20 mm, white; style to c. 45 mm, stigma-lobes c. 10, to 4 mm, whitish. Fruit broadly clavate, c. 20–30 × 17–22 mm, magenta-red at apex, paler below, to white at base. Seeds 1.5 × 1.2 mm, rather narrow at the hilum; testa-cells strongly convex.

Southern caatinga element: on gneiss/granite inselbergs (rarely on limestone outcrops) and stony soil of the *caatinga* and *caatinga / campo rupestre* ecotone, c. 300–1000 m, south-eastern edge of the Chapada Diamantina and margins of the planalto de Maracas, in the Rio de Contas drainage and western flank of the Serra do Espinhaço, central-southern Bahia to central-northern Minas Gerais. Endemic to the core area of Eastern Brazil. Map 24C.


 Conservation Status. Lower Risk (1); PD=3, EI=1, GD=1. Short-list score (1x5) = 5. Lower Risk at present, but its habitat continues to be lost and monitoring is desirable.

A specimen labelled as Lützelburg 32 at Munich (M) and annotated as being the type number of Cereus goebelianus Vaupel by Werdermann cannot be considered a true duplicate of the collection described by Vaupel, since it represents Coleocephalocereus pluricosatus (E Minas Gerais and Espirito Santo), which is unknown from Bahia, where the type of the former was collected, and has much smaller flowers than those described by Vaupel, who does not appear to have studied it. As an examination of his materials has clearly shown, Lützelburg’s numbering and labelling of his collections was rather chaotic and this Munich specimen should not be allowed to further destabilize the nomenclature of the Bahian species (see below).

Until the late 1960s, this unmistakable plant was known by the misapplied name Cephalocereus (Austrocephalocereus) purpureus (= Micranthocereus purpureus (Gürke) Ritter). Vaupel’s description of the stem, ribs and spination are not representative and probably referred to a juvenile plant or juvenile base of the stem, but the original details of cephalium and flower clearly refer to this species. The confusion with M. purpureus began with Britton & Rose (1920: fig. 25) and was compounded by Werdermann (1933), who believed C. goebelianus to be synonymous, having redescribed the true M. purpureus as C. lehmannianus in 1932. Ritter (1968) recognized the problem, but not being sure of the precise identity of Vaupel’s name, redescribed the plant treated here as Coleocephalocereus pachystele.

Subg. Buiningia (F. Buxbaum) P. J. Braun (nos. 5 & 6): plants low (< 1.2 m), caespitose; stems non-mucilaginous; ribs lacking transverse epidermal folds above the areoles; spines very long, finely to stoutly needle-like; flowers diurnal, coloured; seeds with flat testa-cells, hilum broad. NE Minas Gerais (drainage of Rio Jequitinhonha).


Stem solitary or caespitose, mostly erect, 15–115 x 6–22 cm, ovoid to cylindric, rather variable in form; ribs 10-20, low and blunt-edged, epidermis yellow-green to slightly glaucous. Areoles 3–5 mm, white felted, 4–11 mm apart, showing indeterminate growth near stem base. Spines golden yellow (blackish in age and darker in seedlings), flexible, central spine(s) 1–4, to 50 x 1 mm at base, radials c. 10–15, to 15 mm, strong hypertrophic spine growth near stem base in some populations. Cephalium making the stem strongly assymetric in low-growing populations,
reaching c. half the width of the stem, composed of abundant white wool mixed with curved, golden bristle-spines to 30 mm. Flowers 30–42 × 17–20 mm, greenish yellow to green; pericarpel to 5 x 5 mm; tube 20–25 mm; nectar-chamber c. 5 mm; outer perianth-segments to 10 × 3 mm, inner segments c. 8 × 2 mm, erect, expanding to give an opening of only 2–4 mm; stamens c. 15 mm; stigma-lobes c. 5–7, whitish. Fruit red to pinkish red, 16–24 × 13–17 mm. Seed c. 1.35 mm, smooth.

South-eastern *caatinga* (inselberg) element: locally dominant on gneissic inselbergs / *lajedos*, c. 280–910 m, north-eastern Minas Gerais (Rio Jequitinhonha drainage and watershed with Rio Pardo). Endemic to the core area within Minas Gerais. Map 33D.


**CONSERVATION STATUS.** Lower Risk (1); PD=2, EI=2, GD=2. Short-list score (1×6) = 6.

Very variable in habit and stem morphology.


Holotype: Brazil, Minas Gerais, 1972, Horst & Uebelmann 359 (U).


Like *C. aureus*, but stems to c. 80(–87) × 11.5 cm; ribs 12–18, to c. 15 mm high and 23 mm wide, epidermis mid- to dark green; areoles to 5 mm, to 15 mm apart; spines yellow and reddish brown to red, the largest central directed downwards, to 70 × 1 mm at base; cephalium with wool and bristle-spines coloured like those of the stem; flowers magenta, 37–48 × 20–27 mm; style reddish above, stigma-lobes 4–5, 2.5 mm, reddish; fruit red, 16–25 × 11–17 mm; seed c. 1.75 mm.

South-eastern *caatinga* (inselberg) element: on gneissic inselbergs and *lajedos* in *caatinga*, c. 250–300 m, near the Rio Jequitinhonha, north-eastern Minas Gerais. Endemic to the core area within Minas Gerais. Map 33D.


**CONSERVATION STATUS.** Endangered (3) [criteria C2b]; PD=2, EI=1, GD=1. Short-list score (3×4) = 12. Endangered, since the known habitat is close to a road and may be visited by collectors for plants and seed.

The range of this species deserves further investigation, but is clearly much more restricted than that of its sister species, *C. aureus*, and is currently known only from the locality cited above. Uebelmann (1996) states it is from Itaobim, which is here assumed to refer to the Itinga locality, since the former is the closest town of any size and is the likely starting point for the short journey to Itinga. However, it should not be difficult to determine the extent of the species’ range more precisely, working eastwards from the known locality along the Rio Jequitinhonha valley.
MELOCACTUS (L.) Link & Otto


VERNACULAR NAMES. Cabeça-de-Frade, Coroa-de-Frade.


Stem unbranched (unless damaged), highly succulent, scarcely woody except at extreme base, depressed-globose to cylindric, vegetative part rarely to 50 cm, with 8–21 vertical ribs, mucilage absent to abundant; areoles small to large, indeterminate growth absent. Spines (3–)4–21 or more per areole, usually only weakly differentiated into central and radial series, sometimes strongly curved to hooked at apex in seedlings. At reproductive maturity stem apex converted into a terminal cephalium of bristles and dense trichomes, vegetative growth ceasing; cephalium remaining small or sometimes attaining 30 cm in length, to 11 cm in diam. Flowers short lived, expanding mid- to late afternoon, small (15–29 x 4–18 mm), tubular, naked, only the pink, magenta or red perianth and sometimes uppermost part of tube exserted from the cephalium (rarely cleistogamous); pericarpel very small, conspicuously narrower than the swollen nectar-chamber at base of tube; perianth-segments tapered to linear, arranged in 2–4 series; lowermost stamens with filaments enlarged at base to protect nectar-chamber, anthers minute, < 1 mm; style and 4–8 stigma-lobes very slender, equalling stamens or long-exserted and conspicuous. Fruit short- to elongate-clavate (c. 10–45 x 5–12 mm), naked except for the pale floral remains attached at apex, white, pink, magenta or reddish, expressed from the cephalium and sometimes falling down from the plant, funicular pulp often becoming liquid, translucent. Seeds small (0.85–1.75 mm), blackish, globose to ovoid; testa-cells few, large, flat to strongly convex or almost pointed.

One of the most widely distributed genera of Cactaceae, comprising 32 spp., ranging from South-eastern and North-eastern Brazil (15 spp.) and the Amazonian region (3 spp.), northwards to the Caribbean (to N Cuba) (9 spp.), and W to the Andes and Central America (S Peru to W Mexico) (5 spp.). The greatest concentration of taxa and centre of diversity is in Eastern Brazil (especially Bahia), and 20 out of the total of 22 species and heterotypic subspecies recognized here are endemic to the core area. The genus is characteristic of the caatingas-agrestes and Northern campos rupestres, only one species occurring in coastal sand-dunes of the Mata atlântica (contrary to the statement in Porembski et al. 1998: 116). Karyotype information has been presented in two recent papers by Das et al. (1998a & b), but is not included below, since no permanently preserved voucher materials were cited and considerable doubt must exist concerning the identities of the taxa studied, which were of unstated origin from a living collection (the unreliable identity of most living plants offered from commercial sources is well known and compounded by the widespread occurrence of man-made hybrids). The nomenclature used would, if taken at face value, indicate that at least two of the species exist in both diploid and tetraploid races. Nevertheless, such studies, if properly documented, would be valuable to enable an understanding of why some sympatric taxa produce hybrids, while others do not.

Various species occur sympatrically and sometimes form hybrid swarms. The key below does not attempt to account for plants of hybrid origin, which include the following taxa (Taylor 1991a): no. 1a x no. 9, 1b x 13, 2a x 9, 2a x 10, 2a x 12, 7b x 10, 8a x 10, 10 x 13, 12 x 13.

Fruit, seed and edaphic data are essential for precise identification.

1. Fruit entirely white, white but very pale pink at apex, or pale lilac-pink to pink and only 10–20 mm long
1. Fruit red or pinkish magenta, at least at apex, to 45 mm long 12
2. Stem lacking mucilage; fruit length 1.5–2.0 × diam. 3
3. Stem with at least some mucilage in the green cortical tissues or highly mucilaginous; fruit length 2 or more × diam. 4
5. Lowermost radial spine markedly longer than longest central spine; flower pinkish magenta; seed to 1.35 mm, testa-cells strongly convex (granite/gneiss inselbergs, cent.-S Bahia) 5. deinacanthus
3. Lowermost radial spine ± equal to or shorter than longest central spine; flower red, at least without; seed 1.35–1.75 mm, testa-cells almost flat (limestone, N Minas Gerais, W & cent.-S Bahia) 6. levitestatus
4. Fruit white, or white and very pale pink only at apex, or pale pink and seed with almost flat testa-cells 5
4. Fruit lilac-pink to pink; seed with testa-cells strongly convex at end opposite hilum 7
5. Central spine(s) > 20 × 1.5 mm (inland Bahia, limestone) 6
5. Central spine lacking or < 20 × 1.5 mm (coastal sand dunes) 15c. violaceus subsp. margaritaceus
6. Perianth-segments 0.7–1.7 mm wide; cephalium 7–9 cm diam., wool often conspicuous; fruit to 6 mm diam. 7. azureus
6. Perianth-segments 1.4–2.2 mm wide; cephalium 10 cm diam., with very dense fine bristles only; fruit 7–9.5 mm diam. 8. pachyacanthus
7. Stem pale bluish waxy-glaucous, at least when young 8
7. Stem always plain green 10
8. Flowers cleistogamous (SE Pernambuco) 11. lanssensianus
8. Flowers opening prior to fruit development 9
9. Stem 11–16 cm diam., pith chlorophyllous; ribs 8–12; areoles 13–20 mm apart on the ribs 13. concinnus
9. Stem to 25 cm diam., pith white; ribs 10–22; areoles 20–40 mm apart on the ribs 9. zehntneri
10. Spines (3–)4–6 per areole, largest 1.2–2.0 mm thick (cent. & S Bahia, 1100–1500 m) 14. paaicipinus
10. Spines > 6 per areole or only 0.5–1.0 mm thick 11
11. Radial spines 5–10(–11), almost straight, 0.5–1.5 mm thick (restinga and sandy places inland, 0–1100 m) 15. violaceus
11. Radial spines (6–)7–11, ± curved, to 2.5 mm thick (inland, especially in the coastinga) 10. zehntneri
12. Fruit to 16 × 7 mm, dark red to base; cephalium white-woolly throughout, bristles hidden (Bahia: Mun. Morro do Chapéu) 11. glaucescens
12. Fruit to 45 × 12 mm, reddish to magenta at apex, paler below; cephalium with conspicuous bristles or white-woolly only at apex 13
13. Ribs ± rounded in cross-section (but edge often acute) or very low; stems depressed-globose to taller than broad 14
13. Ribs triangular in cross-section; stems broader than tall 17
14. Lowermost radial spine recurved at apex, to 35 mm, central spine 1, to 22 mm; stem hemispheric; ribs very low (Bahia: Mun. Vitória da Conquista) 4. conoideus
14. Lowermost radial spine straight or outcurved at apex, or > 35 mm, central spines > 1, > 22 mm, or stem and ribs not as above 15
15. Lowermost radial spine > 40 mm and < 1.5 mm thick, or stem taller than broad or lacking mucilage and/or flowers with pinkish, long-exserted stigma-lobes; ribs 9–16 16
15. Lowermost radial spine < 40 mm or > 1.5 mm thick; stem depressed to globose, with mucilage in the green cortical tissues; stigma-lobes white, scarcely exserted; ribs 8–12 3. bahiensis
16. Spines 9–14 per areole, lowermost radial 40–80 mm; stem to 15 × 18 cm 1. ores
16. Spines (11–)14–21 per areole, lowermost radial 50–150 mm; stem to 45 × 35 cm 2. ernestii
17. Stem light greyish blue-green or quite glaucous; flower with c. 23 perianth-segments visible from above; spines usually < 40 mm (S & E Bahia) 9. salvadorensis
17. Stem pale to dark green; flower with 25–33 perianth-segments visible from above (rarely cleistogamous); spines to 60 mm (Pernambuco, Bahia & N Minas Gerais) 3. bahiensis

MELOCACTUS OREAS Group (nos. 1–4):


Stem depressed-globose to elongate, 8.5–15.0(–35.0) × 10–18 cm, mid- to dark green; ribs 10–16, rather variable in height, to 40 mm broad near stem base, always ± rounded in cross-section, but edge often acute; areoles 6–9 × 4–6 mm, 10–18 mm apart on the ribs. Spines 9–14, horn-coloured, pale brown or dull reddish brown, acicular, central(s) 1–4, lower 27–45 mm, radials 8–11, lowermost 40–80 mm, slender and flexuous, rarely stout and stiff, outcurved or straight. Cephalium to 12 × 4–8 cm, bristles dark reddish brown. Flowers light to dark pinkish magenta, 17–22 × (7–)9–10 mm. Fruit red at apex, magenta to pinkish below, fading to almost or quite white at base, elongate clavate, 14–28 × 5–9 mm. Seed nearly globose, 0.85–1.20 × 0.8–1.15 mm, testa-cells convex.

This endemic NE Brazilian species is divisible into the following subspecies:

1. Ribs 10–13; stem usually depressed (N Chapada Diamantina, Bahia, 700–1000 m)
1a. subsp. oreas

1b. subsp. cremnophilus

1a. subsp. oreas

Stem subglobose to elongate, 10–15(–35) × 10–18 cm; ribs (11–)12–16, to 15–25 mm high; areoles 9 × 4–6 mm. Spines 9–14, central(s) 1–4, lower 35–45 mm, radials 8–10, lowermost to 40–80 mm.

Eastern caatinga element: on more or less exposed granite/gneiss løjedos and arenitic rocks, caatinga-agreste, within the lower drainage of the Rio Paraguaçu, at < 500 m, eastern Bahia. Endemic to Bahia. Map 32C.


CONSERVATION STATUS. Lower Risk (1); PD=1, El=1, GD=2. Short-list score (1×4) = 4. Lower Risk at present, but further modification of its habitats is likely and it requires monitoring in view of its relatively restricted distribution.

The name M. oreas Miq. is here employed for a plant of relatively limited distribution with up to 16 ribs, the high rib-count being the only detail in Miquel’s original description which positively excludes its application to the more common and widespread M. ernestii Vaupel, which has up to 13(–14) ribs only.
Subspecies *oreas* has been observed sympatric with *M. ernestii* and *M. salvadorensis*. It will occasionally hybridize with the latter. It may also hybridize or intergrade with *M. bahiensis* in north-eastern Bahia.


Like subsp. *oreas*, but stem globose to strongly depressed-globose, usually rather small, 8.5–12.0 × 13.5–14.5 cm; ribs 10–13, often rather low; areoles to c. 6 × 5 mm. Spines 9–13, central(s) 1–4, 27–40 × 1 mm, lower slightly upcurved, radials 8–9, straight to slightly outcurved, lowermost to 55–70 × 1 mm, more strongly outcurved.

*Caatinga / Northern campo rupestre* (Chapada Diamantina) element: on ± exposed crystalline/sandstone and granitic rocks, 700–1000 m, northern part of the Chapada Diamantina, Bahia. Endemic to the core area within North-eastern Brazil. Map 28D.

**CONSERVATION STATUS.** Vulnerable (2) [criteria B1/2c]; area of occupancy estimated to be <2000 km²; PD=1, EI=1, GD=1. Short-list score (2x3) = 6.

Subspecies *cremnophilus* is isolated from subsp. *oreas* by a zone of high forest on the eastern flank of the Chapada Diamantina, Bahia. It has been found sympatric with *M. ernestii*, *M. bahiensis* and *M. concinnus*, and will hybridize with the last-named. The population previously identified as belonging to this subspecies from Pernambuco (Mun. Caetes, 4 km NW of the town, then 0.5 km NE towards a fazenda, 13 Feb. 1991, *Taylor & Zappi* 1627B, K, photos) requires further study (cf. *Taylor* 1991a).


Stem with or without mucilage, subglobose to shortly cylindric, 9–45 × 7–22–(35) cm, light yellow-green to dark green; ribs 9–13–(14), to c. 30 mm high and 70 mm broad near stem base, ± rounded in cross-section but sometimes with an acute edge; areoles to 13 × 9.5 mm, to 28 mm apart. Spines (11–)14–21, red and yellow banded or dull reddish to brownish, centrals (3–)4–8, lower somewhat upcurved or straight, to 32–90 × 1.3 mm, radials 7–13, lowermost to 45–150 × 1.3 mm, straight or outcurved. Cephalium to 18 × 8 cm, composed of pale to bright pinkish red bristles, sometimes covered by white wool at apex. Flower 19.5–29.0 × 9–18 mm; stigmas lobes white, not exserted.

This species is divisible into two subspecies:

1. Stigma-lobes not or scarcely exserted, white; green stem tissues mucilaginous, ribs 10–13(–14); central spines 1–4(–6) (NE Brazil & NE Minas Gerais)

2. subsp. ernestii

2a. subsp. longicarpus

Stem mucilaginous at least in the green cortical tissues, subglobose to shortly cylindric, 10–45 × 14–22(–35) cm; ribs 10–13(–14), to c. 30 mm high and 40–70 mm broad near stem base; areoles to 10 × 9 mm. Spines (11–)14–18, centrals 4(–6), lower somewhat upcurved, to 40–90 × 1.3 mm, radials 7–13, lowermost to 50–150 × 1.3 mm, outcurved. Flower 19.5–25.0 × 9–15 mm; stigmas lobes white, not exserted.

Eastern caatinga element: locally dominant on exposed crystalline/sandstone rocks and especially gneissic inselbergs, including those in brejo forest, 250–1190 m, southern Paraiba, eastern Pernambuco, western Alagoas, western Sergipe, Bahia (E of 42°W) and north-eastern Minas Gerais. Reported from Ceará and Rio Grande do Norte by Lützelburg (1925–26) and likely to occur there. Map 30C.

PARÁIBA: Mun. Esperança, 16 Nov. 1920, Lützelburg 15000 (M); Mun. Pocinhos, July 1921, Lützelburg 12602 (M); between Soledade and Campina Grande, Nov. 1920, Lützelburg 51, 57B (M); Mun. Maturéia, Serra de Teixeira, Pico do Jabe, 1994, M.F. Agra et al. (JPB). 

ALAGOAS: reported from Piranhas etc. by Lützelburg (1925, 1: 107).


MINAS GERAIS: NE Minas Gerais, Mun. Pedro Azul, near the town, Horst 168 (U 531281); Mun. Itatobim, 1 km W of town, 18 Nov. 1988, Taylor & Zappi in Harley 25527 (K, SPF); l.c., 8 km from road BR 116 towards Itinga, 9 Apr. 1983, Martinelli & Leuenberger 9228 (B).

CONSERVATION STATUS. Lower Risk (1); PD=1, EI=2, GD=2. Short-list score (1×5) = 5.

This subspecies can be found sympatric with M. oreas, M. bahiensis, M. salvadorensis, M. zehntneri, M. glaucescens and M. concinnus.

The following may represent a name for hybrids between M. ernestii and M. zehntneri, which have been observed in the municípios of Poçao/Jataíba (F. A. R. Santos 5 & 6, PEUFR, K, photos) and Alagoinha (Taylor & Zappi, K, photos), Pernambuco, but it has yet to be recollected at the type locality: M. horridus Werderm. in Notizbl. Bot. Gart. Berlin 12: 227 (1934). Holotype: Pernambuco, Mun. Serra Talhada, 1932, Werdermann 2934a (B, in spirit; K, photos).

Although the ranges of M. ernestii and M. zehntneri overlap, they are usually separated ecologically, M. ernestii preferring more humid rocks at higher altitudes.


Stem lacking mucilage or with a little in the green cortical tissues, epidermis light to dark green, occasionally somewhat glaucous, 9–20 × 7–20 cm; ribs 9–11–12, to 25–50 mm broad near stem base; areoles to 13 × 9.5 mm. Spines (13–)14–21, sometimes very thinly overlaid with grey, nearly straight, but sometimes strongly curved to hooked at apex in seedlings, centrals (3–)4–8, lower to 32–53 × 1–1.8 mm, radials (8–)10–13, lowermost to 45–90 × 0.8–1.8 mm. Cephalium bristly or densely white-woolly at apex. Flowers often large, 22–29 × 9–18 mm, with whitish, pink or reddish, ± exserted stigma-lobes. Fruit pink to red at apex, elongate-clavate, 16–45 × 6.5–12.0 mm.
Southern caatinga element: on gneissic inselbergs and in other rocky places in caatinga, c. 450–950 m, between the Rio São Francisco and 42°W in southern Bahia, and on west side of the Serra do Espinhago in northern Minas Gerais. Endemic to the core area of Eastern Brazil. Map 24D.


CONSERVATION STATUS. Lower Risk (1); PD=1, EI=1, GD=2. Short-list score (1x4) = 4. Lower Risk at present, but habitats are being disturbed in certain parts of its range; needs to be monitored.

Subspecies longicarpus is sympatric with M. salvadorensis in Mun. Rio do Antônio, Bahia.

Type: Bahia, Mun. Marcionilio Sousa, Rose & Russell 19935 (US, lecto. designated here; NY, lectopara.).


Stem globose, depressed-globose or pyramidal, 9.5–21 × 11–21 cm, pale to dark green, with mucilage at least in the green cortical tissues; ribs 8–14, very low or up to 30 mm high, very variable in shape; areoles 6–14 × 4.5–8.0 mm, to 24 mm apart on the ribs. Spines 9–16, mostly straight, central(s) 1–4, 17–50 mm, radials (7–)8–12, lowestmost to 22–60 mm. Cephalium usually small, rarely more than 5 × 6.5–8.5 cm. Flower pinkish magenta, 20–23 × 10–12.5 mm. Fruit reddish to magenta at apex, paler below, 17–25 × 6.5–9.0(–10.0) mm. Seed 1.05–1.35 × 0.85–1.30 mm, testa-cells convex.

Until recently the name M. bahiensis was commonly misapplied in Brazilian literature to the more widely ranging M. zehntneri. This misuse can be attributed to Werdermann, whose incorrect determinations of herbarium material preserved at Recife (IPA) seem to have misled two generations of botanists and ecologists.

The true M. bahiensis is highly variable. The following infraspecific taxa are recognized:

1. Central spine(s) 1–4, the lower and largest usually > 25 mm, lowestmost radial spine 24–60 mm 2
2. Central spine 1, to 25 mm, lowestmost radial spine 22–32 mm (N Bahia) 3a(ii). subsp. bahiensis f. acispinosus (Permambuco & NE to S Bahia)
3. Ribs rounded to somewhat acute but scarcely triangular in cross-section, or lowestmost radial spine > 40 × 1.5 mm (Permambuco & NE to S Bahia)
3b. subsp. amethystinus (S edge of Bahia to central Minas Gerais: Diamantina)
3. Ribs c. 10, sharply acute at edge, to 60 mm diam.; areoles 8–14 mm; lowermost radial spine to 60 mm (S Bahia)

3a(iii). subsp. bahiensis f. inconcinnus

3. Ribs 8–12, ± rounded, to 45 mm diam.; areoles to c. 8 mm; lowermost radial spine to 50 mm

3a(i). subsp. bahiensis f. bahiensis

3a. subsp. bahiensis

Stem globose to depressed-globose or pyramidal, 9.5–21 × 11–21 cm; ribs 8–12, high and acute to low and rounded, to 60 mm broad; areoles to 8–14 × 6.5–8.0 mm (to only 6 × 4.5 mm in f. acispinosus). Spines 9–16, pale reddish brown overlaid with grey, central(s) 1–4, lower 17–50 × 1–2 mm, porrect, straight or upcurved, radials (7)–8–12, lowermost 22–60 × 1–2 mm. Seed 1.05–1.20 × 0.8–1.05 mm (to 1.35 × 1.3 mm in f. acispinosus).

Eastern caatinga / Northern campo rupestre element: on more or less exposed crystalline rock formations (quartzitic-arenitic, granite/gneiss), quartz gravel etc., rarely on limestone, campo rupestre / caatinga, 300–1300 m, northern and eastern Pernambuco, to c. 14°S in Bahia. Endemic to the core area within North-eastern Brazil. Map 30D.


Conservation status. Lower Risk (1); PD=1, El=1, GD=2. Short-list score (1×4) = 4.

Two distinctive local Bahian forms of this subspecies are distinguished in the key above. Forma acispinosus (Buin. & Brederoo) N. P. Taylor (1991a: 28) is represented by the collections cited from the municípios of Senhor do Bomfim, Ituá and Jacobina, and f. inconcinnus (Buin. & Brederoo) N. P. Taylor (1991a: 30) by those from Paramirim, Livramento do Brumado, Brumado and Ituaçu.

Subspecies bahiensis can be found sympatric with M. oreas, M. ernestii, M. zehntneri, M. concinnus and M. violaceus subsp. ritteri.


Stem depressed-globose to pyramidal, 10–13 x 13–19 cm; ribs 9–14, usually triangular in cross-section, edge acute; areoles 6–10 x 5–7 mm. Spines 9–13, all ± straight, brown to reddish or horn yellow, thinly overlaid with grey, central(s) 1–4, lower 15–33 x 1–1.8 mm, radials 8–10, lowermost 24–40 x 1.2–1.5 mm. Seed 1.1–1.3 x 0.95–1.15 mm.

Eastern caatinga / Northern campo rupestre element: under and between shrubs on mainly crystalline (quarzitic/arenitic) rock formations in the Serra do Espinhaço region and on exposed granite/gneiss further east, campo rupestre / caatinga, 300–1000 m, southern Bahia (S of 14°S) to central Minas Gerais. Endemic to the core area of Eastern Brazil. Map 32D.

BAHIA: Mun. Caetité, Brejinho das Ametistas, 26 July 1989, Zappi 175 (K, SPF), Horst 270 (U 531291); Mun. Presidente Jânio Quadros, reported by Rizzini (1982: 75, fig. 39 above left); Mun. (?), E of Urandi, reported by Braun (1988a: 208–209, as ‘HU 535’).


CONSERVATION STATUS. Lower Risk (1); PD=1, EI=1, GD=2. Short-list score (lx4) = 4.

This subspecies is sometimes sympatric with M. ernestii, M. zehntneri and M. concinnus, but hybrids between them have not been observed.


Stem mucilaginous in the green cortical tissues, strongly depressed-globose to hemispheric, to 10 x 17 cm; ribs 11–15, very low and rounded, to 2.5 cm high, 4 cm wide; areoles 6.5–7.5 x 6.5 mm. Spines dark brown overlaid with grey, central 1, 20–22 x 1.5 mm, radials 8–11, straight to slightly recurved, lowermost 20–35 x 1.5–1.7 mm, recurved near apex. Flower pinkish magenta, c. 22 x 10 mm. Fruit lilac-magenta, 18–21 x 5–6 mm. Seed 1.05–1.25 x 0.9–1.05 mm, testa-cells strongly convex at periphery.
Eastern caatinga / Northern campo rupestre element: under and between shrubs in quartz gravel, campo sujo / cerrado de altitude, c. 1050 m, Serra do Periperi, Mun. Vitória da Conquista, south-eastern Bahia. Endemic to Bahia. Map 32C.


CONSERVATION STATUS. Critically Endangered (4) [criteria B1/2c]; extent of occurrence estimated to be < 100 km²; PD=2, EI=1, GD=1. Short-list score (4x4) = 16. Regrettably, survival of M. conoideus in the wild is severely threatened by extraction of the quartz gravel in which it grows, and through commercial collection for the European horticultural market. Since June 1992 it has been listed on Appendix I of C.I.T.E.S. In 1989 M. conoideus was all but extinct at the type locality in the Serra do Periperi above Vitória da Conquista, BA, where it is sympatric with the widespread M. concinnus. However, Brazilian cactus enthusiasts have recently discovered a healthy extension of this population in an adjacent part of the serra further from the BR 116 highway and this area is now officially protected, although this has so far failed to halt gravel extraction.

MELOCACTUS DEINACANTHUS Group (no. 5):


Stem not mucilaginous, globose to elongate, 15-35 × 12-25 cm; ribs 10-12, acute, to 40 × 60 mm broad near stem base; areoles to 15 × 10 mm, to 33 mm apart on the ribs. Spines 15-21, reddish brown, centrals 4-7, lower to 53 × 3 mm, radials 11-14, lowermost to 80 × 2.5 mm, somewhat recurved. Cephalium to 25 × 9 cm, with exposed bristles at apex. Flowers pinkish magenta, to 26 × 11.5 mm; stigma-lobes whitish, not exserted. Fruit entirely white, shortly clavate, 12-22 × 6-12 mm. Seed 1.15-1.35 × 1.05-1.25 mm, scarcely narrowed or broadest at the hilum, testa-cells strongly convex.


BAHIA: Mun. Bom Jesus da Lapa, Juá, 21 Apr. 1992, Hatschbach & E. Barbosa 56810 (MBM); l.c., 34.5 km SE of Bom Jesus on road BR 430 to Riacho de Santana, south side of road, Morro da Barriguda, 20 July 1989, Zappi 150 (K, SPF); l.c., 22 km from Riacho de Santana, 16 Apr. 1983, Leuenberger et al. 3075 (B, CEPEC); l.c., 1971, Horst 153 (U 531251).

CONSERVATION STATUS. Critically Endangered (4) [criteria B1/2c]; area of occupancy estimated to be < 10 km²; PD=3, EI=2, GD=1. Short-list score (4x6) = 24. It seems to be known from only a single roadside site. Its rarity and vulnerability to commercial exploitation has caused it to be placed on Appendix I of C.I.T.E.S., since June 1992.

M. deinacanthus is readily distinguished from all other members of the genus by the combination of shortly clavate, pure white fruits and uniquely shaped seeds, which are very broad at the hilum and with strongly convex testa-cells. It appears to have a very limited distribution east of the Rio São Francisco and is presently known from only the locality cited above, where it is a co-dominant element of the rupicolous vegetation.

MELOCACTUS LEVITESTATUS Group (no. 6):


Stem without mucilage, light grey-green to dark green, or sometimes rather glaucous and with reddened edges to the ribs, slightly depressed or globose to cylindric, 15-68 × 14–30 cm; ribs 9–12(-15), to 5 × 8 cm; areoles to 11 × 10 mm, with abundant creamy wool at first, to 30–42 mm apart on the ribs. Spines 8–15, brownish red thinly overlaid with grey, central(s) 1–4(-6), 17–33 × 1–2.5 mm, mostly ascending, lower up- or decurved towards apex, radials 7–10, all strongly recurved, lower 3 21–33 × 1.5–2.0 mm. Cephalium to 18 × 7–12 cm. Flower entirely red or deep red with grey, with abundant creamy wool at first, to 30–42 mm apart on the ribs.

Southern Rio São Francisco caatinga element: usually on elevated outcrops of Bambuí limestone amidst high caatinga forest, c. 450–700 m, western and central-southern Bahia and central-northern Minas Gerais. Endemic to the core area of Eastern Brazil. Map 27C.


CONSERVATION STATUS. Lower Risk (1); PD=3, EI=1, GD=2. Short-list score (1x6) = 6. Lower Risk at present, but in need of monitoring in view of the potential threat from limestone quarrying.

MELOCACTUS AZUREUS Group (nos 7 & 8):


Stem mucilaginous in the chlorophyllous cortical tissues, subglobose to cylindric, dark or grey-green to intensely glaucous, 13-45 x 14-19 cm; ribs (9-)10, triangular in cross-section, to 35 x 40 mm; areoles to 13 x 11 mm, to 28-35 mm apart on the ribs. Spines 9-15, blackish or dark brown to reddish overlaid with grey, some hooked in seedlings, decurved or nearly straight, 21-53 x 1-2.2 mm, centrals 1-4, radials 7-11. Cephalium to c. 12 x 7-9 cm, composed of reddish bristles and white wool, the latter abundant and loose, or sparse. Flowers pinkish magenta, 19-23 x 8-11.5 mm. Fruit entirely white, slightly pinkish at apex or pale pink throughout, to 17 x 6 mm. Seed 1.05-1.75 x 0.95-1.50 mm, testa-cells flat and smooth.

An endemic Bahian species divisible into two subspecies:

1. Stem glaucous, at least when young; cephalium apex with brownish tufts of wool, bristles not or scarcely exserted; seeds (1.3-)1.4-1.75 mm 7a. subsp. azureus

1. Stem never glaucous; cephalium apex lacking brownish wool tufts, bristles usually well-exserted; seeds 1.05-1.30 mm 7b. subsp. ferreophilus

7a. subsp. azureus

Stem somewhat depressed-globose to shortly cylindric, pale blue-glaucous, often intensely so, eventually light grey-green, 13-26 x 14-19 cm; areoles to 11 x 7.5 mm. Spines 9-13, all somewhat recurved to decurved or almost straight, lower central 21-43 x 1.5-2.0 mm, radials 8-10, lowermost 21-40 x 1-2 mm. Cephalium with brownish woolly felt-like tufts at apex, wool abundant and sometimes nearly or quite obscuring the bristles. Seed (1.3-)1.4-1.75 x 1.2-1.5 mm.

Northern Rio São Francisco caatinga element: on flat, exposed Bambui limestone in caatinga at c. 450-750 m, in the region of Irecê and lower drainage of the Rio Jacaré, central-northern Bahia. Endemic to Bahia. Map 25C.


CONSERVATION STATUS. Endangered (3) [criteria B1I2bcd]; extent of occurrence = 1102 km²; PD=1, EI=1, GD=2. Short-list score (3x4) = 12. Endangered by actual or potential habitat destruction (agricultural development) at its few known localities, but potentially conserved within the Área de Proteção Ambiental de Gruta dos Brejões.

This subspecies has been observed sympatric with M. pachyacanthus subsp. viridis, q.v.


Stem globose to cylindric, dark to grey-green, 15-45 x 15-19 cm; areoles to 13 x 11 mm. Spines 11-15, lower central to 30-53 x 2-2.2 mm, radials 7-11, lowermost to 40-53 x 2 mm, often strongly decurved towards apex. Cephalium lacking brownish woolly tufts at apex, scarcely woolly in old plants, bristles conspicuous, ± well-exserted. Seed 1.05-1.30 x 0.95-1.10 mm.
Northern Rio São Francisco caatinga element: on raised, exposed Bambuí limestone in caatinga at c. 700–850 m, in the upper drainage of the Rio Jacaré and tributaries, between América Dourada, Barro Alto and Souto Soares, central Bahia. Endemic to Bahia. Map 25C.


CONSERVATION STATUS. Endangered (3) [criteria B1/2cde]; extent of occurrence = 513 km²; PD=1, EI=1, GD=1. Short-list score (3x3) = 9. Endangered from potential limestone quarrying, actual modification of the environment surrounding its habitat and in view of its very limited known area of occupancy (< 50 km²).

At the first locality cited above this subspecies was found sympatric with M. zehntneri and there was evidence of introgression between them. Its epithet was given in the mistaken belief that the limestone upon which it occurs was an iron-rich rock of volcanic origin.


Stem mucilaginous, depressed-globose to ovoid, pale green to grey-green, not glaucous except sometimes when young, 15–30 × 20 cm; ribs 9–11, low, to 25–37 × 50–65 mm; areoles to 13–15 × 9–11 mm, to 25 mm apart on the ribs. Spines 10–12, all very stout, reddish brown overlaid with grey, central(s) 1–3, lower 28–46 × 2–3(–4) mm, porrect or slightly ascending, radials 8–9, straight to slightly recurved, lower 3 25–49 × 2–2.5 mm. Cephalium to 12 × 10 cm, with dull pinkish red bristles, wool conspicuous or sparse. Flowers reddish to deep pinkish magenta, 22–25 × 7–10 mm, sometimes only half-expanded or scarcely exserted from cephalium. Fruit whitish or rather pale pink becoming very pale in lower half, 16.5–20.0 × 7–9.5 mm, somewhat flattened. Seed 1.2–1.4 × 0.95–1.15 mm, testa-cells flat and smooth, some elongate.

An endemic Bahian species divisible into two subspecies:

1. Stem globose to elongate-ovoid, strongly glaucous especially when young
2. Stem depressed-globose, plain green

8a. subsp. pachyacanthus
8b. subsp. viridis

8a. subsp. pachyacanthus

Stem ± glaucous. Cephalium to c. 9 cm diam., with bristles and conspicuous wool.

Northern Rio São Francisco caatinga element: on flat, ± exposed Bambuí limestone in caatinga at 520–620 m, near the Rio Salitre, northern Bahia. Endemic to Bahia. Map 25C.


CONSERVATION STATUS. Critically Endangered (4) [criteria A2c]; area of extent = 1099 km²; PD=1, EI=1, GD=2. Short-list score (4x4) = 16. Critically Endangered by actual or potential habitat destruction (urban/agricultural development) at its few known, widely separated localities.
This subspecies is sometimes partially sympatric with *M. zehntneri*, but can be distinguished by its darker coloured flowers, smooth seeds and stronger spination.


Stem never glaucous. Cephalium c. 10 cm diam., with very dense bristles and little or no wool.

Northern Rio São Francisco *caatinga* element: on flat, ± exposed Bambui limestone in *caatinga* at 700–750 m, in the region of Irecê, central-northern Bahia. Endemic to Bahia. Map 25C.

**CONSERVATION STATUS.** Critically Endangered (4) [criteria B1i2a–e/C2a1D]; PD=1, EI=1, GD=1. Short-list score (4×3) = 12. Almost extirpated by habitat destruction (agricultural development) at its known localities, where less than 50 individuals survive.

Near Irecê, Bahia, subsp. *viridis* has been found sympatric with *M. azureus* subsp. *azureus*, but can be distinguished by its greener epidermis, stouter spination, massive cephalium of very dense bristles and scant wool, less expanded flowers with much broader perianth-segments, larger, more pinkish fruits and smaller seeds. The habitats of these taxa in this region have mostly been destroyed by agricultural development.

**MELOCACTUS VIOLACEUS** Group (nos. 9–15):


Stem with mucilage in the green cortical tissues, pyramidal-globose to depressed-globose, greyish blue-green or quite glaucous, 12–20 × 12–25 cm; ribs 8–14, triangular-acute, 25–30 × 30–50 mm; areoles to 7–8.5 × 7–8 mm, 20–30 mm apart on the ribs. Spines horn yellow to reddish brown, overlaid with grey at first, central(s) 1–4, 15–30 × 1.5–2.5 mm, radials 7–10, lowermost 20–46 × 1.8–2.2 mm. Cephalium to 15 × 6–10 cm, composed of dense reddish bristles and sparse grey-white wool. Flowers pinkish magenta, opening c. 4–5 p.m., to 25 × 12 mm, but sometimes scarcely exserted from cephalium and less expanded. Fruit deep lilac-magenta, clavate, c. 17 × 6.5–9.0 mm. Seed 1.1–1.3 × 0.9–1.15 mm, some testa-cells markedly elongated, others strongly convex, especially at periphery.

Eastern *caatinga* element: usually on or adjacent to exposed gneiss/granitic rocks/inselbergs and in stony soil of the *caatinga*, low elevations to c. 660 m, within the Rio Paraguaçu (Rio Jacuipe) and Rio de Contas (Rio Gavião) drainage systems, eastern and southern Bahia. Endemic to Bahia. Map 32D.


**Conservation Status.** Lower Risk (1); PD=2, EI=1, GD=1. Short-list score (1×4)= 4. Lower Risk at present, but its habitat continues to disappear.

This species can be found sympatric with *M. oreas*, *M. ernestii* (both subspp.), *M. zehntneri* and, probably, *M. bahiensis* and *M. concinnus*. It occasionally hybridizes with *M. oreas* and *M. ernestii* subsp. *ernestii*. It is easily confused with *M. zehntneri*, but has much darker, magenta fruit. Its pollination biology has been studied by Raw (1996).


Type: Bahia, Mun. Juazeiro, *Rose & Russell* 19728 (US, lectotype designated here; NY, lectopara.).

*Cactus zehntneri* Britton & Rose, Cact. 3: 236, with illus. of type, fig. 248 (1922).


Stem highly mucilaginous, at least in the non-chlorophyllous tissues, dark to grey- or light green, often glaucous, but sometimes plain dark green, hemispheric to cylindrical, very variable in shape, 11-48 x (9-)13-25 cm; ribs 10-22, 22-35 x 22-57 mm, with a sharply acute edge; areoles to 12 x 9 mm, set into notches and c. 20-40 mm apart on the ribs. Spines 8-13(-15), horn yellow, brown or dull pink, but usually thickly overlaid with grey except at the dark tips, at least some hooked at apex in seedlings, centrals (0-)1-2(-4), upcurved, 15-40(-45) x 1.3-3.0 mm, radials 7-11, weakly to strongly recurved, lower 1-3 largest, 19-39(-45) x 1.5-2.5 mm. Cephalium to 11(-30) x 6-10 cm, composed of fine, dense, pale pinkish red bristles and sparse to abundant, white to creamy wool. Flowers pale to deep pink, not at all to well-exserted from cephalium, sometimes with the tube exserted also, ± expanded, to 25 x 4-13 mm. Fruit very pale (rarely almost white) to deep lilac-pink, rarely magenta (SE Pernambuco), 12-20 x 5-9(-10) mm. Seed 1.0-1.4 x 0.8-1.35 mm, testa-cells strongly convex at end opposite hilum.

Widespread <i>caatinga</i> / Northern <i>campo rupestre</i> element: in soil or sand and on rocks of various types, including limestone, gneiss/granite (inselbergs), sandstones, quartzitic and other crystalline formations, in the <i>caatinga</i> (rarely on rocks in <i>cerrado</i>, W Bahia, or in <i>campo rupestre</i>, S Bahia), c. 200-1000 m, northern Piauí, northern Ceará and Rio Grande do Norte to southern Bahia. Endemic to North-eastern Brazil. Map 19.

PIAUÍ: N Piauí, Mun. Buriti dos Lopes, 5 km NE of town on road BR 343, rocks by the Rio Pirangi, 19 Feb. 1995, <i>Taylor</i> (K, photos); Mun. Cocal, c. 17 km E of town, 19 Feb. 1995, <i>Taylor</i> (K, photos); SE Piauí, Mun. Dom Expedito Lopes, Gaturianu, <i>Ritter</i> 12066a (U 531268); Mun. Santo Antônio de Lisboa, <i>Horst</i> 444 (U 531289); Mun. Simões, foot of Chapada do Araripe from Marcolândia, 7°36'S, 40°45'W, 5 April 2000, <i>E.A. Roche et al.</i> (K, photos); Mun. Jaciçós, 28 km S of town on road BR 407, 6 April 2000, <i>E.A. Roche et al.</i> (obs); Mun. Canto do Buriti, c. 15 km S of town, partly exposed granite, 5 Feb. 1990, <i>Zappi</i> 215 (HRCB, ZSS); Mun. Paulistana, 25 km S of Paulistana, 1982, <i>Horst</i> 519 (ZSS AV-20-48).

CEARA: Mun. Taurá, 6 km along road to Marrecas / Cocotá from junction with road BR 020 S of Taurá, 30 Jan. 1990, <i>Zappi</i> 209 (HRCB, K, photos).

RIO GRANDE DO NORTE: Mun. Açu, 1978, <i>Horst</i> 480 (ZSS); Mun. Tangará, road BR 226, W of town towards Santa Cruz, 6°14'S, 35°51'W, 1 April 2000, <i>E.A. Roche et al.</i> (K, photos).

PARAÍBA: Mun. Pocinhos, Parque das Pedras, 28 June 1998, <i>E.A. Roche</i> 420 (JPB, PEUF); Mun. Taperoa, Nov. 1920, <i>Lützelburg</i> 54 (M); Mun. Campina Grande, Nov. 1920, <i>Lützelburg</i> 14001 (M); Mun. Irapanga, Serra Água Branca, 7-10 Jan. 1994, <i>M.F. Agrela et al.</i> (JPB); Mun. São João do Cariri, c. 1-2 km from the town, on road BR 412, 29 June 1998, <i>E.A. Roche</i> 426 (JPB); Mun. Sumé, 29-30 June 1994, <i>M. Agrela et al.</i> 2827 (JPB); Mun. Monteiro, s.d., <i>Lützelburg</i> 86 (M), Nov. 1920, <i>Lützelburg</i> 12321 (M).


SERGIPE: Mun. Canindé de São Francisco, 23 Apr. 1981, <i>M. Fonseca et al.</i> 481 (ASE 896); Mun. Monte Alegre de Sergipe, 12.5 km from the town towards Paulo Afonso (Bahia), 11 Feb. 1991, <i>Taylor</i> & <i>Zappi</i> 1617C (K,

BAHIA: W Bahia, Mun. Barreiras, NW of the city, Serra da Bandeira, cliff edges, road to new airport and near Telebahia tower, 18 Jan. 1991, Taylor et al. 1441 (K, ZSS, HRCB, CEPEC) & 1441A (K, HRCB); N Bahia, Mun. Glória, Brejo do Burgu, 27 Aug. 1995, F.P. Bandeira 267 (HUEFS); Mun. Remanso, 11 km E of town, 9°33’S, 42°W, 7 April 2000, E.A. Rocha et al. (K, photos); i.e., c. 30 km from Remanso towards Casa Nova, 10 Feb. 1990, Zappi 220B (K, seeds); Mun. Juazeiro, 6.5 km along dirt road to Rodeodouro from road BA 210, 10 Jan. 1991, Taylor et al. 1389 (K, ZSS, HRCB, CEPEC); Mun. Paulo Afonso, reported by Rizzini (1982: 67, fig. 34 below left); Mun. Sento Sé, 10 km E of turning to Bazuá on road BA 210, Taylor et al. 1390A (K, photo); Mun. Curaçá, 4 km SE of Poço de Fora, 7 Jan. 1991, Taylor et al. 1368A (ZSS, photo); Mun. Uauá, 12.5 km N towards Patamute, 6 Jan. 1991, Taylor et al. s.n. (ZSS, photo); Mun. Campo Formoso, 2.5 km W of Curral Velho, 9 Jan. 1991, Taylor et al. 1386C (K, photo); Mun. Jaguarari, 10 km N of Flamengo on road BR 407 to Juazeiro, 15 July 1989, Zappi 125A (K, frs in spirit, photo); Mun. Xique-Xique, 26 km SE of the town on road BA 052, 13 Jan. 1991, Taylor et al. (obs.); Mun. Jacobina, 10 km from Lajes (Lages) on road to Catinga do Moura, caatinga on limestone, 16 July 1989, Zappi 133A (K, photo); Mun. Gento do Ouro, 16 June 1994, L.P. de Queiroz 3951 (HUEFS, K); i.e., S of Xique-Xique, Serra de Santo Inácio, Horst 266 (U 531294); Mun. Morro do Chapéu, 2.5 km E of América Dourada, south (east) bank of Rio Jacaré (Rio Vereda do Romão Gramacho), N of road BA 052, exposed Bambuí limestone, 17 July 1989, Zappi 138A (K, SPF); Mun. Valente, 6 km N of Valente beside road to Santa Luz, caatinga on fine quartz sand, 14 July 1989, Zappi 121 (K, SPF); Mun. Aracoi, 14.5 km N towards Tucano, 5 Jan. 1991, Taylor et al. 1354A (K, photos); Mun. Ibotirama, few km E of the town, 1986, P.J. Braun 604 (ZSS); S Bahia, Mun. Bom Jesus da Lapa, c. 32 km NE of Bom Jesus da Lapa, just beyond Caldeirão, 43°13’W, 13°10’S, caatinga with damp sandy area, 18 Apr. 1980, Harley 21525 (K, CEPEC); Mun. Macaúbas, Horst 128 (U 531266, 531280); Mun. Paramirim, 43 km W of Livramento do Brumado beside road to Paramirim, 4 km from Caraubas, 28 Nov. 1988, Taylor in Harley 25555 (K, SPF); Mun. Livramento do Brumado, 12 km S of Livramento beside road to Brumado, 23 Nov. 1988, Taylor & Zappi in Harley 25545A (K, frs in spirit); Mun. Dom Basílio, 21 km S of Livramento do Brumado, 21 Mar. 1991, G.P. Lewis s.n. (K, photos); Mun. Brumado, reported by Rizzini (1982: 67, fig. 28 below); Mun. Aracatu, 25 km E along road BR 030 towards Sussuarana, 3 Feb. 1991, Taylor et al. 1542B (K, photo); Mun. Tanhaçu, Ourives, 1964, Ritter s.n. (U 531248); Mun. Palmas de Monte Alto, 1964, Ritter s.n. (U 531249); Mun. Caetité, near Brejinho das Ametistas, c. 1000 m, 26 July 1989, Zappi 177 (K, SPF).

**Conservation Status.** Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1×5) = 5. Lower Risk, but exploited in many parts of its range as cattle fodder, for cactus candy and even for horticultural plantings, as seen in Pernambuco (Taylor 1991a) and elsewhere.

With the exception of one disjunct occurrence in the *cerrado* of western Bahia (near Barreiras), the range of *M. zehntneri* corresponds very closely to the limits of the *caatinga*. It is absent, however, from the *caatingas* of northern Minas Gerais and adjacent southernmost Bahia, and is replaced by the related and similar *M. salvadorensis* (q.v.) in the dry valleys of the Rio Paraguaçu and Rio de Contas in eastern Bahia (E of 41°W). Elsewhere, it can be found sympatric with *M. ernestii*, *M. bahiensis*, *M. azureus* subsp. *ferreophilus*, *M. pachyacanthus*, *M. salvadorensis*, *M. lancssensianus* (fide Braun) and *M. concinnus*. The name *M. horridus* Werderm. may relate to hybrids between *M. zehntneri* and *M. ernestii* (q.v.).

*M. zehntneri* varies greatly in stem size, shape and colour, in spine number, length, thickness and colour, and in the degree to which its flowers are exerted from the cephalium and thus able to expand. Its pollination biology has been studied by Locatelli & Machado (1999a).

Stem highly mucilaginous, depressed-globose, to 8 x 14 cm, bluish grey-green; ribs c. 12, acute, 25-30 mm high, to 40 mm wide near stem base; areoles circular, 5-6 mm in diam., c. 13 mm apart on the ribs. Spines 8-9, pinkish grey to beige, yellowish to brownish at apex, stiff, central 1, upcurved, to 30-35 x 1.5-2.0 mm, radials 7-8, recurved, lowermost longest, to 35-40 x 1.5 mm. Cephalium to 2.5 x 7 cm, with pale red to salmon-coloured bristles. Flowers apparently cleistogamous, drying up without expanding to form 6 mm long floral remains attached to the fruit. Fruit pink, c. 17 x 6 mm, containing 18-32 seeds. Seed 1.1 x 0.9 mm, testa-cells strongly convex.

Eastern caatinga element: on exposed granitic outcrops of serras in caatinga, c. 900 m, Mun. Caetes, south-eastern Pernambuco. Endemic to Pernambuco. Map 31C.

**CONSERVATION STATUS.** Data Deficient.

At its type locality said by Braun, l.c., to occur sympatrically with *M. zehntneri*, but neither species has been observed by the present author in the municipio cited above. The status of this taxon remains uncertain. However, it is not the only cleistogamous plant of this relationship known from the region — the following cleistogamous forms may also belong here (Map 31C):

**PARAÍBA:** Mun. Tacima, near border of Mun. Caçara, inselberg known as 'Pão de Açucar', 6°36'S, 35°28'W, 1 April 2000, E.A. Rocha et al. (K, photos) — like *M. zehntneri*, but stem rather small and spines longer and more slender.

**PERNAMBUCO:** Mun. Serra Talhada, rocky mountain slope c. 1 km north of the town, 13 Feb. 1990, Zappi 223 (HRCB, ZSS, K) — not dissimilar from *M. bahiensis* in some respects and possibly worthy of description as a new taxon (see Taylor 1991a: plate 14).


Stem highly mucilaginous, depressed-globose to pyramidial, intensely light blue-glaucous at first, light grey-green in age, 13-18 x 14-24 cm; ribs 8-15, to 40 mm high and 60 mm broad near stem base; areoles to 8 x 5 mm, to 21 mm apart on the ribs. Spines 6-10, brown thickly overlaid with grey, dark brown to blackish at tip, centrals (0-)1-2, lower 11-20 x 0.8-1.7 mm, ascending and upcurved, radials 5-8, not or scarcely overlapping with those from areoles on adjacent ribs, nearly straight to somewhat recurved, lower 3 11-25 x 1-1.8 mm. Cephalium to 10 x 6-7.5 cm, bristles hidden beneath dense, creamy white wool. Flowers lilac-magenta, c. 25 x 15.5 mm. Fruit entirely deep red, 9.5-16.0 x 5-7 mm, terete or somewhat flattened. Seed 1.1-1.35 x 0.9-1.15 mm, testa-cells strongly convex.

**Caatinga / Northern campo rupestre** (Chapada Diamantina) element: in the open and between low shrubs of the caatinga on flat or sloping, ± exposed, crystalline rock outcrops with accumulation of gravel, 700-900 m, Chapada Diamantina, Mun. Morro do Chapéu, Bahia. Endemic to Bahia. Map 28D.


**CONSERVATION STATUS.** Critically Endangered (4) [criteria B1/2c]; area of occupancy estimated to be < 10 km²; PD=2, EI=1, GD=1. Short-list score (4×4) = 16. In view of its rarity and the threats from commercial collection *M. glaucescens* has been placed on Appendix I of C.I.T.E.S. since June 1992. A local reserve to protect this and other rare species has been proposed.
On account of its striking white-woolly cephalium, lilac-magenta flowers and small, deep red fruits, this is one of the most distinctive species and cannot be confused with any other member of the genus.

*M. glaucescens* is extremely restricted in distribution, being certainly known from only the small area approximately 20–25 km west of Morro do Chapéu, Bahia, on both sides of the road BA 052. At both collection points cited above there is evidence of hybridization with contiguous populations of other members of the genus. At the first locality (Harley 27393) it occasionally hybridizes with *M. ernestii* and the product of these two very different taxa can be identified as *M. xalbicephalus* Buin. & Brederoo in Krainz, Die Kakteen, Lfg 52 (1973). At the second locality *M. glaucescens* has formed a hybrid swarm with *M. concinnus*, although this may not be the only taxon involved (Taylor 1991a: plate 17, below).


[M. macrodiscus var. macrodiscus sensu Ritter, Kakt. Südamer. 1: 133 (1979) non Werderm. (1932).]

Stem highly mucilaginous, with green, chlorophyllous pith, grey-green and glaucous, at least when young, intensely so in seedlings, depressed-globose, 8–12(–13) × 11–16 cm; ribs 8–12, to 20(–30) mm high and 35–60 mm broad near stem base, often laterally creased; areoles to 6.5 × 6 mm, 13–20 mm apart on the ribs. Spines 6–9, red then blackish when developing, later horn yellow or pale reddish brown to brown, thickly overlaid with grey except at the dark tips, central (0-)1, 10–19 × 1 mm, upcurved, radials 6–8, slightly to strongly recurved, lower 1–3 largest, 15–26(–28) × 1–2 mm, sometimes hooked at apex. Cephalium to 5.5 × 4–9 cm, composed of fine, dense, pale pinkish red bristles and creamy wool. Flowers deep pink, scarcely to well-exserted from cephalium, 20–23 × 6–12 mm. Fruit pale lilac-pink to pink, 13–18(–22.5) × 5–8.5 mm, terete or somewhat flattened. Seed 1.05–1.35 × 0.95–1.3 mm, testa-cells strongly convex.

Eastern *caatinga* / Northern *campo rupestre* element: in the open or beneath low to tall shrubs and trees in *caatinga*, *carrasco*, *cerrado de altitude* and *campo rupestre*, in stony soil, quartz sand or gravel, or between crystalline rocks, 550–1300 m, Chapada Diamantina, Serra do Espinhaço and Serra do Periperi (Vitória da Conquista), central Bahia to northern Minas Gerais. Endemic to core area of Eastern Brazil. Map 31C.


CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=2. Short-list score (1×5) = 5. Lower Risk, but some populations affected by burning of vegetation started by man (campos rupestres).

When found sympatric or contiguous with populations of other species M. concinnus not infrequently forms hybrid swarms. These include allied species, such as M. glaucescens, M. zehntneri and M. paucispinus, as well as the unrelated M. oreas subsp. cremnophilus. It is also found with M. bahiensis, M. conoideus and, perhaps, M. salvadorensis. Forms possibly referable to this species, or perhaps to M. zehntneri, found at the northern limits of its range, around Morro do Chapéu, with only 5 curved spines per areole are peculiar, resembling the following species in their spination, but lacking its high ribs. These are said ( fide M. Machado, in litt., 22.11.99) to occur with typical M. concinnus.


Stem highly mucilaginous, strongly depressed, hemispheric or disc-shaped, usually partly buried in the sand, light grey-green, never glaucous even when young, 7–11.5 × 15–20 cm; ribs 9–10, to 2.5–4.0 cm high and 3.7–5.0 cm broad near stem base; areoles c. 3.5–7.0 × 2.5–5.5 mm, to 24 mm apart on the ribs. Spines (3–)4–6, recurved, pale grey with dark brown tips, all radial, lowermost largest, to 10 × 1 mm. Cephalium to 3–6 × 7–8 cm, composed of dense, fine, pinkish red bristles and creamy white wool. Flowers deep pink, (18–)24–26 × (9–)12.5–14.5 mm. Fruit pale lilac-pink, (14–)16.5–19.0 × 5.5–7.5 mm. Seed 1.3–1.6 × 1.2–1.5 mm, testa-cells strongly convex.

Northern campo rupestre element: in sand or quartz gravel, cerrado de altitude and campo rupestre, c. 1100–1500 m, in the Chapada Diamantina and northern Serra do Espinhaço, central to southern Bahia. Endemic to Bahia. Map 28D.

BAHIA: Mun. Seabra, 28.5 km W of Seabra near road BR 242 to Ibotirama, 18 July 1989, Zappi 144 (K, SPF); Mun. Abaira, 9 km N of Catolés, camino de Ribeirão de Baixo a Piata, geralis entre Serra do Atalho e a Serra da Tromba, 13°14'S, 41°55'W, 10 July 1995, L.P. Queiroz et al. 4420 (HUEFS, K); Mun. Érico Cardoso [Água Quente], Pico das Almas, valley near Serra do Pau Queimado, near old road between Mato Grosso do Norte and Água Quente, quartz gravel, 23 Dec. 1988, Hind in Harley 27430 (K, SPF, CEPEC); Mun. Rio de Contas, Pico das Almas, between Rio de Contas and Faz. Brumadinho, 0.5 km before Faz. Brumadinho, 27 Nov. 1988, Taylor in Harley 25554 (K, SPF, CEPEC); Mun. Urandi (?), E of town reported by Braun (1988a: 208, 171, illus. as 'HU 536').
CONSERVATION STATUS. Endangered (3) [criteria B1/2ce]; extent of occurrence = 6585 km², but area of occupancy certainly < 500 km²; PD=2, EI=1, GD=1. Short-list score (3x4) = 12. In view of its restricted distribution, rarity and desirability to collectors, this species has been listed in Appendix I of C.I.T.E.S. since June 1992. Two of the five populations known are small (< 50 individuals).

The strongly depressed stem of *M. paucispinus* seems to be an adaptation to minimize damage caused by fire, which periodically sweeps through its *cerrado / campo rupestre* habitat. By remaining partly buried in sand and exposing only the upper half of its flattened stem, it benefits from the cooler air drawn in at ground level as the fire passes, though the edges of its ribs may still get scorched. This adaptation is identical to that displayed by members of the ecologically comparable genus *Discocactus*, with which juvenile plants of *M. paucispinus* are readily confounded.

A population recently photographed by R. Harley (K, photos), between Piatã and Inûbia (Mun. Piatã, Bahia), appears to represent plants showing introgression with *M. concinnus*, with bluish grey-green epidermis, 11 ribs and mostly 5, well-developed spines per areole. A curious population from Morro do Chapéu, mentioned under *M. concinnus* (q.v.), is not included here at present, although the plants have very similar spination.


Stem highly mucilaginous, dark green, never glaucous even when young, usually broader than tall, often very small, 5–18(–20) x 6–17(–20) cm; ribs 8–15; areoles to 5 x 5 mm, 6–18 mm apart on the ribs. Spines 5–10(–12), brownish but thickly overlaid with grey except at the dark brown to blackish tips, very slender, 0.5–1.5 mm thick, centrals absent or 1, to 19 mm, ascending and often slightly upcurved, radials almost straight or slightly recurved, lower 3–5 largest and nearly equal, 14–24(–26) mm. Cephalium to 5.5(–11) x 3.7–8.5 cm, with abundant white wool and sparse to numerous, ± exserted, pale red, very fine bristles. Flowers deep pink, 15–25 x 6–13.5 mm, scarcely to well-exserted from the cephalium. Fruit pale pink to lilac-pink or white, 12.5–19.0 x 5.5–7.5 mm. Seed 1.2–1.5 x 1–1.4 mm, testa-cells strongly convex.

Two of the 3 subspecies recognized here are endemic to the core area of Eastern Brazil:

1. Fruit lilac- to pale pink
2. Fruit white to very pale pink (NE Bahia, Sergipe & Alagoas) 15c. subsp. *margaritaceus*
2. Flower to 25 x 13.5 mm; spines 6–12; ribs 9–15 (NE Minas Gerais & coastal regions of E Brazil up to 35 km inland, from Rio Grande do Norte to Rio de Janeiro) 15a. subsp. *violaceus*
2. Flower c. 18–22 x 7–10 mm; spines 5–6; ribs 8–10 (Bahia inland: Jacobina & Rui Barbosa) 15b. subsp. *ritteri*
15a. subsp. violaceus

Stem depressed-globose, hemispheric or disc-shaped, 6–16 cm diam.; ribs 9–15, to 10–25 × 40 mm broad near stem base; areoles 6–18 mm apart on the ribs. Spines 6–12. Cephalium to 5.5–(7.0) × 3.7–8.5 cm. Flower ± exserted from cephalium, with 17–25 perianth-segments visible from above.

Widespread humid forest (Mata atlântica/restinga) and Northern campo rupestre (cerrado) element: between shrubs in sand of the coastal restinga, riverine sand-dunes and similar habitats further inland, 0–150 m (in sandy cerrado de altitude at 1100 m, NE Minas Gerais only), Rio Grande do Norte to Rio de Janeiro, but apparently rather discontinuous, perhaps for lack of suitable habitats and due to habitat destruction. Map 12D.


PARAÍBA: Mun. Santa Rita, M.F. Agra (obs.); i.c. (?), plants on sale in market in João Pessoa, assumed to be from Santa Rita site, 1992, McRobb (K, photo ref. BZ 92-151); Mun. Pedras de Fogo, beside sugarcane plantation E of dirt road leading N from Destilaria Giasa, 7°20’S, 35°4’W, c. 150 m, 31 Mar. 2000, E.A. Rocha et al. (K, photos) — c. 30 km from the coast.


SERGIPE: between Penedo (AL) and Pindoba, c. 30–35 km from the ocean, c. 6 km from the Rio São Francisco, 100 m, 1978, Horst 482 (ZSS AV-20-24/41/94).


CONSERVATION STATUS. Vulnerable (2) [criteria A2c]; PD=1, E1=1, GD=2. Short-list score (2×4) = 8. Vulnerable from habitat modification by development for the tourist industry and for pineapple and sugarcane plantations. In Paraíba, the locality at Santa Rita has already been destroyed by a pineapple plantation, while that north of Pedras de Fogo has all but disappeared due to the cultivation of sugarcane.


Stem depressed-globose, 8–13.5 cm diam.; ribs 8–10, to c. 15 × 50 mm; areoles 10–14 mm apart on the ribs. Spines 5–6. Cephalium to c. 5 × 5 cm. Flower with up to 24 perianth-segments visible from above, sometimes scarcely exserted from cephalium.

Eastern caatinga / Northern campo rupestre element: between Vellozia shrubs in fine quartz sand or gravel, campo rupestre, c. 450–860 m, near Jacobina and above Rui Barbosa, central-eastern Bahia. Endemic to Bahia. Map 31C.

CONSERVATION STATUS. Critically Endangered (4) [criteria B1I2c]; extent of occurrence < 100 km²; PD=1, EI=1, GD=1. Short-list score (4×3) = 12. Known from only two small locations totalling < 10 km² and both near to towns.

This very local taxon occurs sympatrically with *M. bahiensis* at both localities cited above. It is very similar to the following in most respects, but has pink fruits like subsp. *violaceus*.


*Melocactus pentacentrus* Lemaire, Cact. Nov. Gen. Sp.: 108 (1839). Type: Bahia [= Salvador], not known to have been preserved.


*M. margaritaceus var. disciformis* Rizz., tom. cit. 78 (1982), nom. inval. (Art. 43.1).

*M. margaritaceus var. salvadoranus* Rizz., tom. cit. 78 (1982), nom. inval. (Art. 43.1).

*M. depressus* sensu Schumann, Gesambt. Kakt. Nachtr.: 129 (1903) pro parte.

Stem depressed-globose, rarely shortly cylindric, 5–15(–25) × 7–13(–20) cm; ribs 8–15, to 20 × 40 mm; areoles 7–10 mm apart on the ribs. Spines 5–10. Cephalium to 5(–11) × 3.7–6.5 cm. Flower exserted from cephalium, with c. 19 perianth-segments visible from above.

Northern humid/subhumid forest (*restinga*) element: on coastal dunes of fine, white sand and inland (Serra de Itabaiana, SE), near sea level to c. 400 m, Alagoas, Sergipe and eastern Bahia (south to Salvador). Endemic to the core area within North-eastern Brazil. Map 15D.


CONSERVATION STATUS. Vulnerable (2) [criteria A2c]; PD=1, EI=1, GD=2. Short-list score (2×4) = 8. Vulnerable from habitat modification by the ever-expanding coastal tourist industry. Away from the coast it is most abundant and currently best protected in the state ecological reserve at the Serra de Itabaiana, Sergipe, managed by the local office of IBAMA.

If this taxon should one day prove to be worthy of specific rank, as Rizzini believed, then the earliest, clearly typified species name for it is *M. ellemeetii* Miquel, l.c. (1858). However, at least one of its northern populations has flowers and very pale pink fruits, which are somewhat intermediate with subsp. *violaceus*, further weakening the differences between them.
Tribe TRICHOCEREEAE F. Buxbaum

As noted earlier, the distinction between this tribe and Cereeae Salm-Dyck is currently unclear when analysed using DNA gene-sequence data (Wallace, ined.), because the informative part of the genome in other tribes investigated is within a 300 base-pair deletion, which appears to be a synapomorphy for this pair of tribes. Their traditional circumscription, based primarily on the presence or absence of hair-spines/spines on the pericarpel and flower-tube, is maintained here, although Espostoopsis F. Buxb. (Trichocereeae) and some species of Cipocereus Ritter (Cereeae) represent exceptions in each case. Harrisia and Uebelmannia are both genera sometimes referred to other tribes, which are included below on the basis of this DNA gene sequence synapomorphy.

24. HARRISIA Britton


Including Eriocereus (A. Berger) Riccobono (1909); Harrisia subg. Eriocereus (A. Berger) Britton & Rose (1920).

A genus of c. 10 species, with a disjunct distribution between the Caribbean (Subg. Harrisia, fruits indehiscent) and central South America (Subg. Eriocereus, fruits dehiscent). Two species are native of Brazil: H. balansae (K. Schum.) N. P. Taylor & Zappi (near Corumbá, Mato Grosso do Sul; cf. Hoehne 1915: 55–56 — Hoehne 3855 (R), Pott et al. 433 (UEC)) and that treated here, which is endemic to the Nordeste and isolated from its nearest congeners by some 1800 km. In its gross morphology it is most similar to the east Andean H. pomanensis (Weber) Britton & Rose (syn. Eriocereus tarijensis Ritter; Argentina & Bolivia). However, gene sequence data (Wallace 1997: 11) indicate that H. adscendens is sister taxon to the Caribbean Subg. Harrisia, linking the two subgenera and indicating the path of radiation of the genus from its presumed origin in the eastern Andes of Bolivia, where it is believed to have a common ancestry with Samaipaticereus Cárdenas.


VERNACULAR NAMES. Rabo-de-raposa, Passa-prá-lá.

Shrubby, to 2 m or more, free-standing or semi-scandent and partly pendulous, sometimes forming dense masses, with basitonic or mesotonic branching, ± segmented. Juvenile growth of markedly different appearance to the adult, the ribs scarcely visible and bearing very small areoles and fine spines. Adult stems erect to decumbent, 2–7 cm diam.; ribs 6–10, low, rounded, tuberculate at the areoles, sinuses sinuous, marked by a dark line (as in H. pomanensis); epidermis pale grey-green, sometimes reddish. Areoles 6–10 mm diam., 25–50 mm apart (much closer in juvenile forms), with white, greyish or brownish, early deciduous hairs, subtended by red scale leaves when first emerging from apical meristem. Central spines 1–3, 15–30 mm, radials 4–7, 3–15 mm. Flower-bearing region not
differentiated; young flower-buds covered in golden hair-spines to 15 mm long, flowers nocturnal, 15–22 × 12–17 cm; pericarpel greenish, covered in tubercles bearing areoles with bristles and triangular bract-scales; flower-tube 5–7 cm, infundibuliform, 1–2 cm diam., bearing scattered areoles with triangular bract-scales and hairs to 1.5 cm; perianth-segments to 6 cm, outer segments reflexed, lanceolate to linear, fleshy, dark red with green shades, inner segments spreading, lanceolate and fimbriate, delicate, white; stamens exerted in relation to the perianth-segments, curved, anthers linear; style 13–20 × 0.3–0.5 cm, stigma-lobes 12–15, exerted; ovary locule ovoid to oblong in longitudinal section. Fruit globose, to 10 cm diam., dehiscent by splitting irregularly, flower remnants deciduous; pericarp greenish then bright orange-red, covered in podaria bearing woolly areoles; funicular pulp white. Seeds c. 3–4 mm, cochleariform, black, shiny; testa-cells flat, smooth.

Widespread central-southern *caatinga* element: common along roadsides, often in farm hedges, amongst semi-open vegetation or scrambling over rocks (inselbergs), *caatinga-agreste*, especially on soils containing clay, c. 50–700 m, from north-western (Xique-Xique), central-northern and -eastern Bahia (drainage of Rio Paraguacu, c. 13°S) northwards to southern Ceará and southern Paraíba (c. 7°S). Endemic to the core area within North-eastern Brazil. Map 21D.

PIAUÍ: reported by Lützelburg (1926, 3: 111), but see comments below.

CEARÁ: S Ceará, Mun. Barro, road CE 292, between Cuncas and border with PB, 7°6′S, 38°42′W, 4 April 2000, E.A. Rocha et al. (K, photos); Mun. Milagres, 2 km E of town on road BR 116, 4 April 2000, E.A. Rocha et al. (obs); Mun. Mauriti, 'Mamalu', road CE 296, shortly after the border with PB, 7°32′S, 38°40′W, 3 April 2000, E.A. Rocha et al. (K, photos); Mun. Jardim, 1.5 km S of town towards Cedro (PE), 4 April 2000, E.A. Rocha et al. (obs).


CONSERVATION STATUS. Lower Risk (1); PD=2, EI=1, GD=1. Short-list score (1×4) = 4.

Although reported from Piauí by Lützelburg (1926, 3: 111), this species has not been seen there by the author. However, its occurrence at Araripina, Pernambuco is close to the border with that state, although it is not known if suitable edaphic conditions exist (soils with clay content).

The places in which this species is commonly found today suggest that its dispersal and establishment is assisted by man and his animals. Its fruits are edible and it is often seen in farmhouse hedges.
25. LEOCEREUS Britton & Rose


An isolated genus comprising a single species endemic to the core area of Eastern Brazil. Its placement in Trichocereae is provisional and awaits confirmation via DNA gene sequence data.

Other species referred to *Leocereus* by Britton & Rose (l.c.) belong in *Arthrocerus*, except for *Cereus oligolepis* (l.c., 225), which is a *Pilosocereus* (Zappi 1994). *L. squamosus* (Gürke) Werdermann (1933) is *Facheiroa squamosa* (Gürke) P. J. Braun & E. Esteves Pereira. For *L. paulensis* Spegazzini, see *Coleocephalocereus fluminensis* (Zappi & Taylor 1992b).


Erect or semi-scandent, to 2(-3) m high, with one or more seldom-branched stems arising from a woody rootstock; stems cylindrical, very woody, lacking mucilage, bright or olive-green, to 200 x 1--2.5 cm; ribs (10--)20, rounded, obtuse, low, c. 1--2 x 2--4.5 mm, sinuses sinuate; areoles circular, 1--2.8 mm, 4--7 mm apart. Spines 8--21, not clearly differentiated into centrals and radials, slender acicular, yellowish to dark brownish or blackish, central(s) 1--9, ± erect, 6--20 mm, radials 7--12, adpressed, 3--5 mm. Flowers subapical, nocturnal, tubular, 40--73 x 20--34 mm, white; pericarpel and tube to c. 50 mm, green, clothed with 2--3 x 0.8--1.0 mm, brownish, triangular-acuminate bract-scales, pericarpel c. 9--10 x 6.5--7.5 mm, with 4 mm, porrect, pale spines in the bract-scale axils, the tube with dark hairs and bristles to 12 mm; nectar-chamber 12--17 x 8--12 mm, narrowed to 6--8.5 mm at base and to 7--11 mm above, apex of tube 12--18 mm diam.; perianth-segments 4--17 x 1.8--4.5 mm, outer series patent to reflexed, green to dull brownish red, oblong-apiculate, inner series suberect, pure white, lanceolate; lowermost stamens with thickened filaments protecting the nectar-chamber, 15--18 mm, anthers cream, 1.6--2.5 mm; style 30--40 x 0.7--1.0 mm, stigma-lobes 6--11, white, 1.5--4.5 x 0.6 mm. Fruit globose to ovoid, 23--36 x 16--32 mm, red, indehiscent, at maturity the spine-clusters becoming detached, floral remains persisting, erect, funicular pulp magenta. Seeds 1.2--1.8 x 1--1.2 mm, black, glossy, hilum oblique, testa-cells flat to slightly convex, with intercellular pits.

Widespread Central & Southern caatinga element: growing between and through shrubs, rocky places in 'caatinga de altitude', campo rupestre and their ecotone, and amongst rocks and cliffs in cerrado (W Bahia), 550--1500 m, northern Bahia to central-northern Minas Gerais (especially in the Chapada Diamantina and Serra do Espinhaco),
northwards to southern Piauí and westwards in the Chapada da Bahia (Espigão Mestre) towards the border with Goiás. On present evidence, endemic to the core area in Eastern Brazil. Map 21C.


**Conservation Status.** Lower Risk (1); PD=4, EI=1, GD=2. Short-list score (1×7) = 7.

*Braun, i.e.* reports the synonymous *L. estevesii* from southern Maranhão, but no corroborating material has been seen by the present author. If *Braun*’s record were substantiated, *Leocereus* would lose its status as a genus endemic to the core area defined in this study.
26. FACHEIROA Britton & Rose


Columnar, erect, treelike, sometimes shrubby, to 8 m; central cylinder woody, solid. Branches 2.4–7.0 cm diam., erect, not constricted, epidermis dull to bright green, not glaucous; ribs 15–20, low, crenate, sinuses straight. Areoles with felt and long hairs; spines weak, flexible to brittle, not very pungent, central spines procerct to deflexed, longer than the numerous radials. Flower-bearing region of stem lateral, subapical or flowers randomly disposed, when differentiated sometimes forming a cephalium that transforms the structure of the stem. Flowers nocturnal, to 5 × 2.5 cm; pericarpel and tube covered in triangular bract-scales subtending tufts of hair; tube cylindric, stout; sometimes with a tuft of hairs between the nectar-chamber and the filament bases; innermost filaments curved towards the style; perianth-segments short, triangular to lanceolate or spatulate, innermost white, pinkish or purplish. Fruit globose to depressed-globose or pear-shaped, indescent, covered in scales and hairs, flower remnant drying brownish, erect. Seeds c. 1–1.5 mm, cochleariform; testa-cells flat or convex; cuticular folds present or absent.

A genus of 3 ± allopatric species, endemic within the core area of Eastern Brazil (Rio São Francisco drainage), mainly in caatinga vegetation, and of uncertain relationship within the Trichocereeae (but cf. *Yungasocereus* Ritter (1980) and *Vatricania* Backeberg (1950), both from the eastern edge of the Andes in Bolivia, the latter genus nowadays sometimes included within *Espostoa* Britton & Rose). Buxbaum (1959) published *Espostoa* subg. *Facheiroa* (Britton & Rose) F. Buxbaum.

1. Flower-bearing part of stem strongly modified, rarely only poorly differentiated
2. Flower-bearing part of stem not at all modified (cent.-S Bahia northwards, non-calcareous rocks) 3. *F. squamosa*
2. Flowers to 3 × 2.8 cm; perianth-segments sometimes pinkish (Bambuí limestone outcrops of SW Bahia and cent.-N Minas Gerais) 2. *F. cephaliomelana*
2. Flowers 4–4.7 × 2 cm; perianth-segments white (cent.-N Bahia, non-calcareous rocks) 1. *F. ulei*


*Facheiroa pubiflora* Britton & Rose, Cact. 2: 173 (1920) ("pubiflora"). Type: Brazil, Bahia, Mun. Xique-Xique, Serra da Cana-brava, Oct. 1917, Zehntner in Rose s.n. (US, lecto. designated here; K, lectopara.)

VERNACULAR NAME. Facheiro-preto.

Treelike or often shrubby, to 6 m or more, much branched. Stems erect, to 7 cm diam.; ribs 18–20, 8–9 × 7–8 mm, epidermis green to grey-green. Areoles 4–5 mm, 10–12 mm apart, long hairs grey. Spines flexible, brown, central spines 2–3, to 18 mm, radials 13–15, 3–15 mm. Flower-bearing region strongly differentiated, lateral, sunken into stem, with greyish wool and bristles to 10 mm. Flowers 4–4.7 × 1.7–2.0 cm; pericarpel and tube wine-coloured, covered in lanceolate to triangular, 2–5 mm bract-scales, bearing tufts of short, reddish to golden brown hairs; flower tube cylindric, to 30 × 22 mm; perianth-segments 8–10 × 3.5–5.0 mm, lanceolate-spathulate; stamens
included in relation to the perianth-segments; nectar-chamber 10 × 12 mm; style 27 mm, stigma-lobes 10–15, exserted; ovary locule saucer-shaped in longitudinal section, 3 × 8 mm. Fruit depressed-globose to pear-shaped, 3.5–6.0 × 4 cm. Seeds c. 1.5 mm, cochleariform, black, shiny.

Northern Rio São Francisco caatinga element: in caatinga at c. 500 m or more, north-western edges of the Chapada Diamantina, from the region of Xique-Xique to the Serra da Chapada, central-northern Bahia. Endemic to Bahia. Map 25D.


CONSERVATION STATUS. Data Deficient.

This taxon has not been studied in the field by the author and little is known about its ecology and relationship with other members of the genus, although it is clearly a distinct species.

Holotype: Brazil, Bahia, Santa Maria da Vitória, 25 July 1974, Horst & Uebelmann 447 (U).


Tree-like or usually shrubby, to 4 m or more, much branched. Stems erect, 2.4–6.0 cm diam.; ribs 18–32, 4–8 × 4–9 mm; epidermis green to grey-green. Areoles 1.5–3 mm, 1–8 mm apart, long hairs grey to brownish. Spines flexible, brown or golden, central spine(s) 1–5, to 40 mm, radials 10–12, 3–15 mm. Flower-bearing region differentiated, lateral, with brownish to greyish or white wool and bristles to 10 mm. Flowers 2.8–3.5 × 1.9–2.8 cm; pericarpel and tube wine-coloured, covered in lanceolate to triangular, 4.5–6 mm bract-scales, bearing tufts of short or long, white to golden brown hairs in their axils; flower-tube 19–20 × 18 mm; perianth-segments 8–10 × 3.5–5.0 mm, lanceolate-spathulate, pink; stamens included in relation to the perianth-segments; nectar-chamber 5–6 × 10–13 mm; style 23–27 mm, stigma-lobes 10–12; ovary locule saucer-shaped in longitudinal section, 3 × 8–10 mm. Fruit depressed-globose to turbinate, 2.5 × 1.8–2.5 cm. Seeds c. 1.2–1.5 mm, cochleariform, brown, dull or shiny.

The distribution of F. cephaliomelana, as broadly circumscribed here, is paralleled or somewhat exceeded by that of other similarly variable cactus taxa exclusive to Bambuí limestone outcrops from the same region, e.g. Tacinga saxatilis, Pilosocereus densiareolatus and Melocactus levitatus. It is divisible into two subspecies:

1. Cephalium somewhat sunken into stem, conspicuous (W Bahia & N Minas Gerais) 2a. subsp. cephaliomelana
1. Cephalium superficial or only weakly developed (cent.-S Bahia, E of the Rio São Francisco) 2b. subsp. estevesii

2a. subsp. cephaliomelana

VERNACULAR NAMES. Facheiro-preto, Xique-xique-preto.
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Southern Rio São Francisco *caatinga* element: locally co-dominant on outcrops of raised Bambui limestone within *caatinga/cerradão*, 550–750 m, south-western Bahia (W of the Rio São Francisco) and central-northern Minas Gerais. Endemic to the core area of Eastern Brazil. Map 27D.


**Conservation Status.** Vulnerable (2) [criteria B1/2bcd]; extent of occurrence = 7554 km²; PD=3, EI=2, GD=2. Short-list score (2x7) = 14. Relatively rare and restricted to isolated limestone outcrops, which may be quarried in future.

This taxon has not been studied in the field by the present author, but the characteristics of the populations treated here have been recorded in some detail by Braun & Esteves Pereira (1986–89).


**Vernacular Names.** Facheiro-da-serra, Xique-xique-amarelo.

Southern Rio São Francisco *caatinga* element: on outcrops of raised Bambui limestone amidst high *caatinga* forest, 600–650 m, central-southern Bahia (E of the Rio São Francisco). Endemic to Bahia. Map 27D.


**Conservation Status.** Endangered (3); [criteria C2b]; PD=3, EI=1, GD=1. Short-list score (3x5) = 15. Restricted to a single, albeit extensive locality, near a town, where there is the potential for limestone quarrying.


*Zehntnerella squamulosa* Britton & Rose, Cact. 2: 177 (1920). Type: Brazil, Bahia, Juazeiro, Serra do Atoleiro, 4 June 1915, Rose & Russell 19760 (US, lecto. designated here; NY, lectopara.).


Diamantina, where it is replaced by a rather variable species in terms of stem size, rib number, flower size and flower-tube & derived substrates, which it appears to avoid, and in the north-western part of the Chapada. The characters utilized by Braun chaetacantha, indumentum colour/abundance etc., the variation being only partly correlated on a regional basis. July 1989, Zappi studied here. The distribution of central-northern Bahia (drainages of Rio Salitre and Rio Jacaré) due to the presence of limestone derived substrates, which it appears to avoid, and in the north-western part of the Chapada Diamantina, where it is replaced by F. ulei.

**Vernacular names.** Facheiro, Facheiro-preto.

Rio São Francisco caatinga element: locally co-dominant with other arborescent cacti on non-calcareous (mostly granite/gneiss) inselbergs or lajedos and in very stony ground of the caatinga (rarely on arenitic rocks in cerrado or at the margins of campo rupestre), 390–1020 m, south-eastern Piauí, western Pernambuco and northern Bahia, and disjunctly in central to southern Bahia, eastwards to the watershed with the Rio de Contas drainage system. Endemic to the core area within North-eastern Brazil. Map 25B.


**Conservation status.** Lower Risk (1); PD=3, EI=2, GD=2. Short-list score (1×7) = 7.

A rather variable species in terms of stem size, rib number, flower size and flower-tube indumentum colour/abundance etc., the variation being only partly correlated on a regional basis. The characters utilized by Braun & Esteves Pereira to maintain the southern-ranging variant, F. chaetacantha, as a separate species do not seem to be consistent on the basis of the materials studied here. The distribution of F. squamosa sens. lat. is markedly disjunct, being interrupted in central-northern Bahia (drainages of Rio Salitre and Rio Jacaré) due to the presence of limestone derived substrates, which it appears to avoid, and in the north-western part of the Chapada Diamantina, where it is replaced by F. ulei.
27. ESPOSTOOPSIS F. Buxbaum


A monotypic genus endemic to the *caatinga* of Bahia and probably related to *Espostoa* Britton & Rose (*sens. str.*), from the central Andes of southern Ecuador and northern Peru. It differs from *Espostoa* in its naked pericarpel and tube, in which it strongly resembles some cephalium-bearing members of tribe Cereeae (*cf. Micranthocereus* Backeb., *sens. lat.*), but in other respects it is extremely similar to the Andean genus and could easily be mistaken for it when in sterile condition. *Gerocephalus* Ritter (see synonymy below) is an illegitimate generic name based on *Cereus dybowskii*, but published one month later than *Espostoopsis* Buxbaum.


VERANOCULAR NAMES. Cabeça-de-velho, Homem-velho, Cabeça-branca, Mandacaru-cabeça-branca, Mandacaru-de-penacho ['perracho'].

Columnar, erect, shrubby to almost treelike, to 5 m, trunk to 80 cm diam. Stems erect, 4–8 cm diam., often braking in the region of the cephalium; vascular cylinder woody, solid, very hard, with scattered perforations, cortex scarcely mucilaginous; ribs 24–33, 2 x 5–6 mm, strongly tuberculate, sinuses straight; epidermis light green with numerous pale stomata; areoles 2–4 mm, to 6 mm apart, with abundant, long, white to grey hairs covering the stem. Spines flexible to brittle, golden or reddish brown, central spines 1–2, to 2(–2.5) cm, radials 10–15, 0.3–1.5 cm. Flower-bearing region a strongly differentiated, lateral cephalium sunken into the stem and markedly protruding from its surface, with abundant, very compact white wool and bristles to 2.5 cm, the flowers developing in an irregular manner (not in order of age of cephalium areoles). Flowers 4–4.2 x 3.5–3.8 cm, all parts turning orange at the slightest touch, then blackening; pericarpel 7 x 10 mm, pale green with minute and scarcely visible bract-scales; tube to 30 x 22 mm, cylindrical, white to pale pink, naked, with broad bract-scales only at apex; perianth-segments 6–7 x 3 mm, lanceolate, acuminate, white; stamens included in relation to the perianth-segments; nectar-chamber 12 x 6–8 mm; style 28–35 mm, stigma-lobes c. 15–16, exserted; ovary locule 6 x 3–4 mm, hemiglobose in longitudinal section. Fruit depressed-globose, 20 x 22 mm, slightly compressed laterally, flower remnants deeply sunken into apex and carrying with them hairs from the cephalium; pericarpel wrinkled, olive-green, pale pink or reddish, becoming exposed at cephalium surface or ± buried. Seeds c. 1.5 mm, cochleariform, black, shiny.

Eastern *caatinga* element: dominant or co-dominant on gneiss/granite inselbergs or quartzitic rock outcrops and in the surrounding *caatinga*, 300–650 m, central-northern and eastern Bahia (markedly disjunct). Endemic to Bahia. Map 31D.


**CONSERVATION STATUS.** Endangered (3) [criteria B1/2bce]; area of occurrence = 5442 km², but area of occupancy < 500 km²; PD=4, EI=2, GD=2. Short-list score (3x8) = 24. All populations of limited extent, the northern one affected by clearance of the *caatinga* in some places, the western of the two southern ones recently burnt. Creation of reserves to accommodate this and associated species at its southern locations in the Rio de Contas valley (between Porto Alegre, Mun. Maracas and Jequie) was recommended by Taylor et al. in Oldfield (1997).

The distribution of this isolated species is markedly disjunct between northern and eastern Bahia (Rio de Contas valley), the southern form showing some differences (notably smaller stems and more exserted olive-brown fruits) that could justify subspecific status.

The better-known northern population, whence the type came, covers an extensive area within the municipio of Jaguarari and in some parts of this region the plant dominates the vegetation, forming impenetrable groves around and upon quartzitic outcrops. It may range beyond this area into the neighbouring municípios of Sento Sé, Campo Formoso, Senhor do Bomfim, Itiuíba and further east to Jeremoabo, as implied by Andrade-Lima (1989: 6) and Lützelburg (1926b: 69), but, despite being so conspicuous, there are no collections or other reports to confirm its presence in these other localities and in northern Bahia it has not been seen outside Mun. Jaguarari by the present author.

The southern populations are found on gneissic inselbergs (not quartzite) and are associated with a quite different suite of *caatinga* Cactaceae. Its disjunct distribution and the differences between the plants from the two areas implies that the species may be an ancient relict in decline.
28. ARTHROCEREUS A. Berger


Shrubby or solitary, 1–2(–4) m tall, basally branched, sometimes with a thickened, corky rootstock. Ribs 9 or more, low. Areoles close together, with felt and long hairs. Spines golden or ferrugineous, translucent, weakly differentiated into centrals and radials, centrals ascending or porrect, pungent, radials numerous, adpressed, bristle-like. Flower-bearing part of stem not differentiated. Flowers salverform, nocturnal (remaining open in the early morning in A. rondonianus); pericarpel globose, it and the tube bearing few to many areoles with hair-spines; tube elongate, cylindric to infundibuliform; perianth-segments narrow; inner segments white to lilac-pink; stamens inserted in ± 2 series, when distinguishable the upper series in a ring at the mouth of the tube; ovary locule hemicircular or rounded in longitudinal section. Fruit indehiscent, globose to obpyriform, with areoles bearing long hair-spines or bristles, funicular pulp white. Seeds ovoid, 1.2–2.0 mm.

An interesting genus endemic to Brazil, with 3 species in Eastern Brazil (campos rupestres of central to SW Minas Gerais) and a fourth, A. spinosissimus (Buin. & Brederoo) Ritter, which is rather similar to no. 1 below, but geographically isolated in Mato Grosso (Chapada dos Guimarães). This last has been separated into subgenus Chapadocereus P. J. Braun & E. Esteves Pereira (1995: 82), but its similarities to A. melanurus would seem to indicate that subdivision of the genus on geographical lines is untenable. The genus is assumed to be related to Echinopsis Zucc. (sens. lat.), but differs in its pollen (Leuenberger 1976), indehiscent fruits and unusual habit form.

In the past the genus Arthrocereus has been used in a broader sense than now, including species presently referred to Echinopsis, ie. E. mirabilis (Argentina), and Pygmaeocereus Johnson & Backeb. (= Echinopsis), ie. P. bylesianus (Peru).

The name of the genus was approved for conservation with a new type, as above, in 1993 (XV Int. Bot. Congress, Tokyo), following the discovery that the former type, Cereus microsphaericus K. Schum. (and its illegitimate, homotypic synonym, C. damazioi Weingart), was misapplied by Berger and is actually identifiable with a species of Schlumbergera Lemaire (Rhipsalidaceae). However, more recently, Eggli & Nyffeler (1996) have cast doubt on whether the generic name can be accepted as validly published by Berger (1929), but this has been contradicted by Doweld & Greuter (submitted).

1. Inner perianth-segments pink, anthers purple (Serra do Cabral) 2. A. rondonianus
1. Inner perianth-segments and anthers white or cream (Serra do Espinhaço and Serra da Mantiqueira) 2
2. Flower-tube ± naked, with only few areoles and hair-spines; stems usually decumbent to ascending, often segmented, sometimes very short to nearly spherical (usually on canga formation) 3. A. glaziovii
2. Flower-tube densely covered in areoles and conspicuous hair-spines; stems ± erect, not segmented (on substrates other than canga) 3

1. Arthrocereus melanurus (K. Schumann) L. Diers, P. J. Braun & E. Esteves Pereira in Kakt. and. Sukk. 38: 312–315 (1987). Type (syntypes): Brasilia, (?) Minas Gerais, Sello 1000 (B†; isosyntype at MO is A. glaziovii); Serra de São João del Rey [Serra do Lenheiro], Glaziou s.n.
Cer


VERNACULAR NAME. Sabugo-do-capeta.

Shrubby or single-stemmed, 0.4-2.0(-4.0) m tall, generally with a corky, thickened rootstock. Branches erect, not segmented; epidermis bright green; ribs 9-19. Areoles to 3 mm diam., 4-6 mm apart, felt greyish, basal areoles with indeterminate growth. Flowers nocturnal, sweetly scented; pericarpel and tube ± covered in triangular bract-scales with hairy areoles; perianth-segments linear, acuminate, fleshy, pale green with brownish shades, strongly reflexed, touching the outside of the flower tube at full anthesis, inner segments linear-lanceolate, slender, delicate, cream or whitish, erect; stamens in 2 series; stigma-lobes exserted.

The following subspecies are recognized:

1. Flowers 9-11.5 cm; pericarpel and tube densely covered in areoles with dark, ferrugineus, hair-spines; perianth-segments 23-40 mm (Rio Grande drainage, SW Minas Gerais) 1a. subsp. melanurus
   1. Flowers 10-16 cm; pericarpel and tube covered in areoles with pale brown or pinkish, soft hair-spines; perianth-segments 40-60 mm 2
   2. Plants with few or no basal branches, reaching 2 m or more, stout rootstock not visibly developed; ribs 12-19 (Serra do Ibitipoca, MG) 1b. subsp. magnus
   2. Plants shrubby, branching freely at base, not > 1 m, stems slender; rootstock well-developed; ribs 9-12 (Rio São Francisco drainage, E foot of Serra do Cipó, MG) 1c. subsp. odor us

1a. subsp. melanurus

Shrubby, to 80 cm tall, with a corky, thickened rootstock. Branches to 4.5 cm diam., tapering to 1.5 cm, erect; ribs 10-17, 3 x 5 mm. Spines yellow to reddish brown, central spines 5-7, stout, porrect, to 3.2 cm, radials numerous, thin but bristle-like and flexible, 4-5 mm. Flowers 9.2-11.5 x 6.5-8.0 cm; pericarpel and tube completely covered in triangular bract-scales with densely hairy areoles and yellow, brown or ferrugineus stiff hairs to 1.5 cm; tube 5-6 x 1 cm at its narrowest point; outer perianth-segments to 23-40 x 4-6 mm, inner segments to 32 x 3.5-5.0 mm; the innermost stamens inserted at 2.5 cm above pericarpel, with long filaments, the outermost series at the apex of tube, filaments 10 mm, anthers to 1.9 mm; ovary locule to 7 mm diam.; style 6-7.7 mm, stigma-lobes 12-13, exserted, 8-10 x 0.4 mm, slender. Fruit rounded, c. 3.0 cm diam., pericarp green, densely covered in bract-scales and trichomes. Seeds c. 1.1 mm, testa-cells convex, with cuticular folds.

CONSERVATION STATUS. Vulnerable (2) [criteria B1/2c]; extent of occurrence = 9669 km²; PD=3, EI=1, GD=1. Short-list score (2x5) = 10.


Erect, single-stemmed or somewhat branched at base, to 2(-4) m. Stems stout, 3.5-5.0(-8.0) cm diam.; ribs 12-19, 3 \times 7 mm. Spines golden brown, central spines to 2-3.5 cm, radials 8-10 mm. Flowers c. 16 cm, perianth-segments > 50 mm. Fruit to 45 x 50 mm; pericarp green with orange tinge, areoles hairy. Seeds 1.9-2.0 mm.

South-eastern campo rupestre (Rio Preto / Rio Paraiba do Sul drainage) element: amongst rocks in campo rupestre, c. 1500 m, Serra do Ibitipoca, southern Minas Gerais. Endemic to the core area within Minas Gerais. Map 39.


CONSERVATION STATUS. Endangered (3) [criteria C2b]; area of occupancy estimated to be < 50 km²; PD=3, EI=1, GD=1. Short-list score (3x5) = 15. Endangered due to its very limited range, but located within a protected area and thus possibly Lower Risk and Conservation Dependent.

An unidentified illustration of this giant subspecies in the above habitat can be found in Leme & Marigo (1993: 68).


Shrubby, to 1 m tall, branching at base, with a corky, thickened rootstock. Branches to 2-3.3 cm diam., erect or hanging from cliffs; ribs 9-12, 2-3 x 5 mm. Spines yellow to reddish, central spines 6-7, stout, the largest porrect, to 4(-6) cm, radials numerous, thin to bristle-like and flexible, 4-5 mm. Flowers 10--16 x 8-10 cm; pericarpel and tube partially covered in triangular bract-scales with pale to pinkish brown hairs to 1.5 cm in their axils; tube 4-8 x 0.8--1.9 cm at its narrowest point, ridged; outer perianth-segments 40 x 5-7 mm; inner segments 40--50 x 6-9 mm; the innermost stamens inserted at 4 cm above pericarpel, with long filaments, the outermost series at the apex of tube, filaments 15--18 mm, anthers to 2.2 mm; ovary locule 8 mm diam.; style 10-13 cm, stigma-lobes 12-13, 10 mm, slender. Fruit rounded to ovate, 3-4 cm diam., pericarp green, covered in bract-scales and pale brown trichomes. Seeds c. 1.2-1.8 mm, testa-cells convex, with cuticular folds.

South-eastern campo rupestre (Serra do Cipó) element: amongst rocks in campo rupestre, c. 900 m, central-southern Minas Gerais. Endemic to the core area within Minas Gerais. Map 39.


Shrubby or single-stemmed, to 1 m tall or more, with a corky, thickened rootstock; stems 1.5-3.0 cm diam., erect, not segmented; epidermis bright green; ribs 13-18, 3 x 4 mm. Areoles to 3 mm diam., 5-7(-10) mm apart, felt greyish. Spines yellow to pale brown, central spines 6-7, stout, the largest porrect, to 7 cm, radials numerous, thin to bristle-like and flexible, 5-10 mm. Flowers nocturnal, remaining open until early morning, 10-13 x 9 cm, not scented; pericarpel and tube with scattered triangular bract-scales with hairy areoles and pale to pinkish brown hairs to 1.5 cm; tube 6-7 x 0.8 cm at its narrowest point, curved and ridged; outer perianth-segments to 50 x 4 mm, linear-lanceolate, fleshy, pale green with pinkish shades or pale pink, strongly reflexed, inner segments to 8-12 cm, stigma-lobes 10-11, exerted, whitish. Fruit rounded to ovoid, 4 x 3 cm; pericarp purplish to brownish, with bract-scales, bristles and trichomes. Seeds c. 2 mm, testa-cells convex, with cuticular folds.

South-eastern campo rupestre (Serra do Cabral) element: between rocks and in bushy places, campo rupestre, c. 700-1200 m, Serra do Cabral, central Minas Gerais. Endemic to the core area within Minas Gerais. Map 37C.


CONSERVATION STATUS. Endangered (3) [criteria B1/2c]; area of occupancy estimated to be < 500 km²; PD=3, EI=1, GD=1. Short-list score (3 x 5) = 15. Known from an area of rather limited extent, there being only c. 20 km separating the two adequately localized sites recorded above.

The lilac-pink flowers of this species are both striking and beautiful.


[A. microsphaericus sensu (K. Schum.) A. Berger, Kakteen: 337 (1929) et auct., non Cereus microsphaericus K. Schum. (= Schlumbergera microsphaerica (K. Schum.) Hövel).]


[Trichoereus damazioi sensu (Weingart) Werderm., Bras. Säulenakt.: 94 (1933), non Cereus damazioi Weingart, nom. illeg.]

Procumbent or erect, shrubby, 20–30 cm tall, stems rarely to 60 cm or more. Branches 3–4(–4.5) cm diam., erect or decumbent, generally segmented, sometimes losing the growing point and the segments becoming very short or almost spherical; epidermis dark green; ribs 10–16, 2–3 × 4–6 mm. Areoles to 2.5 mm diam., 4 mm apart, felt greyish. Spines yellow to dark reddish brown, central spines 4–8, stout, the largest porrect, to 4 cm, radials numerous, thin to bristle-like and flexible, to 8 mm. Flowers nocturnal, 8–15 × 5–8.5 cm, sweetly scented; pericarp and tube bearing few triangular bract-scales with hairy areoles and few, pale hairs; tube 60–75 × 6–8 mm at its narrowest point, ridged; outer perianth-segments to 30 × 6 mm, linear, acuminate, fleshy, pale brownish pink or greenish, strongly reflexed; inner segments to 18 × 5 mm, linear, acute, slender, delicate, cream or whitish, erect; stamens in two poorly distinct series, the innermost inserted at 2.5–3.5 cm above pericarpel, with long filaments, the outermost series at the apex of tube, filaments 5–10 mm, anthers to 1.5 mm; ovary locule 8–9 mm diam.; style 5–9 cm, stigma-lobes 7–12, exserted, 6 mm, slender. Fruit depressed-globose to obpyriform, 2–3 cm diam.; pericarp reddish brown, naked or nearly so. Seeds c. 1.5–1.8 mm, testa-cells convex, with cuticular folds.

South-eastern campo rupestre element on iron-rich rock (canga) in campo rupestre, to 1300–1750 m, east and south of Belo Horizonte, central-southern Minas Gerais. Endemic to the core area within Minas Gerais. Map 39.


Without locality or date, Sello 1000 (MO) [isosyntype no. for A. melanurus, q.v.].

CONSERVATION STATUS. Endangered (3) [criteria B1/2bcd]; extent of (historical) occurrence = 672 km²; PD=3, EI=1, GD=2. Short-list score (3×6) = 18. Many of its former habitats have been eliminated through the mining of iron ore and its isolated populations are very small (< 100 individuals).

Further field studies are needed to evaluate the status of the erect and prostrate forms of this species.

**VERNACULAR NAMES.** Roseta-do-diabo, Coroa-de-frade.

Stems depressed-globose, often half buried in the ground, non-mucilaginous, lacking woody tissues, very small or to c. 10 × 25 cm, remaining solitary or sprouting offsets; ribs 9–26, well-defined or broken up into tubercles; areoles small to large but soon becoming glabrous, indeterminate growth absent. Spines relatively few, usually 3–17 per areole, sometimes very stout or minute. At maturity stem apex transformed into a white-woolly and often bristly cephalium, bearing flowers and fruit from its deeply sunken apex. Flowers salverform, nocturnal, sweetly scented (hawkmoth syndrome), 1–6 or more rapidly developing at the same time; pericarpel ovoid, usually quite naked, tube (including the nectar-chamber) elongate, bearing leafy bract-scales glabrous in their axils; perianth-segments narrowly oblanceolate, the outermost often greenish, brownish or even deep pink, inner series white, rarely pale pinkish; stamens numerous, inserted along the inside of the tube, and at its apex, on short filaments, sometimes the lowermost inserted above a whorl of hairs which protect the nectar-chamber; style long or short, stigma-lobes c. 5–6, slender, whitish. Fruit clavate, usually naked, dehiscing by longitudinal splits in the pericarp, red, orange-yellow, greenish or white, pulp scanty, but very attractive to ants. Seeds 0.8–2.0 × 0.8–2.2 mm, hat-shaped, black, very shiny, testa tuberculate, the tubercles sometimes elongated and pointed.

A genus of 6, very closely related species, all of which occur in Eastern Brazil (Ceará, Piauí, Bahia to N-cent. Minas Gerais), 5 being endemic and mostly either patchy in distribution or extremely local, rare and often in danger of extinction (the whole genus has accordingly been placed in Appendix I of C.I.T.E.S. since 1992). However, the complex species, *D. heptacanthus* (here recorded from NW Minas Gerais, W & S-cent. Bahia & SW Piauí), ranges as far as northeastern Paraguay and eastern Bolivia, through Mato Grosso do Sul, Goiás and Mato Grosso. It is curious that, except for a single population of *D. heptacanthus* subsp. *catingicola* from Mun. Paramirim and *D. zehntneri* subsp. *boomianus* near Morro do Chapéu, the genus has not been recorded from central and southern Bahia (east of the Rio São Francisco), although suitable habitats exist, eg. in the Chapada Diamantina. Instead, such habitats are characterized by similarly adapted *Melocactus* species (eg. *M. paucispinus*, *M. conoideus*, *M. concinnus*, *M. violaceus*).

As the generic name implies, the plants are disc-shaped, and over much of its range *Discocactus* is found in habitats through which fire passes regularly (notably the *cerrado* and associated *campo rupestre*). This depressed, ground-hugging habit protects the plant against the worst effects of burning, since the region a few centimeters above the ground is usually much cooler from air being drawn in as the fire passes. Three of the rarer, northern species, however, occur in the *caatinga* and apparently are not normally subjected to fire.

*Discocactus* is clearly very closely related to the much larger genus, *Gymnocalycium* Pfeiffer ex Mittler (1844), which replaces it to the south and south-west, in Southern Brazil, Paraguay, Argentina and eastern Bolivia. *Gymnocalycium* differs mainly in lacking a cephalium, in having broader, diurnal, brightly coloured flowers and in displaying a greater diversity in seed-morphology. It may prove to be paraphyletic with respect to *Discocactus* and the latter name has priority, raising the fraught question of which name should be preferred or conserved.

1. Radial spines 3–8 per areole, often > 1.5 mm thick; stem solitary or offsetting when damaged by fire, > 11 cm diam.
1. Radial spines > 8 per areole, to 1.5 mm thick; stems freely offsetting, or solitary and < 11 cm diam.

2. Exposed part of vegetative stem with only 3 areoles visible per rib; ribs not broken up by tubercles (N Bahia to Piauí and Ceará)

2. bahiensis

2. Exposed part of vegetative stem with > 3 areoles per rib and/or ribs tuberculate with deep sinuses between successive areoles

3. Seed 1.5-2.0 mm; fruit white or greenish, rarely pinkish red at apex; ribs 9-26, ± tuberculate; spines often flattened, > 1.5 mm thick

4. Ribs 9-26, acute-edged, with shallow sinuses between areoles on the same rib (Minas Gerais: E of Rio São Francisco)

4. placentiformis

4. Ribs 10-12, composed of rounded tubercles with deep, acute-edged sinuses between areoles on the same rib (SW Piauí, W & cent.-S Bahia & NW Minas Gerais)

3. heptacanthus subsp. catingicola

5. Ribs not tuberculate; stem solitary, dark purplish green to brownish; spines minute, adpressed, claw-like (N Minas Gerais: near Grão Mogol, sand)

5. pseudoinsignis

5. Ribs ± tuberculate; stem usually offsetting, light green or spines not as above (N Bahia)

6. horstii

5. Ribs strongly developed, spiralled, obscuring the ribs


Solitary or strongly caespitose; stem 3-7 × 2-12 cm, light to dark green; ribs 12-21, broken up into ± spiralled tubercles; areoles to c. 15 mm apart on the ribs. Spines creamy white to grey, interwoven and ± hiding the stem, centrals 0-2, radials 9-18. Cephalium to 3.5 × 4.5 cm, white-woolly, with 7-60 mm, erect, dark bristles at its margin. Flowers 33-77 × 35-55 mm, greenish in bud; outer perianth-segments 19-28 × 3.5-6.0 mm, green to yellowish, inner segments 17-25 × 4-6 mm, white. Fruit commonly bright red, rarely white-tinged-green, 18-46 × 6-9 mm. Seed 0.8-2.0 × 0.8-2.2 mm, testa densely covered by elongate tubercles.

This species is divisible into two subspecies:

1a. subsp. zehntneri

Solitary or sparingly offsetting, stems globose to elongate; ribs c. 12-13, tubercles 10 × 15-20 × 15-20 mm; areoles c. 9-10 × 5-6 mm. Central spines 0-2, to 70 × 2 mm, radials c. 11, to 25-75 × 1.5 mm. Fruit red.

Northern Rio São Francisco caatinga element: on exposed arenitic rocks and gravelly soil in caatinga, 450-500 m, Mun. Sento Sé, northern Bahia. Endemic to Bahia. Map 25D.


CONSERVATION STATUS. Endangered (3) [criteria B1/2bcd]; PD=1, EI=1, GD=2. Short-list score (3x4) = 12. Part of its former habitat has been submerged beneath the Represa [Lago] de Sobradinho.


Offsetting freely, stems depressed, sometimes ± buried when growing in sand; ribs 13-21, tubercles 3-11 x 2-13 x 2-13 mm; areoles 3-7 x 1.5-3 mm. Central spine 0-1, to 60 mm beneath the cephalium, radials 4-30 x <1 mm. Fruit red, or white, tinged green.

Northern campo rupestre (Chapada Diamantina) element: on exposed arenitic rocks often with an accumulation of gravel or in pure quartz sand, caatinga / campo rupestre, c. 700-1000 m, northern Bahia. Endemic. Map 28C.

CONSERVATION STATUS. Vulnerable (2) [criteria B1/2c]; PD=1, EI=1, GD=2. Short-list score (2x4) = 8. Habitats fragmented and subject to collection, at least one being directly accessible from a main road, although soon to be designated as a protected area.


[D. placentiformis sensu Britton & Rose, Cact. 3: 220, fig. 233 (1922) non (Lehm.) Schumann.]

VERNACULAR NAME. Frade-de-cavalo.

Solitary or freely offsetting in age, 4-7 x 5.5-18.0 cm, grey- to light or yellow-green; ribs 10-15, to 30 x 20 mm, sometimes composed of tubercles to c. 7-10 x 15-30 x 15 mm; areoles oval, c. 6-10 x 3-8 mm, 10-23 mm apart, sometimes only 3 visible per rib above ground. Spines 5-11, all radial, strongly recurved, sometimes hooked at apex, in some forms interwoven with those of adjacent areoles, pale yellow to pinkish brown at first, later greyish or dark brown to blackish, to 35(-45) x 0.5-2.5(-3.0) mm, the uppermost 1-3 in each areole very small when present. Cephalium low, to 47 mm diam., with soft whitish wool, bristles when present hairlike, to 30 mm, yellow or brownish. Flowers 40-72 x 30-54 mm; outer perianth-segments green, yellow or pinkish brown, inner segments 8--
Northern *caatinga* element: on exposed, gravelly river terraces amongst limestone or iron-stained quartzite, and seasonally inundated river plain, under and between jurema-preta (*Mimosa tenuiflora*) and carnaúba (*Copernicia prunifera*) within the *caatinga*, 380–650 m, Rio São Francisco drainage of northern Bahia (probably in adjacent Pernambuco), Ceará and northwestern Piauí (Rio Canindé). Map 21A.

CEARA: unlocalized, photograph communicated by Prof. Mattos, UFCE (K).


PERNAMBUCO: vaguely reported from near Santa Maria da Boa Vista, Uebelmann (ms).


**CONSERVATION STATUS.** Endangered (3) [criteria A1ac]; PD=2, El=1, GD=2. Short-list score (3×5) = 15. Part of its range was eliminated by permanent inundation from the Represa de Sobradinho (BAfPE) in the 1970s and the remainder has been heavily impacted by agriculture and road/ house construction; some of its few sites being accessible by road and visited by collectors.

The distribution of this taxon seems rather disjunct but remains inadequately known at present. It is related to the preceding species, occasionally bearing red fruits (cf. Rose & Russell 19742) and both are assumed to have been derived from within the *D. heptacanthus* complex, sharing similarities with the geographically close *D. heptacanthus* subsp. *catingicola* (q.v.).

The plant described as *D. subviridigriseus* Buin. *et al.* is connected to typical *D. bahiensis* by a series of forms from northern Bahia, comprising Braun 642, Horst 437 (*D. bahiensis* sensu Buining), the actual type of the species (Rose & Russell 19783) and Horst & Uebelmann 633. The ‘*D. subviridigriseus*’ form extends into Piauí and Ceará and may be expected to occur in Pernambuco. It seems to be an ectotype of river flood plains in the *caatinga*, where in northern Bahia, at least, it is associated with semi-barren habitats with bushes of jurema-preta (*Mimosa tenuiflora* (Willd.) Poir.) and carnaúba palms, and is evidently at times subjected to temporary inundation. It does not merit recognition as a subspecies in view of the gradual intergradation with typical *D. bahiensis* already noted (cf. Braun & Esteves Pereira, l.c.).


Only the following subspecies is found in Eastern Brazil:


Solitary, 4–9 x 11–20 cm, plain green; ribs 10–12, completely broken into tubercles, which are 15–20 x 22–40 x 15–30; areoles positioned slightly below and sunken into tubercle apex, oval, 6–8 x 4–5 mm, 15–30 mm apart, 4–5 visible above ground on each rib. Central spine 0–1, to 20 mm, radials 5–8, weakly recurved, pale yellow then grey to brownish in age, to 36 x 1.25–2.50 mm. Cephalium 3–7.5 cm diam., with white wool and 35–45 mm, yellow to dark brownish bristles. Flowers 50–60 x 40–60 mm, light brown to olive-green in bud; outer perianth-segments 22–24 x 7–8, white to greenish without, inner segments 18–20 x 5–7, white. Fruit white or faintly pinkish, 40–45 x 8–13 mm. Seed 1.5–2.0 x 1.5–2.0 mm, with irregularly spaced, elongate, pointed tubercles.

Western cerrado element: on exposed gravel or sand, cerrado and cerrado-caatinga ecotone, 450–700 m, south-western Piauí, western and central-southern Bahia and north-western Minas Gerais. Endemic to the core area within Eastern Brazil. Map 35B.


BAHIA: W Bahia, Mun. Barreiras, near old airport, Horst 205A (U, ZSS, K); Mun. São Desidério, west of Sitio Grande at waterfall, Horst 392 (U); Mun. Santana, near Porto Novo, Horst 448 (U, ZSS); I.c. (?), Braun 341 (ZSS); Mun. Santa Maria da Vitória, airport, Horst & Uebelmann 760 (ZSS, K); Mun. Coribe, 8 km south of Coribe, Horst & Uebelmann 760A (ZSS); cent.-S Bahia, Mun. Paramirim, 28 Nov. 1988, Taylor in Harley 25558 (K, SPF, CEPEC).


Conservation Status. Vulnerable (2) [criteria B1/2c]; area of occupancy estimated to be < 2000 km²; PD=1, EI=1, GD=2. Short-list score (2x4) = 8. Vulnerable due to the fragmented nature of its distribution and small population size. In need of regular monitoring, since the cerrado and caatinga habitats are undergoing much destructive change.

Despite Buining's use of the epithet eatingicola, this subspecies is more typical of the cerrado and probably occurs in the caatinga only at its eastern and north-western limits. D. heptacanthus subsp. heptacanthus (sensu lato) replaces it to the west and subsp. magnimmamus (Buining & Brederoo) N. P. Taylor & Zappi (1991: 86) occurs in parts of Mato Grosso do Sul and Paraguay. The collections cited from south-western Piauí and central-southern Bahia (Harley et al. 25558, which is not precisely localized for conservation reasons) are somewhat intermediate with D. bahiensis and would be an argument for synonymizing the latter taxon as a further subspecies of D. heptacanthus.

The synonymy given above under the species name refers only to names based on types collected within eastern Brazil, as treated here and in the adjacent parts of Minas Gerais, Tocantins and Goiás. All other Discocactus names published up to the end of 1999, which are not accounted for under other species, are additional synonyms of D. heptacanthus, sensu lato.


D. tricornis Monv. ex Pfeiffer, Abbild. Beschr. Cact. 2: t. 28 (1850). Type: not known to have been preserved. Lectotype (designated here): Pfeiffer, l.c., t. 28 (1850).


Very variable; stem solitary unless damaged by fire, 3.5–10 × 12–25 cm, light to dark green; ribs 9–26, well-defined, but weakly to strongly tuberculate, with shallow sinuses between successive tubercles, to 30 mm high and 40 mm wide near stem base, the tubercles 8–15 × 20–30 × 12–25 mm; areoles circular to oval, 4–9(–15) × 3–8(–12) mm, somewhat sunken, 15–25 mm apart on the ribs, 3–7 visible per rib above ground level. Spines 3–8(–10), whitish, dull yellow, brownish, pinkish or reddish, later grey, central spine 0(–1), to 20 mm, lower 3–5 radials to 40(–45) × 4 mm, mostly flattened and slightly recurved, sometimes splitting longitudinally, other spines when present much smaller. Cephalium 1–7 × 4–11 cm, white-woolly, with or without 30–45 mm, brownish bristles. Flowers 45–85 × 40–80 mm, pale green, brown or deep pink in bud; outer perianth-segments 24–35 × 3–7 mm, inner segments 15–30 × 2–5 mm, white or pale pinkish. Fruit 30–50 × 5–15 mm, white to pink or reddish at apex. Seed 1.5–1.9 × 1.4–2.0 mm, testa with irregularly spaced, short to elongate, pointed tubercles.

Widespread South-eastern campo rupestre / cerrado element: on arenitic rocks, quartz sand and gravel, cerrado / campo rupestre, rarely within the southern limits of the caatinga, 550–1275 m, east of the Rio São Francisco, central and northern Minas Gerais. Endemic to the core area within Minas Gerais. Map 35D.


**Conservation Status.** Vulnerable (2) [criteria B2b(3)c/d]; extent of occurrence = 42111 km², but area of occupancy almost certainly < 2000 km²; PD=2, EI=1, GD=2. Short-list score (2×5) = 10. Vulnerable, since most populations are small and isolated from one another.

Typical *D. placentiformis* (Lehm.) Schumann is assumed to be the plant found about Diamantina, Minas Gerais. This region was visited before 1827 by botanists such as Riedel (see Urban 1906: 90), who was cited as the collector of the type of the synonymous *D. linkii* Pfeiffer (*Melocactus besleri* Link & Otto pro parte), based on material contemporary with that of *Cactus placentiformis* Lehmann. The illustration in Martius, Flora brasiliensis 1 (1, Tabulæ physiognomicae): t. XLVI (1855) is presumably intended to depict this species growing in the Serra do Ouro Branco, and should, perhaps, be put down to artistic licence, since there is no other evidence to suggest that it ever ranged much further south than the last municipio cited above.

The large-stemmed, many-ribbed, thick-spined form of this species (syn. *D. pulvinicapitatus, D. latispinus, D. pseudolatispinus*), from the western slopes of the Serra do Espinhaço, and from the Serra do Cabral and northwards (municipios Claro dos Poços, Jequitai, Bocaiuva, Francisco Dumont & Buenópolis), is distinctive and may be worthy of recognition as a subspecies. It is connected to typical forms of the species by populations found near the western edge of Mun. Diamantina (syn. *D. multicolorispinus*). The form from the north-eastern population (Mun. Grão Mogol, syn. *D. pugionacanthus*) is also distinctive for its ± strongly tuberculate stem and could be mistaken for *D. heptacanthus*. Some plants from the region north of Diamantina, eg. *Horst & Uebelmann* 232 cited above, superficially resemble *D. pseudoinsignis* (see below) in their spination.


Solitary, 7–9 × 12–21 cm, light to dark green; ribs 12–13, almost straight and even, not tuberculate, 15–25 mm high, 20–40 mm broad; areoles 6 × 4–5 mm, 10–30 mm apart and 5–6 visible per rib above ground. Spines 5–8(–9), ± terete or at least isodiametric, grey to blackish, central 0–1, 10–30 × 0.5–1.5 mm, radials 5–7(–8), lower 3 c. 25–42
\*1-1.5 mm, straight or variously curved, others much smaller. Cephalium to 5 × 10 cm, white-woolly, usually with exserted, to 40 mm, dark brownish bristles. Flowers c. 75 × 60 mm, pale brownish olive-green in bud; outer perianth-segments c. 30 × 4 mm, inner segments c. 22 × 2 mm, white. Fruit 32–45 × 5–9 mm, orange-yellow to reddish at apex. Seed 1–1.4 × 1.0 mm, regularly tuberculate.

South-eastern campo rupestre (Grão Mogol) element: in pure quartz sand or sand between arenitic rocks, campo rupestre, 700–1000 m, Mun. Cristália and Mun. Grão Mogol, northern Minas Gerais. Endemic to the core area within Minas Gerais. Map 36B.


CONSERVATION STATUS. Endangered (3) [criteria B1I2c]; extent of occurrence = 89 km² (probably under-recorded); PD=2, EI=1, GD=1. Short-list score (3×4) = 12. Population numbers affected by habitat modification.

Following the discovery of this species in the early 1970s, Buining (1980) misidentified it as *D. insignis* Pfeiffer, a name previously and correctly referred to the synonymy of *D. placentiformis* (Lehm.) Schumann by previous authors (see Taylor 1981: 40). Pfeiffer’s 19th Century description calls for a plant with only 10 ribs (consistently 12–13 in *D. pseudoinsignis*) and, together with his illustration of the type, clearly indicates that the bract-scales on the flower-tube and outer perianth-segments of the flower were deep pink, which is a feature of some forms of *D. placentiformis*, but not of *D. pseudoinsignis* (outer segments pale brownish olive-green).

*D. pseudoinsignis* is similar to the variable *D. placentiformis* and falls within the geographical range of the latter (which is recorded from the northern part of Mun. Grão Mogol, Serra da Bocaina), but can be distinguished by its non-tuberculate ribs, slender spines and smaller seeds. Its closest relative is probably the following, with which it is partly sympatric.


Solitary, to 2 × 6 cm, dark brown- to purplish green; ribs 15–22, straight and narrow, 6–8 mm high, c. 4 mm wide at the rounded edge, and to 10 mm apart, not tuberculate; areoles oval, c. 1.5 × 1.0 mm, very slightly sunken into the ribs, to 5 mm apart, 4–6 visible per rib above ground level. Spines 9–11, all radial, pectinate, tightly adpressed to stem, claw-like, brown with a grey coating, to 3.5 × 0.75 mm. Cephalium to 1.5 × 2 cm, white-woolly, with erect, dark brown, 20 mm bristles. Flowers solitary or paired, 60–75 × 60 mm, pale yellow-brown in bud; tube only 4–5 mm diam. at narrowest point; perianth-segments white, outer 30–35 × 3.5–8.0 mm, inner 20–24 × 6–9 mm. Fruit 30 × 4 mm, white. Seed 1–1.1 × 0.9–1.0 mm, tuberculate.

South-eastern campo rupestre (Grão Mogol) element: in quartz gravel and sand beneath shrubs in campo rupestre, c. 1000 m, Serra do Barão, northern Minas Gerais. Endemic to the core area within Minas Gerais. Map 36B.

MINAS GERAIS: Mun. Grão Mogol [precise location withheld for conservation reasons], *Horst 360 (U), 1987, P.J. Braun 851 (ZSS).*

CONSERVATION STATUS. Critically Endangered (4) [B1I2c]; extent of occurrence < 100 km²; PD=2, EI=1, GD=1. Short-list score (4×4) = 16. Now known from two adjacent populations, one heavily impacted by collectors in the recent past and by ongoing habitat modification through quartz extraction. A state reserve has recently been
established ('Reserva Estadual da Serra do Barão') and should result in increased protection, the authorities being well aware of the interest in the plant (M. Machado, *in litt.*, 20.05.2000).

A dwarf neotenic ally of *D. pseudoinsignis*, and perhaps the most remarkable of all Brazilian cacti. Heavily collected in the early 1970s for the European horticultural market (Buining 1974a: 70) and regarded as 'Critically Endangered'. *D. woutersianus* Brederoo & Broek in *Succulenta* 59: 203 (1980) was said to have been based on material of *Horst* 360, but according to Riha in *Kaktusy* 26: 59 (1990) it is identifiable as the hybrid *D. horstii* × *D. pseudoinsignis* ['*D. insignis*'] originating in cultivation and now also reported from the wild (Uebelmann 1996: HU 1497).

The name *D. subnudus* Britton & Rose (1922: 217) was based on a photograph of a badly damaged plant said to emanate from the coast of Bahia. No *Discocactus* has subsequently been reported from coastal Brazil and the provenance of this plant and its identity remain doubtful. Lützelburg (1926, 3: 69, 111) combined this epithet as *Echinocactus subnudus*, but may have applied it to *Melocactus violaceus* in error.
30. UEBELMANNIA Buining


Globose to elongate, usually single-stemmed, 5–100 cm; vascular cylinder not woody, outer cortex generally with gummiferous cells (disintegrating and fusing vertically into ducts in U. gummifera) and positioned within or close to the ribs. Seedlings globose, sometimes developing beneath the surface of the substrate. Stems erect to decumbent, 5–17 cm diam., epidermis bright to grey-green, whitish, reddish or dark brown, distinctly roughened; hypodermis with dense accumulations of pectin; ribs c. 13–40, broken or not into tubercles. Areoles with felt and white or brownish long hairs; spines hard, golden to greyish, central spines porrect, radials sometimes absent. Flower-bearing region of stem apical, not differentiated. Flowers diurnal, yellow or reddish, 1.5–2.5 x 1–2.5 cm; pericarpel and tube with bract-scales, hairs and eventually bristles; tube rotate; perianth-segments triangular to lanceolate, spreading to reflexed. Fruit narrowly turbinate, few-seeded, flower remnant drying whitish, erect; pericarpel with bract-scales and some glabrescent hairs, red; funicular pulp translucent. Seeds 1.1-2.4 mm, cochleariform, brown to black, with the hilum-micropylar region depressed; testa-cells flat or convex; cuticular folds absent.


A remarkable, taxonomically isolated genus of 2–3 species, endemic to a relatively small region of central Minas Gerais (campos rupestres, sensu lato) and since 1992 placed on Appendix I of C.I.T.E.S. in view of its rarity and the potential risks to its survival from commercial and private collection in the wild. Marlon Machado (in litt., 04.02.2000; see also Schulz & Machado 2000) has studied the genus extensively in habitat and has concluded that the grounds for recognising more than 2 species may be weak, U. buiningii potentially being only a local form of U. gummifera. However, relatively few plants of each have been investigated for the crucial anatomical differences that are currently used to distinguish them, so it seems premature to make taxonomic changes here. The distribution maps for this genus presented in Chapter 4 are partly based on data kindly supplied as GPS co-ordinates by Marlon Machado, which are not given here in order to protect these rare plants from unscrupulous collectors.

It is assumed that the flowers are adapted for visits by hymenoptera, as observed by Schulz & Machado (2000), but Heek & Strecker (1995) have also noted hummingbirds visiting the flowers of U. gummifera.

The genus is only provisionally placed in Trichocereeae. Its correct position is very uncertain at present and will probably only become clearer when additional molecular evidence becomes available.

1. Ribs not broken up into tubercles; flowers to 18 x 10 mm; fruit reddish to deep pink, conspicuous; seeds with flat testa-cells (Subg. Leopoldohorstia) 3. pectinifera

1. Areoles borne on pronounced tubercles; flowers > 20 x 15 mm; fruit yellowish or greenish, inconspicuous; seeds with convex testa-cells (Subg. Uebelmannia) 2

2. Ribs 15–22; stem cortex with mucilage cells but lacking ducts 1. buiningii

2. Ribs 22–42; stem cortex with vertically arranged mucilage ducts 2. gummifera

Subg. Uebelmannia

See Key, above. Found only on quartz sands and gravels.

Globose to subcylindric, solitary, to 12 × 8 cm; without gummiferous ducts under the epidermis. Epidermis greenish red to brownish, rough. Ribs 16–18, strongly tuberculate; tubercles conical, deflexed, to 7.5 mm high and 6 mm broad, c. 5 mm apart. Areoles on top of the tubercles, 2 mm diam., with sparse greyish wool when young, later glabrescent. Spines yellow-brown, black tipped, soon becoming whitish, curved upwards, flattened on upper surface, central spines 2–6, to 15 mm, radials 0–4, to 5 mm. Flower to 27 × 25 mm; tube c. 9 mm, with bract-scales, white hairs and brownish bristles; perianth-segments deep yellow; style 14 mm; stigma-lobes 6–7. Fruit 5–6 × 4–5 mm, yellowish. Seed 1.2–1.4 × 0.8–0.9 mm, cochleariform to reniform, black; testa-cells convex.

South-eastern *campo rupestre* (Serra Negra) element: in quartz sand, *campo rupestre*, c. 1200 m, Serra Negra, Minas Gerais. Endemic to the core area within Minas Gerais. Map 38B.


**CONSERVATION STATUS.** Critically Endangered (4) [criteria C2]; PD=3, EI=1, GD=1. Short-list score (4×5) = 20. According to Braun & Esteves Pereira (I.c.) and Schulz & Machado (2000) this species is on the verge of extinction and is scarcely if at all in cultivation, where it has proved very difficult. Affected by collection of plants and seed.


**VERNACULAR NAMES.** Coroa-de-frade, cabeça de frade.

Globose to cylindrical, elongate, solitary, 5–30(-40) × 6–15 cm; with gummiferous ducts under the epidermis. Epidermis greenish red to brownish, rough. Ribs c. 30–40, strongly tuberculate; tubercles conical, deflexed, to 4.5 mm high and 4–5 mm broad, c. 4 mm apart. Areoles on top of the tubercles, 2 mm diam., when young with sparse greyish wool, later glabrescent. Spines greyish or whitish, correct or curved upwards, flattened on upper surface, central spines 2–6, 10–25 mm long, radials 0–4, to 8 mm. Flower 20–25 × 18–30 mm; tube c. 10 mm, with triangular bract-scales and white hairs; perianth-segments deep yellow; style 12 mm; stigma-lobes 7–8. Fruit 6–8 × 4–6 mm, yellowish or greenish. Seed 1.1–1.3 × 0.8–0.9 mm, black or dark reddish brown; testa-cells convex.

South-eastern *campo rupestre* (Serra Negra / Serra do Ambrósio) element: in quartz sand, *campo rupestre*, 900–1600 m, Serra Negra, Minas Gerais. Endemic to the core area within Minas Gerais. Map 38C.

K), 5 Aug. 1988, Eggli 1086, 1088 (ZSS); l.c., Serra do Ambrósio, 1938, Mello-Barreto s.n. (RB); l.c., Faz. do Sr José Batista, 15 July 1984, A.M. Giulietti et al. in CFCR 4511 (SPF, SP), 6 Mar. 1988, Zappi & Prado in CFCR 11821 (SPF).

Conservation Status. Endangered (3) [criteria B2ce/3d]; extent of occurrence = 198 km²; PD=3, EI=1, GD=2. Short-list score (3x6) = 18. Subpopulations often large, but overall range of species very limited and some habitats affected by charcoal production and collection of plants and seed. Local morphological variation significant.

See Key, above. Found on crystalline rocks. Type and only species:


U. ammophorus hort., nom. nud.

Vernacular Name. Quiabo-da-lapa.

Globose to fusiform or cylindric, elongate, solitary or aggregated, 10–50(-100) x 10–17 cm; with gummiferous ducts under the epidermis. Epidermis green to grey-green, with or without waxy plates, rough. Ribs 13–29, straight, not tuberculate, to 5 mm high and 5–7 mm broad. Areoles 2 mm diam., very condensed to 3 mm apart, with sparse greyish or brownish wool when young, later glabrescent. Spines greyish, whitish or yellowish brown, porrect or spreading, straight, flattened in upper surface, central spines 2–6, 10–40 mm long, radials 0–3, spreading. Flower 8–16 x 6–10 mm; tube c. 8 mm, with triangular bract-scales, white hairs and bristles; perianth-segments pale yellow, tinged reddish or greenish; style 6–7 mm; stigma-lobes 7–8. Fruit 15–25 x 6–8 mm, pericarp with few glabrescent or slightly woolly bract-scales, reddish to bright pinkish. Seed 1.7–2.4 x 1.3–1.6 mm, cochleariform, keeled, brown, shiny, smooth; testa cells flat.

A variable species, comprising a complex of numerous local forms, the following subspecies probably representing an over-simplification of the situation in nature (cf. Schulz & Machado 2000):

1. Plants with grey-green, white-scaly epidermis; ribs 13–20(-26) 3a. subsp. pectinifera
1. Plants with green epidermis, white scaly plates absent; ribs (16–)18–29 2
2. Spines yellow, ascending, organized in rows following the edge of the rib; plants to 50 cm 3b. subsp. flavispina
2. Spines greyish, spreading, not organized in rows; plants to 100 cm 3c. subsp. horrida

3a. subsp. pectinifera

Plants 20–85 cm tall, with grey-green, white-scaly epidermis; ribs 13–20(-26). Spines greyish or whitish, ascendent, organized in rows following the edge of the ribs, central spines 2–4, 10–25 mm, radials 0–3.

South-eastern campo rupestre (Diamantina) element: crystalline rocks in campo rupestre, c. 650–1250 m, Serra do Espinhaço, north-east and south of Diamantina, Minas Gerais. Endemic to the core area within Minas Gerais. Map 38D.

CONSERVATION STATUS. Endangered (3) [criteria B1/I2e]; extent of occurrence = 765 km²; PD=3, EI=1, GD=2. Short-list score (3×6) = 18. Endangered from collection of plants and seed throughout its limited range, where populations are mostly small (area of occupancy < 500 km²).

The form reported from Inhai seems somewhat morphologically and geographically intermediate between all three subspecies recognized here.


U. warasii Ritter, nom. nud.

Plants to 50 cm tall, with green epidermis; ribs (16-)21-29. Spines yellow, ascendent, organized in rows following the edge of the rib, central spines 2-4, 10-25 mm.

South-eastern campo rupestre (Diamantina) element: crystalline rocks in campo rupestre, c. 1200-1350 m, Serra do Espinhaço, west of Diamantina, Minas Gerais. Endemic to the core area within Minas Gerais. Map 38D.


CONSERVATION STATUS. Endangered (3) [criteria B1/I2e]; extent of occurrence = 131 km²; PD=3, EI=1, GD=2. Short-list score (3×6) = 18. Subjected to the collection of plants and seed throughout its very restricted range.


Plants to 100 cm tall, with green epidermis; ribs 23-27. Spines greyish, spreading, not organized in rows; central spines 3-6, 20-40 mm.

South-eastern campo rupestre (Rio São Francisco drainage) element: on sandstone outcrops on the western slopes of the Serra do Espinhaço ('Serra Mineira'), c. 700-850 m, Mun. Bocaiúva, Minas Gerais. Endemic to the core area within Minas Gerais. Map 37D.

CONSERVATION STATUS. Critically Endangered (4) [B1/2cc]; PD=3, EI=1, GD=1. Short-list score (4x5) = 20. Known from only a single small locality, close to agricultural activities and highly sought-after by collectors.

Apparently disjunct from the remainder of the genus, but the region in between is very poorly known.

The untypifiable name *Uebelmannia centeteria* (Lehmann ex Pfeiffer) Schnabel (*Echinocactus centeterius* Lehmann ex Pfeiffer, Enum. Cact.: 65. 1837) is doubtfully referred to the Chilean species, *Eriosyce curvispina* (Colla) Kattermann, by Hunt et al. (1994: 146). It was stated by Pfeiffer, i.e., to have originated from Minas Gerais, but this is assumed to be an error.