Taxonomy and phytogeography of the Cactaceae of eastern Brazil

Thesis

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TAXONOMY AND PHYTOGEOGRAPHY
OF THE CACTACEAE OF
EASTERN BRAZIL

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Eastern Brazil is a vast tropical area known to be rich in cactus diversity and endemism. Early explorers documented little of this due to the difficulty cacti present for preservation and description of living and museum specimens. Most taxa now known were discovered in the past 100 years, the majority being named and classified by horticulturists, whose activities greatly distorted their number and geographical range. Extensive literature, field and herbarium studies enabled better determination of generic and specific limits, correct nomenclature and details of distribution and ecology. Keys have been written to facilitate identification of the 30 genera, 134 species and 43 heterotypic subspecies here recognised.

In Eastern Brazil cactus biodiversity is concentrated in Bahia and Minas Gerais — each having > 90 taxa and 30 or more state endemics. The most likely explanation for this is greater complexity and discontinuity of habitats, leading to isolation of taxa and increased speciation. Cactus phytogeography lends support to recent hypotheses on historical plant migration routes in South America, while analysis of distribution patterns indicates > 94% of taxa as ± restricted to one of 3 major vegetation categories: (1) Mata atlântica, (2) Caatingas & Northern campos rupestres and (3) Cerrados & South-eastern campos rupestres. Significantly, the campos rupestres are rich in endemic cacti, but divisible into two areas on the basis of cactus diversity. Of taxa included in category (2), > 70% belong to one of three major geographical-ecological areas, ranged west to east.

Conservation status has been determined using information gathered for the above inventory and applying IUCN 1994 'Red List Categories' combined with Farjon & Page criteria (‘phylogenetic distinction’, ‘ecological importance’, ‘genetic diversity’). As guidance to conservationists, prioritised shortlists of threatened taxa and Area Hotspots are provided. The South-eastern campos rupestres are of the greatest concern in terms of threatened taxa.
Mandacaru¹
Quando fulora² na seca
É o sinal que a chuva chega no setão³
Toda menina que enjoia da boneca
É o sinal que o amor já chegou no coração
Meia comprida, não quer mais sapato baixo
Vestido bem cintado, não quer vestir timão

Ela só quer
Só pensa em namorar
Ela só quer ...

De manhã cedo já tá pintada
Só vive suspirando, sonhando acordada
O pai leva ao doutor
A filha adoentada
Não dorme, não estuda
Não come, não quer nada

Ela só quer ...

Mas o doutor
Nem examina
Chamando o pai de lado
Lhe diz logo, em surdina
Que o mal é da idade
É que pra tal menina
Não há um só remédio
Em toda medicina

Ela só quer ...

[Xote das Meninas' by
Luiz Gonzaga⁴ & Zé Dantas]

¹ Cereus jamacaru De Candolle, a cultural symbol in the cactus flora of Eastern Brazil
² floresce
³ in this sense, the caatinga
⁴ cultural spirit of the Nordeste Brasileiro, a sanfoneiro

To Dani, for being the Brasileira she is
To 'Nessa, for being the lady she is
And to Bichiz, for being Bichiz
— My long-suffering family
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Chapter 1

INTRODUCTION

1.1. Aims

In the author’s application to register for an Open University Research Degree, in 1996, the following were indicated to represent the aims of the investigation:–

1. ‘To develop a monographic taxonomic treatment of the species of native and naturalized Cactaceae of Eastern Brazil, including identification aids’,

2. ‘Assessments of their conservation status and’

3. ‘Analysis of distribution patterns’. 

Item no. 1, above, has been completed but, in view of its size (>135,000 words), an abridged synopsis — including the accepted names, identification keys, summarized distribution and ecological data and taxonomic commentary — is submitted as part of the thesis itself (Chapter 3.2). The full floristic monograph, annexed as Supplement 1, remains a source of essential supporting information, containing the many individual distribution records and conservation assessments, nomenclatural documentation etc., upon which Chapters 2–5 are based.

Items 2 & 3 are represented by Chapters 5 & 4, respectively, which are preceded by chapters including the history of discovery, inventory and classification of Cactaceae in Eastern Brazil (Chapter 2) and the synoptical taxonomic treatment just referred to. The phytogeographic analysis presented in Chapter 4 aims to establish a basis from which other families of plants from Eastern Brazil can be compared to determine whether there exist
similar and repeating patterns of endemism in unrelated plant groups. By the application of cladistic biogeography it would be possible to determine whether such similarities are due to common evolutionary pathways driven, for example, by historic climatic events (Funk & Brooks 1990), or merely due to random chance. This, however, requires a sufficient number of robust and comparable phylogenies, necessarily based on or backed up by molecular data (cf. Chapters 2.7 & 3.1), which, unfortunately, have been beyond the resources of the present study. Nevertheless, distribution patterns established here can be evaluated in this manner at a later date while, for the present, delimitation of the areas and taxa involved combined with assessment of conservation status (Chapter 5) can enable the identification of conservation area hot-spots and lead to recommendations for action to protect both taxa and areas. Even without a significant number of phylogenetic hypotheses, the recording and analysis of distribution patterns and extra-Brazilian phytogeographical links have the potential to contribute data to the study of past vegetational/climatic history in the neotropics (cf. Pennington et al. 2000).

1.2. Significance of the geographical area chosen

In the biodiverse neotropics the cactus family, with more than 1300 species (Hunt 1999a: 160), represents the second in order of size amongst higher plant groups that are ± endemic (the first being Bromeliaceae). The Cactaceae has 4 major geographical centres of diversity in the Americas (Taylor in Oldfield 1997: 18–19), of which the first in order of importance is Mexico and the south-western USA. Baseline floristic-monographic treatments of cacti from this North American region have been published in the last 25 years (cf. Hunt 1992b). The second centre of diversity is within the Andean chain, Peru and Bolivia being especially rich, but significant parts of this region have not been safe to work in until quite recently and the taxonomic complexities of the family in the central Andes are too great and currently too little understood for the kind of study presented here to be attempted (cf.
Taylor et al. in Oldfield 1997: 111). The third centre in order of importance is Eastern Brazil, a large but discrete region largely cut off from other areas of cactus diversity by broad environmental zones that are ecologically unsuitable for most members of this primarily dryland family (see ‘Background’ below and Chapter 4 for fuller explanation of how ‘Eastern Brazil’ has been delimited). The last monographic-floristic treatment of the Cactaceae in Brazil was published 110 years ago (Schumann 1890) and accounted for only 13 of the 134 native and introduced species now recorded from Eastern Brazil, most of which are endemic, making this area a priority for taxonomic inventory and conservation.

As delimited here ‘Eastern Brazil’ includes the habitats of all cacti native to the vegetation known as caatinga, its ecotones with the Atlantic Forest (agreste), and all but 7 species endemic to campo rupestre and other, geographically associated rupicolous formations within the contiguous cerrados (for vegetation details, see Chapter 4.3). The 7 taxa excluded are from the adjacent parts of the Brazilian states of Goiás, Tocantins and Minas Gerais*, but expanding the study area westwards would mean including elements of 2 more Brazilian Regions (‘Grandes Regiões’), i.e. Central-western and Northern Brazil, and for relatively little gain, since these are without significant cactus floras. Expanding further southwards would increase the number of epiphytic Rhipsalideae to be treated, but as noted below, these are now better understood and less deserving of study than the cacti of the Brazilian drylands. The size of the taxonomic survey presented here can be judged by reference to Appendix 2, which lists more than 1000 botanical names applied to cactus taxa found in Eastern Brazil, c. 800 of these being treated as synonyms.

1.3. Study methods

The author is a trained plant taxonomist of 18 years’ service in the Kew Herbarium (1977–1995), with field experience in Nepal, Mexico, Venezuela and Chile gained during the

* Namely, Pilosocereus albisummus, P. flexibilispinus, P. vilaboensis, P. diersianus (Zappi 1994), Cereus sp. nov. (Tocantins), Arrojadoa sp. nov. (Goiás) and Micranthocereus estevesii (see Appendix 3).
period 1981–1990. In order to build a comprehensive understanding and documentation of morphology, ecology and geographic distribution, herbarium and living materials were studied and field collections (and photographic records) were made in Eastern Brazil, the latter deposited at Kew (K)

Methods employed have already been described in Taylor (1991a: 2–4) and Zappi (1994: 11) and field excursions are detailed in Table 1.1, below. Field studies are especially important for Cactaceae, because the difficulties that face the collector in their preparation for the herbarium and for subsequent identification have meant that the family has tended to be ignored by professional botanists and has in general remained poorly represented in museum collections (see Chapter 2). Nevertheless, materials at the following 50+ herbaria were studied for the project and often augmented

(institutions are listed by their standard Index Herbariorum codes, those indicated in bold typeface being the more important for Cactaceae in Eastern Brazil, some of the remainder being significant at the state level): ALCB, ASE, B†, BAH, BHCB, BM, BONN†, BR†, C (list by D. R. Hunt consulted), CEN, CEPEC, CESJ, E†, EAN, ESA†, F, GUA, HB, HNT, HRB, HRCB†, HUEFS, IAN, IPA, JP, L, M†, MAC, MBM, MBML, MEXU, MG, MO, NY†, P (loan only), PEUF, R, RB†, RSA, S (loan only), SI, SP, SPF, SPSF, U†, UB, UEC, UFG, UFMT†, UFP, US, VIC, W, WAG, ZSS† (the symbol † indicates that associated living collections were also examined). Most of the above-cited institutions have been visited in person, so that all of their materials could be studied (rather than relying upon non-specialists selecting loans), this because of the need to have a view of taxon distribution as comprehensive as possible. Another major source of distributional data has been the author’s many contacts, both in Brazil and amongst the cactus hobbyist community in the U.K. and elsewhere. The extensive literature on Cactaceae has also been consulted and published records and details of type localities were particularly helpful in completing distribution maps for taxa from beyond Eastern Brazil, as discussed in Chapter

* Duplicates have been deposited in one local herbarium in each state of collection and by D. C. Zappi at SPF or HRCB.
4 (Maps 2–9). The author’s rationale in the development of taxonomic concepts is described in Chapter 3.1.

Distribution maps and calculations of ‘extent of occurrence’ for phytogeographic and conservation purposes were produced digitally with assistance from Kew’s Geographical Information Systems Unit (GIS Unit, Herbarium), employing ArcView software and a convexhull algorithm run on a networked desktop computer with a 21", high resolution screen. It has become obvious that over-reliance on latitude and longitude coordinates determined by collectors and their assistants prior to the advent of global positioning systems equipment (GPS) can introduce disturbingly great errors. Such records, therefore, have been localized using other label data aided by various GIS overlays, eg. road and river systems. Obviously erroneous coordinate label data have been excized from the records cited in Supplement 1. GIS overlays have also been checked against a diverse range of available printed maps acquired in Brazil during the course of this study and also compared with actual routes travelled on the ground, revealing significant discrepancies in some areas. Would-be phytogeographers certainly ‘have it easy’ with the now freely available and cost-effective, hand-held GPS readers, that have become the modern standard for any field excursion. The digital maps created have been electronically imported into the text of Chapters 4 & 5 and could not have been completed in the time available, if mapping pen and manually applied symbols were still being used!

1.4. Background

The present study has its origins in a field excursion to Eastern Brazil led by Dr Ray Harley (Herbarium, Royal Botanic Gardens, Kew), which departed the U.K. at the close of September 1988. This excursion, in which the author was invited to participate as a Cactaceae specialist with an interest in Brazilian taxa (Taylor 1980, 1981, 1982), was part of a long-term collaborative project to study the flora of the East Brazilian Highlands and
especially the *campos rupestres* of the Chapada Diamantina, Bahia (cf. Stannard 1995). The collaboration involved RBG Kew, the Instituto de Biociências of the Universidade de São Paulo (São Paulo state) and the herbarium of the Centro de Pesquisas de Cacau (CEPEC), Ilhéus (Bahia state), and was carried out under the terms of a *convênio* (agreement) and of a collecting permit issued by the Brazilian authorities (Conselho Nacional de Pesquisas Científicas e Tecnológicas, CNPq and Instituto Brasileiro do Meio Ambiente, IBAMA). Whilst this excursion focused on the highland areas, including visits to various localities in the state of Minas Gerais as well as the Pico das Almas in Bahia, participating specialists were allowed time and resources to make field collections of their chosen plant families in other vegetation types. Thus, the author, accompanied by Brazilian postgraduate, Daniela Zappi, was able to study and sample some of the Cactaceae characteristic of the *caatinga* and *cerrado* biomes. Prior to returning from Brazil, in February 1989, there was also an opportunity to study members of the family in the Atlantic Forest (*Mata atlântica*) of São Paulo state, once again guided by Zappi.

Having gained an insight into the ecology and variation patterns of Brazilian cacti in habitat, the author accepted an invitation from Zappi in 1989 to accompany her on an initial field excursion towards a taxonomic revision of the genus *Pilosocereus* Byles & Rowley, the subject selected for her doctoral thesis (Zappi 1994). This also greatly furthered progress with a long-running project to revise the genus *Melocactus* Link & Otto in Central and South America (Taylor 1991a), whose centre of diversity is in Bahia, which was extensively travelled by Zappi and the author during 3 weeks in July 1989. Following this rewarding experience, approval was gained from the Keeper of the Herbarium at Kew, Prof. Gren Lucas, to begin a regional taxonomic monograph of the family, to be entitled ‘The Cacti of Eastern Brazil’. The decision to take this project forward was based on three factors: (1) the perceived high levels of endemism of Cactaceae in this area, (2) the apparent lack of knowledge about their taxonomy and distribution, and (3) the established
series of collaborations and floristic treatments already realized by RBG Kew in the North-
eastern region of Brazil (eg. Harley & Mayo 1980, Renvoize 1983, Harley & Simmons

However, whereas the above-cited treatments had focused on Bahia state, or
particular sites in its mountainous interior, ‘The Cacti of Eastern Brazil’ project, with a
more modest number of taxa, could afford to be more ambitious and cover a wider area.
Initial field studies suggested this should be the most species-rich parts of North-eastern
Brazil and the adjacent South-eastern state of Minas Gerais, which holds many endemic
taxa besides being the southern limit of range of many others. Ultimately the area chosen
has expanded further to encompass NE Brazil in its entirety and the northern half of South-
eastern Brazil, limited at 22°S and 46°W. Hence the convenient term, ‘Eastern Brazil’, an
area amounting to c. 2 million km².

From 1990 further field excursions were planned and executed, as summarized in
Table 1.1, and opportunities taken to collaborate with other students and their professors,
besides giving papers and mini-courses at Brazilian botanical congresses and universities.
In the interests of gaining a better knowledge of the largely epiphytic cactus flora of the
Atlantic Forest — a vegetation type that has been all but comprehensively destroyed within
Eastern Brazil — additional field excursions within the contiguous South-eastern region of
Brazil, in the states of Rio de Janeiro and São Paulo, were also carried out. These
contributed to a precursory treatment of the tribe Rhipsalideae (Barthlott & Taylor 1995),
whose species found in Eastern Brazil would have been difficult to interpret, since their
centre of greatest diversity is outside the area dealt with in this thesis. Prior to visiting
Brazil for the first time, 7 weeks of field studies had been conducted in Venezuela (Dec.
1987 – Jan. 1988), a country whose cactus flora is now known to hold considerable
interest, in terms of phytogeography, in relation to that of Eastern Brazil.
During 1993, when the present doctoral studies were first contemplated, the author had already begun developing ideas on the phytogeography and conservation status of the cacti of Eastern Brazil (Taylor 1991c, Taylor & Zappi 1992a, Taylor et al. in Oldfield 1997: 111–124, 143–144), which have since become the focus of the work presented here, backed up by the detailed taxonomic inventory represented by Supplement 1.

<table>
<thead>
<tr>
<th>Dates</th>
<th>Areas visited</th>
<th>Main purpose of excursion</th>
<th>Collaborator(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>July 1989</td>
<td>Bahia, N Minas Gerais</td>
<td>Collecting material for D. C. Zappi's revision of <em>Pilosocereus</em></td>
<td>D. C. Zappi</td>
</tr>
<tr>
<td>Dec. 1990</td>
<td>NE &amp; SE Minas Gerais, W Espírito Santo</td>
<td>Collecting material for 'Cacti of Eastern Brazil' project</td>
<td>D. C. Zappi</td>
</tr>
<tr>
<td>April 1992</td>
<td>N &amp; E Bahia</td>
<td>Noting/photographing additional distribution records</td>
<td>D. C. Zappi</td>
</tr>
<tr>
<td>Feb. 1995</td>
<td>E Bahia, E Alagoas, cent.-N Pernambuco, E &amp; S Paraíba, N Piauí, NW Ceará</td>
<td>As above</td>
<td>a) A. M. Carvalho (BA)</td>
</tr>
<tr>
<td>Aug. 1998</td>
<td>NE Bahia (by bus), E Sergipe</td>
<td>Determine identity of <em>Pilocereus rupicola</em> Werdermann (Serra da Itabaiana, Sergipe)</td>
<td>M. L. Santos (SE)</td>
</tr>
</tbody>
</table>

Table 1.1. Field excursions directly related to the project involving the author (1988–2000).
Chapter 2

HISTORY OF DISCOVERY, NAMING AND CLASSIFICATION OF THE CACTACEAE OF EASTERN BRAZIL

2.1. Introduction

The history of the discovery and naming of Cactaceae from Eastern Brazil, as defined here, is detailed for each taxon in Appendix 1 and can be resolved into 4 major periods. First, however, it is necessary to make some remarks about this subject in more general terms.

Being for the most part highly succulent, normally unpleasantly spiny, yet unusual to look at, cacti have always been worthy of study and comment, but never easy to preserve by conventional methods, nor to draw accurately. Early botanical expeditions to Brazil undoubtedly encountered many cacti, but while even the most illustrious authorities, such as von Martius, frequently refer to them in their field notebooks and scientific publications (Martius 1832, 1846), remarkably few actually succeeded in bringing significant numbers of preserved specimens back to their herbaria and museums. Many, however, attempted and were evidently successful in sending live material back for cultivation in Europe, e.g. Melocactus violaceus subsp. violaceus (M. depressus)*, sent back to Britain from Pernambuco by George Gardner (Hooker 1838). Once introduced to the stove house, their naming and description soon followed, but frequently the living specimens were never subsequently

* Botanical authorities for E Brazilian cactus names are not cited here but can be found in Chapter 3.2.
preserved, either because they were considered too precious as items of horticultural interest, or as simply incapable of transformation into an 'hortus siccus'. Thus, until relatively recent times, detailed knowledge of the majority of species has been hampered by a profound lack of both museum specimens and reliable literature, and this to an extent much greater than with other, more 'conventional' plants.

The last and only comprehensive study that focused on the Cactaceae from this vast region of Eastern Brazil was made by Karl Moritz Schumann, as part of Martius's monumental Flora brasiliensis (Schumann 1890). For the reasons just explained his treatment is rather limited in its coverage, since many conspicuous species that were accessible to, and very probably noticed by 17th and 19th Century collectors in Brazil are either missing or not distinguished, for lack of adequate material, eg. the ubiquitous Xique-xique (Pilosocereus gounellei). Unluckily for Schumann, the 20th Century's golden age of cactus discovery in Brazil was still to come, as the following notes and Appendix 1 hopefully make clear. The lack, since Schumann's time, of any kind of satisfactory taxonomic treatment of the Cactaceae of the huge eastern regions of Brazil therefore justified the work from which the present study is derived. Here, a greater than 12-fold increase in diversity, with 161 native taxa at the ranks of species and subspecies (heterotypic), is reported. Schumann (1890) accounted for only 13 of these!

2.2. Count Johan Maurits in North-eastern Brazil: 1637–1644

Our knowledge of Brazilian cacti begins with the Dutch occupation of North-eastern Brazil, during the years 1630–1654. This included a seven-year period, commencing in 1637, under the command of Governor General Johan MAURITS of Nassau-Siegen, whose company included two accomplished scientists, Willem Pies (latinized to the more familiar PISO) and Georg MARCGRAF (also written Marcgrave, Markgraf etc.), and also two talented artists, Albert ECKHOUT and Frans POST. Whitehead & Boeseman (1989) have brought together a
substantial body of information on the work of the Maurits team, amongst which six cactus species can be confidently identified from the illustrations they cite and reproduce: *Tacinga palmadora, Brasiliopuntia brasiliensis, Cereus fernambucensis, C. jamacaru, Pilosocereus gounellei* and *Melocactus violaceus* (see Appendix 1). They also illustrate what may be *Harrisia adscendens* (l.c., tt. 89b & 99b) and refer to a *Rhipsalis* species that remains to be identified (l.c., 84). Although the Dutch were mostly restricted to the coastal regions of the Nordeste, ranging from Salvador (Bahia), to São Luís (Maranhão), maps drawn by Marcgraf indicate that they travelled far inland, via the Rio São Francisco. This explains how they encountered *caatinga* species, such as *Cereus jamacaru, Pilosocereus gounellei, Tacinga palmadora* and, perhaps, *Harrisia adscendens*.

While other kinds of plants illustrated during the Dutch occupation were described in the 18th Century by Linnaeus and his contemporaries, no cacti appear to have been named from this source until 1814, when Willdenow published *Cactus brasiliensis* (= *Brasiliopuntia brasiliensis*), followed in 1828 by *Cereus jamacaru* De Candolle, both of these based on illustrations in Piso (1648). The latter is now a conserved name, since the illustration specifically cited by De Candolle is identifiable as *C. fernambucensis*, but subsequent authors consistently employed the name for the much larger *caatinga* species we know today (Taylor & Zappi 1992c).

**2.3. 19th Century collectors**

After the Dutch natural historians left North-eastern Brazil about 170 years passed before records of additional cactus species were made from the region covered here. With the Brazilian capital and principal port of entry now situated at Rio de Janeiro, which is outside the geographical limits of this study, many of the humid forest and coastal sand-dune species were first recorded from around that city long before they turned up further to the north. Certainly, parts of Rio de Janeiro were intensively botanized in the 19th Century, as was the
southern half of Minas Gerais (Urban 1906). However, during the period 1815–1860, only 6 additional species and one heterotypic subspecies were collected in the area treated here (N of 22°S) and 4 of these — *Pereskia grandifolia, Rhipsalis lindbergiana, Arthrocereus glaziovii, Discocactus placentiformis* — were found in the states of Minas Gerais and Espírito Santo, which are those closest to Rio de Janeiro. The others — *Rhipsalis baccifera* subsp. *hileiabaiana, Pilosocereus pentaedrophorus, Melocactus oreas* — were discovered in the state of Bahia, close to, or within a few days' journey of its capital and principal sea port of Salvador. The *Pilosocereus* was obtained by a French collector, MOREL, who could also have been the discoverer and source of *Melocactus violaceus* subsp. *margaritaceus*, which was originally described as *Mellemeetii* in 1857–58. The collectors of *Discocactus placentiformis* and *Melocactus oreas* are unknown, although the type of one of the contemporary synonyms of the former was said to have been obtained by RIEDEL (see Supplement 1, for details of synonyms). Four of the remaining taxa mentioned above were gathered as herbarium specimens by other famous European collectors from this period, including Prince WIELD-NEUWIED, SAINT-HILAIRE, SELLO and BLANCHET (see Urban 1906, for details).

Two collectors, who were active during the remaining period up to the end of the century, are worthy of particular mention: the Dane, WARMING, who spent 6 years at Lagoa Santa in Minas Gerais during the 1860s, and the Frenchman, GLAZIOU, who sent collections from the same state to Schumann prior to 1890. These individuals are notable for reasons besides their relative productivity. Warming’s collections from the gallery forests, mountains and Bambui limestone outcrops around Lagoa Santa were mostly lost or spoilt (Zappi 1994: 80–82), but he subsequently discussed and illustrated the plants (Warming 1908), so that it is possible to be sure about their identity (here using modern nomenclature): *Hylocereus setaceus, Lepismium warmingianum, Cereus jamacaru* subsp. *calcirupicola* and *Pilosocereus floccosus*. Glaziou probably can be credited with the discovery of *Arthrocereus melanurus* and *Cereus hildmannianus*, but his claims to have personally collected *Tacinga (Opuntia)*
inamoena and T. braunii (the latter described and named more than a century later) are almost certainly not genuine. The Tacinga species are indeed found in Minas Gerais, but not in the southern parts of the state that Glaziou is known to have visited and thus it is fairly clear that here we have a further instance of his mis-appropriation of material from another and as yet unidentified collector (cf. Wurdack 1970).

2.4. The golden age of cactus discovery: 1900–1950

From the beginning of the 20\textsuperscript{th} Century until around 1930 six field collectors made major contributions to our knowledge of the Cactaceae of Eastern Brazil. Between 1906 and 1907 the German, Ernst ULE, made a series of long expeditions into the interior of Piauí and Bahia, partly in search of plants that would provide a source of rubber (Zappi 1994: 135). This was the first time that any serious attempt to collect the cacti of the \textit{caatinga} had been made and so nearly everything that Ule found was new to science. Most of these new taxa were named by Gürke at Berlin-Dahlem from 1906 onwards, the great cactologist-monographer, Schumann, having died in 1903. The following key \textit{caatinga} species are amongst the many significant discoveries made by Ule: \textit{Pereskia bahiensis}, \textit{Stephanocereus leucostele}, \textit{Arrojadoa penicillata}, \textit{A. rhodantha}, \textit{Pilosocereus catingicola}, \textit{P. pachycladus} (the earliest definite record, but named much later), \textit{P. piauiensis}, \textit{Melocactus ernestii}, \textit{Harrisia adscendens} (see above), \textit{Facheiroa ulei} and \textit{F. squamosa}. He also made the first collection of the most widespread of the Chapada Diamantina’s \textit{campo rupestre} cacti, \textit{Micranthocereus purpureus}.

The Swiss-german emigré, Leo ZEHNTNER, who is known to have established a cactus garden at Juazeiro in northernmost Bahia, remains a little-researched figure in the history of Brazilian plant collectors, yet there is no doubting his importance in relation to Cactaceae. As a collector he was apparently most active during the period 1912–1920 and seems to have complemented the activities of Ule, visiting a number of Bahian sites the latter did not reach.
He is justly commemorated in the generic names of the cereoids, *Zehntnerella* (= *Facheiroa*) and *Leocereus*, both East Brazilian endemics, and in the epithets of many other Brazilian cacti named by Britton & Rose (1919–1923). This eponymy reflected the considerable assistance he gave to the American collectors, Rose & Russell, as discussed below, who made field studies in 1915 in connexion with the great monograph of the family by the above-cited authors. At this period Zehntner must have relied extensively on access to habitats in Bahia by means of the fluvial highway of the Rio São Francisco and via the few railway systems that had already been constructed. Amongst the taxa he is believed to have collected for the first time are: *Pereskia stenantha*, *Quiabentia zehntneri*, *Tacinga funalis*, *Pseudoacanthocereus brasiensis*, *Pilosocereus gounellei* subsp. *zehntneri*, *Micranthocereus flaviflorus*, *Coleocephalocereus goebelianus*, *Leocereus bahiensis*, *Discocactus zehntneri* and *D. bahiensis*. Another little-known collector from the earliest part of this century was **Dybowsk**, the discoverer of the remarkable *Espostoopsis dybowskii*.

Ule and Zehntner between them are the most important discoverers of cacti from the North-east Region of Brazil until quite recent times. Others amongst their contemporaries, however, improved our knowledge of distribution, while also finding a few novelties. Phillip von **Lützelburg**, another phytographer of Germanic origin, made extensive journeys over much of North-eastern Brazil and also through Espirito Santo state during the period 1913–1933, while in the employ of the Brazilian government. However, his 3-volume work, *Estudo Botânico do Nordeste*, published by the Inspetoria Federal de Obras Contra as Secas (Lützelburg 1925–1926), is more important as a source of information and illustrations than are the few cactus collections that survived these expeditions. Unfortunately, as Werdermann (1933) noted, much of Lützelburg’s cactus material was lost, and the present study has revealed that the part which did survive suffers from many confusions of labelling, rendering his data unreliable and his published lists of species ± unverifiable. His certain discoveries include *Cereus fernambucensis* subsp. *sericifer*, *Stephanocereus luetzelburgii* (the remarkable
bottle-cactus of Bahia), *Pilosocereus brasiliensis* subsp. *ruschianus*, *P. chrysostele* and *Coleocephalocereus pluricostatus*, but only two of these were described from his material.

More important as collectors were the two aforementioned Americans, *Rose* and his assistant *Russell*, who spent a couple of months collecting in Bahia, via the railway system, in 1915. Apart from their obviously successful collaboration with Leo Zehntner and the use made of his living collections at Juazeiro, they made numerous gatherings in northern Bahia and a significant contribution at the margins of the *caatinga-agreste* in eastern Bahia, utilizing railway lines that formerly connected the cities of Juazeiro and Jequié with Salvador and thence southwards in the direction of Minas Gerais. Amongst their discoveries were *Tacinga werneri*, *Rhipsalis russellii*, *Cereus albicaulis*, *Melocactus bahiensis* and *M. zehntneri*, but their extensive herbarium records, preserved at US, NY, K and elsewhere, are perhaps more important for documenting the distribution of already known taxa in parts of the region which have since suffered much habitat destruction (eg. at Jaguaquara ['Toca da Onça']).

During the period 1930–1950 a greater number of collectors made mostly small but worthy additions to our knowledge of the cacti of Eastern Brazil. By far the most important of these was the German cactus specialist, Erich *Werdermann*, from the Berlin-Dahlem Botanical Garden & Museum. He planned and executed a very successful expedition during 1932, which was reported the following year in his entertaining botanical travelogue entitled *Brasilien und seine Säulenkakteen*, an English translation appearing 9 years later (*Werdermann* 1933, 1942). Werdermann and colleagues began their journey in Pernambuco, then spent a considerable period in Bahia, before passing through Minas Gerais *en route* to São Paulo. Much of the journey was made by Ford Zeppelin car, but the condition of roads in the Brazilian interior left much to be desired and his account tells of the many stops they made to effect repairs. Werdermann made numerous collections, including living specimens and some in spirit, but sadly much of his material was subsequently destroyed at Berlin during the second World War (cf. Leuenberger 1978). Amongst the taxa he discovered are
Cipocereus minensis, Pilosocereus tuberculatus, P. glaucochrous, Micranthocereus polyanthus and Melocactus salvadorensis. He also collected and described a significant number of entities that have passed into synonymy, besides creating some confusions of identity that survive even to this day (eg. he used the name Melocactus bahiensis for the much more widespread *M. zehntneri*). Other collectors who made notable contributions contemporary with that of Werdermann included resident Brazilian botanists as well as foreign explorers, eg. Bento PICKEL (especially at the easternmost limits of the *caatinga-agreste* in Pernambuco), MARKGRAF et al. (Minas Gerais, discovered Brasilicereus markgrafii), MELLO-BARRETO (Minas Gerais, *Uebelmannia gummifera*), HERINGER (Minas Gerais), CUTLER (Ceará), DROUET (Ceará, Pilosocereus flavipulvinatus), BRADE (Minas Gerais and Espírito Santo, *Cipocereus bradei, Arthrocereus rondonianus*), DUARTE (Minas Gerais, *Cipocereus minensis* subsp. *pleurocarpus, Pilosocereus densiareolatus*) and PINTO (Bahia, *Pereskia aureiflora*).

2.5. Modern collectors: post 1950

In modern times, cactus discovery in Eastern Brazil began with the arrival of the German, Friedrich RITTER, in 1959 (Eggli *et al.* 1995) and was closely followed in the 1960s by his compatriot, Leopold HORST, the latter’s Swiss nurseryman sponsor, Werner UEbelmann and Dutch collaborator, Albert BUINING (Uebelmann 1996). These collectors were largely motivated by the horticultural trade and cactus hobbyist interests, especially in Europe, where new discoveries were eagerly sought. However, although many so-called ‘spec. nov.’ were collected, introduced to cultivation and swiftly named, the number of genuine first discoveries of taxonomically ‘good’ species was far less than it seems, for two reasons. First, many of the taxa that these and subsequent cactus plant hunters claimed as new discoveries had already been collected much earlier by professional botanists and deposited in herbaria, which these amateurs did not usually consult (see Appendix 1). Secondly, the taxonomic concepts they

Horst and his associates, Uebelmann and Buining, were even more successful than Ritter, since they were evidently able to devote more time to exploration of the remote Brazilian interior (the 'sertão') and this by means of suitable vehicles on roads that were steadily improving. Over a period of some 30 years, starting in the mid-1960s, a steady stream of novelties were reported in journals and catalogues back in Europe and the USA, and plant material was distributed to avid cactophiles via Uebelmann’s nursery. No less than 26 distinct new taxa can be attributed to the efforts of their explorations, although, as already indicated, the number they actually claimed as new was probably in terms of hundreds (a measure of this can be gained from the number of names listed for relevant Brazilian genera in Eggli & Taylor 1991). The following distinct novelties were discovered between the years 1966 and 1982:— *Arrojadoa dinae* subsp. *eriocaulis, Pilosocereus pentaedrophorus* subsp. *robustus, P. fulvilanatus* (2 subspp.), *P. magnificus, P. aureispinus, Micranthocereus violaciflorus, M. auriazureus, M. dolichospermaticus, Coleocephalocereus buxbaumianus*.
subsp. buxbaumanus, C. purpureus, Melocactus conoideus, M. deinacanthus, M. azureus (2 subsp.), M. pachyacanthus, M. lanssensianus, M. glaucescens, Discocactus zehntneri subsp. boomianus, D. heptacanthus subsp. catingicola, D. pseudoinsignis, D. horstii, Uebelmannia buiningii, U. pectinifera (3 subsp.). The significance of the achievement of these collectors is reflected in the fact that many of the above are extremely localized and figure amongst the threatened taxa discussed in Chapter 5.

Other collectors that have been active during this period include professional botanists. The Argentinian cactus specialist, Alberto CASTELLANOS, made frequent visits to Eastern Brazil while resident in Rio de Janeiro and collected cacti on a number of occasions. In 1968 he collected material of a Pilosocereus, P. azulensis, which was only recognised as new quite recently (Taylor & Zappi 1997). He is known to have made other herbarium collections from the core area, but it is believed that an important part of his material was destroyed in a fire (M. Vianna [GUA], pers. comm.). Around the mid 1960s Paulo MARTINS collected Rhipsalidaceae at the behest of Prof. F. Brieger (Universidade Federal de Brasília) and discovered Rhipsalis paradoxa subsp. septentrionalis in Bahia, which was not described until 1995 (Barthlott & Taylor 1995). Dárdano de ANDRADE-LIMA, Raymond HARLEY (discoverer of Melocactus oreas subsp. cremnophilus), Leopoldo KRIEGER (discoverer of Arthrocereus melanurus subsp. magnus) and Gustavo MARTINELLI are amongst a handful of mostly Brazilian botanists that included cacti in their general field collections for the herbarium during the 1970s. In particular Andrade-Lima deserves praise for his many collections in areas that have since undergone considerable habitat modification, and for his various helpful publications on Brazilian cacti (cf. Prance & Mori 1982).

During the 1980s and 90s there has been much more field activity, both by Brazilian botanists and their European collaborators, as well as amateur cactophiles, but this has resulted in fewer discoveries of genuinely new taxa. Some of those that have been found are extreme rarities, narrow endemics or plants from more or less inaccessible habitats.
Nonetheless, a steady stream of novel plants has been reported in the specialist cactus & succulent literature. In 1981, a team of botanists from universities in São Paulo state, including Antônio FURLAN and Inês CORDEIRO, discovered a peculiar new *Arrojadoa, A. bahiensis*, restricted to nearly vertical cliffs in the Chapada Diamantina, Bahia (Taylor & Zappi 1996). In the same year another remarkable cactus, *Melocactus paucispinus*, which imitates the unrelated genus *Discocactus*, was discovered in the same region by the German cactophiles, HEIMEN *et al.* In 1984, Brazilian amateur, Eddie ESTEVES PEREIRA, found two new subspecies at a locality in southern Bahia (*Tacinga saxatilis* subsp. *estevesii* and *Facheiroa cephaliomelana* subsp. *estevesii*), while the following year VAN HEEK and VAN CRIEKINGE discovered the very rare *Micranthocereus streckeri* in central Bahia. In 1986, Prof. Werner RAUH and Roberto KAUTSKY collected a series of little-known or undescribed *Rhipsalideae* from the region of Domingos Martins in Espírito Santo state: *Rhipsalis pacheco-leonis* subsp. *catenulata*, *R. cereoides*, *R. sulcata*, *R. clavata*, *R. pilocarpa* and *Schlumbergera kautskyi*. The following year Countess Beatrix ORSSEICH obtained the extraordinary, red-flowered *Rhipsalis hoelleri* from the same area (Barthlott & Taylor 1995). Also in 1987, Brazilian botanists Daniela ZAPPI and Vera SCATENA found a most unusual new cereoid cactus, *Cipocereus laniflorus*, on slopes of the Serra do Caraça in central-southern Minas Gerais, while the following year the present author and Zappi discovered the ‘Critically Endangered’ *Melocactus pachyacanthus* subsp. *viridis* in central-northern Bahia (Taylor 1991a). Since the last-mentioned no further new discoveries of really distinct taxa (other than presumed hybrids) have been made over the past decade, during which time extensive field studies focused on Cactaceae, and on a scale never before attempted, have been carried out by the present author and collaborators, Daniela ZAPPI, Urs EGGLI, Emerson ROCHA and Marlon MACHADO. Others, especially Luciano de QUEIROZ and his team from the University of Feira de Santana, Bahia, have made significant herbarium collections in the Nordeste and, unlike
many botanists, have not been afraid of including substantial numbers of cacti amongst these, greatly extending our knowledge of geographical distribution.

2.6. Taxonomic history of the Cactaceae from Eastern Brazil: 1890–1979

In terms of monographic and synoptic taxonomic treatments, the following authors’ names are particularly relevant in relation to the cacti of Brazil, amongst those that published prior to the 1980s: Schumann, Britton & Rose, Berger, Werdermann, Backeberg, Buxbaum, Hunt and Ritter. The first treatment that merits mention is that by SCHUMANN (1897–98), the Gesamtbeschreibung der Kakteen, which followed closely on the heels of his accounts for Martius’s Flora brasiliensis and Engler & Prantl’s Das Pflanzenfamilien (Schumann 1890, 1894). Schumann’s classification was, by present standards, extremely conservative at generic level, where he recognized the following ‘hold-all’ genera: Cereus Miller (including a variety of Brazilian columnar-cereoid and scandent species, plus some rhipsaloids now referred to Schlumbergera Lemaire, but excluding part of the modern Pilosocereus Byles & Rowley as Pilocereus Lemaire), Rhipsalis Gaertner (for a variety of epiphytic taxa belonging to tribe Rhipsalideae DC., but also including some now referred to tribe Hylocereae Buxbaum), Echinocactus Link & Otto (for all the low-growing globular forms like Discocactus Pfeiffer, but not Melocactus) and Opuntia Miller, this last being used in the traditional broad sense that has persisted until quite recent times. In addition he accepted Melocactus Link & Otto and Pereskia Miller in their current senses, Hariota DC. (nom. illeg. = Hatiora Britton & Rose), Pilocereus Lemaire (in a sense excluding its type), Phyllocactus Link (correctly Epiphyllum Haw.), Epiphyllum (for part of what is now Schlumbergera) and Zygocactus Schumann (= Schlumbergera). Schumann classified the genera of Cactaceae into 3 subfamilies, Pereskioideae, Opuntioideae and Cereoideae (correctly Cactoideae), an arrangement which has remained little changed until
very recently (Maithuenia (Weber) Schumann, which he placed in Pereskioidae, is now in its own subfamily).

In their great 4-volume work, *The Cactaceae*, BRITTON & ROSE (1919–1923) recognized Schumann’s 3 subfamilies as tribes and otherwise radically changed the classification of the family at generic level, liberally dividing his hold-all genera and describing many new ones to account for the numerous discoveries made in the early years of the 20th Century. In total they recognised 124 genera for the family. A good part of the changes they made to the abundant cereoid species was considerably influenced by Alwin Berger’s detailed subgeneric rearrangement of *Cereus* (Berger 1905), some of whose subgeneric names and/or taxa they upgraded to generic status. Thus, Schumann’s concept of *Cereus* became restricted to the group immediately close to the type species, *C. hexagonus* (L.) Miller. However, *Pilocereus* was included in *Cephalocereus* Pfeiffer, whose type (*Cactus senilis* Haw.) and Brazilian taxa are nowadays placed in different tribes (Pachycereae and Cereeae, respectively). The scandent cereoids including Brazilian species were separated into the new genera, *Hylocereus* and *Mediocactus*. The then known E Brazilian globular cacti were placed in the reinstated *Discocactus*, but allied with *Melocactus*, for which Britton & Rose dug up the abandoned name *Cactus* L. These were the only genera included in their subtribe Cactinae (*Melocactus* is now seen as the most derived element in tribe Cereeae, while *Discocactus* is referred to Trichocereaeae; Taylor & Zappi 1989). Britton & Rose also split up the E Brazilian elements in Schumann’s concept of *Rhipsalis*, recognizing *Lepismium* Pfeiffer, *Erythrorhipsalis* A. Berger (1920) and *Epiphyllanthus* A. Berger (1905), as well as *Hatiora* Britton & Rose. New genera were created for various taxa that had been described in *Cereus* and *Cephalocereus* shortly after Schumann’s death, namely, *Arrojadoa*, *Leocereus*, *Facheiroa* and *Zehntnerella*. New opuntioid genera were also created for recently discovered taxa: *Quiabentia* (for a leafy species initially described as a *Pereskia*) and *Tacinga* (for a curious, scandent species).
While some commentators welcomed these new generic names, others, especially in Germany, where Schumann's view still held sway, rejected some or all, or even hedged their bets, eg. Berger (1929), who ambiguously treated many of Britton & Rose's genera simultaneously as subgenera and genera in his handbook, *Kakteen*.

Werdermann (1933, 1942), in dealing with the cereoid cacti of Eastern Brazil, adopted a compromise position, recognizing some of the segregates employed by Britton & Rose, but sinking others. For example, *Trichocereus* (Berger) Riccobono he accepted for some of the Brazilian taxa subsequently realigned by others in *Arthrocereus* A. Berger (1929), but Britton & Rose's *Arrojadoa* went into the synonymy of *Cephalocereus*, from which he separated *Pilocereus*. In the latter genus he placed the curious *Cereus luetzelburgii*, and also *C. leucostele*, for which Berger (1926) had recently created the then monotypic *Stephanocereus*. Another of Berger's splits he did not accept was *Brasiliopuntia* A. Berger (1926), which he referred back to *Opuntia*, although he seems to have been prepared to accept *Tacinga* Britton & Rose.

If Britton & Rose started a trend towards the splitting of genera, then the German cactus nurseryman, Curt Backeberg (1938, 1958–62), went many stages further, his 6-volume monograph promulgating a more than 10-fold increase in genera over Schumann's treatment (220 vs 21)! His poorly researched innovations, typological species concepts, disregard for taxonomic and nomenclatural conventions and unsatisfactory suprageneric classification (Barthlott 1988) resulted in little less than a state of taxonomic and nomenclatural chaos, which probably frightened off most professional botanists from serious study of the family until the mid-1960s. In 1938 he established 3 very poorly defined genera, which have turned out to be worthy of recognition, now that the family is better understood in Eastern Brazil: *Brasilicereus, Micranthocereus* and *Coleocephalocereus*. At the same time he published *Austrocephalocereus*, which modern authors now agree should be subsumed in *Micranthocereus*, according to the type species he cited for
the former (*Cephalocereus purpureus* Günke), although it is very doubtful whether he was using that binomial in its correct sense! He also accepted nearly all previous generic splits involving E Brazilian species. His great adversary and critic was the cactus evolutionary morphologist, Franz BUXBAUM, who supported the description of perhaps the most distinct of all the newer genera to emanate from Eastern Brazil — *Uebelmannia* Buining (1967) — and it is surprising that Backeberg failed to recognize this group, having described its earliest-known species himself (*Parodia gummifera* Backeberg & Voll).

David HUNT, in John Hutchinson’s *The Genera of the Flowering Plants* (vol. 2; Hunt 1967), provided a comprehensive botanical account of the Cactaceae down to generic level, adopting a more conservative attitude than both Britton & Rose and Backeberg, and classifying the genera within a modified version of the former monographers’ tribal/subtribal scheme. In total, he recognised 84 genera for the family and in their arrangement was partly influenced by the morphological-phylogenetical studies of Buxbaum (see below). Notable in Hunt’s treatment was his use of *Cephalocereus* in a very broad sense to include both North American and Brazilian columnar taxa bearing cephaloid structures, ie. *Arrojadoa, Stephanocereus, Micranthocereus, Austrocephalocereus, Coleocephalocereus* and *Pilosocereus*. The only Brazilian exception to this was *Facheiroa*, which was subsumed into the Andean genus *Espostoa* Britton & Rose, a move earlier proposed by Buxbaum (1959). Similarly, *Rhipsalis* was used in a more inclusive sense than either Schumann or Britton & Rose, but *Schlumbergera* was circumscribed in the manner accepted today. Both *Leocereus* and *Arthrocereus* were recognised, but the latter, besides Brazilian taxa, included a divergent Argentinian species now placed in *Echinopsis* (*E. mirabilis* Speg.).

The aforementioned Friedrich RITTER based his classification scheme on very careful observation of the plants in the field, which knowledge he had gained during many years of exploration (Eggli *et al.* 1995). In 1959 he was the first to recognize the generic
status of what later was named *Uebelmannia* Buining (1967), for which his manuscript name was ‘*Gummocactus*’ (Ritter 1979). Later, in a paper on Brazilian cephalium-bearing cacti (Ritter 1968) he independently recognised the distinctness of the rare Bahian endemic, *Cereus dybowskii*, which he named *Gerocephalus dybowskii*, this, unfortunately, a few weeks after Franz Buxbaum had published the priorable generic name, *Espostoopsis*, for the same plant (Buxbaum 1968). He was also the first among modern authors to recognize that the globular-stemmed genus, *Melocactus*, was closely related to the cereoid *Coleocephalocereus* (Ritter, l.c., Taylor 1991a: 17). Subsequently, when writing up his many years’ results of cactus study in South America, he published a series of new genera reflecting his excellent knowledge of the Cactaceae (Ritter 1979). Of these, *Pseudoacanthocereus* and *Cipocereus* are recognized today, but *Floribunda* and *Mirabella* have passed into the synonymy of *Cipocereus* and *Cereus*, respectively (Zappi & Taylor 1991, Taylor 1991b, 1992a). Although Ritter lacked a proper training in plant systematics, his generic concepts were certainly more realistic than those of either Backeberg or Buxbaum, as is evidenced by his treatment of *Pilosocereus* as including *Pseudopilocereus* Buxbaum, of *Micranthocereus* including *Austrocephalocereus*, and of *Coleocephalocereus* including *Buiningia* Buxbaum, all of which are circumscriptions followed in standard treatments today (eg. Hunt 1992b, 1999a, Barthlott & Hunt 1993, Zappi 1994).

While Buxbaum described and named a new genus and a few new subgenera amongst the cacti of Eastern Brazil, as well as rearranging some others, the major contribution he made to the study of the Cactaceae as a whole was the evolution of a tribal classification based on a comprehensive understanding of morphology (Buxbaum 1950–1954). His system was first presented in 1958 with further notes and adjustments appearing over the next 16 years (Buxbaum 1958, 1959, 1962, 1968a & b, 1975; Endler & Buxbaum 1974). His studies, terminology and tribal nomenclature still form the basis for current schemes of classification, as described in the following section (Chap. 2.7), which also
accounts for the present author's involvement in the consensus developed under the auspices of the International Organization for Succulent Plant Study (IOS), by its Cactaceae Working Party. Towards the close of the period under discussion a new tool for investigating micro-morphology and especially that of pollen and seeds, was becoming important for classification of cacti — the Scanning Electron Microscope (Leuenberger 1976, Barthlott & Voit 1979). Influenced by data derived from these sources, the last treatment of the Cactaceae to appear prior to the 1980s recognised a little over 100 genera (Barthlott 1977, 1979).

2.7. Systematics of Cactaceae 1980–2000 and the IOS consensus initiatives

An unusual feature of Cactaceae systematics over the past two decades is the degree to which its proponents have been organised. Since 1950, the International Organization for Succulent Plant Study (IOS) has encompassed a significant group of cactus specialists (as well as those with wider interests in succulent plants), a notable exception being the wayward Curt Backeberg, whose major detractors were mostly IOS members! A study of the names of those in attendance at successive biennial IOS congresses highlights the opportunities that have existed for those interested in 'cactology' to exchange ideas (Supthut 1999). Thus, it was perhaps not surprising that a proposal by IOS Secretary, David Hunt, to establish a Cactaceae Working Party, which would aim towards a 'consensus classification', was made at the Frankfurt-am-Main congress of the organization in 1984 (Anderson 1999). This consensus approach was partly driven by the need of two of its major protagonists, David Hunt and Wilhelm Barthlott, to complete treatments of the family for major reference works on vascular plants (Walters et al. 1989: 202–301, Barthlott & Hunt 1993). Such treatments were at risk of being hampered by the singular lack of orthodox taxonomic revisions of individual genera and the widely contrasting approaches adopted in modern 'standard works' on the family, such as those by
the ‘splitters’, Curt Backeberg and Friedrich Ritter (see Chap. 2.6) and ‘lumper’, Lyman Benson, whose circumscription of *Cereus* Mill. was as broad as that of its 18th Century author, Phillip Miller, taking in elements placed in at least 4 of Buxbaum’s tribes (Benson 1982).

In these circumstances, and recognizing that a considerable body of knowledge existed amongst the IOS membership, but was fragmentary in nature, the drawing together of a Working Party at annual meetings could bring benefits. This process was agreed in 1984 and meetings have been held at least annually since then, facilitated by the decision to hold ‘inter-congress’ meetings of IOS between its biennial congresses, starting in 1985. Following a second meeting of the Working Party a draft list of genera was published in 1986 (Hunt & Taylor 1986). This recognized a total of 86 genera in 3 categories: ‘unanimously accepted’ by the majority of Working Party participants (51 genera), ‘less than unanimously accepted’ by at least a third of participants (26 genera) and the remainder (9 genera) to be retained out of nomenclatural expediency or because they were considered ‘*incertae sedis*’. This first ‘consensus’ list was relatively conservative, but as the Working Party grew, and with it the sources of useful information, there was a gradual inflation of genera, so that the next list published (Hunt & Taylor 1990) recognized a total of 93, once again in 3 categories (55 accepted by at least 80% of participants, 21 accepted by c. 60% and 17 for nomenclatural reasons or as *incertae sedis* and accepted by 35–60%). The genera accepted in the second list were determined by a postal ballot, which attracted responses from more than 20 specialists. Proposed changes to the previous list were justified in a series of short printed notes and accompanied by the sometimes contrasting views of particular participants, the present author included (Hunt & Taylor 1990: 98–104). Further thoughts and views were subsequently aired by consensus participants in a paper printed the following year (Hunt & Taylor 1991) and opportunities were taken to publish new names for use in the first edition of the CITES Cactaceae Checklist (Hunt
1992b), which closely followed the IOS consensus list, but accepted a further 8 genera in the third category, bringing the total for the family to 101. This Checklist went down to the level of species and consequently drew attention to those whose generic placement was particularly controversial. A series of short papers by members of the Working Party, as well as by others not necessarily connected with the IOS, have continued to appear (e.g. Hunt & Taylor 1992 and in the newsletters, Cactaceae Consensus Initiatives nos. 1–8, 1996–99, Cactaceae Systematics Initiatives no. 9, 2000). Besides these shorter commentaries, more substantial monographic, synoptic and cladistic treatments of larger or complex groups by members of the IOS Working Party have begun to appear, those with relevance to Brazil including *Pereskia* (Leuenberger 1986), *Facheiroa* (Braun & Esteves Pereira 1986–89), tribe Cerceae (Taylor & Zappi 1989), *Melocactus* (Taylor 1991a), *Pilosocereus* (Zappi 1994), tribe Rhipsalideae (Barthlott & Taylor 1995) and *Uebelmannia* (Nyffeler 1998). Most recently, a second edition of the CITES Checklist has appeared (Hunt 1999a), drawing heavily on the above-cited treatments and accepting 108 genera, with their included taxa listed down to the level of subspecies.

Since 1992, as with other groups of organisms, our understanding of Cactaceae systematics has become heavily influenced by molecular data, in the form of phylogenies derived from analysis of gene sequence variation (DNA/RNA), and this has been further supported by anatomical, phytochemical, pollen and seed micro-morphological information, which the molecular data are beginning to help interpret (Stuppy & Huber 1991, Wallace 1995, Wallace & Cota 1996, Maffei et al. 1997, Santos et al. 1997, plus various soon-to-be-published studies by Barthlott & Hunt, Nyffeler, Stuppy, Wallace & students). The ways in which the IOS consensus process and subsequent studies have contributed to the classification of the 30 cactus genera here recognized for Eastern Brazil are summarized in Table 2.1.
<table>
<thead>
<tr>
<th>E Brazilian genus</th>
<th>IOS Consensus status</th>
<th>Comments / justification</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>PERESKIOIDEAE Schumann:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. <em>Pereskia</em> Mill. 1754</td>
<td>Unanimously accepted since 1986</td>
<td>Earliest generic name in subfamily, though potentially paraphyletic as currently circumscribed (Table 2.2)</td>
</tr>
<tr>
<td><strong>OPUNTOIDEAE Schumann:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. <em>Quiabentia</em> Britton &amp; Rose 1923</td>
<td>Sunk into <em>Pereskiopsis</em> 1986 &amp; 1990; recognised by Hunt (1992b, 1999a)</td>
<td>Seed anatomy (Stuppy submitted) supports separation from <em>Pereskiopsis</em></td>
</tr>
<tr>
<td>3. <em>Tacinga</em> Britton &amp; Rose 1919</td>
<td>Unanimously accepted 1986 &amp; 1990, but only in original circumscription (<em>sens. str.</em>) including 2 spp.</td>
<td>Recognized in an expanded sense here for 6 spp., based on seed anatomy and floral similarities (Taylor &amp; Stuppy submitted)</td>
</tr>
<tr>
<td>4. <em>Brasiliopuntia</em> (Schumann) A. Berger 1926</td>
<td>Sunk into <em>Opuntia</em> / 1986 &amp; 1990</td>
<td>Recognized here based on seed- and pollen-morphology (lacks reticulate exine of <em>Opuntia sens. str.</em>) and unique, autapomorphic habit and behaviour (Taylor &amp; Stuppy submitted)</td>
</tr>
<tr>
<td>5. <em>Nopalea</em> Salm-Dyck 1850</td>
<td>Sunk into <em>Opuntia</em> / 1986 &amp; 1990</td>
<td>Recognized here based on pollen-morphology (lacks reticulate exine of <em>Opuntia sens. str.</em>) and floral differences</td>
</tr>
<tr>
<td>6. <em>Opuntia</em> Mill. 1754</td>
<td>Unanimously accepted since 1986 with <em>sens. lat.</em> circumscription</td>
<td>Earliest generic name in subfamily, here recognized <em>sens. str.</em> for taxa with unique autapomorphic reticulate pollen exine and sensitive stamens</td>
</tr>
<tr>
<td><strong>CACTOIDEAE (HPE clade)—Hylocereae:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9. <em>Epiphyllum</em> Haw. 1812</td>
<td>Unanimously accepted since 1986</td>
<td>Earliest generic name in tribe</td>
</tr>
</tbody>
</table>

38
<table>
<thead>
<tr>
<th><strong>CACTOIDEAE (HPE clade?)</strong></th>
<th><strong>-Echinocereeae(?)</strong></th>
<th><strong>CACTOIDEAE-Rhipsalideae:</strong></th>
</tr>
</thead>
</table>

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<tr>
<th><strong>CACTOIDEAE-Rhipsalideae:</strong></th>
<th><strong>Cereae:</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>11. <em>Lepismium</em> Pfeiffer 1835</td>
<td>Accepted to include only the Brazilian type species for reasons of nomenclatural expediency in 1986, then in an expanded sense by a minority of IOS WP members in 1990; accepted by Hunt (1992b, 1999a)</td>
</tr>
</tbody>
</table>

| 12. *Rhipsalis* Gaertner 1788 | Unanimously accepted 1986–90 | Earliest generic name in the tribe, whose present circumscription is supported by phylogenetic analyses. See Chapter 3.1 |

| 13. *Hatiora* Britton & Rose 1915 | Unanimously accepted 1986, then by only a minority in 1990; subsequently accepted by Hunt (1992b, 1999a) | Circumscription employed here defined on the basis of stem- and floral-morphology, as described by Barthlott (1987) and Barthlott & Taylor (1995). *E* Brazilian type species shown to be part of a monophyletic group (*Hatiora* subg. *Hatiora*) on the basis of phylogenetic analyses, but genus becomes paraphyletic if taxa referable to *Rhipsalidopsis* Britton & Rose are included. See also Chapter 3.1 |

| 14. *Schlumbergera* Lemaire 1858 | Unanimously accepted since 1986 following expanded circumscription employed in revision by Hunt (1969) | Recognition of this genus is supported by gene sequence data (Wallace ined.). See Chapter 3.1, Fig. 1 |

<table>
<thead>
<tr>
<th><strong>CACTOIDEAE (BCT clade)– Cereae:</strong></th>
<th><strong>Cereae:</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>15. <em>Brasilicereus</em> Backeberg 1938</td>
<td>Included in <em>Monvillea</em> Britton &amp; Rose 1920 in 1986, but accepted by a minority of IOS WP members in 1990, following recommendations in Cereae paper by Taylor &amp; Zappi (1989); accepted by Hunt (1992b, 1999a)</td>
</tr>
</tbody>
</table>

<p>| 16. <em>Cereus</em> Mill. 1754 | Unanimously accepted since 1986 | Earliest generic name in the tribe |</p>
<table>
<thead>
<tr>
<th>S.No.</th>
<th>Genus</th>
<th>Status and Features</th>
</tr>
</thead>
<tbody>
<tr>
<td>17.</td>
<td>Cipocereus Ritter 1979</td>
<td>Lumped with Pilosocereus in 1986, then accepted (incl. Floribunda Ritter) by a minority of IOS WP members in 1990, following recommendations in Cereeae paper by Taylor &amp; Zappi (1989); accepted by Hunt (1992b, 1999a)</td>
</tr>
<tr>
<td>18.</td>
<td>Stephanocereus A. Berger 1926</td>
<td>Accepted to include only the type species for reasons of nomenclatural expediency in 1986, then in an expanded sense by a minority of IOS WP members in 1990; accepted by Hunt (1992b, 1999a)</td>
</tr>
<tr>
<td>19.</td>
<td>Arrojadoa Britton &amp; Rose 1920</td>
<td>Unanimously accepted since 1986</td>
</tr>
<tr>
<td>22.</td>
<td>Coleocephalocereus Backeberg 1938</td>
<td>Accepted by a majority of IOS WP members in 1986, then by fewer votes in 1990, following the suggestion that it might be paraphyletic in respect of Melocactus by Taylor &amp; Zappi (1989). Accepted by Hunt (1992b, 1999a)</td>
</tr>
<tr>
<td>23.</td>
<td>Melocactus Link &amp; Otto 1828</td>
<td>Unanimously accepted since 1986</td>
</tr>
</tbody>
</table>

**CACTOIDEAE (BCT clade) - Trichocereeae:**

<table>
<thead>
<tr>
<th>S.No.</th>
<th>Genus</th>
<th>Status and Features</th>
</tr>
</thead>
<tbody>
<tr>
<td>24.</td>
<td>Harrisia Britton &amp; Rose 1908</td>
<td>Unanimously accepted since 1986 in the broad sense including Eriocereus Riccobono (1909)</td>
</tr>
<tr>
<td>25. <strong>Leocereus</strong> Britton &amp; Rose 1920</td>
<td>Accepted less than unanimously by IOS WP members in 1986 (when it was hinted that <em>Arthrocereus</em> A. Berger might be included), then fully accepted as a monotypic entity in 1990, following commentary by the present author (l.c. 100) and data in Taylor &amp; Zappi (1990)</td>
<td>Fruit- and seed-morphology unique within the BCT clade and sister group as yet unidentified. Position awaits confirmation based on molecular data.</td>
</tr>
<tr>
<td>26. <strong>Facheiroa</strong> Britton &amp; Rose 1920</td>
<td>Accepted less than unanimously by IOS WP members in 1986 &amp; 1990; accepted by Hunt (1992b, 1999a)</td>
<td>Sister group within tribe at present uncertain and its position remains to be elucidated with molecular data.</td>
</tr>
<tr>
<td>27. <strong>Espostoopsis</strong> Buxbaum 1968</td>
<td>Maintained as a synonym of <em>Austrocephalocereus</em> in 1986 (which had been Buxbaum's later view, cf. Leuenberger 1976), then recognized by a minority of IOS WP members in 1990, following recommendations by Taylor &amp; Zappi (1989); accepted by Hunt (1992b, 1999a)</td>
<td>In stem and habit characters this plant strongly resembles the Andean genus, <em>Espostoa</em> Britton &amp; Rose, but has naked flowers and polycolpate pollen. Its placement in Trichocereeae, rather than Cereeae, is provisional and based on the strong suspicion that its floral features are merely convergent with Cereeae, where it appears to lack any obvious relatives</td>
</tr>
<tr>
<td>28. <strong>Arthrocereus</strong> A. Berger 1929</td>
<td>Tentatively referred to <em>Leocereus</em> in 1986, then accepted by a minority of IOS WP members in 1990, following debate reported in l.c., 99–100; accepted by Hunt (1992b, 1999a)</td>
<td>Close to the very large and complex genus, <em>Echinopsis</em> Zucc., but differing in its pollen (Leuenberger 1976) and indehiscent fruits. Molecular evidence is needed to confirm its generic status or otherwise</td>
</tr>
<tr>
<td>29. <strong>Discocactus</strong> Pfeiff. 1837</td>
<td>Unanimously accepted since 1986</td>
<td>Assumed to be the sister group of the much larger <em>Gymnocalycium</em> Pfeiff. ex Mittler 1844, but distinguished by having 12–15-colpate (vs 3-colpate) pollen (Leuenberger 1976) and the presence of a terminal cephalium — a parallelism with <em>Melocactus</em></td>
</tr>
<tr>
<td>30. <strong>Uebelmannia</strong> Buining 1967</td>
<td>Accepted less than unanimously by IOS WP members in 1986, then unanimously in 1990; accepted by Hunt (1992b, 1999a)</td>
<td>Apparently a member of the BCT clade, but presently without obvious allies and thought to be an isolated relict</td>
</tr>
</tbody>
</table>

Table 2.1. Status of genera of Cactaceae found in Eastern Brazil according to the IOS consensus process (Hunt & Taylor 1986, 1990), CITES Checklist editions (Hunt 1992b, 1999a) and their present treatment, with brief justifications and notes. (See further discussion in Chapter 3.1/3.2.)

Relationships are clearly defined on molecular and other evidence at the subfamily level (ie. *Pereskioideae*, *Opuntioideae* and *Cactoideae*, see Table 2.2; Barthlott & Hunt 1993, Wallace 1995, Wallace & Cota 1996, Wallace & Dickie submitted, Stuppy 41.
submitted), but in the complex Cactoideae, comprising > 100 genera, the situation is less clear, though there appear to be c. 7 major clades of uneven size.

<table>
<thead>
<tr>
<th>Subfamily</th>
<th>Characters / molecular markers</th>
</tr>
</thead>
<tbody>
<tr>
<td>PERESKIOIDEAE Schumann</td>
<td>Woody, with essentially non-succulent stems bearing broad, functional, scarcely succulent leaves and un-barbed spines; seeds of 'common ancestral centrospermous type' (Barthlott &amp; Hunt 1993); pollen 3–15-colpate. Has no shared cpDNA restriction site changes with the putatively basal Maihuenioideae (Maihuenia only), but may be paraphyletic in respect of Cactoideae (Wallace 1995: 9)</td>
</tr>
<tr>
<td>OPUNTIOIDEAE Schumann</td>
<td>Stems succulent, at least at first, bearing cylindrical to awl-shaped or rarely flattened, succulent and often caducous leaves and two distinct kinds of barbed spines; seeds covered in a bony aril formed from the funicle (unique in the centrosperms); pollen mostly 12–18-porate. Has autapomorphic deletion in the plastid gene accD, ORF 512, from the large single copy portion of cpDNA (Wallace, pers comm.)</td>
</tr>
<tr>
<td>CACTOIDEAE</td>
<td>Stems succulent, leaves reduced to minute ephemeral scales or usually entirely absent; spines un-barbed; seeds various, lacking an aril or this a corky appendage at the hilum only; pollen mostly 3(–12)-colpate. Has autapomorphic c. 700 base-pair deletion from the chloroplast encoded gene rpoC1 intron (Wallace &amp; Cota 1996)</td>
</tr>
</tbody>
</table>

Table 2.2. Characters defining the subfamilies of Cactaceae represented in Eastern Brazil.

Unfortunately, much of the molecular research already conducted is yet to be published, although regular presentations and updates have been provided by Robert Wallace and his students (Iowa State Univ., USA) at IOS and other meetings, and most recently by him and also Reto Nyffeler (Harvard Univ. Herbaria, USA; cf. Nyffeler 1999) at the 26th IOS congress in Zürich, March 2000.

These investigations have demonstrated that the Brazilian Rhipsalideae DC. are a monophyletic group and in Eastern Brazil their delimitation into 4 genera based on morphological characters is well supported (by the trnL-F intergenic spacer and rpl16 intron markers, fide Wallace). As already argued by Barthlott (1988), this strongly contradicts Buxbaum’s tribal arrangement (Buxbaum 1958 etc., cf. Leuenberger 1976),
where the slender-stemmed, small-flowered South American rhipsaloid epiphytes were included within the Hylocereae, which are larger-growing epiphytes and climbers with a centre of diversity in Central America.

In-so-far as they have been sampled, the remaining E Brazilian Cactoideae divide into two groups of Buxbaumian tribes (based on the \textit{rpl}16 intron and \textit{rbcL} markers, \textit{fide} Wallace): the so-called Hylocereeae-Pachycereeae-Echinocereeae clade (HPE, also includes Leptocereeae \textit{pro parte} and \textit{Corryocactus} Britton & Rose) and the Browningieae-Cereeae-Trichocereeae (BCT) clade. In the Taxonomic Synopsis in Chapter 3 the Rhipsalideae are positioned between the HPE and BCT clades to emphasize their separation, but it is important to note that the basal topology of these major evolutionary lines is as yet unresolved, so their order has no other significance. The HPE clade includes the large-flowered, robust climbers and epiphytes belonging to the Hylocereeae \textit{(Hylocereus, Epiphyllum etc.)} to which should probably be added the similar if enigmatic \textit{Pseudoacanthocereus}, whose position awaits confirmation with molecular evidence. In an earlier molecular analysis the Hylocereeae appeared as the most basal element in Cactoideae (Wallace 1995: Fig. 11), but that position has now been taken by \textit{Calymmanthium} Ritter, an aberrant Peruvian cereoid.

The BCT clade is robustly monophyletic, characterised by a substantial deletion of some 300 nucleotide base-pairs, but since this, the evolutionarily active part of the \textit{rpl}16 intron has been deleted, there is currently little scope for further resolution of relationships within the clade with this marker. Unfortunately, the clade represents 16 out the total of 30 cactus genera of Eastern Brazil. However, evidence from a phytochemical source suggests that at least the ± naked-flowered Cereeae Salm-Dyck (8 or 9 genera) may be a monophyletic component within BCT, since, in a recent family-wide survey, the cuticular \textit{n}-alkanes of \textit{Cereus, Pilosocereus} and \textit{Melocactus}, representatives of markedly different parts of the tribe (Taylor & Zappi 1989: Figs 2–5), are reported to be much more similar to
each other than to those of other tribes (Maffei et al. 1997). *Brasilicereus* is provisionally included in Cereae here, but has aberrant, scaly flowers and potentially might represent the Browningieae component of BCT or belong to the Trichocereae Buxbaum. The presumed Trichocereae component is 7 genera, of which *Leocereus*, *Espostoopsis* and *Uebelmannia* are each aberrant in different ways and their inclusion in the tribe is provisional at present. Unlike the naked-flowered Cereae this tribe is characterised by pericarps/flower-tubes ± clothed in hair-spines and/or sometimes spines or bract-scales, although *Espostoopsis* has almost naked flowers.

The remaining major clades of Cactoideae recognizable on molecular evidence, that are absent from Eastern Brazil, are the Cactae (N Hemisphere), Notocacteae Buxbaum (S South America), *Calymmanthium* (Peru) and *Copiapoa* Britton & Rose (Chile), the latter two lacking tribal names at present. A comparison of Buxbaum’s higher level classification of Cactaceae with that implied by modern molecular phylogenies is offered in Table 2.3, together with brief notes on the circumscription of his groupings.

<table>
<thead>
<tr>
<th>Tribes/subtribes of Buxbaum, principal included genera [* = native in E Brazil] and their characteristics</th>
<th>Status based on molecular data (gene sequence variation)</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>LEPTOCEREEAE Buxbaum <em>Leptocereus</em>, <em>Calymmanthium</em>, <em>Armatocereus</em>, <em>Neoraimondia</em>, <em>Samaipaticereus</em> etc. Erect columnar-cereoid taxa with few high stem ribs and shortly tubular flowers bearing areoles and spines</td>
<td>Buxbaum’s circumscription is not supported by molecular data and these genera should be dispersed amongst the tribes that follow, except for <em>Calymmanthium</em>, which probably merits its own tribe</td>
<td>Buxbaum was grouping these taxa on the basis of what are now seen to be symplesiomorphies</td>
</tr>
<tr>
<td>HYLOCEREEAE Buxbaum: 5 subtribes <em>Nyctocereus</em>, <em>Peniocereus</em>, <em>Acanthocereus</em>, <em>Harrisia</em> <em>, Aporocactus</em>, <em>Selenicerus</em>, <em>Deamia</em>, <em>Hylocereus</em> <em>, Epiphyllum</em> <em>, Disocactus</em>, <em>Pseudorhipsalis</em>, <em>Pfeiffera</em>, <em>Hattiora</em> <em>, Schlumbergera</em> <em>, Rhipsalis</em> <em>, Lepismium</em> etc. Suberect shrubs, lianas and epiphytes (both erect and pendent) with few-ribbed or flattened stems, very diverse flowers and ± smooth seedcoats (except <em>Harrisia</em>)</td>
<td>Molecular evidence requires the removal of the small-flowered, S Hemisphere epiphytes as the Rhipsalideae DC., sens. str. (excl. <em>Pseudorhipsalis</em>). <em>Acanthocereus</em>, <em>Leptocereus</em> (see above), <em>Deamia</em> and the Hylocereae sens. str. are basal to the Echinocereae (Pachycereae) elements in the HPE clade. <em>Harrisia</em> belongs in Trichocereae</td>
<td>As circumscribed by Buxbaum, the Hylocereae should have been called the Rhipsalideae DC., which is an older name</td>
</tr>
</tbody>
</table>

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<table>
<thead>
<tr>
<th>Tribe</th>
<th>Description</th>
<th>Example</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>PACHYCEREEAE</strong> Buxbaum: 4 subtribes</td>
<td>These form a significant part of the HPE clade, to which must be added the relevant parts of Buxbaum’s Leptocereae and Hylocereae, and the Echinocereae (q.v.)</td>
<td>Buxbaum included Pilosocereus p.p. (tribe Cereaeae) in Cephalocereus.</td>
</tr>
<tr>
<td><em>Pterocereus, Escontria, Pachycereus, Stenocereus, Carnegiea, Neobuxbaumia, Cephalocereus, Myrtillocactus</em> etc.</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>BROWNINGIEAE</strong> Buxbaum</td>
<td>Part of Browningia sens. lat. belongs to the BCT clade, but recent reports suggest that Castellanosia is part of the HPE clade (Hunt 2000)</td>
<td></td>
</tr>
<tr>
<td>Browningia, Castellanosia etc.</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>CEREEAE</strong> Salm-Dyck</td>
<td>With the exception of Jasminocereus, which belongs with Armatocereus in the HPE clade, the remainder included here by Buxbaum, where sampled, are BCT clade members and those having the assumedly synapomorphic naked pericarpel are referable to Cereeae. Is Stetsonia Browningioid?</td>
<td>The positions of the putative sister taxa, Praeacereus and Brasiliocereus, await clarification on the basis of molecular markers. Are they Cereeae?</td>
</tr>
<tr>
<td>Erect columnar-cereoid taxa with densely scaly tubular flowers</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>TRICHOCEREEAE</strong> Buxbaum: 4 subtribes</td>
<td>All elements included here by Buxbaum belong in the BCT clade, but as noted above some taxa are now referred to the Cereeae on the basis of their floral morphology, and various other BCT-Trichocereae were misplaced in the Notocacteae. Samaipaticereus (Leptocereae) and Harrisia (Hylocereae sensu Buxb.) belong here (Wallace 1997)</td>
<td>The position of Leocereus remains to be clarified on the basis of molecular markers</td>
</tr>
<tr>
<td>Erect columnar-cereoid taxa, bearing ± naked, tubular, mostly nocturnal flowers and ± naked fruit</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>NOTOCACTEAE</strong> Buxbaum: 5 subtribes</td>
<td>Notocacteae in its strictest sense (<em>Austroacereus, Eriosyce, Parodia sens. lat. and Frailea</em>) is strongly supported by molecular data, but the tribe sensu Buxbaum is otherwise a complete mixture, including elements of at least 4 other major lines, eg. the BCT clade, the HPE clade (<em>Corryocactus</em>, <em>Copiapoa</em> and Cactaeae (<em>Astrophytum</em>))</td>
<td>The Notocacteae as now defined are recognizable on the basis of floral characters (woolly pericarpel with bristles above) in combination with unique seedcoat morphology</td>
</tr>
<tr>
<td>Corryocactus, Austroacereus, Eriosyce, Eulychnia, Copiapoa, Parodia, Frailea, Uebelmania*, Astrophytum, Gymnocalycium, Sulcorebutia [= Rebutia p.p., see above], Discocactus*, Melocactus* etc.</td>
<td></td>
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</tr>
<tr>
<td>Mostly globular-stemmed, ribbed or tuberculate cacti, bearing diurnal short-tubed flowers with mostly scaly and/or bristly and woolly pericarpels; many unique seedcoat characters</td>
<td></td>
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</tr>
<tr>
<td><strong>ECHINOCEREEAE</strong> Buxbaum</td>
<td>Not recognizable as a discrete entity on molecular data, being an integral part of the large HPE clade and close to Stenocereus (Pachycereae)</td>
<td>Echinocereae will likely prove to be the oldest name for the HPE clade.</td>
</tr>
<tr>
<td>Bergerocactus, Echinocereus.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low-growing, shortly cereoid cacti bearing diurnal flowers with areolate-spiny pericarpels</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>CACTEAE</strong>: 4 subtribes</td>
<td>Well-defined major clade strongly supported by molecular data and other data when the North American Astrophytum is included from Buxbaum’s Notocacteae.</td>
<td>The majority of taxa are characterized by a suite of apomorphic seedcoat characters that sets them apart from all other cacti</td>
</tr>
<tr>
<td><em>Echinocactus, Sclerocactus, Thelocactus, Turbinicarpus, Lophophora, Strombocactus, Ariocarpus, Ferocactus, Escobaria, Mammillaria, Coryphantha</em> etc.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mostly globular-stemmed, ribbed or tuberculate cacti, bearing diurnal short-tubed flowers with naked, scaly and/or woolly pericarpels</td>
<td></td>
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</tbody>
</table>

Table 2.3. Buxbaum’s tribal arrangement of Cactaceae-Cactoideae (after Leuenberger 1976) evaluated by modern molecular data (Wallace, pers. comm.) etc. For terminology, see Chapter 3.2.
The ‘molecular revolution’ that has taken over our thinking about Cactaceae phylogeny and systematics has greatly improved our ability to compare like with like and interpret the characters that were formerly used, identifying convergencies and paraphyletic groups. However, as in other groups of angiosperms this has not always resulted in more clearly defined groups based on easily observable characters. The more derived taxa within the Cactoideae, such as the Rhipsalideae, Notocacteae and Cacteae are definable on the basis of such characters, as are isolated aberrant elements, like *Calymmanthium*, but distinguishing some of the unrelated yet morphologically convergent genera between the speciose columnar or cereoid HPE and BCT clades will be difficult unless there exist observable characters that we are currently ignoring. Hence, it is unlikely, or so it seems at present, that a workable field key based on gross morphological characters can be written to identify all the major lineages of Cactoideae classified using molecular data.
3.1. Generic and Specific concepts and characters employed by the author

Generic concept. Unlike specific concepts, where many taxonomists can agree that it is possible to recognize well-defined entities in nature whose circumscription is often relatively unambiguous, concepts that group species into genera are much more liable to differ in breadth. Cactaceae systematics is a classic exemplar of this, 'with the archetypal lumpers and splitters traditionally engaged in regular and unwearied conflict' (Hunt 1999b: 3). The key point, however, is that for the purpose of communicating evolutionary relationship the group defined should have a single common ancestor and include all taxa derived from that ancestor, ie. it is monophyletic. Thus, in an earlier, morphologically-based, cladistic treatment of the genera of Cereeae (the largest cactus tribe in Eastern Brazil), involving the author, it was stated that 'the operational taxonomic units to be employed ... as far as our knowledge permits ... are monophyletic' (Taylor & Zappi 1989: 15). This is still very much the principle embodied here, so that *Melocactus* Link & Otto and *Coleocephalocereus* Backeberg are each regarded as monophyletic (they are held to be sister taxa on the basis of the synapomorphy of fruits expressed from the cephalium). *Melocactus* has autapomorphies of a terminal
cephalium, slender-clavate fruits, seeds with relatively few testa-cells and pollen with simple tectal perforations (Taylor & Zappi 1989, Taylor 1991a: 17–18), while its potentially paraphyletic sister taxon is now believed to be monophyletic on the basis of having fruits dehiscent by means of a small basal pore (see Plate 1.4), all of these character states being unique within tribe Cereeae.

Independent cladistic analyses of Rhipsalideae DC., based on morphological characters (Taylor ined. [1996]) and molecular data (Wallace ined., see Fig. 1), when taken together, suggest that in comparison to the plesiomorphic, mesotonically branched Lepismium Pfeiffer (Barthlott 1987), the more derived E Brazilian genera of the tribe are each potentially monophyletic, as follows: (1) based on acrotonic branching, freely disarticulating old/diseased stem-segments and expanded flowers with ± colourless perianth-segments (Rhipsalis Gaertner); (2) these same vegetative states combined with strictly determinate stem-segments and ± erect (vs pendent habit), but perianth highly coloured and its inner segments only half-expanded (Hatiora Britton & Rose, sens. str. [2 spp.]); and (3) all the above derived stem-segment character states combined with the presence of a well-developed perianth-tube, highly coloured flower and stamens inserted in 2 series (Schlumbergera Lemaire). The structural modifications of Hatiora and Schlumbergera are here interpreted as independent adaptations towards pollination by hummingbirds. However, in the molecular analysis (Fig. 1), Hatiora is paired with Rhipsalis pachyptera, indicating Rhipsalis as paraphyletic, but the morphological evidence clearly places this species (and all other members of R. subg. Phyllarthrorhipsalis, see Chap. 3.2) together with the remainder of Rhipsalis. Defined on this basis Rhipsalis, Hatiora (sens. str.) and Schlumbergera, are easily recognized and may well be monophyletic, but there are also theoretically less clear cut, yet practical considerations that flavour some of the generic circumscriptions presently adopted in other tribes of the family.
Thus, various genera are recognised here on the basis of 'obvious morphological characters' (Judd et al. 1999: 29) that are assumed to be autapomorphies, but cannot be proved to be such, at least partly because of the lack of molecular phylogenies that would help determine the polarities of the character states employed, e.g. characters defining taxa in the major tribes Cereeae and Trichocereeae (see Chapter 2.7 for explanations). In other cases it may not even be wise to state that such obvious morphological characters can be assumed to be autapomorphies, but their significance is that the taxa they define cannot be allied with any other group and seem isolated taxonomically. This latter situation describes and is used to justify the recognition of *Pseudoacanthocereus* Ritter, *Leocereus* Britton & Rose (as a monotype) and *Uebelmannia* Buining (see Table 2.1), each of which possesses a unique suite of characters and whose inclusion in any other genus — and it is hard to decide which this

![Cladogram of Rhipsalideae](image-url)
might be (!) — would greatly increase the risk of creating at least a paraphyletic, if not a polyphyletic assemblage. These uncertainties stem from a lack of sufficient characters that can be safely employed in phylogenetic analysis (Taylor & Zappi 1989: 14), since the highly specialized and reduced nature of cactus morphology effectively limits the features that can be used, many being strongly linked to environmental factors and homoplasious. This said, a comprehensive investigation into anatomy (as begun by Mauseth 1996) and stem chemistry might well add valuable data sets for Brazilian and other South American taxa, as it has for the North American Pachycereeae (Gibson & Horak 1978). In the short term, molecular data look to be those most likely to contribute to a better understanding of generic relationships in Brazilian cacti and various teams of researchers, including Brazilians (eg. Drs Amaral & Bittrich at UNICAMP, São Paulo), are currently seeking new sources of informative gene sequences.

In a couple of other cases it is not so much a lack of knowledge as the needs of practical convenience that have shaped decisions on the circumscriptions adopted, it being arguably better to be aware of a problem than to use ignorance as one’s excuse — the situation described in the previous paragraph. For example, based on molecular data (Wallace 1995: 9, Butterworth ined.) the species comprising *Pereskia* Miller fall into 4 distinct clades whose relationship to one another at present cannot be further resolved and, as noted already (Tables 2.1/2.2), a more serious problem is that the genus is potentially paraphyletic in respect of the Cactoideae (see Fig. 2). It could, in theory, be broken up and in that case the Brazilian taxa would end up being distributed between 3 different genera (see Chap. 3.2), not that this would be either helpful for identification purposes or more informative than their recognition as subgenera or sections. However, although the genus is implicitly circumscribed here to include
all its named species, the element that makes it paraphyletic in respect of the Cactoideae (represented by 'Leptoqua' in Fig. 2) is *P. lychnidiflora* DC., a native of Central America, not Brazil. A not dissimilar situation is presented by the treatment of *Cereus* Miller adopted here. Two sympatric subgenera are recognized, Subg. *Cereus* and Subg. *Mirabella* (Ritter) N. P. Taylor (1991b, 1992a), but the latter lacks the potential autapomorphy for the genus, which is the early-deciduous spent perianth (inclusion of Subg. *Mirabella* has required *Cereus* to be keyed out twice in the 'Key to genera'). However, on other characters there is no reason for its exclusion from *Cereus* and it is particularly close in habit, flowers and fruit to another allopatric-vicariant element known as *C. subg. Ebneria* (see Map. 3, Chap. 4), which has the early-deciduous perianth. In these circumstances the author prefers to await molecular evidence that may help determine whether the persistent perianth in Subg. *Mirabella* represents the plesiomorphic state or an apomorphic reversal. The same remark must apply to another case where, in contrast, two taxa have been kept apart. This concerns *Pilosocereus* Byles & Rowley and *Micranthocereus* Backeberg (see section 3.2, below, for details), where there is an unclear relationship and fragile distinctions between two taxa that have never been combined hitherto (the much larger and more widespread genus is *Pilosocereus*, which has the younger of the two generic names involved and in the interests of nomenclatural stability would need to be conserved, if they were lumped as a single genus).

Besides the already-mentioned *Leocereus*, the status of two other monotypic genera treated below merits particular justification. It could be argued that a monotype is an admission of failure on the part of the taxonomist/systematist, since the otherwise conveniently informative binomial system of nomenclature in this case does not indicate the relationship of the species involved. Thus, the names of *Espostoopsis dybowskyi* and *Brasiliopuntia brasiliensis* do not give an immediate clue as to their relationship, although the
Figure 2. Cladogram of *Pereskia* taxa (Pereskioideae) with *Leptocereus* ('Leptoqua', Cactoideae); *Maihuena* ('Maipoe', Maihuenioideae) and *Talinum* (Portulacaceae) are outgroups; based on gene sequence analysis of the *rpl16* intron of ribosomal protein L16. *Pereskia* comprises 4 unresolved clades, the upper 3 including Brazilian taxa (© Feb. 2000, C. Butterworth, Iowa State Univ., USA).
well-informed may get a steer from the generic etymologies. In fact, their names do indeed explain the putative relationship of *Espostoopsis* and *Brasiliopuntia*, which are potentially close to *Espostoa* Britton & Rose and *Opuntia* Miller, respectively. In the case of *Espostoopsis* its inclusion in *Espostoa* (tribe Trichocereeae) would be premature on current evidence and require an expansion of the latter's circumscription, which would make for difficulties in writing a simple key to South American columnar genera. Alternatively, the various unusual features or combinations of characters that *Espostoopsis dybowskii* displays argue against its inclusion in any of the genera of tribe Cereeae (Taylor & Zappi 1989), where its similarities look suspiciously like convergence. On the basis of robust evidence from gene sequences and seed anatomy (Wallace & Dickie submitted, Stuppy submitted) *Brasiliopuntia* belongs in the same clade as *Opuntia* Miller and shares some obvious morphological similarities (eg. combination of flattened stem-segments and flowers with spreading stamens). However, the previously ill-defined 'dustbin genus' *Opuntia* can now be most conveniently recognized in a restricted sense on the basis of the autapomorphic character state of pollen with a reticulate exine (a unique feature within the centrosperms, according to Wilhelm Barthlott, pers. comm.). This circumscription is further supported in more practical terms, since all species to be included in *Opuntia sens. str.* can be readily identified by flowers possessing sensitive stamens, which excludes *Brasiliopuntia* and other genera in the *Opuntia* clade (Taylor & Stuppy submitted). In relation to most of these the habit, dimorphic stems and pollen characters of *Brasiliopuntia* (see section 3.2, below) are clearly strong autapomorphies, while its inclusion in any of them would likely result in the creation of a paraphyletic group or at least one which was difficult to key out and comprehend (the somewhat similar Caribbean

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genus, *Consolea* Lemaire, differs in having seeds with very distinct funicular envelope anatomy and flowers with numerous small ovules, and is regarded as convergent).

In the artificial 'Key to genera' below, *Arrojadoa, Stephanocereus, Cipocereus* etc. are keyed out twice and this merits explanation. Excepting *Cereus*, which has been discussed already, this has been done to avoid making the key over-complicated to use and interpret, so that the user who is relatively uninformed about the morphology/diversity of Brazilian cacti should have an easier choice between the options presented and be able to reach an identification with greater confidence. The generic characters in these taxa are either not the easiest to employ in a dichotomous key, or are not observable for much of the year, and so other features have been used in the initial couplets resulting in more numerous but easier choices in subsequent couplets. In the case of *Stephanocereus*, comprising only two monotypic subgenera of markedly different habit (see Table 2.1), the infrageneric taxa have been keyed out as such, to flag up the full range of options to the first-time user. This is desirable because each taxon somewhat mimicks representatives of other genera with which it might otherwise be confounded (Subg. *Stephanocereus* is like *Arrojadoa rhodantha*, while Subg. *Lagenopsis* is like *Melocactus*). The same applies to *Arrojadoa* and *Cipocereus*, each including aberrant taxa which resemble species of other genera.

Specific concept and use of subspecies. Judd et al. (1999: 128–130, Table 6.4) describe more than seven different species concepts and admit that 'there is no consensus about species concepts in plants'. Earlier they note that 'The ascendency of phylogeny as an organising principle in systematics motivated a phylogenetic species concept'. This has various potential interpretations, but that favoured here is the definition advanced by Nixon & Wheeler (1990) of a phylogenetic species as the 'smallest aggregation of populations (sexual) or lineages
(asexual) diagnosable by a unique combination of character states in comparable individuals'. If such combinations of characters are fixed, diagnosable and testable by phylogenetic analysis, then we have a better method of recognizing species than that which has, in fact, been applied here — essentially the phenetic species concept, based on 'the overall similarity of members of a species, which are separated from other species by a gap in variation' (Judd et al., l.c.). For reasons explained in the preceding paragraphs it is difficult to employ phylogenetic methods for testing species concepts in Brazilian cacti and where it has been attempted (eg. Zappi 1994: 29) the robustness of the clades identified could easily be questioned. Such techniques were attempted in the investigative stages of the author's revision of Melocactus (Taylor 1991a), but the phylogenies deduced for the species level treatments were not published because of their inherent weaknesses. A sufficient number of characters that can be confidently polarized into plesiomorphic and apomorphic states is necessary and this has proved difficult enough at the generic level (Taylor & Zappi 1989), let alone at the rank of species, without access to molecular data. The size of the treatment realized here (> 125 native species) has unfortunately prevented the application of molecular techniques and phylogenetic methodology in a uniform way at this level. Furthermore, this will only become a feasible and meaningful activity when the generic relationships and, therefore, the significance of the characters and their states, can be clarified in the tribes Cereeae and Trichocereeae.

In employing a phenetic species concept this study has, however, taken into account, wherever possible, the reproductive strategy and inferred breeding system of the plants, as observed in nature and in cultivation (where the author has studied a considerable diversity of taxa over many years). Understanding reproductive strategy is important if similarities or differences and suites of linked characters that relate to pollination and dispersal syndromes are not to be over-valued. For example, it seems that some Brazilian cacti are probably able to
take advantage of different pollinators by quite minor changes to floral morphology and timing of anthesis, e.g. *Micranthocereus (Austrocephalocereus) purpureus* (Taylor & Zappi 1989: 22) and *Pilosocereus glaucochrous* (Zappi 1994: 78). Little is known at the cytological level about the breeding systems of cacti, but circumstantial evidence strongly implies that the majority of Brazilian taxa (as is true of cacti in general) are self-incompatible and outbreeders (cf. Ross 1981). The actual mechanism has recently been investigated in one Brazilian genus, namely *Schlumbergera* (Boyle 1997, O'Leary & Boyle 1998), but its operation in the rest of the family is presently unknown. However, exceptions to the obligate outbreeder status of most cacti from Eastern Brazil are known or suspected. Many, but not all *Melocactus* species appear to be self-compatible, at least in cultivation (Taylor 1991a: 16), and there is evidence that a couple of taxa are cleistogamous (see *M. lanssensianus* and other geographically disjunct look-alikes of uncertain status discussed in Supplement 1). The species definition that has been maintained in this latter circumstance is somewhat different, since there can be no gene exchange between such lineages and thus it is possible that a series of very narrowly defined taxa could be recognized if this phenomenon should prove to be more widespread than current field knowledge suggests. Going down that road might mean abandoning a pragmatic phenetic species concept in favour of the largely discredited biological species concept (Judd *et al.*, l.c.) and for the time being the temptation to recognize more narrowly defined taxa has been resisted.

The very few chromosome counts so far obtained for E Brazilian cacti, e.g. in *Pereskia* (Leuenberger 1986) and Rhipsalideae (Barthlott 1976), indicate that nearly all are diploids, although Das *et al.* (1998a&b) have recently presented some poorly documented evidence of tetraploids in *Melocactus*. Clearly, there is much work to be done here and studies of North American members of the family have painted a more interesting picture, with significant
numbers of polyploids in members of the Cactoideae (especially the 'HPE clade') and Opuntioideae (Pinkava 1999).

Field studies of cacti conducted in Brazil and elsewhere indicate that related taxa, and especially sister taxa, are only rarely sympatric and suggest that speciation has probably occurred by allopatric means in a majority of cases. When species belonging to the same genus occur together they can hybridize (eg. see treatments of Tacinga, Cipocereus, Arrojadoa and Melocactus, below), but this is not the norm and few hybrids have been recorded in the large genera Pilosocereus and Rhipsalis, whose species are frequently sympatric (cf. Zappi 1994: 35, Barthlott & Taylor 1995, Taylor 1999). However, even if inability to interbreed is a good criterion for defining some species, its obvious limitation is the converse situation, since more distantly related taxa hybridize on occasion and can produce viable offspring, eg. Pilosocereus pentaedrophorus × Micranthocereus purpureus, known from two sites at the eastern edge of the Chapada Diamantina, Bahia. Likewise, no one would seriously wish to suggest that Tacinga inamoena and T. palmadora, or for that matter Arrojadoa rhodantha and A. penicillata, should be lumped together as more broadly defined species because they hybridize at some (and certainly not all) sites of sympatry. In these cases the individual species here recognized can each be separated on suites of mutually exclusive characters and the Tacinga species would deserve being classified in different sections were the genus not so small as to make this of limited value.

Leaving aside theoretical concepts it is worth recording the author's experience that it has been a relatively straightforward task to delimit species amongst the cacti of Eastern Brazil. Straightforward, at least once the necessary fieldwork has been completed, because most initial uncertainties have revolved around regional or local variation, in the case of a number of widespread taxa, and the geographical area to be surveyed has been substantial. The
initial difficulties have been created through the use of typological species concepts by amateur 'cactus hunters', whose desire to discover and publish something new has been greater than that to understand the overall patterns of variation (Chapter 2.5). Put another way, their approach to defining and naming taxa has not been synthetic, but driven only by a search for differences. While species have often been more broadly defined here than in previous treatments, their regional variation is now better understood and many of the more widespread taxa have been subdivided into subspecies. In nature, many such cactus species, eg. *Arrojadoa rhodantha* and *Pilosocereus pachycladus*, are comprised of numerous geographically sequential races, none of which is sufficiently distinct to be worthy of being named (though many have). In some cases, however, these races can grouped on a geographical basis into subspecific taxa sharing mutually exclusive similarities. Thus, the races of *P. pachycladus* have been grouped into two subspecies defined on numbers of stem ribs correlated with amount of areolar wool. At their points of contact in northern Bahia they are scarcely distinguishable, whereas towards their margins it is likely that additional subspecies will be required once further field studies have been made. A somewhat different situation where the rank of subspecies has been employed is exemplified by *P. fulvianatus*. This is not as wide-ranging as its aforementioned relative and much less variable, but it includes a rather disjunct population that has begun to evolve some constant differences suggestive of incipient speciation (*P. fulvianatus* subsp. *rosae*). Here similarities greatly outweigh differences, but geographical separation makes its recognition as a subspecies appropriate and informative.

The most problematical taxa encountered in this study have been those in 2 of the 3 largest genera that have already been monographed, ie. *Melocactus* and *Pilosocereus*. Here there remain doubts about the circumscriptions of the *M. oreas / M. bahiensis* and the *P. machrisii* complexes, but it is anticipated that even these can be resolved by more field studies.
Characters employed by the author. It is not the intention here to enumerate all characters utilized in the definition of taxa in this study, but since not all of these are obvious from the keys presented in the next section it seems desirable to discuss a selection and give some specific examples of their use. Various characters have been discussed in detail before (Taylor & Zappi 1989) and others have already been mentioned above, eg. in Tables 2.1/2.3, because they were advanced in support of generic circumscriptions adopted by members of the IOS Working Party.

- **Stem mucilage.** While cactus floral tissues appear to be invariably mucilaginous there is much more variation that can be readily observed in stem tissues. The adaptive significance of this is still not completely understood (Gregory & Baas 1989). It may be involved in the water regime of the plant or offer protection from insect herbivores or high insolation (Nyffeler 1997). The basal Pereskioideae have it in abundance, so it is possible that its loss or reduction could represent an apomorphy, but this is far from clear. Also, it is rarely, if ever totally absent from stem tissues, but its relative abundance and precise location vary markedly within some genera, eg. *Micranthocereus*, *Coleocephalocereus*, *Melocactus*. For example, *Cereus hildmannianus* and *C. jamacaru* are both found in dry forest formations: the former has highly mucilaginous stems, the latter with mucilage obvious only at the actively growing stem apex. In *Uebelmannia* subg. *Uebelmannia* the two putative species are distinguished on the presence or absence of mucilage ducts.

- **Branching pattern.** This is likely to be more than one character, ie. comparable character states are not homologous. In Rhipsalideae, where 3 genera form a clade (Fig. 1, above), this is defined by the synapomorphic possession of acrotonic origin of new stem-segments, which arise from the apex of subtending segments whose growth has ceased, an unusual
condition within the Cactoideae (but more common in Opuntioideae). A second, presumably non-homologous case distinguishes *Pilosocereus* subg. *Gounellea* from *P.* subg. *Pilosocereus*. The former is characterised by new branches being initiated in a subacrotonic position, immediately below the apex of the actively growing subtending axis, as opposed to a mesotonic or basitonic origin in the latter. This 'subacrotonic' pattern is unique within Cereeae and by outgroup comparison was determined to be an apomorphy by Zappi (1994); it is presumed to have evolved in parallel in some Pachycereeae (e.g. *Myrtillocactus* Console) and in *Stetsonia* Britton & Rose (Browningieae?).

- **Seed-morphology.** This heading covers a range of different characters, including the anatomy of the funicular envelope (Stuppy submitted), seed shape and relative size and position/orientation of the hilum (e.g. see key to *Brasilicereus*, below), testa-cell size and shape and cuticular ornamentation. Seed size and colour also varies significantly in some groups. Seed characters are useful at all levels in the Cactaceae, as a family-wide survey will shortly demonstrate (Barthlott & Hunt in press), and this is also true in relation to the cacti of Eastern Brazil. Here seed-morphology has been investigated for most taxa studied using the Scanning Electron Microscope. Ample examples of this have already been published, so these will not be repeated now (Taylor 1991a, Taylor *et al.* 1992, Zappi 1994), but a few additional cases merit brief mention. However, it is important to recognize that we understand little about the influence of ecology (environment, dispersal syndromes etc.) on, for example, testa-morphology, and the use of such characters in phylogenetic analysis needs to be done with great care and in combination with unrelated character sets to ensure that such ecological influences are minimized. Thus, in the Cereeae, *Coleocephalocereus goebelianus* and *Stephanocereus leucostele* share
remarkably similar and distinctive drop-shaped seeds, but on most other characters they are clearly not closely related and there must be a strong suspicion that their shared seed-morphology is connected with dispersal, eg. by ants, even though their fruits differ markedly. The 5 species included in *Cipocereus* divide into 2 groups based on seed colour and testa-cell shape (periclinal walls) and ornamentation. These features correlate with stem rib number and it is likely that the peculiar testa ornamentation of the *C. minensis* Group will prove to be a unique synapomorphy, distinguishing it from all other Cereae.

- **Fruit-morphology.** This is a suite of characters that have tended to be ignored or under-valued until quite recently and yet there is often more diversity displayed here than in floral structures. The 'Key to genera' makes frequent mention of fruit characters and Plate 1 gives some examples of their diversity in tribe Cereae. In *Cereus*, the vegetatively very similar *C. jamaicaru* and *C. hildmannianus* can be readily separated when bearing ripe fruit. The former has fruit dehiscent by means of a sub-basal lateral split in the pericarp, while the latter opens at its apex along 3 lines like an expanding flower (Plate 1.1). It seems likely that they are dispersed by different vectors, the fruits of *C. jamaicaru* have frequently been seen with small birds hanging from beneath them, while those of *C. hildmannianus* have a form that could be accessed by bats (see Table 4.7). *Melocactus* (Cereae) and *Discocactus* (Trichocereae) are highly convergent, both being low-growing plants bearing (uniquely in Cactaeae) non-chlorophyllous terminal cephalia. On this basis they were once classified in their own tribe (see Chapter 2.6) and they even share slender clavate fruits. However, the fruits of *Melocactus* are indehiscent and eaten by lizards and birds, while those of *Discocactus* are laterally dehiscent by means of 2 or more splits and the seeds are eagerly sought by ants (as in the proposed sister genus, *Gymnocalycium*).
Plate 1. Examples of fruit diversity in tribe Cereeae. 1.1 (top left), *Cereus hildmannianus* (ovoid, apically dehiscent, perianth remains deciduous); 1.2 (top right), *Pilosocereus gounellei* (depressed-globose, subapically/laterally dehiscent, perianth remains persistent); 1.3 (bottom left), *Cipocereus bradei* (ovoid, indehiscent, with translucent funicular pulp, pericarp intensely blue-waxy); 1.4 (bottom right), *Coleocephalocereus buxbaumianus* (clavate, dehiscent by basal pore). [Plate 1.1 © RBG Kew]
3.2. Taxonomic Synopsis of the Cactaceae of Eastern Brazil

As its scope this treatment 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). Accepted names with their botanical authorities, bibliographic citations and types (seen unless indicated as 'n.v.'), summarized ecological and distributional data (for maps, see Chapter 4) and taxonomic commentary are presented, but detailed documentation of synonymy, morphological descriptions, distribution records and conservation assessments can be found in Supplement 1. An index to names and epithets, including all synonyms is also appended (Appendix 2). The genera are arranged in subfamilies and tribes, while the species of the more diverse genera are divided into subgenera or informal groups. Dichotomous keys to facilitate identification are provided for genera, species and subspecies. In these, unqualified measurements refer to length (or height in the case of erect plants); those connected by a multiplication sign (×) refer to length followed by width/diameter. Dimensions of the whole plant or its stems are always given exclusive of the spines; and distances between structures that themselves have a size, eg. between areoles on a rib, are given from organ centre to centre. The author wishes to make it clear that he does not accept this thesis as a vehicle of 'effective publication' and any new names and typifications are to be regarded as provisional and invalid under the International Code of Botanical Nomenclature, Arts 7.10 & 34.1 (Greuter et al. 2000).

A few cactus terms employed below, and in Supplement 1, need brief explanation:

(1) areoles are the felted cushions (actually highly telescoped short shoots) found on various parts of the cactus plant, bearing trichomes, spines (≡ modified leaves), hair-spines 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 (eg. as seen on the fruit in Plate 2.5);

(4) pericarpel is the cactaceous structure comprising the specialized stem or receptacle into which the ovary of the inverted cactus flower is sunken (eg. see Plates 2.4, 3.1, 3.4, 4.1 & 5.1);

(5) the flower-tube is the hollow or partially hollow structure above the pericarpel 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 (see Plates 3.1, 4.1, 4.4, 4.5 & 5.3);

(6) a cephalium is a ± modified part of the stem, whether apical or lateral (see Plates 4.4, 4.6, 5.2 & 5.4), 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 (ie. terete) or deformed, as in the case of so-called 'sunken' cephalia.

**Key to genera**

1. Actively growing stems bearing broad or awl-shaped leaves
   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. Leaves broad (SW Bahia & Cent.-N Minas Gerais)
   2. Quiabentia
   3. Leaves awl-shaped (widespread)

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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, drought-deciduous; seed 8–10 mm

4. Brasiliopuntia

4. Trees to < 4 m, or shrubs, subshrubs or lianas; stems/stem-segments not as above; seed to c. 5 mm

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)

5. 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. Stamens long-exserted and perianth-segments erect, not spreading; spineless and with few glochids (introduced/cultivated)

6. Nopalea

6. Stamens not as above or perianth-segments spreading to strongly reflexed and/or stems spiny

3. Tacinga

7. Flower > 10 cm long, or 8–10 cm and tube bract-scales bearing hairs (hair-spines) in their axils

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)

8. Fruit not as above; seed blackish

10. Pseudoacanthocereus

9. Stems flat, trigonous or 3-winged

9. Stems with > 3 wings/ribs

10. Pericarpel and flower-tube bearing conspicuous spines/bristles or broad-based bract-scales; perianth > 15 cm diam.

11. 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

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

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)

16. Flowers ± zygomorphic, tube to 8 mm long or more (S Espirito Santo & SE Minas Gerais)

16. Flowers actinomorphic, tube lacking or < 3 mm long

17. New stem-segments (excluding greatly elongated and usually basal extension shoots) arising mostly two or more together from the apices of older segments (branching acrotomic), 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- to mesotomic), not separating at the segment joints when old or diseased

18. Flowers whitish or not strongly coloured, or developed laterally on stem-segments of ± indeterminate growth; plant ± pendent

18. Flowers bright yellow or orange, from composite areoles at the apex of ultimate or penultimate segments of strictly determinate growth; plant ± erect

7. Hylocereus

8. Selenicereus

9. Epiphyllum


13. Schlumbergera

14. Harrisia

28. Arthrocereus

11. Lepismium

12. Rhipsalis

13. Hatiora
19. Plant unbranched or branched at or below ground level (caespitose), never abruptly segmented, shortly columnar, ± globose or depressed-globose, with or without a non-chlorophyllous bristly-woolly terminal cephalium

19. Plant branched above ground, slender cylindric to tall columnar, or plants single-stemmed 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, true 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.

24. Fruit with white or translucent pulp, spineless, or if spiny then stem > 2 cm diam.

25. Pericarpel and tube bearing areoles and bristle-spines; fruit covered in an intensely blue waxy bloom (Cent.-S Minas Gerais)

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

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

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

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)

27. Fruit not as above, or < 2 cm diam.; stems various
28. Stems segmented, with bristly/woolly ring cephalia at the joints and apex of distal stem-segments
29. Stems not as above; cephalium, if present lateral and ± continuous or elongate-terminal
30. Flowers green without, 8–10 cm long (Bahia, caatinga) 18. Stephanocereus subg. Stephanocereus
30. 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. Flower-bearing areoles ± modified or comprising a lateral cephalium; fruit not as above
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. Coleocephalocereus
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. 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: Bambui limestone) 21. Micranthocereus
PERESKIOIDEAE Schumann

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). Plate 2.1.

1. **PERESKIA** Miller


Including *Rhodocactus* Backeberg & Knuth (1936).

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

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* Griseb. (Mato Grosso do Sul) and *P. nemorosa* Rojas (Rio Grande do Sul), and are related to nos. 2–4 from Eastern Brazil (see Fig. 2, above). The East Brazilian taxa are restricted to various phases of the *Mata atlântica*, *agreste* and southern *caatingas*.

1. Scrambling or climbing plant, spines on vigorous shoots paired, recurved; flower white or cream 1. aculeata
   1. Erect shrubs or trees, spines always straight, spreading, never paired-recurved; flower yellow, pink, magenta, orange or red
   2. Flower bright yellow; fruit globose, 1–3-seeded 2. aureiflora
   2. Flower pink, magenta, orange or red; fruit turbinate, with > 3 seeds 3
3. Leaves narrowly elliptic to obovate-lanceolate; lateral veins (7-)10–13; seeds (5–)6–7 mm (*Mata atlântica, s.l.*)

2. *grandifolia*

3. Leaves ovate to broadly elliptic-ovate; lateral veins 5–7; seeds 4–5.5 mm (*caatinga*)

4. Flowers with campanulate to urceolate perianth; flower-buds orange; perianth-segments reddish pink, erect, recurring at apex only, stamens and style enclosed

4. *stenantha*

4. 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 absent.


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.

**PERESKIA GRANDIFOLIA** Group (nos. 2–4): sclereids fusiform-aggregated; stomata on stem present; periderm formation retarded; brachyblast leaves present. Fusiform-aggregated sclereids
are also found in *P. nemorosa* and *P. sacharosa* (SE South America, see Map 7), which, together with *P. grandifolia* subsp. *violacea*, are indicated as potentially basal members of this Group in molecular phylogenies (based on cpDNA restriction site variation and the plastid gene rpl16 intron) produced by Wallace (1995: 9) and C. Butterworth (*in litt.*, 10 Feb. 2000) at Iowa State University, USA (Fig. 2, above).


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 Espírito Santo, cultivated in N Minas Gerais & S Bahia)  
   2b. subsp. *violacea*

2a. subsp. *grandifolia*

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


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 Espirito Santo, apparently cultivated elsewhere. Endemic to the core area within South-eastern Brazil. Map 16A.

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, recent studies of plastid DNA gene sequences, conducted by Wallace (1995) and Butterworth (ined.), have indicated that this taxon may be worthy of specific status and that it is the basal element amongst the E Brazilian taxa belonging to the P. GRANDIFOLIA Group (see Fig. 2, above). 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 has been observed regenerating from stumps remaining in recently cut primary forest.

Central-southern (Bahian) *caatinga* element: *caatinga* surrounding the Chapada Diamantina, planalto de Maracás, northern Serra do Espinhaço and Serra Geral (Bahia), 300–900 m, east of the Rio São Francisco. Endemic. Map 23.

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, well beyond the known range of *P. stenantha*, had somewhat intermediate flowers, and in the region of Caitité 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).


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 lacking; periderm formation early; brachyblast leaves present. Other members of this group are from northern South America (P. guamacho Weber, sister species of P. aureiflora; see Map 6) and the eastern Caribbean islands (4 spp.).


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.

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 recently been confirmed in gene sequence phylogenies obtained by Wallace (1995) and Butterworth (ined., see Fig. 2).
OPUNTIOIDEAE Schumann

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). Plates 2.2–2.4.

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 *Pereskiopsis* Britton & Rose, *Quiabentia*, *Cylindropuntia* (Engelm.) F. Knuth and *Grusonia* Britton & Rose (Wallace & Dickie submitted). The broad flattened leaves of *Quiabentia* and *Pereskiopsis* may represent a synapomorphic reversal, since both *Austrocylindropuntia* Backeb., *Cumulopuntia* Ritter and the subfamily's plesiomorphic potential sister group, the Maihuenioideae, 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 Chaco and its periphery of Argentina, Paraguay and Bolivia (see Map 8). Its Brazilian counterpart, treated below, is of restricted 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, Bom Jesus da Lapa, Rio São Francisco, 15–16 Nov. 1912, Zehntner 630 (US, lecto. designated here; NY, lectopara.).

Southern Rio São Francisco *caatinga* element: on ± naked or thinly wooded limestone (Bambuí) outcrops or gneiss/granite inselbergs amidst high *caatinga* forest, 450–750 m, both sides of the Rio São Francisco valley, west-cent./southern Bahia and cent.-northern Minas Gerais. Endemic to the core area of Eastern Brazil. Map 26B.

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 (Taylor & Stuppy submitted). Other genera included in this lineage, but absent from Brazil, are *Miqueliopuntia* Ritter (N Chile), *Tunilla* Hunt & Iliff (*Opuntia* group AIRAMPO, Argentina) and *Consolea* Lemaire (E Caribbean). The following genus appears to have 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


Literature: Taylor & Stuppy submitted.

As recently amplified, a genus of 6 species named as an anagram after the *caatinga* of Eastern Brazil, where it is frequent, also ascending into the included *campos rupestres* (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 and 5 & 6 are known or suspected, but only that involving 4 & 6 is mentioned in the key 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

3. Stamens exserted (cultivated)  

   *Nopalea cochenillifera*

4. Stamens included (Eastern caatinga-agrestes)

3. Fruit greenish to reddish or purple outside, to 3 cm, funicular pulp yellowish  

4. Fruit greenish white, sometimes with faint pink shades, 4–5.5 cm, funicular pulp bright pink

5. Plants low-growing, rarely exceeding 1 m, mostly subshrubs; stem-segments always flattened; spines absent or fine and slender, to 15 mm (widespread, especially on rocks)

6. Plants taller, to 2 m or more, scandent, with at least the lower parts of stems perfectly cylindric; spines absent (NE Minas Gerais to W Pernambuco, caatinga)

5. Joints spineless (present in some areoles of T. xquipa); areoles well spaced, 10–20 mm apart

6. Joints with minute spines; areoles congested, 1–14 mm apart

6. All stem-segments perfectly cylindric; flowers green to purplish (S to NW Bahia & W Pernambuco)

6. Ultimate stem-segments ± flattened; flowers green (Rio Jequitinhonha valley, NE Minas Gerais)

1. **Tacinga funalis** Britton & Rose, Cact. 1: 39–40 (1919). Type: Brazil, Bahia, Joazeiro, 1915, Rose & Russell 19723 (US, lecto. designated here; NY, lectopara.).

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.
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 characteristic in the southern part of its range, but recorded northwards to at least Mun. Cafarnaum, central Bahia. These variants do not appear to exhibit obvious vegetative differences and the flowers of Backeberg's var. zehntneroides, as described, seem to be of somewhat intermediate colour. More collections and observations during its late winter (August/September) flowering period are needed.


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.


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

The flowers and fruit of this species provide a clear link between T. funalis, T. braunii and the following species.

† New name not accepted by the author in this thesis
A plant of probable hybrid origin, involving *T. werneri* and *T. inamoena*, has been observed near Pedra Azul, Minas Gerais.


Eastern *caatinga* element: in *caatinga-agreste* and *carrasco*, frequent on deep sandy substrates, c. 200–1020 m, Rio Grande do Norte to southern Bahia (from central Pernambuco and the Chapada Diamantina / northern Serra do Espinhaço eastwards). Endemic to North-eastern Brazil. Map 30A.

Apart from a single sighting unsupported by herbarium material (c. 60 km SE of Macaúbas, Bahia), this species appears to have a mainly eastern distribution, ranging from southern Bahia northwards to Rio Grande do Norte. Its pollination biology has been studied by Locatelli & Machado (1999a). It exhibits considerable regional variation.


Holotype: Brazil, Minas Gerais, Montes Claros, 1959, *Ritter* 1035 (U).

This is 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

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† New name not accepted by the author in this thesis
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)  
   \[ \text{5a. subsp. saxatilis} \]

1. Areoles very densely disposed, 1–6 mm apart; perianth-segments lanceolate (Mun. Iuiú, S Bahia)  
   \[ \text{5b. subsp. estevesii} \]

5a. subsp. saxatilis

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.

The hybrid \( T. \) saxatilis subsp. saxatilis \( \times T. \) inamoena has been observed and collected in western Bahia together with both parental taxa.

5b. subsp. estevesii \((P. \ J. \ Braun) \ N. \ P. \ Taylor \ & \ Stuppy\) in Succulent Pl. Res. 6: 00 (2001).  
Holotype: Brazil, Bahia, [Serra de Iuiú], 1984, E. Esteves Pereira 191 (UFG; ZSS, iso.).


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\( \dagger \) New name not accepted by the author in this thesis
6. Tacinga inamoena (K. Schumann) N. P. Taylor & Stuppy \footnote{New name not accepted by the author in this thesis} in Succulent Pl. Res. 6: 00 (2001).

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

Widespread Eastern Brazil element: usually on rocks (including inselbergs) or very stony ground, open \textit{caatinga} and \textit{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 \textit{cerrado} of western Bahia. Endemic to Eastern Brazil. Amongst the commonest of cacti from the region. Map 19.

The type locality, as given by Glaziou, l.c., 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 ‘\textit{Opuntia rubescens}’ [sensu Schumann (1890), non DC.], Glaziou 14865, which is \textit{Tacinga braunii} (q.v.), immediately precedes that for \textit{T. inamoena} (Gl. 14864) and both species grow together in the valley of the Rio Jequitinhonha, north-eastern Minas Gerais, where \textit{T. braunii} is endemic. It seems probable, therefore, that the type of \textit{T. inamoena} came from north-eastern Minas Gerais, where it reaches its southern limit.

Braun & Esteves Pereira (1989: 272) remark that \textit{Opuntia [Tacinga] 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 \textit{T. inamoena} has spineless stem-segments as in \textit{T. funalis} and \textit{T. braunii}, but, like 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:


Type: Brazil, Pernambuco, without date or collector (Pt).

\[T. inamoena × T. palmadora\]

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.

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

This is 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.

\* New name not accepted by the author in this thesis
A very distinct, highly specialized, monotypic, arborescent genus, which is allied to *Opuntia sensu stricto* on the basis of seed-morphology/anatomy (Stuppy submitted), 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, cylindric 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 a stronger shoot of indeterminate growth arising from a cotyledon axil. 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. The flowers and fruits contain few, large ovules and seeds, resp.

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).

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, north-western Paraíba, central-southern and eastern Pernambuco, Alagoas, Sergipe, north-western, northern and eastern Bahia, north-eastern and central-southern Minas Gerais and Espírito
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 a population sampled in northern Bahia (Erskine 132, see Supplement 1) 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 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 precise 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, so that 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.).
Plate 2. Diversity of Cactaceae in Eastern Brazil. 2.1 (top left), example of Pereskioideae: *Pereskia bahiensis*; 2.2–2.4, examples from Opuntioideae: 2.2 (bottom left), *Brasiliopuntia brasiliensis* (Caruaru, Pernambuco), 2.3 (top right), *Tacinga inamoena* (Tacima, Paraiba), 2.4 (centre right), *T. funalis* (cult., Desert Bot. Museum, Tucson, USA); 2.5 (bottom right), example from Cactoideae-Hylocereeae: *Hylocereus setaceus* (fruit, Itarana, Espirito Santo). [2.2 & 2.5 © D Zappi]
*5. NOPALEA Salm-Dyck


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


Introduced: on cultivated land (native to Mexico and Central America).

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

6. OPUNTIA Miller


A genus of at least 100 species, even when narrowly circumscribed (as here), 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/naturalised) *2. dillenii
1. Areoles spineless or with few or dark brownish spines; segments obovate, elliptic or rhomboid 2
2. Segments dark green; fruits proliferating 1. monacantha
2. Segments generally somewhat glaucous; fruits never proliferating (cultivated) *3. ficus-indica


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.

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 unequivocably 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 can probably not 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-easter limit. The collections from central-eastern Minas Gerais are rather disjunct on present knowledge, but 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).


Introduced and sometimes escaping by the sea; planted inland for hedging; native of Caribbean coasts and southwards to Ecuador; widely introduced elsewhere in warmer regions.

Benson (1982: 497–501) treats *O. dillenii* as a variety of the scarcely spiny, more narrowly segmented *O. stricta* (Haw.) Haw., and on such authority they were synonymized in the first edition of the CITES Cactaceae Checklist (Hunt 1992b), but subsequently retained as separate
species (Hunt 1999a). Further studies are needed in the Caribbean region where these taxa are native (cf. Howard 1989).


Introduced and planted about houses and farms. According to Kiesling (1999) originally domesticated in Mexico about 9000 years ago, having back-crossed with its putative wild ancestors known as *O. streptacantha* and *O. megacantha*; subsequently introduced throughout the warmer parts of the world and sometimes becoming a serious pest.

An important source of cattle fodder during drought in the *sertão*, where it is increasingly planted, often at the expense of native cactus habitats (eg. *Pilosocereus tuberculatus*). 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. Plates 1.1–1.4 & 2.5–5.4.

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
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 gene sequence data, presented at IOS meetings or otherwise communicated by R. Wallace (Iowa State Univ., USA) since 1993 and by R. Nyffeler at the IOS Congress in Zürich, March 2000.

Tribe HYLOCEREEAE F. Buxbaum

The Brazilian representatives of this tribe are robust climbers or large epiphytes, with flattened or trigonous stems and large flowers > 20 cm long. Plate 2.5.

7. HYLOCEREUS (A. Berger) Britton & Rose


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. Salmodyckia 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. Salmodyckia 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. trigonus (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.

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*


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.

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

† New name not accepted by the author in this thesis
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 quoad 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. 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.

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, igapô). 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:


Dillenius, Hortus elthamensis: t. 64, fig. 74 (1732).

Widespread neotropical element: epiphyte in *Mata atlântica*, *caatinga-agrest*, *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.

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 and Bahia. 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 (Wallace, in prep.). It is placed in this tribe, including the former Leptocereeae (ie. Echinocereeae subtribe Leptocereinae D. Hunt, ined.), only because the genus from which it was separated, ie. *Acanthocereus* (Berger) Britton & Rose, is currently placed there. Plate 3.1.

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:


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.

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']. It seems unlikely that this plant would occur in coastal vegetation and this record is therefore to be discounted as a probable misidentification.

**Tribe RHIPSALIDAEAE DC.**

In terms of numbers of species, this is the second largest tribe of Cactoideae in Eastern Brazil (after Cercoideae). All the species treated here are epiphytes and/or lithophytes in the core area of Eastern Brazil, with flowers < 6 cm long. Plates 3.2–3.3.


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 atlântica* in Eastern Brazil.
1. Distal parts of stems flattened, with conspicuous marginal teeth to at least 4 mm long

1. houlletianum

1. Stems flattened or 3–6-winged/angled/ribbed, with strongly adpressed marginal teeth/crenations to at most 2 mm long

2. Areoles woolly at anthesis and subsequently; flowers immersed in the areoles, 1 or more per areole, whitish to deep pink (Pernambuco southwards)

2. Areoles not woolly; flowers 1 per areole, not sunken, whitish (SE Brazil)

2. warmingianum


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.

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.

2. Lepismium warmingianum (K. Schumann) Barthlott in Bradleya 5: 99 (1987). Type (syntypes): Brazil, Minas Gerais, Lagoa Santa, Warming s.n. (B†, lectotype designated by Britton & Rose 1923: 238); ibid., Caldas, Lindberg 511 (B†). Lectotype (Barthlott & Taylor

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.

Also reported from Bahia and Paraíba 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.


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.

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


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 Espírito Santo, Rio de Janeiro and São 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. However, 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. *hileiabaiana*, 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 (Barthlott & Taylor 1995).
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. Stems flat, angled, winged, strongly to weakly ribbed or terete with ± raised podaria subtending ± fleshy scale leaves (or cylindrical 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

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

4. Stem-segments of indeterminate growth, branching often only subacrotonic, with numerous discontinuous ribs (S Espirito Santo)

5. Stem-segments terete, not ribbed, but sometimes with raised podaria subtending the scale-leaves (widespread)

6. Stems 3–4-angled in cross-section, the angles discontinuous and not forming ribs (widespread)

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)
8. Ultimate stem-segments stouter, to 2 mm or more thick (excluding midrib) in living material, margins strongly
crenate-lobed, the areoles to 5–6 mm from the outermost part of margin; flowers 1–5 per areole,
developing during the dry season (Pernambuco)

4. crispata

9. Stems mostly pendulous or sprawling, > 25 mm wide, flat or 3–5-winged

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. All stems of ± indeterminate growth, not forming composite areoles at apex; flowers and fruits always lateral
(widespread)

13. Pericarpel shorter than perianth; fruit globose to shortly barrel-shaped, to c. 5 x 4 mm; flowers/fruit mostly
lateral (S Minas Gerais)

14. Basal extension shoots of indeterminate growth apparently lacking or to only c. 12 cm long, all other stem-
segments determinate and < 7 cm; stamens white 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-adipressed, bristle-like spines; fruit bristly

18. Flower 20–25 × 20 mm; fruit globose-ovoid, c. 10 mm long; plant flowering when < 1 m long

18. Flower c. 15 × 12 mm; fruit truncate, c. 6 mm long; plant attaining 2 m before flowering

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 day and night, 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.


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

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. The single collection
known from Minas Gerais sometimes produces flowers almost devoid of fertile stamens in
cultivation.

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

2. Rhipsalis elliptica Lindberg ex K. Schumann in Martius, Fl. bras. 4(2): 293 (1890). Type
(syntypes): Brazil, Mosén 3630, Glaziou 14859 & Schenck 1218 (B†). Lectotype (Barthlott &

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.

Lützelburg (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.

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

R. oblonga is very similar to R. goebeliana from Bolivia (Yungas) and to R. occidentalis Barthlott 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.


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.

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 (eg. 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 19th Century in Europe, where it was becoming widespread in cultivation under Haworth's epithet (eg. 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. *Goniohipsalis* 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 sunken into the stem (less so in nos. 8–9), areoles rarely flowering > once. South America. Type: *R. paradoxa* (Pfeiffer) Salm-Dyck.

**5. Rhipsalis floccosa** Salm-Dyck *ex* Pfeiffer, Enum. cact.: 134 (1837). Type: a living plant, presumed not to have been preserved. Neotype (Barthlott & Taylor 1995: 55): Brazil, Bahia,

The most widespread and commonest *Rhipsalis* taxon in Eastern Brazil, from Pernambuco southwards, but rather variable and requiring further study in the field.

1. Flowers 12–20 mm in diameter or larger; fruit usually deep pink

   5c. subsp. pulvinigera

1. Flowers to c. 12 mm in diameter; fruit whitish

   2

2. Stem-segments with conspicuous swollen podaria

   5a. subsp. floccosa

2. Stem-segments almost perfectly cylindrical, without obvious podaria

   5b. subsp. oreophila

**5a. subsp. floccosa**

Widespread humid forest element: epiphytic or epilithic in Mata atlântica, including mata de brejo and the eastern foot of the Chapada Diamantina (Bahia), near sea level to c. 900 m, eastern Pernambuco to Espírito 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* (Ritter) Barthlott & N. P. Taylor in eastern Paraguay and north-eastern Argentina, by subsp. *tucumanensis* (F. A. C. Weber) Barthlott & N. P. Taylor in the eastern Andes of Argentina, Bolivia and Peru (Junín) and by subsp. *pittieri* (Britton & Rose) Barthlott & N. P. Taylor in northern Venezuela. Map 14C.

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

Holotype: Brazil, Minas Gerais, mountains E of Monte Azul, 1964, *Ritter* 1247 (SGO 125604, lectotype of *R. monteazulensis* Ritter, the replaced synonym).

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.

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:


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 Espírito Santo; South-eastern and Southern Brazil (to Rio Grande do Sul). Map 18B.

Typical *R. floccosa* subsp. *pulvinigera* is distinguished from its northern relatives by its generally smaller and more evenly sized, somewhat shiny, smoother, often 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 magenta when ripe (more rarely whitish). Beyond Eastern Brazil it ranges from Rio de Janeiro (Serra dos Órgãos) to Rio Grande do Sul (Mun. Guaíba) and replaces subsp. floccosa in the coastal regions of South-eastern and Southern Brazil. They can be reliably distinguished only on the basis of fertile material.


Only the following heterotypic subspecies is found in Eastern Brazil:


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.

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

Only to the following heterotypic subspecies is found in Eastern Brazil:


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

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* (Lindberg) Schumann by Britton & Rose (1923).

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


Southern humid forest element, but ecology and range poorly understood; known only from Domingos Martins, Espírito Santo.

Until recently this species was known only in cultivation, where it was often misidentified as *R. micrantha* (Kunth) DC. (central Andes to Central America). It seems to be a member of the *R. pacheco-leonis / R. pentaptera* Pfeiffer complex, although it strongly resembles *R. floccosa*, differing most obviously in its clearly angled/ribbed stem-segments, less conspicuously erumpent flower-buds and scarcely woolly fertile areoles post-anthesis. It was likely 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 by only a single collection from southern Espírito Santo.

Scheinvar (1985) misapplies the name *R. sulcata* to specimens of *R. trigona* Pfeiffer (SE & S Brazil: 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.


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-agreste (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 South-eastern Brazil (to W Rio de Janeiro & SE São Paulo). Map 12B.

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 Hilêia Baiana of eastern Bahia. R. lindbergiana is somewhat variable in stem thickness, the stoutest forms including that described as R. densiareolata Löfgren.
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 Eastern Brazil are referred to the following form:


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

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

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 (Maranhão to E Pernambuco)  
   12a. subsp. *baccifera*

12a. subsp. *baccifera*

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.

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.

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, Chapada Diamantina, eastern and central Bahia. Endemic to Bahia. Map 12C.

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. Eyrthrorhipsalis 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.

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).

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


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

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. from 1857), but this is too poorly typified to be applied with confidence and has been variously misapplied by previous authors (as discussed in Barthlott & Taylor 1995).

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.

Only a collection by Zappi (n° 259) and one from the Serra Negra have been seen as living plants and suggest the above identity, although neither has been examined in flowering condition. Other collections from Ibitipoca (Mun. Lima Duarte, MG) 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 named *R. ormindoi* N. P. Taylor & Zappi (1997), from the adjacent parts of Rio de Janeiro, to take into account.


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). Map 18C.
Collections seen from Rio de Janeiro and Espírito Santo are definitely *R. clavata*, but those cited in Supplement 1 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 the distinctive *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.).

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.

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.

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.

This, 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, Epallagogonium, 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.


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

This recently described species is closely related to *R. puniceodiscus* Lindberg (Rio de Janeiro to Santa Catarina), which it strongly resembles in vegetative characters (Taylor 1999). Its red flowers are presumed to be an adaptation for pollination by hummingbirds.

13. **HATIORA** Britton & Rose


A genus of 2 or 5 species, depending on the circumscription adopted, 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.

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Disjunct humid forest element: epiphytic or lithophytic, *Mata atlântica, mata de brejo, mata de grotão* and *mata de neblina*, c. 600–1750 m, central (E Chapada Diamantina) and eastern Bahia, central-southern Minas Gerais (S Serra do Espinhaço and Serra da Mantiqueira), southern Espírito Santo and northern Rio de Janeiro, but northern records markedly disjunct; South-eastern and Southern Brazil (to Paraná). Map 12C.

This species presents very diverse morphology, 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. They can be distinguished as follows:

1. Segments globose, ovoid or inverted bottle-shaped
   1a. *f. salicornioides*

1. Segments uniformly cylindric, or somewhat thicker at base
   1b. *f. cylindrica*

*Forma cylindrica* (Britton & Rose) Süßpiele (Barthlott & Taylor 1995: 73) has stem-segments of ± constant size, bearing conspicuously felted and often bristly, composite areoles only at their apices, which readily distinguishes non-flowering plants from superficially similar *Rhipsalis*
spp., eg. *R. cereuscula*. The distribution of forma *cylindrica* seems markedly disjunct on present knowledge, including two adjacent sites in eastern Bahia and one in Espírito Santo. Beyond Eastern Brazil it occurs in only four further sites, in south-western Minas Gerais (Camanducaia), Rio de Janeiro (Ilha Grande & Parati-Mirim) and São Paulo (Serra da Bocaina), and appears to be much rarer than the ‘typical’ form.

A single collection of the magenta-flowered sister-species, *Hatiora herminiae* (Campos-Porto & Castellanos) Barthlott (1987), 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 SE São Paulo (Campos do Jordão), at higher elevations (> 1600 m), epiphytic on *Araucaria*.

14. SCHLUMBERGERA Lemaire


Including *Epiphyllanthus* A. Berger (1905).


An endemic Brazilian genus of 6 species, ranging from southern Espírito 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. Terminal segments orbicular to obovate or truncate in outline, laterally compressed

2. Joints almost unarmed, but margins toothed; flowers scarcely zygomorphic

2. Joints covered in areoles with pungent, very thin spines; flowers strongly zygomorphic


Southern humid forest (inselberg) element: lithophytic on inselbergs, rarely epiphytic, \textit{Mata atlântica}, 900–1300 m, central-southern Espírito Santo. Endemic. Map 18D.

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


Southern humid forest element: lithophytic or epiphytic, \textit{mata de neblina}, at > 2000 m, Serra do Caparaó, Minas Gerais / Espírito Santo; Rio de Janeiro (Serra de Itatiaia). Map 18D.

The name \textit{S. microsphaerica} must be used in preference to the more familiar \textit{S. obtusangula} (Schumann) D. Hunt, since the former, as \textit{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.

Holotype: Brazil, Rio de Janeiro, Itatiaia, 2400 m, 11 June 1902, Dusén 1530 (R).

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.
Plate 3. Diversity of Cactaceae in Eastern Brazil. 3.1 (top left), example from Cactoideae-Echinocereae (?): *Pseudoacanthocereus brasiliensis* (Itinga, Minas Gerais); 3.2–3.3, examples from Cactoideae-Rhipsalideae: 3.2 (top right), *Rhipsalis crispata* (neotype collection), 3.3 (bottom left), *R. lindbergiana* (near São João da Sapucaia, Minas Gerais); 3.4 (bottom right), example from Cactoideae-Cereae (?): *Brasilicereus phaeacanthus* (near Livramento do Brumado, Bahia). [3.2 © RBG Kew]
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. Plates 1.1–1.4, 3.4–4.6.

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., Nyffeler, ined.). These have failed to resolve the tribes Cereeae, Trichocereeae and Browningieae (pro parte) as distinct units in cladistic analyses due to the synapomorphic deletion of c. 300 base-pairs from the ITS (internal transcribed spacer) of the rpl16 intron, which represents 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 (Plate 3.4), and may belong elsewhere.

15. BRASILICEREUS Backeberg

Type: Braslicereus phaeacanthus (Gürke) Backeberg (Cereus phaeacanthus Gürke).

An endemic genus of 2 species, related to Praecereus F. Buxbaum (with 2 widespread South American species, P. euchlorus (Weber) N. P. Taylor 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 (part of which may be closer to 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)  


Type: Brazil, Bahia, near Maracas, Sep. 1906, Ule 7022 (HBG, lecto. designated here).


Type: Brazil, Bahia, near Maracás, Sep. 1906, Ule 7022 (HBG, lecto. designated here).


Type: Brazil, Bahia, near Maracás, Sep. 1906, Ule 7022 (HBG, lecto. designated here).

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. Maps 24B & 40.

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 they illustrate from Jequié under the number 'HU 746' is very far from typical of the species, having a peculiar naked pericarpel.


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.

This species is clearly differentiated from the widespread and variable *B. phaeacanthus* by the acute pericarpel bract-scales and curved seeds.
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 three described species, C. spegazzinii F. A. C. Weber, C. kroenleinii 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

1. Floral remnant not deciduous from fruit or breaking off above its base to leave a blackened appendage on the strongly angular unripe fruit; rootstock rhizomatous-tuberous; semi-scandent shrubs to < 3.5 m, with non-erect branches to 5 cm diam. (Subg. Mirabella) 5

2. Fruit (when undamaged) opening from apex into c. 3 segments (S Minas Gerais) 6. hildmannianus

2. Fruit opening by a single, initially basal or lateral split 3
3. Tree-like, often with a well-defined trunk and to > 4 m; fruit pinkish- to purplish-red (*caatinga/agreste* and on limestone etc. in other ecosystems, NE Brazil to cent. Minas Gerais)

5. jamaicaru

3. 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. Ribs 3-5; flowers 14-25 cm (mainland Brazil)

3. fernambucensis

4. Ribs 5-9; flowers c. 13 cm (Fernando de Noronha)

4. insularis

5. Ribs (2-)3-5(-6), acute; wood yellow beneath the bark (*caatinga*, Piauí, Pernambuco, N & S Bahia to cent.-N Minas Gerais)

2. albicaulis

5. 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. paxtonianus* 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 (1992) 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 protologue of *C. cavendishii*).


*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). Map 34.

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.

Widespread *caatinga* element: in *caatinga de altitude*, *caatinga* and *carrasco*, usually 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 North-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 half 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 by Britton & Rose as an *Acanthocereus*, 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 *campos rupestres* (rare).

The specific epithet is correctly spelled with ‘f’ and should not be corrected to ‘pemambucensis’ 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.) Hummelnck, 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

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.
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).


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 Espírito Santo and southernmost Minas Gerais, to adjacent Rio de Janeiro (Rio Paraiba drainage). Endemic to South-eastern Brazil. Map 16B.

This subspecies represents a distinct inland race of the otherwise littoral *C. femambucensis*. Apart from its yellow fruit it differs from subsp. *femambucensis*, 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.


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

This taxon may represent a further subspecies of *C. femambucensis*, from which it is separated by c. 350 km of Atlantic Ocean, but molecular studies are desirable before any taxonomic
changes are proposed. *Cereus insularis* is apparently very variable in habit and spination, some forms being completely covered in fierce spines, the stems 5–9-ribbed. 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. A provisional synonym, *C. ridleii* Backeb., based on a plant discovered by the respected Dárdano Andrade-Lima, is known only from his original habitat photograph, depicting a distinctive tree-like specimen (c. 3–5 m tall), 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.

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 various populations further to the south, 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 a 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 (N Minas Gerais northwards from Diamantina, especially drainage of the Rio Jequitinhonha) 5a. subsp. *jamacaru*

1. Juvenile plants (between 10 cm and 1 m high) passing through a stage with 5–8 ribs and uniformly short, dark red-brown spines; mature stem-segments broadest near base; flower 10–15 cm diam.; pericarpel and tube to 21 cm, bract-scales green or brownish, inconspicuous; largest perianth-segments 5–7 cm (W Bahia to central Minas Gerais, to 20°S, Rio São Francisco drainage, often on limestone) 5b. subsp. *calcirupicola*

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 to region of Diamantina and frequent on inselbergs), sometimes cultivated further south as well as within its natural range, ranging northwards to western Maranhão, northern Piauí and Ceará; Northern Brazil (Tocantins and Pará)? Map 19.

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, degree of pseudo-segmentation of the stem (more or less constricted and convex or parallel-sided) and spine development. There are various regional variants, one being that found in southern Rio Grande do Norte and adjacent Paraíba and Ceará, which has many ribs as a seedling and little-constricted parallel-sided adult stems. 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 Prov. Santa Cruz), Bolivia, which has been named *Piptanthocereus colosseus* Ritter (1980: 553). Braun & Esteves Pereira (1995) refer this taxon to *C. lamprospermus* Schumann, however.


*Caatinga / mala 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 (Goiás and Distrito Federal). Map 27A.
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 west and south 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) with forms found further west on limestone outcrops in Goiás and the Distrito Federal. Some populations on isolated limestone outcrops have developed into distinctive variants, such as that described as var. *pluricostatus* by Ritter (see Supplement 1). However, these are equalled by similar variations seen in subsp. *jamacaru*.


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

6a. subsp. *hildmannianus*

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).

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 in the key to species (above) and, together with the highly mucilaginous stem tissues, would seem to provide a means for distinguishing C. hildmannianus from C. fernambucensis subsp. fernambucensis and sericifer, with whose ranges it slightly overlaps, and from the related but allopatric C. jamaicaru. 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 in Supplement 1 (see also 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 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 not infrequent 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 East Brazilian Cereaeae, of which the first is judged to contain 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 quoad typ.

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-morpholgy (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 (C. CRASSISEPALUS Group)

2. Ribs > 8, rounded in section; areoles with short, brown or white felt, long hairs absent; central and radial spines alike or upper areoles unarmed (C. MINENSIS Group)

3. Areoles contiguous; flowers and fruits bearing areoles with spines and long hairs (Serra do Caraça, MG)

1. laniflorus

2. Areoles distinct; flowers and fruits naked (Diamantina MG, eastwards & north-eastwards) 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. bradei

3. Stems 2.5–5.0 cm diam., densely spiny; transverse folds absent; epidermis grey-green or bright green

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. Flower blue outside, tube smooth, glabrous; perianth-segments patent to reflexed at anthesis; fruits not ridged, smooth (Serra da Bocaina, Grão Mogol & Serra do Cabral, southwards, disjunctly, to Serra do Caraça & Itabirito, 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 & Serra da Lapinha, MG)

4b. minensis ssp. pleurocarpus

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.

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.


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 Espinhaço, Minas Gerais. Endemic to the core area within Minas Gerais. Map 38A.

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

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 Espinhaco, Minas Gerais. Endemic. Map 37A.

Where *C. bradei* is found growing with *C. minensis* there is often evidence of introgression.


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 & westwards) 4b. subsp. *pleurocarpus*

4a. subsp. *minensis*

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.

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


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.


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.

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 preference.
18. STEPHANOCEREUS A. Berger


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*


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*).


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

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


Including *Pierrebraunia* E. Esteves Perreira (1997).


A genus of 4–5 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.

The Subgenus Albertbuiningia P. J. Braun & E. Esteves Pereira (1995b: 81) was established 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, cliffs, 1000–2000 m)  
   1. bahiensis

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

2. Stems 10–50 × 2 cm, sometimes arising from a tuberous, rhizomatous rootstock; flowers bicoloured (anthesis p.m.), inner perianth-segments contrasting with flower-tube (Serra do Espinhaço: Caí vité 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

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.

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*.


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

   b. subsp. eriocaulis

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 Bocaiúva) in the Serra do Espinhaço (and Serra Geral). Endemic to the core area within Eastern Brazil. Map 28B.

Very variable in stem morphology and flower colour. On present knowledge, the typical northern populations and the southern forms (described as A. beateae P. J. Braun & E. Esteves Pereira and A. heimenii van Heek & Strecker) appear to be disjunct, being interrupted by the following subspecies.


Northern campo rupestre element: in sandy cerrado, 700–950 m, eastern drainage of Serra do Espinhaço, northern Minas Gerais. Endemic to the core area within Minas Gerais. Map 28B.
Variable in flower colour. The plant described and illustrated as *A. eriocaulis* var. *rosenbergeriana* by van Heek & Strecker (see Supplement 1) appears to be somewhat intermediate between the two subspecies recognized.


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.

This species has a more restricted range than the following and is not nearly as common, nor as variable. Their different habitat preferences deserve further analysis: they are seldom truly sympatric despite the considerable overlap in distribution.


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-eastern 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 × 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 following collection seems to confirm its presence:

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. above Caetite (Bahia) and east of Monte Azul (Minas Gerais).

3 × 4: *Arrojadoa penicillata × Arrojadoa rhodantha*

*Caatinga* in the drainage of the Rio Paraguacu and Rio Brumado / Rio de Contas, 300–450 m, southern Bahia.

Sometimes forming a complete range of intermediates between the parents in places within the areas of sympathy.
20. PILOSOCEREUS Byles & Rowley


Including *Pseudopilocereus* F. Buxbaum (1968).


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, eg. *P. gounellei*, *P. catingicola* and *P. pachycladus*. The Brazilian species are classified into two subgenera and various species-groups.

1. Branching candelabriform, 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

1. Branching erect and/or plants branched only at base, the new branches first developing well below the apex of the stems subtending them; floral remnants pendent, deeply immersed in apex of fruit, forming a linear insertion point (Subg. Pilosocereus) 3

2. Treelike, with a well-defined trunk, not branching near base; ribs 4–7; flower-bearing areoles without long trichomes

1. *tuberculatus*

2. Shrubblike, 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*
3. Treelike or shrubby, branching above the base; vascular cylinder strongly to moderately woody
4. Apical, subapical and flower-bearing areoles without long hairs (at least in habitat)
5. Epidermis blue, covered in wax
6. Spines brown to greyish, opaque; flower-buds acute; flower opening wide, 6–7 × 4–5 cm, tube straight
   (restinga, SE Brazil & S Bahia)
7. Epidermis greyish, pale or olive-green, not strongly waxy
8. Areoles > 2 mm apart, distinct
9. Flower-bearing areoles with scarce, white long hairs; young spines golden, flexible
10. Spines brownish, reddish or blackish, opaque
11. Spines golden, translucent
12. Ribs 5–12; 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
14. Fertile part of stem without or with few bristles, long hairs white, silky; ribs 13–19
   153
14. Spines golden; ribs wider than high; fertile part of the stem apical or subapical, not strongly modified (caatinga, N Bahia and Pernambuco) 12b. pachycladus ssp. pernambucoensis

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

15. Ribs 4–6, or some stems with up to 7 ribs 17

16. Areoles 8–16 mm apart on the ribs; seeds 2–2.3 mm (NE Brazil) 3. catingicola

16. Areoles 5–7 mm apart on the ribs, seeds 1.5–1.6 mm (NE Minas Gerais) 4. azulensis

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. catingicola

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) 6. brasiliensis

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 8–27, 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

19. Flower exterior reddish or pinkish brown; flower-tube infundibuliform; ribs 8–17 20

19. Flower exterior green to brownish; flower-tube cylindric, straight to curved; ribs 12–27 21

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

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

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

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

Subg. Gounellea Zappi (nos. 1 & 2):


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

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 (n° 19, M!), bearing a label indicating southern Paraíba (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.


The neotype chosen (Zappi 1994) was collected by Lützelburg in the adjacent state of Paraíba (*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. ('mandacaru') and *Tacinga inamoena* (K. Schum.) N. P. Taylor & Stuppy ('quipá'), is one of the most common and widespread cacti of Eastern Brazil.

This extremely variable species is divided into 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)

2a. subsp. gounellei

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)

2b. subsp. zehntneri

2a. subsp. gounellei

*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.

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 Werdermann (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 described in Andrade-Lima (1981: 160).

Rio São Francisco *caatinga* element: rupicolous, on outcrops of Bambui 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.

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 ‘sunken’ cephalium and glaucous epidermis. Study of diverse populations of *P. zehntneri* and *P. braunii* suggests that there is 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*.


This species is divided in two subspecies:

1. Branches (6-)8–12 cm diam., ribs 4–6, spines stout, 10–40 mm (Bahia)

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)

3a. subsp. *catingicola*

3b. subsp. *salvadorensis*

3a. subsp. *catingicola*

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.

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.


Widespread caatinga / humid forest (restinga) element: in dense or sparse restinga on sand-dunes north of Salvador (BA) to Rio Grande do Norte (to Natal), extending somewhat inland in southern Paraiba, eastern Pernambuco and in the São Francisco River valley 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.

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 (Alagoas/Sergipe), where it apparently develops into exceptionally tall specimens with many erect branches.

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

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. ARRABIDAE 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. floccosus subsp. quadricostatus and one of the other Pilosocereus from the area (eg. P. multicostatus, P. pachycladus), does not seem plausible given the characters it displays.


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.

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. 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 *caatinga* of the Rio São Francisco valley.


Two subspecies are recognized as follows:

1. Branches dark green; ribs 4–5  
   6a. subsp. *brasiliensis*

1. Branches greyish green to glaucous; ribs (4–)5–7  
   6b. subsp. *ruschianus*

**6a. subsp. brasiliensis**

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. Map 17D.
Variable in the degree of areolar wool developed in some populations.

Holotype: not extant. Lectotype (Zappi, l.c.): Brazil, Espírito Santo, Mun. Colatina, Buin. & Brederoo, in Kakt. and. Sukk. 31: 33, photograph, above right (iconotype).

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.


Northern *caatinga* element: in the *caatinga/cerrado* ecotone, dense, high and low shrubby *caatinga*, open, seasonally flooded carnaúba (*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, central and south-eastern Piauí (to c. 8°S) and along the border regions between Piauí and Maranhão; (?) to northern Tocantins. Endemic to North-eastern Brazil? Map 20.

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 n°. 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.


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**

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.
8b. subsp. **robustus** Zappi in Succulent Pl. Res. 3: 74 (1994). Holotype: Brazil, Bahia, Mun. Livramento do Brumado, 11 km S of town on road to Brumado, 450 m, 13°45'S, 41°49'W, 23 Nov. 1988, **Taylor & Zappi** in **Harley** 25544 (SPF; CEPEC, K, isos.).

Eastern *caatinga* element: in dense *caatinga-agreste* of the Rio de Contas (Rio Gavião) 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.

Variable in rib number and stem thickness. Intergeneric hybrids between *P. pentaedrophorus* 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. pentaedrophorus*, in the drainage of the Rio Pardo, *P. pentaedrophorus* subsp. *robustus* can be found sympatric with *P. floccosus* subsp. *quadricostatus*.


*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.

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.


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.

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 semiarid 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*

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.

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.

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


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

PILOSOCEREUS ULEI Group (nos. 11–13).

Found in *caatinga-agreste*, *caatinga* and *campo rupestre*.


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***

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.

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.


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.
Although it has not been possible to study populations of subsp. *rosae* in the field, its striking morphological and ecological similarities with *P. fulvianatus 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. *fulvianatus* (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 Município of Augusto de Lima, Minas Gerais.


Holotype: Brazil, Bahia, Urandi, 1964, Ritter 1223 (U).

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 unequivocably 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’, page 181). 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 significant number of heterotypic synonyms described by Ritter, Buining & Brederoo, and Braun (see Supplement 1). 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–)12–19, 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*
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 inselbergs, 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.


Northern caatinga element: locally co-dominant with other woody vegetation in dense or sparse caatinga and agreste, on sandy or rocky substrates (including sandstone and gneissic inselbergs), c. 350–750 m, northern Bahia (north of 10°S), Alagoas, Pernambuco, Paraiba, Rio Grande do Norte, south-eastern Piauí, southern and north-western Ceará (W, S & E escarpments of Chapada do Araripe, Chapada da Borborema & plateau of the Serra da Ibiapaba). Endemic to North-eastern Brazil. Map 20.

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 high numbers of ribs (mostly 13–19) and fine, golden spination, and 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, presenting 10–15 ribs and relatively fine spination.
P. pachycladus subsp. pernambucoensis may present either coerulescent blue or greyish green epidermis, the former predominating in its western populations, the latter being characteristic of its eastern range, in central and eastern Pernambuco, Paraíba and Rio Grande do Norte, where plants have much narrower stems. These north-eastern populations may represent an as yet unnamed subspecies, which displays little variability when compared to the subspecies as a whole.

Britton & Rose and Werdermann confused populations of P. pachycladus subsp. pernambucoensis with Cereus piauhyensis Gürke (1907), which they combined as Cephalocereus piauhyensis (Gürke) Britton & Rose (1920), and Pilocereus piauhyensis (Gürke) Werdermann (1933). The type material of Cereus piauhyensis Gürke was collected by Ule in the Serra Branca, north of São Raimundo Nonato (Piauí), beyond the western extent of P. pachycladus subsp. pernambucoensis, which appears to terminate before 42°W. This error also appears in Andrade-Lima (1989), where he follows the concept of Britton & Rose and Werdermann and illustrates and describes P. pachycladus subsp. pernambucoensis as P. piauhyensis. However, Andrade-Lima (1989) places the southern forms of P. pachycladus (ie. subsp. pachycladus) under Pilosocereus glaucescens (A. Linke) Byles & Rowley, a name of uncertain application.

Egler (1951: 587, fig. 6) and Uebelmann (1996) confuse this widespread northern subspecies with Facheiroa squamosa, which in Pernambuco is restricted to the southernmost part of the state, adjacent to Bahia.

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.

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

PILOSOCEREUS AURISETUS Group (nos. 14–16)

Stems branching only at base. Found on or amongst rocks in cerrado and in campo rupestre.


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.

The recently described *P. estevesii* P. J. Braun is tentatively referred here (see Supplement 1). 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 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 a proposed relationship with the *P. PENTAEDEPHORUS* Group (Zappi 1994), whereas those of *P. estevesii*, as described and illustrated, 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*.


One of the specific features of *P. aurisetus* is found in its fruit, which characteristically splits across the apex, often 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 Espinhaço) 15a. subsp. *aurisetus*
Plants to 3 m; branches 4.5–7.0 cm diam., ribs 10–17; flower-bearing areoles with golden hairs (Serra do Cabral)

15b. subsp. aurilanatus

15a. subsp. aurisetus

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

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.


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.

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. aurisetus via the form of the latter described under the synonym, *P. supthutianus* P. J.
Braun. The most striking feature of subsp. *aurilanatus* is its stouter, taller stems with dense, golden hairs on the flower-bearing areoles.


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

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* (L. Diers & E. Esteves Pereira) P. J. Braun, 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.


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

*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, recall *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.


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) Werderm. Both authors had not seen living 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 P. J. Braun & E. Esteves Pereira 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. P. piauhyensis occupies a crescent-shaped northern and western distribution zone peripheral to that of P. chrysostele.


Northern caatinga element: on whitish to grey, granitic inselbergs, with the surface broken into large blocks of stone, associated with highland caatinga, 430–1190 m, Pernambuco, Paraíba, Ceará and Rio Grande do Norte. Endemic to North-eastern Brazil. Map 20.


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.

Variable in stature and in the extent of cephalium wool developed.

Probable hybrid with *P. pachycladus* subsp. *pachycladus*:


Braun & Esteves Pereira’s recently described species is here regarded as a putative hybrid, with little hesitation, since it characters are strongly suggestive of such an origin, involving *P. pachycladus* and *P. densiareolatus*, the latter being reported as sympatric by the above authors. *P. pachycladus* certainly also occurs in this region and similar hybrids have been observed in western Bahia.
*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 on closer examination the branching pattern is completely different, being candelabromform 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; ‘Cereastreae 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 unequalled and its stated rarity lends further 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* Britton & Rose with *Pachycereus* Britton & Rose (×*Pachocactus* Rowley) and, separately, with *Myrtillocactus* Console (×*Myrgerocactus* Moran) in 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 Cereaeae, 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.
Plate 4. Diversity of Cactaceae in Eastern Brazil. 4.1–4.6, examples from Cactoideae-Cereae: 4.1 (top left), *Cereus albicaulis* (near Nova Petrolina, Pernambuco), 4.2 (top right), *Ciriocereus laniflorus* ('clonotype', cult. RBG Kew), 4.3 (centre left), *Arrojadoa bahiensis* (cult. RBG Kew, ex Mucugê, Bahia), 4.4 (centre right), *Stephanocereus leucostele* (Aracatu, Bahia), 4.5 (bottom left), *Pilosocereus pachycladus* (near Morro do Chapêu, Bahia), 4.6 (bottom right), *Melocactus cf. lanssensianus* (Mun. Tacima, Paraiba). [4.2–4.3 © RBG Kew; 4.5 © U Eggli; 4.6 © E Rocha]
21. MICRANTHOCEREUS Backeberg


The relationships of this endemic Brazilian genus within tribe Cereeae are unclear, but fruits with non-impressed, ± superficial floral remnants and stems bearing lateral cephalia are found in *Pilosocereus* subg. *Gounellea* (cf. *P. gounellei* subsp. *zehnneri*) 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. The possession of hypertrophic spines is most likely linked to the rupicolous habitat (Porembski et al. 1998) and not an indicator of relationship. More significantly, 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 more 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 restricted 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, campos rupestres, Serra do Espinhaço and Chapada Diamantina) 2

1. 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

2. Flowers > 30 × 20 mm, anthesis predominantly nocturnal 3

2. Flowers slender, < 25 × 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*.


Northern *campo rupestre* (N Serra do Espinhaco) 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 29A.

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 hypertrophic 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).

Holotype: Brazil, Minas Gerais, Mato Verde, 950 m, Aug. 1972, Buining in Horst 348 (U).

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 29B.

This is the southern sister species of the following.


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 29B.

The basionym, *Cephalocereus purpureus* Gürke, 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* Werderm. Lützelburg (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. Lützelburg 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 Ituacu.

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.


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.

According to the list in Uebelmann & Braun (1984), Uebelmann (1996) and the label on the holotype 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).

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

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.


Northern campo rupestre element: in quartz sand amongst crystalline rocks, c. 900–1000 m, Mun. Caitité, southern Bahia. Endemic. Map 29C.

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.


Northern *campo rupestre* (Chapada Diamantina) element: in the *campo rupestre / 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 29C.

The distribution of this variable 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 calcareous soils, which would not suit it and thus it is probable that its distribution is highly fragmented, justifying a conservation status of ‘Vulnerable’.

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.


Southern Rio São Francisco *caatinga* element: on Bambuí 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.
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 threatened 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).

22. COLEOCEPHALOCEREUS Backeberg


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

1. Flowers diurnal (often a.m.), inner perianth-segments scarcely expanding, yellow-green or magenta; seeds smooth, testa-cells flat; ribs lacking transverse folds (Rio Jequitinhonha drainage, NE Minas Gerais) 5

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*

2. Spines < 17 in areoles remote from the cephalium and stem base, not or scarcely hooked in seedlings, or hypertrophic spination developed at ground level; stem tissues mucilaginous (NE Minas Gerais & Espírito Santo southwards) 3

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

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.

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.

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.

Southern humid/subhumid forest (inselberg) element: on gneissic inselbergs or lajedos, 100–1000 m, south-eastern and south-western Minas Gerais (disjunct). Endemic to the core area within Minas Gerais. Map 16D.

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.


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 to Rio de Janeiro etc.)  
   2a. subsp. fluminensis

1. Stem decumbent except at the inclined apex, to 6 cm diam. (NE Minas Gerais)  
   2b. subsp. decumbens

2a. subsp. fluminensis

Southern humid/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 Espírito Santo; Rio de Janeiro and off-shore islands of São Paulo (to Ilha Queimada Grande). Map 16C.

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*.


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.

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 Paraiso (MG) and the Rio Doce in Espírito Santo (eg. municípios Nova Venêcia and Pancas, ES), 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.

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.

A 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 Supplement 1). Their use of subspecific status needs to be evaluated in the light of future 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).

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:


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.

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 pluricostatus (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 Ritter.
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).


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.

Very variable in habit and stem morphology.


Holotype: Brazil, Minas Gerais, 1972, Horst & Uebelmann 359 (U).

South-eastern caatinga (inselberg) element: on gneissic inselbergs and lajedos in caatinga, c. 250–300 m, near the Rio Jequitinhonha, east of Itinga, north-eastern Minas Gerais. Endemic to the core area in Minas Gerais. Map 33D.

The range of this species is poorly known, but it is clearly much more restricted than that of its sister species, C. aureus, and is currently known from only a single locality. However, it should not be difficult to determine the extent of the species' range more precisely, working eastwards from the known locality just east of Itinga.
23. **MELOCACTUS (L.) Link & Otto**


One of the most widely distributed genera of Cactaceae, comprising 32 species, 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 18 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 has not been taken into account, since no permanently preserved voucher materials were cited and considerable doubt must exist concerning the identities of the taxa studied, being 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 by Das *et al.* 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 × no. 9, 1b × 13, 2a × 9, 2a × 10, 2a × 12, 7b × 10, 8a × 10, 10 × 13, 12 × 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
2. Stem lacking mucilage; fruit length 1.5–2.0 × diam.
3. Lowermost radial spine markedly longer than longest central spine; flower pinkish magenta; seed to 1.35 mm, testa-cells strongly convex (single site on granite/gneiss, cent.-S Bahia)
4. Fruit white, or white and very pale pink only at apex, or pale pink and seed with almost flat testa-cells
5. Central spine(s) > 20 × 1.5 mm (inland Bahia, limestone)
6. Central spine lacking or < 20 × 1.5 mm (coastal sand dunes)
7. Stem pale bluish waxy-glaucous, at least when young
8. Flowers cleistogamous (Pernambuco & Paraíba)
9. Flowers opening prior to fruit development
10. Stem always plain green
11. Fruit red or pinkish magenta, at least at apex, to 45 mm long
12. Stem with at least some mucilage in the green cortical tissues or highly mucilaginous; fruit length 2 or more × diam.
13. 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)
14. Fruit red or pinkish magenta, at least at apex, to 45 mm long
15. Perianth-segments 0.7–1.7 mm wide; cephalium 7–9 cm diam., wool often conspicuous; fruit to 6 mm diam.
16. Perianth-segments 1.4–2.2 mm wide; cephalium 10 cm diam., with very dense fine bristles only; fruit 7–9.5 mm diam.
17. Stem pale bluish waxy-glaucous, at least when young
18. Flowers opening prior to fruit development
9. Stem 11–16 cm diam., pith chlorophyllous; ribs 8–12; areoles 13–20 mm apart on the ribs

9. Stem to 25 cm diam., pith white; ribs 10–22; areoles 20–40 mm apart on the ribs

10. Spines (3–)4–6 per areole, largest 1.2–2.0 mm thick (cent. & S Bahia, 1100–1500 m)

10. Spines > 6 per areole or only 0.5–1.0 mm thick

11. Radial spines 5–10(–11), almost straight, 0.5–1.5 mm thick (restinga and sandy places inland, 0–1100 m)

11. Radial spines (6–)7–11, ± curved, to 2.5 mm thick (inland, especially in the caatinga)

12. Fruit to 16 × 7 mm, dark red to base; cephalium white-woolly throughout, bristles hidden (Bahia: Mun. Morro do Chapéu)

12. Fruit to 45 × 12 mm, reddish to magenta at apex, paler below; cephalium with conspicuous bristles or white-woolly only at apex

13. Ribs ± rounded in cross-section (but edge often acute) or very low; stems depressed-globose to taller than broad

13. Ribs triangular in cross-section; stems broader than tall

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)

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. 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

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

16. Spines 9–14 per areole, lowermost radial 40–80 mm; stem to 15 × 18 cm

16. Spines (11–)14–21 per areole, lowermost radial 50–150 mm; stem to 45 × 35 cm

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)

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)

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MELOCACTUS OREAS Group (nos. 1–4):


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)

1b. subsp. cremnophilus

1. Ribs 12–16; stem depressed to elongate (E Bahia < 500 m)

1a. subsp. oreas

1a. subsp. oreas

Eastern caatinga element: on more or less exposed granite/gneiss lajedos and arenitic rocks, caatinga-agreste, within the lower drainage of the Rio Paraguacu, at < 500 m, eastern Bahia. Endemic to Bahia. Map 32C.

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.

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.

Subspecies cremnophilus is isolated from subsp. oreas by a zone of dense 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. Cactés, Taylor & Zappi 1627B, K, photos) requires further study (cf. Taylor 1991a).


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) (widespread in the Eastern caatinga-agrestes)  
2a. subsp. ernestii

1. Stigma-lobes exserted, often pinkish red; stem lacking mucilage or with traces in the green cortical tissues, ribs 9–11; central spines 4–8 (between the Rio São Francisco and 42°W, S Bahia & N Minas Gerais)  
2b. subsp. longicarpus

2a. subsp. ernestii

Eastern caatinga element: locally dominant on exposed crystalline/sandstone rocks and especially gneissic inselbergs, including those in brejo forest, 250–1190 m, Paraíba, central-eastern Pernambuco (Chapada da Borborema), western Alagoas, western Sergipe, Bahia (E of 42°W) and north-eastern Minas Gerais. Also reported from Ceará and Rio Grande do Norte by Lützelburg (1925–26). Map 30C.

This subspecies can be found sympatric with M. oreas, M. bahiensis, M. salvadorensis, M. zehntneri, M. glaucescens and M. concinnus.

The following from Pernambuco may represent a name for hybrids between M. ernestii and M. zehntneri, which have been observed in the municípios of Poção/Jataúba (F. A. R. Santos 5 & 6, PEUFR, K, photos) and Alagoinha (Taylor & Zappi, K, photos), 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.

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 Espinhaço in northern Minas Gerais. Endemic to the core area of Eastern Brazil. Map 24D.

Subspecies longicarpus is sympatric with *M. salvadorensis* in Mun. Rio do Antônio, Bahia.


Type: Bahia, Mun. Marcionílio Sousa, *Rose & Russell* 19935 (US, lecto. designated here; NY, lectopara.).

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 following infraspecific taxa are recognized:

1. Central spine(s) 1–4, the lower and largest usually > 25 mm, lowermost radial spine 24–60 mm

1. Central spine 1, to 25 mm, lowermost radial spine 22–32 mm (N Bahia) 3a(ii). subsp. bahiensis f. acispinosus

2. Ribs rounded to somewhat acute but scarcely triangular in cross-section, or lowermost radial spine > 40 × 1.5 mm (Pernambuco & NE to S Bahia)

2. Ribs acute and triangular in cross-section; lowermost radial spine to 40 × 1.5 mm (S Bahia & N Minas Gerais) 3b. subsp. amethystinus

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

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.

Two distinctive local Bahian forms of this subspecies are distinguished in the key above. Forma acispinosus (Buin. & Brederoo) N. P. Taylor (1991a: 28) occurs in the municípios of Senhor do Bomfim, Itiúba and Jacobina, and forma inconcinnus (Buin. & Brederoo) N. P. Taylor (1991a: 30) in Paramirim, Livramento do Brumado, Brumado and Ituacu.

Subspecies bahiensis can be found sympatric with M. oreas, M. ernestii, M. zehntneri, M. concinnus and M. violaceus subsp. ritteri.


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) and northern Minas Gerais. Endemic to the core area of Eastern Brazil. Map 32D.

This subspecies is sometimes sympatric with M. ernestii, M. zehntneri and M. concinnus, but hybrids between them have not been observed.


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.

**MELOCACTUS DEINACANTHUS Group (no. 5):**


Southern Rio São Francisco *caatinga* element: on a gneissic inselberg in *caatinga* east of the Rio São Francisco, 500–600 m, central-southern Bahia. Endemic to Bahia. Map 27C.

*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 one locality (Morro da Barriguda, Juá, Mun. Bom Jesus da Lapa).

**MELOCACTUS LEVITESTATUS Group (no. 6):**

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.

**MELOCACTUS AZUREUS** Group (nos 7 & 8):


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**

Northern Rio São Francisco *caatinga* element: on flat, exposed Bambuí 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.

This subspecies has been observed sympatric with *M. pachyacanthus* subsp. *viridis*, q.v.

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.

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.


An endemic Bahian species divisible into two subspecies:

1. Stem globose to elongate-ovoid, strongly glaucous especially when young

8a. subsp. *pachyacanthus*

1. Stem depressed-globose, plain green

8b. subsp. *viridis*

8a. subsp. *pachyacanthus*

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.

This subspecies is sometimes partially sympatric with *M. zehntneri*, but can be distinguished by its darker coloured flowers, smooth seeds and stronger spination.

Northern Rio São Francisco caatinga element: on flat, ± exposed Bambuí limestone in caatinga at 700–750 m, in the region of Irecê, central-northern Bahia. Endemic to Bahia. Map 25C.

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):


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 Jacuípe) and Rio de Contas (Rio Gavião) drainage systems, eastern and southern Bahia. Endemic to Bahia. Map 32D.

This species can be found sympatric with *M. ores, M. ernestii* (both subspp.), *M. zehntneri* and, probably, *M. bahiensis* and *M. concinnus*. It occasionally hybridizes with *M. ores* and *M.*
ernstii subsp. ernstii. 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.).

Widespread *caatinga* / Northern campo rupestre element: in soil or sand and on rocks of various types, including limestone, gneiss/granite (inselbergs), sandstones, quartzitic and other crystalline formations, in the *caatinga* (rarely on rocks in *cerrado*, W Bahia, or in campo rupestre, 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.

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 (east of 41°W). Elsewhere, it can be found sympatric with *M. ernstii*, *M. bahiensis*, *M. azureus* subsp. *ferreophilus*, *M. pachyacanthus*, *M. salvadorensis*, *M. lanssensianus* (fide Braun) and *M. concinnus*. The name *M. horridus* Werderm. may relate to hybrids between *M. zehntneri* and *M. ernstii* (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 exserted from the cephalium and thus able to expand. Its pollination biology has been studied by Locatelli & Machado (1999a).

Eastern *caatinga* element: on exposed granitic outcrops of serras in *caatinga*, c. 900 m, Mun. Caetés, south-eastern Pernambuco and, perhaps, elsewhere to the west and north (cent.-N Pernambuco and eastern Paraíba). Map 31C.

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 município cited above. The status of this taxon remains uncertain; likewise, the identities of other, similar, cleistogamous plants provisionally referred here (see Supplement 1).


*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.

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, where there is evidence of hybridization with contiguous populations of other members of the genus. At the eastern edge of its range 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). To the west M. glaucescens has formed a hybrid swarm with M. concinnus, although this may not be the only taxon involved (Taylor 1991a: plate 17, below).


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.

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*.


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.

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 Inúbia (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.

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. *margariteus*

2. Flower to 25 × 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 × 7–10 mm; spines 5–6; ribs 8–10 (Bahia inland: Jacobina & Rui Barbosa)  

15b. subsp. *ritteri*

15a. subsp. *violaceus*

Widespread humid forest and Northern campo rupestre (cerrado) element: between shrubs in sand of the coastal restinga (and in similar forest up to 35 km inland), c. 0–150 m, or far inland 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. Map 12D.


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.
This very local taxon occurs sympatrically with *M. bahiensis* at both its localities. It is very similar to the following in most respects, but has pink fruits like subsp. *violaceus*.


Northern humid/subhumid forest (*restinga*) element: on coastal dunes of fine, white sand and inland (Serra de Itabaiana, Sergipe), 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.

If this taxon should one day prove to be worthy of specific rank, as Rizzini (1982) believed, then the earliest, clearly typified species name for it is *M. ellemeetii* Miquel, published 1858. However, at least one of its northern populations has very pale pink fruits and flowers, 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., Nyffeler, 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. Plates 5.1–5.4.

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 (Schumann) N. P. Taylor & Zappi (near Corumba, Mato Grosso do Sul; cf. Hoehne 1915: 55–56 — Hoehne 3858 (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. However, gene sequence data 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 has common ancestry with *Samaipaticereus* Cárdenas (Wallace 1997: 11). Its closest relative may be *Harrisia pomanensis* (F. A. C. Weber) Britton & Rose (Argentina & Bolivia).

1. *Harrisia adscendens* (Gürke) Britton & Rose, Cact. 2: 155 (1920). Type: Brazil, Bahia, 1906, Ule 7072 (B, lecto. designated here; K, photo ex B; HBG, lectopara.).

Widespread central-southern *caatinga* element: common along roadsides, amongst semi-open vegetation or scrambling over rocks (inselbergs), and especially in disturbed areas, *caatinga-agreste*, often on soils with a clay content, c. 50–700 m, from north-western (Xique-Xique), north-eastern and central-eastern Bahia (drainage of Rio Paraguacu at c. 13°S) northwards to southern Ceará and Paraíba (at c. 7°S). Endemic to the core area within North-eastern Brazil. Map 21D.

Although reported from Piauí by Lützelburg (1926, 3: 111), this species has not been seen there by the author and suitable edaphic conditions may be lacking.

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, either planted or spontaneous.
25. **LEOCEREUS** Britton & Rose


An isolated genus comprising a single species endemic to the core area of Eastern Brazil. Its placement in Trichocereeae is provisional and awaits confirmation via DNA gene sequence data.

Other species referred to *Leocereus* by Britton & Rose (l.c.) belong in *Arthrocereus*, except for *Cereus oligolepis* Vaupel (Britton & Rose, l.c., 225), which is a *Pilosocereus* (Zappi 1994). *Leocereus squamosus* (Gürke) Werdermann (1933) is *Fácheiroa squamosa* (Gürke) P. J. Braun & E. Esteves Pereira. For *Leocereus paulensis* Spegazzini, see *Coleocephalocereus fluminensis* (Zappi & Taylor 1992b).


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 Espinhaço), northwards to southern Piauí and westwards in the Chapadão da Bahia (Espigão Mestre) towards the border with Goiás. On present evidence, endemic to the core area in Eastern Brazil. Map 21C.
26. FACHEIROA Britton & Rose


Including Zehntnerella Britton & Rose (1920); Facheiroa subg. Zehntnerella (Britton & Rose)


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 included within Espostoa Britton & Rose). Buxbaum (1959) published Espostoa subg. Facheiroa (Britton & Rose) Buxb.

1. Flower-bearing part of stem strongly modified, rarely only poorly differentiated
   2
   1. Flower-bearing part of stem not at all modified (cent.-S Bahia northwards, non-calcareous rocks) 3. F. squamosa
   2. Flowers to 3 x 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 x 2 cm; perianth-segments white (cent.-N Bahia, non-calcareous rocks) 1. F. ulei


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.
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).

The distribution of *F. cephaliomelana*, as broadly circumscribed here, is paralleled or somewhat exceeded by that of other similarly variable cactus taxa exclusive to Bambui limestone outcrops from the same region, e.g. *Tacinga saxatilis*, *Pilosocereus densiareolatus* and *Melocactus levitestatus*. 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

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.

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).

Southern Rio São Francisco caatinga element: on outcrops of raised Bambuí limestone amidst high caatinga forest, 600–650 m, central-southern Bahia (E of the Rio São Francisco). Endemic to Bahia. Map 27D.


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.

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 (Ritter) P. J. Braun, 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 sterile.


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 (disjunct). Endemic to Bahia. Map 31D.

The distribution of this isolated species is markedly disjunct between northern and central-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 município 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, Itiúba and further east to Jeremoabo, as implied by Andrade-Lima (1989: 6) and Lützelburg (1926, 3: 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.
Plate 5. Diversity of Cactaceae in Eastern Brazil. 5.1–5.4, examples from Cactoideae-Trichocereae: 5.1 (top left), *Facheiroa squamosa* (Mun. Curaçá, Bahia), 5.2 (top right), *Espostooapis dybowskii* (E of Porto Alegre, Mun. Maracas, Bahia), 5.3 (bottom left), *Arthrocereus melanurus* (cult. R. Mottram, ex São João del Rei, Minas Gerais), 5.4 (bottom right), *Discocactus placentiformis* (Mun. Claro dos Poções, Minas Gerais). [5.1 © U Eggli; 5.3 © R Mottram]
28. ARTHROCEREUS A. Berger


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), see Map 8. 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 Speg. (Argentina), and Pygmaeocereus Johnson & Backeb. (= Echinopsis), ie. P. bylesianus Andreae & Backeb. (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 Schumann (and its illegitimate, homotypic synonym, C. damazioi Weingart), was misapplied by Berger and is actually identifiable with a species of Schlumbergera Lemaire (Rhipsalideae). However, more recently, Nyffeler & Eggli (1996) have cast doubt on whether the generic name can be accepted as validly published by Berger (1929), but this view is contradicted by Doweld & Greuter (submitted).
1. Inner perianth-segments pink, anthers purple (Serra do Cabral)  
2. Inner perianth-segments and anthers white or cream (Serra do Espinhaço and Serra da Mantiqueira)  
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)  
1. A. melanurus

1. Arthrocereus melanurus (K. Schumann) L. Diers, P. J. Braun & E. Esteves Pereira in Kakt. and. Sukk. 38: 312–315 (1987). Type (syntypes): Brasília, (?) Minas Gerais, Sello 1000 (B†; isosyntype at MO is A. glaziovii); Serra de São João del Rey [Serra do Lenheiro], Glaziou s.n. (living plant, assumed not to have been preserved). Lectotype (designated here): Schumann, in Martius, Fl. bras. 4(2): t. 39 (1890).

The following subspecies are recognized:

1a. subsp. melanurus

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)  
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. 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. odorus

1a. subsp. melanurus


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.

For an illustration of this giant subspecies in habitat, see Leme & Marigo (1993: 68).


Holotype: Brazil, Minas Gerais, Serra do Cipó, 1964, *Ritter* 1354 (U).

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.


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.

The lilac-pink flowers of this species are both striking and beautiful.

Holotype: Brazil, Minas Gerais, Pico d’Itabira do Campo, 20 Dec. 1888, Glaziou s.n. (B; K, SPF, photos ex B).

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.

Field studies are needed to evaluate the status of the erect and prostrate forms of this species.

29. *DISCOCACTUS* Pfeiffer


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 north-eastern 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, eg. *M. paucispinus*, *M. conoideus*, *M. concinnus* and *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* appears 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 in lacking a cephalium, in having broader, diurnal, brightly coloured flowers, tricolpate (vs. 12–15-colpate) pollen and in displaying a greater diversity in seed-morphology. It might be paraphyletic in respect of *Discocactus* and the latter name has priority.

1. Radial spines 3–8 per areole, often > 1.5 mm thick; stem solitary or offsetting when damaged by fire, > 11 cm diam.

2. Radial spines > 8 per areole, to 1.5 mm thick; stems freely offsetting, or solitary and < 11 cm diam.

3. Exposed part of stem with only 3 areoles visible per rib; ribs not broken up by tubercles (N Bahia to Piauí and Ceará)

4. Exposed part of stem with > 3 areoles per rib and/or ribs tuberculate with deep sinuses between areoles

5. 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

6. Seed 1–1.4 mm; fruit yellow-orange at apex; ribs 12–13, scarcely tuberculate; spines ± terete, to 1.5 mm thick (N Minas Gerais: near Grão Mogol)
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 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, in pure quartz gravel) 6. horstii

5. Ribs ± tuberculate; stem usually offsetting, light green or spines not as above (N Bahia) 6

6. Tubercles strongly developed, spiralled, obscuring the ribs 1. zehntneri

6. Tubercles weakly developed, arranged in clearly defined ± vertical ribs 2. bahiensis


This species is divisible into two subspecies:

1. Solitary or 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 25–75 × 1.5 mm; fruit red 1a. subsp. zehntneri

1. Offsetting freely, stems depressed, sometimes ± buried when growing in sand; ribs 13–21, tubercles 3–11 × 2–13 × 2–13 mm; areoles 3–7 × 1.5–3.0 mm; central spine 0–1, to 35 × 1 mm, but to 60 mm beneath the cephalium, radials 4–30 × <1 mm; fruit red, or white tinged green 1b. subsp. boomianus

1a. subsp. zehntneri

Northern Rio São Francisco caatinga element: on exposed arenitic rocks and gravelly soil in caatinga, 450–500 m, northern Bahia. Endemic to Bahia. Map 25D.


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.


Northern *caatinga* element: on exposed, gravelly river terraces amongst limestone or quartz stones, and seasonally inundated river flood plain with 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 north-western Piauí (Rio Canindé). Map 21A.

The distribution of this taxon seems rather disjunct, but remains inadequately known at present. It is related to the preceding species and occasionally bears red fruits (normally greenish white) 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 (see Supplement 1). This plant extends into Piauí and Ceará and may be expected to occur in Pernambuco. It seems to be an ecotype of river flood plains in the *caatinga*, where in northern Bahia, at least, it is associated with jurema-preta and carnaúba on ± barren, flat ground with stained quartz pebbles, evidently at times subject to
temporary inundation. It does not seem to merit recognition as a subspecies in view of its gradual intergradation with typical *D. bahiensis*.


Only the following subspecies occurs in Eastern Brazil:


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.

Despite Buining’s use of the epithet *catingicola*, 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. Collections from south-western Piauí and central-southern Bahia are somewhat intermediate with *D. bahiensis* and would be an argument for synonymizing the latter taxon as a further subspecies of *D. heptacanthus*. 

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Widespread South-eastern *campo rupestre / cerrado* element: on arenitic rocks, quartz sand and gravel, *cerrado / campo rupestre*, 550–1275 m, east of the Rio São Francisco, central and northern Minas Gerais. Endemic to the core area within Minas Gerais. Map 35D.

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, but 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 region of Lagoa Santa.

The large-stemmed, many-ribbed, thick-spined form of this species (syn. *D. pulvinicapitatus*, *D. latispinus*, *D. pseudolatispinus* — see Supplement 1), from the western slopes of the Serra do Espinhaço, and from the Serra do Cabral and northwards (municípios Claro dos Poços, Jequitai, Bocaiúva, 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 superficially resemble *D. pseudoinsignis* (see below) in their spination.


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.

Following the discovery of this species in the early 1970s Buining (1980) misidentified it as *D. insignis* Pfeiffer, a name correctly referred to the synonymy of *D. placentiformis* (Lehm.) Schumann by previous authors (see Taylor 1981: 40). Pfeiffer’s 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), but it can be distinguished by its non-tuberculate ribs, slender spines and smaller seeds. Its closest relative is probably the following species, with which it is partly sympatric.

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.

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 thought to be heading for extinction, but now known to be more abundant and protected in a reserve. The name *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


A remarkable, taxonomically isolated genus of 2–3 species, endemic to a relatively small region of central Minas Gerais (*campos rupestres, sensu lato*). 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 the variable *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. Part of the data upon which the distribution maps for this genus are based (Chapter 4) was supplied as coordinates by Marlon Machado and are not given in Supplement 1 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*.

1. Ribs not broken up into tubercles; flowers to 18 × 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 × 15 mm; fruit yellowish or greenish, inconspicuous; seeds with convex testa-cells (Subg. *Uebelmannia*)

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 37
Subg. Uebelmannia

See Key, above. Found only on quartz sands and gravels.


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.


South-eastern campo rupestre (Serra Negra / Serra do Ambrosio) element: in quartz sand, campo rupestre, 680–1600 m, Serra Negra, Minas Gerais. Endemic to the core area within Minas Gerais. Map 38C.


See Key, above. Found on cristalline rocks. Type and only species:

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. Spines yellow, ascending, organized in rows following the edge of the rib; plants to 50 cm  
   2

2. Spines greyish, spreading, not organized in rows; plants to 100 cm

   3b. subsp. flavispina

3a. subsp. pectinifera

South-eastern campo rupestre (Diamantina) element: crystalline rocks in campo rupestre, 650–1350 m, Serra do Espinhaço, north-east and south of Diamantina, Minas Gerais. Endemic to the core area within Minas Gerais. Map 38D.

The form reported from Inhaí seems somewhat morphologically and geographically intermediate between all three subspecies recognized here.


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.


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.

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.c., to have originated from Minas Gerais, but this is assumed to be an error.
Chapter 4

PHYTOGEOGRAPHY OF CACTACEAE NATIVE TO EASTERN BRAZIL

4.1. Introduction

Following detailed study of the systematics, habitats and range of the Cactaceae native in Eastern Brazil it becomes obvious that there are some more or less well-defined distribution patterns into which the majority of taxa can be classified. These patterns generally correspond with geographical, climatic, edaphic and other ecological phenomena and thus may offer help in defining phytogeographical regions and give clues about past vegetational history (Harley 1988, Prado & Gibbs 1993). Such studies are also important from the standpoint of conservation, since they indicate the minimum number, range and diversity of areas and habitats that need to be considered for protection (for priorities, see Chapter 5: Table 5.3).

Perhaps the most interesting and potentially informative aspect of this study is to use the areas defined below as a model to compare with other floristically important plant groups found in Eastern Brazil, especially those with ecological preferences similar to Cactaceae, such as Araceae (eg. Philodendron, Anthurium) and Bromeliaceae (eg. Dyckia, Encholirium), both of which are frequently lithophytic. However, before this can be done, it is necessary to have a rather detailed knowledge of the group concerned, especially in the field, and to make monographic studies to enable the careful determination of species limits, relationships,
geographical range and reproductive dispersal strategies. This is perhaps the first study of its kind to focus on a taxonomic group of reasonable size and complexity. Hopefully, there will be future opportunities to evaluate its significance for other families found in Eastern Brazil.

4.2. Choice of area studied

This phytogeographical study attempts to account for all taxa of Cactaceae that are native of the North-eastern region (‘Nordeste’) of Brazil, and of its South-eastern region (‘Sudeste’) north of c. 22°S and east of c. 46°W, as indicated on Map 1. For this purpose only taxa between the ranks of genus and subspecies have been considered, since these are defined by ± stable morphological characters in combination with a distinct geographical range. The total of native species and heterotypic subspecies is 161 (for completeness sake the Taxonomic Synopsis in Chapter 3 also deals with introduced, naturalized and frequently cultivated taxa, as well as giving other conventional information, such as botanical authorities, which are omitted here). Thus defined, the area chosen includes all Brazilian Cactaceae endemic to the great caatingas dominion (Andrade-Lima 1981) and all but two of those endemic to the campos rupestres, the vegetation type that characterizes the East Brazilian Highlands (Harley in Stannard 1995: 25), whose western part, with few cacti (W Minas Gerais & Goiás), is excluded (see Map 1). Nearly 76% (122) of the native species and heterotypic subspecies of cacti found in E Brazil are believed to be endemic and this justifies its choice for study.

While the whole of this geographical area has been considered, initial field and herbarium investigations suggested focusing on a somewhat smaller core area delimited at c. 7°S and c. 46°W, ie. including southern Piauí, the southernmost tip of Ceará, the southern half of Paraíba, then southwards to 22°S, in which there is a much greater diversity of taxa. *Cereus insularis* (Fernando de Noronha), is the only endemic from the Nordeste that does not enter this core area. Table 4.1 indicates taxa ranging beyond the core area and those endemic to it, the latter being 66.5% (107 taxa) of the overall total. A significant part of the territories of the northernmost states of the Brazilian Nordeste, comprising Maranhão, Piauí, Ceará, Rio Grande do Norte and Paraíba, has a relatively poor cactus flora, none having more than 16 native taxa. Only Minas Gerais and Bahia have significant numbers of state endemic taxa.

Possible explanations for these differing levels of diversity will be discussed below.

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Table 4.1. Distribution of species and subspecies of Cactaceae native in E Brazil by state. Key: † = taxon endemic to the total area included in this table; ‡ = taxon endemic to core area; § = single-site endemic; + = definitely recorded as native; ± = record requiring confirmation or of dubious identity; +? = possibly native or cultivated; c = cultivated; FN = Fernando de Noronha (PE) only; MG1/RJ1 = excl. W of c. 46°W and S of c. 22°S. For the locations of, and 2-letter codes for the states, see Map 1.
4.3. Definition of vegetation types

In most cases, the terminology used below to identify Brazilian vegetation types follows that employed by Prado (1991) and Harley in Stannard (1995: 7-11, 13-27, 37-40, 47-50, 52-66), which should be consulted for more detailed treatments including numerous valuable references. The definitions and terms employed by the Brazilian government (IBGE) have not been followed. Azevedo (1972), Cavalcanti Bernardes (1951), Domingues (1973), King (1956) and Nimer (1973) have been consulted for edaphic, geological and climatic data.

*Mata atlântica* (Atlantic Forest, Plate 6.1). In its broadest sense this term covers a wide range of evergreen and semi-evergreen forest formations, beginning at the coast, from the high tide mark, and stretching far inland until, in NE Brazil, the deciduous *caatinga* is reached. It also reappears, in fragmented form, at the base of the eastern side of the Chapada Diamantina in Bahia and as riverine forest along the Rio São Francisco (Brandão 2000: 75; Maps 14A–14C). In SE Brazil such vegetation extends much further inland, on to the *planalto central*, and there once formed extensive tracts of semi-humid 'mata do planalto' (eg. see Map 14A), which is considered a part of the Atlantic Forest system by many Brazilian botanists. In some areas the forest includes extensive outcrops of smooth gneissic rocks or larger inselbergs and these represent an important habitat for rupicolous cacti in such areas, especially from south-eastern Bahia (Santa Cruz da Vitória) southwards and south-westwards to Rio de Janeiro, where, for example, *Pilosocereus brasiliensis* and *Coleocephalocereus* subg. *Coleocephalocereus* are characteristic rupicolous taxa (Maps 16A–16D). Although normally thought of as a very humid environment, this is by no means uniformly the case, since rainfall can vary from more than 2000 mm down to less than 800 mm per annum and often includes a more or less well-marked dry season. The cactus flora varies considerably with levels and frequency of precipitation and, as a consequence, many taxa show markedly disjunct distributions. Minimum temperatures vary in line with latitude.
and altitude, but are probably never less than 0°C anywhere in the regions considered in this study, and are never < 12°C, from Rio Grande do Norte to coastal S Bahia (Nimer 1973: 42).

In the drier or rocky and less dense phases of the Mata atlântica large, terrestrial (ie. non-epiphytic) cacti are able to compete with other forest species, such as in the coastal forests around the border regions of Bahia and Sergipe (eg. *Cereus jamacaru* — typically a caatinga species), in eastern Minas Gerais and central Espírito Santo (eg. *Pereskia grandifolia* subsp. *violacea*) and in the lowlands of southern Espírito Santo and north-eastern Rio de Janeiro (eg. *Brasiliopuntia brasiliensis*). At or near the coast the forest is termed restinga and even in more humid areas frequently includes edaphically dry sand-dunes in which an open or denser scrub, or taller, forest supports a variety of non-epiphytic cacti. However, the dense, multilayered forest in areas where there is rain every month of the year includes only cactus epiphytes, but even these can be absent or rare in some phases of this ecosystem, eg. the 'mata de tabuleiro', found on elevated Tertiary 'Barreiras’ formations in parts of coastal Bahia and Alagoas. Further landwards the 'brejo' forests (mata de brejo) represent isolated patches of more humid, evergreen vegetation on mountain ridges surrounded by seasonally dry Atlantic Forest or even caatinga (Map 10). These benefit from lower average temperatures, greater cloud cover and overnight dews (Rodal et al. 1998), which compensate for rain during dry periods. They are sometimes rich in epiphytes, often including a variety of Cactaceae tribe Rhipsalideae (see Table 5.1, Chapter 5). Finally, in eastern parts of the Chapada Diamantina (Bahia) and Serra do Espinhaco (N Minas Gerais) there occur isolated montane cloud forests ('mata de neblina’ at 1200–1800 m), which, at the highest elevations, are extremely humid. These are treated as part of the campo rupestre mosaic here (see below), because their flora lacks various of the more widespread cactus epiphytes characteristic of forests further east and even includes an endemic subspecies (*Rhipsalis floccosa* subsp. *oreophila*). Connecting the extremes of perhumid coastal
rainforest and dry inland *caatinga* is the ecotonal type known as *agreste* (here used to include *Mata de cipó*). Like much of the *Mata atlântica* (Myers et al. 2000), most of this has been destroyed eliminating an important habitat for certain cacti.

*Caatinga* (Plate 6.2–6.4). The low forest or semi-open thorny thicket vegetation most prevalent in NE Brazil, in which the great majority of species is drought-deciduous (see Map 40). There is a pronounced dry season, which can be of unpredictable duration (2–12+ months), the total annual rainfall being less than 1000 mm and sometimes less than 500 mm. Soils vary from very shallow and stony to deep and sandy, but many of the cacti are restricted to rock outcrops of various kinds, including gneiss/granite, sandstone and limestone. The minimum temperature throughout the area never drops below 8°C and the maximum can reach 40°C (Nimer 1973: 49). This vegetation is normally encountered at less than 750 metres altitude, occurring at sea level at its northern limits in coastal Ceará, but occasionally at more than 1100 metres (*‘caatinga de altitude’*), such as c. 50 km to the west of Seabra (Mun. Ibitiara, Bahia) and on the Pico do Jabre (Mun. Maturéia, Paraíba). Its southern limit is uncertain, but in the Rio São Francisco valley islands of taller, dry forest (deciduous *mata seca*) on limestone outcrops extend far to the south of the main *caatinga* area. Andrade-Lima (1981) divides *caatinga* vegetation into 12 different types, only some being rich in Cactaceae.

*Cerrado* (Plate 6.5). This is the Brazilian savanna woodland, which occupies a huge area in the Central-Western and South-eastern regions of the country, occurring in only a few, mostly small patches in the North-east where precipitation and soil conditions allow. It is an open woodland comprising a more or less evergreen layer of trees with curious contorted trunks and a mixed herbaceous and woody ground flora. The plants show many adaptations against high insolation and fire: sclerophyllous foliage, xylopodia, thick bark etc. Usually around 1500 mm or more of rain falls each year, but there is a regular dry season during winter when fires sometimes sweep through. The soils are very deep and strongly leached of
nutrients, often with a very low pH. Cacti are rare or quite absent, except in open areas on some deep sandy or gravelly substrates, or restricted to rock outcrops protected from the fire. In Eastern Brazil cerrado vegetation is usually found below 750 metres altitude; when occurring above this elevation it is generally included with the following type.

*Campo rupestre* (Plate 6.6). This is often described as a mosaic of different vegetation types, which reflects the intimate mixture of different topographies, substrates and microclimates, resulting from the juxtaposition of mountain ridges, grassy or marshy valleys, bare rocks, sand and gravel deposits and sharp diurnal fluctuations in temperature, humidity and light, all combined with elements of the 3 preceding vegetation types (hence the terms 'mata de neblina', 'caatinga de altitude' and 'cerrado de altitude'; also 'carrasco' — used for the caatinga / campo rupestre / cerrado ecotone). However, campo rupestre is most commonly and intricately associated with cerrado, so that the distinction between the two is often difficult to make and, therefore, in Area No. 4, below, the two are treated together. Rainfall is rather variable, but frequently well in excess of 1000 mm per annum and accompanied by heavy dews and mist. Maximum temperatures are lower than in the other vegetation types mentioned above and winter minima can descend to between 0°C and -4°C at the highest elevations (Nimer 1973: 46). Cacti are mainly restricted to the rock outcrops and areas of deep sands and gravels, from c. 750–1950 m, eg. Pico das Almas, BA (*Arrojadoa bahiensis*) and Pico do Itambé, MG (*Cipocereus minensis*), although vegetation of this nature sometimes descends to less than 400 metres (eg. near Andarai, BA: *Micranthocereus purpureus*). Such vegetation is commonest along the mountain backbone of Eastern Brazil formed by the Serra do Espinhaço and Chapada Diamantina (Serra da Moeda, MG, northwards to Jacobina, BA), but also occurs in smaller pockets further to the east on more isolated ridges, such as at Rui Barbosa and Monte Santo (BA), and further south in the Serra da Mantiqueira (Serras do Lenheiro and Ibitipoca, MG) — see Map 41.
Plate 6. Habitat types. 6.1 (top left), Atlantic Forest / *Mata atlântica* (descent to Caraguatatuba, São Paulo); 6.2 (top right), *caatinga-agreste* (near Rui Barbosa, Bahia); 6.3 (centre left), shrubby *caatinga* (near Casa Nova, Bahia); 6.4 (centre right), inselberg in *caatinga-agreste* (Pedra Azul, Minas Gerais); 6.5 (bottom left), *cerrado* (between Montes Claros and Januária, Minas Gerais — a habitat of *Cereus mirabella*); 6.6 (bottom right), *campo rupestre* (Mun. Érico Cardoso, NW of the Pico das Almas, Bahia).
4.4. Endemism, barriers to dispersal, vicariance and phytogeographical links

As stated above, the core geographical area defined within Eastern Brazil and particularly focused on in this study has been recognized primarily for its remarkable endemism of Cactaceae genera and species, especially those of the caatinga of the North-eastern states and associated highland campos rupestres, both of which extend into the northern part of the SE Brazilian state of Minas Gerais, where the highest concentration of Cactaceae taxa is found. Vegetation including a significant representation of cacti also reaches into the Mata atlântica of eastern Minas Gerais and the neighbouring state of Espírito Santo, where a substantial area drained by the Rio Doce and adjacent river systems receives less than 1000–1250 mm of rain per year (see map 'isóietas anuais 1914–1938' in Azevedo 1972; Nimer 1973: 40, fig. 18). In this substantial core area representatives of the family appear to have evolved for long periods in isolation, so that many distinctive taxa without parallel elsewhere have arisen. It is also true that various major cactus genera, widespread in the neotropics, are absent from this region. These include Selenicereus (assuming S. subg. Salmdyckia = Hylocereus), Disocactus, Pseudorhipsalis, Echinopsis and Cleistocactus, besides others mentioned below, which, unlike the above, are replaced in Eastern Brazil by obvious, closely related vicariants. Genera from the widespread, species-rich, South American Notocacteae are likewise absent. Other significant neotropical genera are represented by only a single native species in each case, eg. Opuntia (sens. str.), Hylocereus, Epiphyllum and Harrisia. In the case of Opuntia, the single species, *O. monacantha*, is only marginally represented, being a rarity at the northern limits of its range.

It is perhaps not difficult to see why this should be so, since today the region is effectively cut off from other centres of cactus diversity by very broad zones of habitat unfavourable to most members of the family. To the north-west of the dry region of North-eastern Brazil is the nearly constantly humid Amazonian region, with its rainforests and
included cerrados, where only few specialized cacti are able to compete with other plants (see Appendix 3). Amongst these is the epiphyte, *Rhipsalis baccifera* subsp. *baccifera*, whose range southwards into Eastern Brazil stops at c. 8°S in the coastal forest of Pernambuco (at Recife), potentially indicating the southern limit of Amazonian floristic influence. To the west, in Central-western Brazil, are the extensive fire-swept cerrados, which are avoided by most cactus genera (except *Discocactus* in gravelly areas), although included rock outcrops and gallery forests do provide some suitable habitats (eg. for *Rhipsalis russellii*, *Pilosocereus machrisii* and allies, *Cereus* spp. and *Arthrocereus spinosissimus*) and have probably permitted a limited amount of migration to and from the caatingas, *Mata atlântica* and campos rupestres in the past (cf. Prado & Gibbs 1993). To the south the diversity of non-epiphytic cacti abruptly decreases as humidity increases, and these are replaced by numerous epiphytic species from tribe Rhipsalideae (Barthlott & Taylor 1995) until the grasslands (or campos) of Rio Grande do Sul are reached. Here the diversity of non-epiphytic cacti suddenly increases again; these, however, are globular species from tribe Notocacteae, which is absent from E Brazil. Such ecological barriers in recent times must have severely limited migration of cactus species and genera to and from neighbouring regions of high diversity, such as the Caribbean, the Andes and the part of south-eastern South America where the Notocacteae are most abundant. However, such barriers have not been constant, climatic fluctuations during the Pleistocene having allowed migration in other groups (Ab'Sáber 1974, Prado 1991), although these seem to have been relatively few in Cactaceae (cf. Table 6.1, pages 376–377).

*Endemism: Pereskioideae.* *Pereskia,* nowadays the only genus included in this subfamily, is comprehensively represented in Eastern Brazil in terms of diversity, since elements of the 3 major groups of species recognised by Leuenberger (1986) are present and give a total of 5 species, with 3 endemic to the core area. The endemic species (*P. bahiensis*, *P. stenantha* and
P. aureiflora) are restricted to the caatinga-agreste, while P. aculeata and P. grandifolia (and its endemic subsp. violacea, which may be specifically distinct) are Mata atlântica species.

Opuntioideae. In terms of species, the 4 rather distinct genera of Opuntioideae native of Eastern Brazil are very small, with only 9 species in total (6 belonging to Tacinga, sens. lat., an endemic of the NE and SE regions of Brazil). At first sight this seems hard to explain, since elsewhere this subfamily is generally species-rich in the dry zones of the Americas, eg. in the Andes, Mexico and south-western United States, where they invariably constitute a major component of cactus floras. So why have so few taxa evolved in Eastern Brazil? The answer may lie in the origin of the subfamily. It includes taxa resembling the genus Maihuenia (Maihuenioideae, cf. Wallace 1995), the plesiomorphic sister group of Opuntioideae (Nyffeler, ined.), which strongly resembles some members of the Portulacaceae, a part of this being the sister group of the Cactaceae (Hershkovitz & Zimmer 1997, Savolainen et al. 2000: Fig. 2). Maihuenia is a genus of temperate South America (Patagonia etc.) and the Opuntioideae in major part are also represented by plants of cooler mountainous regions (Andes) or higher plateau-lands (northern Mexico etc.), perhaps suggesting that they are generally less well adapted to life in the constantly warm, lowland parts of the tropics. In the drier parts of such tropical regions the Opuntioideae have, however, evolved some highly specialized and derived forms (derived when compared to a supposed Maihuenia-like ancestor), such as Tacinga (including 2 spp. of cactus lianas, E Brazil), Brasiliopuntia (1 treelike sp., neotropics south of the River Amazon), Consolea (c. 8 treelike spp., Caribbean islands) and Pereskiopsis (6 semi-scandent or treelike spp., trop. Mexico & Cent. America). Quiabentia (2 treelike spp., Chaco region & E Brazil) is not included in this list, since at least its western species comes from a region that experiences frost in winter (Map 8) and its Brazilian counterpart is confined to the more seasonal south-western caatingas. Tacinga, sens. lat. (6 spp.), extends considerably beyond the E Brazilian
core area into the northernmost caatingas (T. inamoena), and slightly beyond it to the west, in Minas Gerais, on edaphically dry limestone outcrops (T. saxatilis), but completely replaces Opuntia, sensu stricto, in Eastern Brazil, except towards the southern margins of the core area where there are a few records of O. monacantha, at its northern limit of range.

Cactoideae. Out of the 8 tribes and 3 or more other major clades of Cactoideae currently recognised (Wallace 1995 & pers. comm., Nyffeler, ined.; see Chap. 2.7) nearly all E Brazilian cactus genera of this relationship fall into tribes Cereeae (9 genera), Trichocereeae (7 genera) and Rhipsalideae (4 genera), with only Hylocereus (1 sp.) and Epiphyllum (1 sp.) in the Hylocereeae and Pseudoacanthocereus (1 sp.) doubtfully in Echinocereeae, sens. lat. (incl. Leptocereeae & Pachycereeae). Therefore, Eastern Brazil is apparently rather lacking in diversity at the tribal level or equivalent.

At generic level the situation is different. Cereeae has its major centre of diversity in Eastern Brazil (Taylor & Zappi 1989) and many of its genera and subgenera are endemic: Cipocereus (5 spp.), Brasilicereus (2 spp.), Stephanocereus (2 spp.), Micranthocereus subg. Micranthocereus (4 spp.), M. subg. Austrocephalocereus (3 spp.), Coleocephalocereus subg. Buiningia (2 spp.) and C. subg. Simplex (1 sp.). Micranthocereus (9 spp.) and Arrojadoa (4–5 spp.) are almost endemic, the first with only M. estevesii (M. subg. Siccobaccatus) located outside the core area on limestone outcrops between southernmost Tocantins and NW Minas Gerais, the second with a recently discovered taxon in NE Goiás. Flower and fruit characters suggest that Cipocereus, Arrojadoa and Stephanocereus comprise a campo rupestre / caatinga lineage with no obvious relatives outside E Brazil. The Trichocereeae, while represented by relatively few species, are also diverse at generic level, with 4 out of 7 genera being endemic: Uebelmannia (3 spp.), Facheiroa (3 spp.), Espostoopsis (1 sp.) and Leocereus (1 sp.). The stronghold of this tribe in Eastern Brazil at species/subspecies level is in the South-eastern campos rupestres and adjacent cerrados, where they total nearly half of
the Cactaceae. All 4 genera of Rhipsalideae are found in Eastern Brazil, but none is endemic
and few species and subspecies are endemic, since the *Mata atlântica* they mostly inhabit
extends well beyond the limits of the core area to the south and south-west. Excepting
*Rhipsalis baccifera*, their range northward terminates at the northern border of Pernambuco.

**Vicariance and phytogeographical links.** Amongst the endemic genera and subgenera there
are some which have obvious sister taxa or close relatives beyond the bounds of Eastern
Brazil (see also discussion on generic relationships, Chap. 2.7 & 3.2). For example, the genus
*Brasilicereus*, with a pair of allopatric species (see Areas Nos. 3 & 4, below), is probably
related to the widespread *Praecereus* (N South America to N Argentina; Hunt 1999a), which
it replaces in Eastern Brazil (Taylor 1992a, 1997a&b): Map 2. The occurrence of *P.
euchlorus*, sens. lat., ranging westwards and northwards from São Paulo and Paraná, Brazil,
through NE Argentina (Misiones), E Paraguay, Bolivia, Peru, Ecuador, Colombia and
Venezuela, when complemented by that of *Brasilicereus* in Eastern Brazil (Minas Gerais &
Bahia), conforms closely to the extended Pleistocene Arc distribution pattern described by
Prado & Gibbs (1993) for dry seasonal woodlands in South America. Another vicariant pair
of taxa comparable with the *Praecereus/Brasilicereus* case is that of *Cereus* subg. *Mirabella*
(2 spp., Areas Nos. 3 & 4, below), which replaces *C. subg. Ebneria* in Eastern Brazil (the
latter comprises 6–7 species, ranging through Central-western Brazil, Bolivia, Paraguay and
Argentina; Taylor 1992a): Map 3. A different and much more disjunct example of vicariance
is that of *Espostoopsis* (see Area No. 3d(i), below) and its presumed relative, the central
Andean genus, *Espostoa* — Map 4. The genus *Discocactus* ranges from eastern Paraguay and
easternmost Bolivia (1–2 spp.) into Eastern Brazil, where 5 other species are endemic. Its

Map 2 (next page). Distribution of *Praecereus* [■] and *Brasilicereus* [●]. South America.
presumed sister taxon is Gymnocalycium (c. 50 spp.), from W Argentina and E Bolivia eastwards, and it is assumed to represent an element originating from this south-western flora. The depressed stems of Discocactus are adapted to withstand the cerrado's fires.

Below generic rank there is a high level of endemism amongst the cacti of Eastern Brazil and most of the endemics have no close relatives outside of this region. However, some notable exceptions provide clear phytogeographical links with other, more or less remote cactus floras (in addition to those already noted above). The most important of these involve the Caribbean, northern South America and Amazonia. Thus, the Pilosocereus Pentaedrophorus Group (8 spp., 5 in E Brazil, 3 endemic to the core area) includes one markedly disjunct species in Roraima and the Guianas (P. oligolepis; Zappi 1994), while the Melocactus violaceus Group (10 spp., 7 in E Brazil, 5 endemic to the core area) includes the geographically isolated M. smithii and M. neryi in the Amazonas-Orinoco drainage region and M. matanzanus in Cuba (Taylor 1991a). A gene sequence phylogeny (Wallace 1997: 11) suggests that the geographically isolated caatinga endemic, Harrisia adscendens, links members of the basal H. subg. Eriocereus (E Bolivia, Paraguay, Argentina & Uruguay) with the Caribbean taxa of Subg. Harrisia, indicating their path of radiation: Map 5. This would seem to have been via an eastern route, rather than a western Andean route, as is suggested by the Praecereus/Brasilicereus example given in the previous paragraph. Equally interesting links are those between the caatinga-agreste of Eastern Brazil and similar dry habitats in northern South America (Colombia & Venezuela): Pereskia aureiflora (see 3a(iii) below) and P. guamacho (Wallace 1995: 9); Pseudoacanthocereus brasiliensis (see 3d(i) below) and P. sicariguensis (Taylor et al. 1992). These vicariant species-pairs are disjunct across the

humid Amazonas-Orinoco region: Map 6. A geographically similar case, but not so disjunct, involving a pair of species, or perhaps a single widespread species with regional forms, is that of the E Brazilian *Cereus jamacaru* and the Venezuelan/Amazonian *C. hexagonus*. Links with the cactus flora of SE Bolivia, Argentina, Paraguay and immediately adjacent parts of Central-western and Southern Brazil are provided by an E Brazilian group of 3 *Pereskia* spp. (*P. grandifolia, P. bahiensis, P. stenantha*) and *Quiaihentia zehntneri*, which have south-western counterparts in the taxa comprising *P. nemorosa / P. sacharosa* and *Q. verticillata* (a species ranging in and around the western part of the Chaco): Maps 7 & 8. The *Pereskia* species-group is another which conforms to the Pleistocene Arc distribution pattern described by Prado & Gibbs (1993) and *Quiabentia* is the only clear link between Chaco and *caatinga* (cf. Prado 1991). *Arthrocereus* is a genus of four species, with 3 native to E Brazil (Area No. 4c) and one disjunct in the Chapada dos Guimarães, Mato Grosso (*A. spinosissimus*): Map 8. Further examples include *Pilosocereus machrisii* and *Discocactus heptacanthurus*, *sens. lat.*, from Central-western & Northern Brazil etc., both ranging into the western part of Eastern Brazil and having endemic sister taxa in Minas Gerais and/or Bahia: *P. aurisetus* and *D. placentiformis / D. bahiensis* etc. Other such links involve the *Mata atlântica*, as provided by *Rhipsalis cereuscula*, ranging from NE & SE Brazil via S Brazil and Paraguay to the west as far as the east Andean Yungas of Bolivia. The widespread and almost endemic *R. lindbergiana* is morphologically most similar to *R. baccifera* subsp. *shaferi*, which ranges between São Paulo state (Campinas) and the eastern Andes. Two *Lepismium* species, *L. cruciforme* (NE to SE Brazil) and *L. warmingianum* (SE & S Brazil), have sister taxa in the eastern Andes of Bolivia (in the Yungas) and north-western Argentina — *L. incachacanum* and *L. lorentzianum*, respectively: Map 9. *Pereskia aculeata* has a bimodal distribution north

Map 4 (next page). Distribution of *Espostoa, sens. str.* [■] and *Espostoopsis* [●]. South America.
and south of the Amazon basin (Leuenberger 1986), mainly on the eastern side of the neotropics (see Area No. 2a, below). Its allies are all Andean (Wallace 1995: Fig. 10).

The phytogeographical links discussed here are summarized on the basis of the Brazilian vegetation types they represent in Tables 4.2, 4.3 & 4.6 (see the area categories to which these relate, below) and also account for the various cactus species of Eastern Brazil ranging into, or providing links with, the immediately adjacent parts of Northern, Central-western and South-eastern/Southern Brazil (see Appendix 3). Such links lend support to the various migratory routes hypothesized by Prado (1991: 222–231, Fig. 8.3) and add to the cactus evidence he was already aware of.

4.5. Discussion of distribution patterns of Cactaceae and phytogeographic areas

The phytogeographical Areas and their subdivisions elaborated below are largely defined by the distribution patterns of cacti indigenous to Eastern Brazil. The lines delimiting Areas 2–4 on Map 10, with a few exceptions, reflect the recorded native occurrences of the taxa described and documented in Supplement 1 (records of cultivated plants excluded), except where they have been drawn by extrapolation from known vegetation/climatic boundaries in the absence of cactus records. In this regard, significant gaps in the author’s field knowledge, and where herbarium records are also lacking, are indicated on Map 10*, so that any extrapolated lines and other assumptions can be identified. Nearly 95% of the taxa (including c. 12% thought to be single-site endemics) have distributions that show a strong correlation with the major vegetation types and topographic features, falling into one of the 3 major categories described below (Areas Nos. 2–4, see Maps 14A & 40). All available

*By state, from north to south, areas deserving of further investigation in the field are as follows. Maranhão: northernmost (coastal dunes) and southernmost limits (towards Piauí); SW Piauí; Ceará (most of state except NW & S); northern Rio Grande do Norte; SE Pernambuco; N & W Alagoas (especially around Mata Grande); southernmost coastal Sergipe; Bahia: NE (Raso da Catarina & coast N of Salvador until Sergipe), cent.–W (the entire region N & S of road BR 242, including land draining into the Rio São Francisco from its E side, to the borders with Minas Gerais, Goiás and Piauí) & SE inselbergs (BA/MG/ES border region); Minas Gerais: NW, NE (drained by Rios Jequitinhonha & Mucuri), E (Caratinga eastwards) & SW (towards 46°W); and Espírito Santo: NW (inselbergs) & S (at > 600 m for Rhipsalideae).
distributional information is fully documented and can be consulted in the detailed taxonomic treatment that represents the key reference for this account (Supplement 1).

Leaving aside the first distribution category (No. 1, below), the other major categories recognised, ie. Areas Nos. 2, 3 & 4, are as delimited on Map 10, with minor exceptions, ie. where disjunct occurrences of one vegetation type are found inside the area of another or as rare disjunct records of particular taxa, these being noted in the discussion under each Area heading. In terms of vegetation types, Area No. 2 corresponds with the Mata atlântica (Atlantic Forest) and its constituent sub-types, such as restinga (at the coast) and mata de brejo (on higher ground well inland). Further west, Area No. 3 corresponds to the caatinga in its entirety, which also surrounds and includes the campos rupestres/cerrados of the northern part of the East Brazilian Highlands and disjunct islands of dry forest on limestone outcrops beyond its vaguely defined southern limits. Area No. 4 comprises the western cerrados and the campos rupestres of the south-eastern part of the East Brazilian Highlands, which are bounded by the Mata atlântica (Area No. 2) on their eastern slopes. At the borders between these adjacent Areas species assigned to one or other may sometimes be sympatric over a small distance, eg. upon gneissic rocks south of Padre Paraíso, Minas Gerais (Nos. 2 & 3) and in the municípios of Grão Mogol and Bocaiúva, MG (Nos. 3 & 4). Apart from these, the zones of overlap, usually ecotonal in character, are not very extensive or do not appear to be so today due to their widespread destruction, as is the case, for example, with the agrestes, which lie between the caatinga and Mata atlântica. At their southern limits, as indicated on Map 10, Areas 2–4 can no longer be distinguished geographically, differing only as ecological concepts. This means that species referred to No. 2 or to No. 3 may sometimes grow in very close proximity to campo rupestre taxa from No. 4.
Map 6. Vicariant species-pairs: *Pereskia guamacho* [▲] and *P. aureiflora* [●]; and *Pseudocactus*:*P. sicariensis* [*] and *P. brasiliensis* [★]. N. South America & E. Brazil.
From the above it should be obvious that each of the Areas Nos. 2, 3 and 4 broadly corresponds to a major vegetation type, namely the *Mata atlântica*, *caatinga* and *cerrado*. However, the *campos rupestres* are divided between Areas Nos. 3 and 4, which reflects the very strong divergence in cactus genera and species between the northern and south-eastern parts of the East Brazilian Highlands. These differences are discussed under their respective Areas, below.

**Distribution patterns and phytogeographical areas**

NB. the symbol '‡' indicates that a taxon is endemic to the core area as defined above; and '§' identifies taxa believed to be, or which are probably single-site endemics (ie. known from a single, if sometimes partly fragmented, population). The distributions of nearly all of the taxa listed below are presented in the accompanying maps.

1. *Eastern Brazil in its entirety*: taxa that are widespread and/or non-specific or disjunct between different vegetation/area categories within E Brazil (9 taxa; < 6% of total)

   Under this heading are listed the taxa which cannot be fitted into any of the more specific vegetation/area categories or patterns outlined below (Nos 2–4). Only one is endemic to Eastern Brazil, and the remainder includes a few taxa very widely distributed in the neotropics as well as those ranging into other parts of Brazil but not beyond. That most of these are epiphytes confirms the assessment made in Ibisch et al. (1996), in relation to Peru, that epiphyte taxa show lower levels of endemism than terrestrial taxa (see also Area No. 2).

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Map 7 (next page). Distribution of the *PERESKIA GRANDIFOLIA* Group: *P. sacharosa* [●] and *P. nemorosa* [▲] (after Leuenberger 1986: 106, fig. 42); and *P. grandifolia s.l.* [■], *P. bahiensis* [○] & *P. stenantha* [□]. Central & E South America. See also Chapter 3, Fig. 2.
Map 8. Distribution of *Arthrocereus*: *A. spinosissimus* [□], *A. melanurus sens. lat.* [■], *A. rondonianus* [●] and *A. glaziovii* [▲]; and of *Quiabentia*: *Q. verticillata* [+] and *Q. zehntneri* [★]. Eastern Andes, Central-western and Eastern Brazil.
Map 9. Vicariant species-pairs in *Lepismium*: *L. incachacanum* [■] and *L. cruciforme* [●]; and *L. lorentzianum* [▲] and *L. warmingianum* [★]. Eastern Andes and Eastern & Southern Brazil etc.
la. Very widespread/non-specific in Areas 2–4 (2 taxa, Map 11)

**Hylocereus setaceus, Epiphyllum phyllanthus.**

These are wide-ranging neotropical taxa of broad ecological tolerance, being strongly xerophytic epiphytes and lithophytes. They belong to tribe Hylocereeae, which phylogenetic research based on gene sequences (Wallace 1995 & pers. comm.) has shown to be amongst the most basal branches in the Cactoideae or its HPE clade. It is also possible that these species themselves are rather old, as is suggested by their very extensive distributions in tropical America, which in the case of *H. setaceus* could represent the combined trans-Amazonian and Andean historical migration route hypothesized by Prado (1991). Note that the widespread neotropical *Rhipsalis baccifera* subsp. *baccifera* is but marginally represented in the core area of Eastern Brazil, reaching southwards only as far as the coastal forests in Pernambuco state. The species is better represented in the core area, however, by the endemic subsp. *hileiabaiana* (see 1b, below).

1b. Ranging between Area No. 2 and No. 3 or No. 4, in restinga / Mata atlântica / mata de brejo / mata de neblina / campo rupestre / caatinga / agreste etc. (7 taxa, Maps 12A–13)

**Brasiliopuntia brasiliensis, Rhipsalis lindbergiana, R. baccifera subsp. hileiabaiana,** R. russellii, **Hatiora salicornioides, Pilosocereus cataringica subsp. salvadorensis,** **Melocactus violaceus subsp. violaceus.**

Taking the epiphytes first (Maps 12B/12C), *Rhipsalis baccifera* subsp. *hileiabaiana*

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Map 10 (next page). Eastern Brazil, showing the principal phytogeographic divisions, Areas 2, 3 & 4 (demarcated by heavy line – see text), 750 metre contour (- - -) on this and all subsequent maps, Chapada Diamantina (CD), Serra do Espinhaço (Sa Esp) and areas of potential interest that await investigation (‘?’). Key: Area 2 = Mata atlântica (• = brejo forest, partly within Area 3), Area 3 = Caatingas and Northern campos rupestres, Area 4 = Western cerrados and South-eastern campos rupestres. Taxa used to define the lines A–B etc.: Harrisia adscendens, Brasilicereus phaeacanthus, Melocactus ernestii, M. bahiensis subsp. amethystinus, M. zehntneri, Pereskia grandifolia subsp. violacea, P. bahiensis, P. stenantha, Pilosocereus gounellei, P. fulvilanatus, P. pachycladus, Tacinga braunii, T. inamoena, Cereus mirabella, C. jamacaru subsp. calcirpicola, *Rhipsalis floccosa* subsp. *floccosa*, R. paradoxa, Cipocereus laniflorus, Arthrocereus rondonianus.
Map 11. Distribution pattern 1a, represented by *Hylocereus setaceus*. Eastern Brazil. [? = record whose identity requires confirmation]
and *Hatiora salicornioides* occur in areas of relatively high rainfall in the *Mata atlântica/ mata de brejo* (Area No. 2) and in *campos rupestres* and montane cloud forests of the East Brazilian Highlands further west (Chapada Diamantina, Area No. 3). Strictly speaking, the *Hatiora* occurs in Areas 2–4, but is common only in the southern part of Area No. 2, so hardly qualifies for inclusion in the previous category, 1a. The disjunction of *R. baccifera* subsp. *hileiabaiana*, a plant restricted to habitats with very high rainfall, is striking and is unlikely to be an artefact of poor collecting or habitat destruction (likewise, that of *H. salicornioides*). In Eastern Brazil *Rhipsalis russellii* is known only from cent.-E/SE Bahia and two disjunct collections from central/southern Minas Gerais (as an epiphyte) and southern Espírito Santo. From there it ranges into Goiás and Mato Grosso, where its habitat details are unknown at present. *R. lindbergiana* has most of its range within Eastern Brazil, ranging from Pernambuco to the border region between eastern São Paulo and Rio de Janeiro. It is found in the *restitinga / Mata atlântica* on the coast and in *mata de brejo* on the Serra Negra (Pernambuco), and more rarely in semi-humid forests surrounding the East Brazilian Highlands, as well as in patches of more humid forest within the *caatinga* area east of the Chapada Diamantina (BA) and in *mata seca* west of the Serra do Espinhaço, MG.

*Melocactus violaceus* subsp. *violaceus* (Map 12D) is primarily coastal, being found in open, shrubby vegetation on sands, at c. 0–150 m alt., from Rio de Janeiro to Rio Grande do Norte, but it has also been collected in north-eastern Minas Gerais, in a very sandy phase of *cerrado de altitude* at 1100 metres elevation (Taylor 1991a: 56). This is an example of the links between the montane and coastal floras of Eastern Brazil, such as have been reported for other plant groups (Giulietti & Pirani 1988: 47, 53, 60; Harley 1988: 100).

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Maps 12A–12D (next page). Distribution pattern 1b, represented by (A) *Brasiliopuntia brasiliensis*, (B) *Rhipsalis russellii* [○] and *R. lindbergiana* [*•*], (C) *R. baccifera* subsp. *hileiabaiana* [▲] and *Hatiora salicornioides* [○] and (D) *Melocactus violaceus* subsp. *violaceus*. Eastern Brazil (B & C core area).
Brasiliopuntia (Map 12A) is a most unusual cactus, inhabiting semi-humid, high forest where it forms a tree with a well-developed trunk (Plate 2.2, page 85). It ranges from dry restinga forest at the coast into the agrestes and caatinga (eg. in Sergipe), reaching further inland into north-western Paraíba, central & eastern Pernambuco and western Alagoas (in brejo forest), reappearing in north-western Bahia (at Formosa do Rio Preto) and then on limestone outcrops amongst mata seca in central Minas Gerais (Area No. 3). It is wide-ranging beyond Eastern Brazil, through eastern Paraguay and the Misiones nucleus (Argentina), reaching the eastern Andes of Peru and Bolivia via Mato Grosso, and is a clear example of the Pleistocene Arc distribution pattern described by Prado & Gibbs (1993).

Pilosocereus catingicola subsp. salvadorensis appears to be the only cactus that is frequently found in both restinga and true caatinga (Map 13). It also occurs as a small population in dry rocky vegetation near the summit of the Serra da Itabaiana, Sergipe, which rises out of the Mata atlântica. While its range is primarily littoral, from Salvador (BA) northwards along the coast erraticly to Rio Grande do Norte, it is also a significant component in caatinga and similar vegetation of the rather dry climate characteristic of the lower parts of the Rio São Francisco’s drainage, from the southern foot of the Serra Negra (PE) and the Raso da Catarina (BA) eastwards, through northern Sergipe and southern Alagoas. (P. catingicola subsp. catingicola is endemic to the caatinga-agreste of E and NE Bahia and other members of this small species-group are P. azulensis, from agreste of NE Minas Gerais, and P. arrabidae, restricted to the coastal restinga from S Bahia southwards.)

Map 13 (next page). Distribution pattern 1b, represented by Pilosocereus catingicola subsp. salvadorensis. Eastern Brazil. See Map 31B for distribution of P. catingicola subsp. catingicola.
2. **Humid/subhumid, evergreen/semi-evergreen forest, including Mata atlântica, restinga, mata de neblina, mata de brejo, agreste in part etc.** (Map 10, east of line C–D; summary in Map 14A) (41 taxa; c. 25% of total)

As might be expected, the high proportion of epiphytic taxa in this category means that there are fewer endemics in this part of the core area of Eastern Brazil in comparison with Area Nos. 3 & 4 (*caatingas / campos rupestres*). Nevertheless, in Eastern Brazil this vegetation type is characterised by some distinctive and widespread taxa (eg. the endemic *Rhipsalis paradoxa* subsp. *septentrionalis*, Map 14C) and there are some interesting disjunctions of non-endemic taxa. In its northern parts, north of the Rio Paraguacu (BA), the *Mata atlântica* becomes a generally rather narrow coastal band, of which the more humid phases sometimes reappear further inland on higher ground as isolated stands of *mata de brejo*. These are located at or near the limit with Area No. 3 (*caatingas*), or actually within it, west of the line on Map 10, but are assigned to Area No. 2 (see Maps 14B & 15A–15C).

It should also be re-emphasized that Area No. 2 includes extensive zones receiving less than 1000–1250 mm of rain/year (see map ‘isoietas anuais 1914–1938’ in Azevedo 1972; Nimer 1973: 40, fig. 18), such as that located between eastern Minas Gerais, central & western Espírito Santo (Rio Doce drainage) and northern Rio de Janeiro, at less than 1000 metres altitude (Maps 16A–16D). Although this particular region includes all 5 representatives (4 endemic) of *Coleocephalocereus* subg. *Coleocephalocereus* (the two other subgenera are restricted to the *caatingas*, Area No. 3), it clearly belongs to the *Mata atlântica* in view of the widespread presence of *Pereskia aculeata*, a species characteristic of the *Mata atlântica* and its ecotone with the *caatinga* (the *agreste*), but not found in the *caatinga* proper.

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Maps 14A–14D (next page). (A) E Brazilian cacti restricted to *Mata atlântica* (incl. *brejo* forest); distribution pattern 2a, represented by (B) *Pereskia aculeata* [o] and *P. grandifolia* subsp. *grandifolia* [●], excl. cult. records, (C) *Rhipsalis floccosa* subsp. *floccosa* [●] and *R. paradoxa* subsp. *septentrionalis* [o] and (D) *Cereus fernambucensis* subsp. *fernambucensis*. E Brazil (C core area).
(Map 14B). It also lacks any of the typical taxa from Area No. 3, such as Tacinga, *Pseudoacanthocereus*, *Cereus jamacaru* etc., and instead is characterized by vicariant subspecies of widespread *Mata atlântica* species, such as *Pereskia grandifolia* subsp. *violacea* and *Cereus fernambucensis* subsp. *sericifer*. However, its lower rainfall appears to interrupt the ranges of various species characteristic of more humid phases of the *Mata atlântica* (eg. *Lepismium cruciforme*, *Rhipsalis floccosa*, *R. oblonga*, *Hatiora salicornioides*) and sites of high diversity and endemism of Rhipsalideae are thus restricted to the relatively small areas of much wetter habitats in southern Espírito Santo (eg. Serra do Caparaó, Domingos Martins, Santa Teresa), which are effectively isolated from the stronghold of this group further southwest, in the mountains of Rio de Janeiro etc. Such isolation can also be used to explain the morphological divergence of the northern and southern taxa now recognized in the widespread species, *Rhipsalis paradoxa*, the southernmost record for subsp. *septentrionalis* (at Domingos Martins, ES) being separated by some 500 km from the nearest of subsp. *paradoxa* (near Parati, Rio de Janeiro).

2a. Widespread taxa and those from SE Brazil or beyond with disjunct occurrences in brejo forests of NE Brazil (8 taxa, Maps 14B–15B)


*Cereus fernambucensis* subsp. *fernambucensis*.

*Pereskia aculeata* is a scrambling shrub or semi-liana with a bimodal distribution in the E Caribbean / N South America (to Guyana) and SE South America (Leuenberger 1986). It inhabits scrubby restinga vegetation and gneissic outcrops of the *Mata atlântica*, reaching the edge of drier vegetation in the agrestes of eastern Bahia and adjacent Minas Gerais, as
well as being found in the drier parts of subdivision No. 2d(i), which is generally avoided by other taxa included here. *Rhipsalis paradoxa* is a typical *Mata atlântica* species, its apparently rare but widespread subsp. *septentrionalis* replacing the southern-ranging subsp. *paradoxa* (south-western Rio de Janeiro to Southern Brazil) in Minas Gerais, Espírito Santo, Bahia and Pernambuco. The range of *R. floccosa* subsp. *floccosa* is similar (Map 14C), but it is much more frequent and ranges further inland in SE Brazil, beyond the western limits of the area considered here (it is replaced by subsp. *pulvinigera* in southern Espírito Santo, cent.-southern Minas Gerais, the mountains of Rio de Janeiro, coastal São Paulo and Southern Brazil).

*Lepismium cruciforme, Rhipsalis crispata* and *R. cereuscula* are Rhipsalideae whose range in NE Brazil is restricted to *brejo* forest (Maps 10, 15A/15B), where all three reach their north-eastern limits of distribution in Pernambuco. They are mostly of more frequent occurrence in SE Brazil and two range much further in a south-westerly direction, *R. cereuscula* attaining Argentina and central Bolivia. Of these, *R. crispata* is a remarkable and interesting example of disjunction between subhumid *restinga* of eastern Rio de Janeiro (from near the state capital to Cabo Frio), forests of the planalto of inner São Paulo and *brejo* forest rising out of the *caatinga-agreste* in eastern Pernambuco.

Populations of taxa in Area category No. 2a are mostly under considerable threat in North-eastern Brazil due to the destruction of their forest habitats, which, in some instances, is the most probable explanation for the apparently extreme disjunctions in their distribution patterns.

Maps 15A–15D (next page). Distribution pattern 2a, showing occurrence in *mata de brejo* in the Nordeste, represented by (A) *Lepismium cruciforme*, and (B) *Rhipsalis crispata* [■] and *R. cereuscula* [○]; pattern 2b, represented by (C) *R. baccifera* subsp. *baccifera* [●] and *Cereus insularis* [★, Fernando de Noronha, Atlantic Ocean]; and pattern 2c: (D) *Melocactus violaceus* subsp. *margaritaceus*. Eastern Brazil (A, B & D core area).
2b. Ranging mainly to the north of the core area (2 taxa, Map 15C)

**Rhipsalis baccifera** subsp. **baccifera**, **Cereus insularis**.

In terms of Cactaceae, *Rhipsalis baccifera* subsp. *baccifera* potentially marks the limits of Amazonian floristic influence, or past expansions of its flora (cf. Oliveira-Filho & Ratter 1995: 144). It is the only member of the large tribe Rhipsalideae recorded from the northern third of E Brazil. The *Cereus* is an endemic of the Atlantic archipelago of Fernando de Noronha and is a very close ally of *C. fernambucensis* (Map 14D) — an argument against the referral of these islands to the caatingas dominion by Andrade-Lima (1981).

2c. **Restingas etc. between Alagoas and Salvador, Bahia** (Map 15D)

**Melocactus violaceus** subsp. **margaritaceus**‡.

This taxon is the cactus representative amongst other endemics known from the extensive coastal sand-dunes that begin north of Salvador, Bahia (cf. Harley 1988: 100–101) and also occurs in restinga-like vegetation at up to 400 metres elevation on the eastern slopes of the Serra da Itabaiana, Sergipe. It is morphologically very similar to *M. violaceus* subsp. *ritteri* from Area category No. 3d(i).

2d. **Southern subhumid and perhumid forest** (SE Bahia southwards) (30 taxa):

2d(i). **Taxa characteristic of less humid, seasonally dry habitats, especially gneiss/granite inselbergs below 1000 metres altitude** (8 taxa, Maps 16A–16D)

**Pereskia grandifolia** subsp. **violacea**‡, **Cereus fernambucensis** subsp. **sericifer**, **Pilosocereus brasiliensis** subsp. **ruschianus**‡, **Coleocephalocereus buxbaumianus**‡ (2 subspecies), **C. fluminensis** (2 subsp.: subsp. **decumbens**‡), **C. pluricostatus**‡.

The 5 taxa (4 endemic) of **Coleocephalocereus** subg. **Coleocephalocereus**, plus the quasi-endemic **Cereus fernambucensis** subsp. **sericifer** (which ranges only a little beyond the
southern limit of 22°S), have extensive distributions in the drainage basins of the Rios Mucuri (MG/BA), Doce (MG/ES) and Paraíba do Sul (MG/RJ), with Co. buxbaumanianus subsp. flavisetus reaching westwards to the watershed between the Rio Grande and Rio São Francisco (MG). These six, plus the more northerly-ranging Pilosocereus brasiliensis subsp. ruschianus (Map 16A), are characteristic inhabitants of this region’s abundant, smooth, gneiss/granite inselbergs, which do not retain much water or permit the accumulation of soil and are otherwise home mainly to certain bromeliads and specialized bulbs, besides annual herbs and other, more wide-ranging cacti (eg. Pereskia aculeata, Hylocereus setaceus). Pereskia grandifolia subsp. violacea is an endemic plant with a similar distribution area, but not always associated with inselbergs and occasionally recorded above 1000 metres altitude at the western limits of the Area (Map 16A). It may be specifically distinct and represents the basal element of the P. GRANDIFOLIA Group within Eastern Brazil (see Chapter 3, Fig. 2).

2d(ii). Taxa from more humid habitats (22 taxa, Maps 17A–18D)


Of those included here, 10 are Rhipsalideae with the major part of their range outside the core area, ie. in South-eastern Brazil, or further afield, and are not, so to speak, ‘typical’

Maps 16A–16D (next page). Distribution pattern 2d(i), represented by (A) Pereskia grandifolia subsp. violacea [●], excluding presumed cultivated records, and Pilosocereus brasiliensis subsp. ruschianus [¤], (B) Cereus fernambucensis subsp. sericifer, (C) Coleocephalocereus fluminensis subsp. fluminensis [¤] & subsp. decumbens [■] and (D) C. buxbaumanianus subsp. buxbaumanianus [▲] & subsp. flavisetus [▲] and C. pluricostatus [★★]. Eastern Brazil (core area).
members of the cactus flora of Eastern Brazil. Only 3 taxa in this category are endemic and are presumed to have very restricted ranges (S Espírito Santo). This tribe has a considerable number of species endemic to the region comprising E São Paulo, SE Minas Gerais, S Espírito Santo and Rio de Janeiro, where its centre of diversity is located. The non-endemic *Rhipsalis oblonga* (Map 17C) appears to be restricted to the 'Hiléia Baiana' or Bahian phase of the Atlantic forest, but this could reflect lack of collecting, eg. in Espírito Santo (where there is one doubtful record from Lützelburg). Its occurrence seems to be linked to regions of very high rainfall (ie. 1750 mm/year or more). It reappears to the west of the city of Rio de Janeiro, reaching coastal São Paulo and represents an ecological vicariant of *R. crispata* (see No. 2a, above). *Pilosocereus arrabidae* and *P. brasiliensis* subsp. *brasiliensis* (Map 17D) are restinga taxa almost endemic to the area, reaching southwards to the city of Rio de Janeiro. *Opuntia monacantha*, a widely distributed species from SE South America and at its northern limit in Eastern Brazil, has a mainly littoral range in South-eastern and Southern Brazil (coast of S Espírito Santo south-westwards), but has also been recorded from *campo rupestre* dunes near Diamantina and Pedra Menina (Mun. Rio Vermelho), central-eastern Minas Gerais, at c. 1000 metres altitude (Map 17A), which is considered atypical here. It is also known from a few inland sites in São Paulo state (near Lorena, Piracicaba and Congonhas).

Floristic links provided by cactus taxa widespread in, or characteristic of, the East Brazilian Humid/subhumid Atlantic forest are less diverse than those of the following major area, but are, nevertheless, worthy of examination (see Table 4.2). As would be expected these links are mainly with the forests of South-eastern and Southern Brazil, but there are also clear Floristic links provided by cactus taxa widespread in, or characteristic of, the East Brazilian Humid/subhumid Atlantic forest are less diverse than those of the following major area, but are, nevertheless, worthy of examination (see Table 4.2). As would be expected these links are mainly with the forests of South-eastern and Southern Brazil, but there are also clear

Maps 17A–17D (next page). Distribution pattern 2d(ii), represented by (A) *Opuntia monacantha* excluding cultivated records, (B) *Lepismium houlletianum* [□] and *L. warmingianum* [●], (C) *Rhipsalis oblonga* [●] and *R. elliptica* [□], and (D) *Pilosocereus arrabidae* [●] and *P. brasiliensis* subsp. *brasiliensis* [★]. Eastern Brazil (core area).
connexions with the humid forests of the Eastern Andes and in one case with the Caribbean and North-eastern South America (*Pereskia aculeata*). According to recent molecular phylogenies (Wallace 1995: 9; Butterworth, ined.), *Pereskia grandifolia s.l.* is indeed basal to the *caatinga* species-pair, *P. bahiensis / P. stenantha*, supporting the hypothesis by Rizzini (1979) that part of the *caatinga* flora has its origins in the *Mata atlântica* (Prado 1991: 230).

The most diverse tribe of Cactaceae in this major area are the epiphytic Rhipsalideae, but all of these appear to have a southern or south-western origin (*Rhipsalis baccifera*, sens. *lat.*, provides a connexion with the Amazon region and beyond, but is also linked with the south-western floras through its subsp. *shaferi*). Thus, the Cactaceae of the *Mata atlântica* can be said to show little direct floristic affinity with those of the Amazonian rainforest.

<table>
<thead>
<tr>
<th>E Brazilian humid/subhumid forest species</th>
<th>Other area(s) and linking taxon/taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pereskia aculeata</em></td>
<td>a) Caribbean &amp; NE South America / <em>P. aculeata</em>. b) Andes / other members of <em>P. ACULEATA Group</em>.</td>
</tr>
<tr>
<td><em>Rhipsalis baccifera</em> subsp. <em>hileiabaiana</em> (1 record from Chapada Diamantina, Bahia)</td>
<td>Caribbean, N South America &amp; Amazonia / <em>R. b. ssp. baccifera</em></td>
</tr>
<tr>
<td><em>Lepismium cruciforme</em></td>
<td>E Andes (Bolivia) / <em>L. incachacanum</em> (sister sp.)</td>
</tr>
<tr>
<td><em>Rhipsalis cereuscula</em></td>
<td>E Andes (Bolivia) &amp; SE South America / <em>ibidem</em></td>
</tr>
<tr>
<td><em>Coleocephalocereus</em> subg. <em>Coleocephalocereus</em></td>
<td>E Brazilian Southern <em>caatingas</em> / C. subg. <em>Simplex</em> &amp; subg. <em>Buiningia</em></td>
</tr>
<tr>
<td><em>Pereskia grandifolia</em> (s.l.)</td>
<td>E Brazilian <em>caatingas</em> and dry forests of the Piedmonte and Misiones nuclei / <em>P. bahiensis, P. stenantha, P. sacharosa, P. nemorosa</em></td>
</tr>
<tr>
<td><em>Rhipsalis paradoxa</em> (s.l.), <em>Hatiora salicornioides, Cereus fernambucensis</em> (s.l.)</td>
<td>SE &amp; S Brazilian <em>Mata atlântica</em> &amp; restinga / <em>ibidem</em></td>
</tr>
</tbody>
</table>

Table 4.2. Significant floristic links provided by cactus taxa between the East Brazilian humid / subhumid forest and other areas (excl. species known only from margins of category 2d or which range only slightly beyond the core area). For links with the East Brazilian Highlands, see Table 4.6.

Maps 18A–18D (next page). Distribution pattern 2d(ii), represented by (A) *Rhipsalis teres* [●] and *R. pilocarpa* [c], (B) *R. floccosa* subsp. *pulvinigera*, (C) *R. juengeri* [★], *R. clavata* [●] and records of uncertain identity from this pair of taxa etc. [?], and (D) *Schlumbergera kautskyi* [●], *S. microsphaerica* [□] and *S. opuntioides* [▲]. Eastern Brazil (core area).
3. Caatingas & Northern campos rupestres (& included cerrados) / caatinga-agreste / mata seca (Map 10, north of line A-D) (83 taxa; c. 51.5% of total)

This major area category includes all that considered here as part of the caatingas dominion in Eastern Brazil (cf. Andrade-Lima 1981), plus the following:— those areas referred to caatinga to the west of the Rio São Francisco (Andrade-Lima 1975); the areas of campo rupestre and cerrado from the northern part of the East Brazilian Highlands (ie. the northern parts of the Serra do Espinhaço and Chapada Diamantina, and their extensions eastwards); ecotones at the southern limits of the caatinga and mata seca in northern Minas Gerais; and part of the agreste or ecotonal vegetation between the caatinga and Mata atlântica in the east. (Much of the agreste has now been so severely altered or destroyed that its cactus flora is mainly to be inferred from a few herbarium records and scrappy extant remnants of what was once an extensive vegetation zone.) In addition, to the west and south of the caatinga proper, in western Bahia, south-western Piauí and central Minas Gerais (Rio São Francisco drainage), a few taxa characteristic of this area occasionally appear on dry rock outcrops, eg. Melocactus zehntneri, Leocereus bahiensis, Pilosocereus flavipulvinatus and Cereus jamacaru subsp. calcirupicola. These outcrops are located inside Area No. 4, but represent disjunct extensions from Area No. 3. The same applies to rare occurrences of Cereus jamacaru and Pilosocereus pentaedrophorus in the Mata atlântica to the east (Area No. 2). A cactus-based approximation to the caatingas area is offered in Map 40 (p. 336).

Area No. 3, as delimited here, makes good sense on the basis of endemism of Cactaceae, as the following list hopefully makes clear. At generic level the endemics are: Facheiroa (3), Stephanocereus (2), Espostoopsis (1) and Leocereus (1), with Arrojadoa (4 spp.) almost endemic. Then there are infrageneric taxa in Pilosocereus, Micranthocereus, Coleocephalocereus and Melocactus. Facheiroa and Espostoopsis are typical caatinga elements. However, the diverse species of Arrojadoa and Stephanocereus are equally divided
between the *caatingas* and Northern *campos rupestres* and this pair of genera is believed to have common ancestry with *Cipocereus*, a more southerly ranging, endemic genus from Minas Gerais, which is associated with *campo rupestre* and is without other close allies (Taylor & Zappi 1996). This indicates an autochthonous E Brazilian source for some of the most characteristic elements of the *caatinga*’s cactus flora, such as *A. penicillata*, *A. rhodantha* and *S. leucostele*, and this is also true of the majority of species in the largest *caatinga* genera, *Pilosocereus* and *Melocactus* (Zappi 1994, Taylor 1991a). *Micranthocereus* subg. *Austrocephalocereus* is a Northern *campo rupestre* endemic.

The southernmost records of cactus species that can be considered as typical elements of the *Caatinga* / Northern *campo rupestre* flora are, west to east:— *Pilosocereus pachycladus* (near Francisco Dumont, MG), *Melocactus concinnus* (Peixe Cru, Mun. Turmalina, MG — Map 31C), *M. bahiensis* (Mercês, Diamantina, MG — Map 32D) and *Brasilicereus phaeacanthus* (near Padre Paraíso, MG — Map 24B). However, this is not intended to suggest that all of these species are actually found in *caatinga* vegetation at these southern sites. The southern limit of *caatinga* vegetation proper is uncertain and depends on one’s definition but, in the Rio São Francisco valley, deciduous thorn forest including cacti, such as *Pereskia stenantha* (Map 26A), *Pilosocereus pachycladus* and *Arrojadoa rhodantha* (Map 21A), extends southwards at least as far as the municípios of Varzelândia, Janaúba and Porteirinha, MG (c. 15°40’S). South of there cacti interpreted as belonging to the *caatingas* are found only on edaphically dry, exposed rock outcrops, mostly of limestone (Bambuí) and gneiss/granite, and are represented by taxa from category Nos. 3a & 3b, below. The southernmost occurrences on such outcrops are those of *Tacinga saxatilis*, *Cereus jamacaru* subsp. *calcirupicola* and *Pilosocereus floccosus* subsp. *floccosus*, the latter two (Maps 27A/27B) inhabiting *mata seca* as far south as the region of Lagoa Santa (c. 19°40’S). *Arrojadoa dinae*, from the Northern *campo rupestre* flora, has its southern limit at c. 17°30’S.
Further east, crossing the Serra do Espinhaco, the south-easternmost caatingas are isolated in the middle section of the Rio Jequitinhonha valley between Mun. Jacinto (16°10'S) and Mun. Araçuaí (16°50'S), as determined by the ranges of species representative of category Nos. 3a & 3d(ii) (Maps 33A-D). However, as noted above under Area No. 2 (Mata Atlântica), cactus-rich vegetation on gneiss/granite outcrops receiving less than 1000–1250 mm of rain per year continues further to the south into eastern Minas Gerais, western Espírito Santo and north-eastern Rio de Janeiro (Rio Doce valley and adjacent drainage systems to the north and south), where Coleocephalocereus is the dominant genus (Maps 16A–16D).

Floristic connexions between this great caatinga region of Eastern Brazil and elsewhere in South America, judged solely on the basis of Cactaceae, are complex, including links with northern South America and the Caribbean, the central Andes (S Ecuador & Peru), the western Chaco (only one clear link) and other parts of SE South America (Table 4.3).

<table>
<thead>
<tr>
<th>E Brazilian caatinga-agreste taxon</th>
<th>Phytogeographical link: geography / taxon</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pereskia aureiflora</td>
<td>Venezuela &amp; N Colombia / ( P. ) guamacho</td>
</tr>
<tr>
<td>Pseudoacanthocereus brasiliensis</td>
<td>N Venezuela &amp; N Colombia / ( P. ) sicariguensis</td>
</tr>
<tr>
<td>Cereus jamacaru (both subspecies ranging beyond the limits of typical caatinga-agreste)</td>
<td>S Caribbean, N South America &amp; Amazonia / ( C. ) hexagonus</td>
</tr>
<tr>
<td>Espostoopsis</td>
<td>Central Andes of Ecuador &amp; Peru / Espostoa, sens. str.</td>
</tr>
<tr>
<td>Facheiroa</td>
<td>E Andes / ( Yungasocereus ) etc?</td>
</tr>
<tr>
<td>Quiabentia zehntneri</td>
<td>W Chaco &amp; margins / ( Q. ) verticillata (syn. ( Q. ) pflanzii etc.)</td>
</tr>
<tr>
<td>Harrisia adscendens</td>
<td>E Andes, SE South America, Caribbean / Harrisia subg. ( Eriocereus ) (especially ( H. ) pomanensis) &amp; subg. Harrisia</td>
</tr>
</tbody>
</table>

Table 4.3. Long distance phytogeographical links between the caatinga-agreste and other South American cactus floras.

Cactaceae characteristic of campo rupestre vegetation and endemic to this Area are about 45% fewer than those endemic to the South-eastern campos rupestres (Area No. 4c below), although the northern area is actually much greater in extent (cf. Maps 10 & 41).

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The geography of cactus taxa within this large Area is not at all random and a series of well-defined patterns of distribution and endemism can be recognized:–

3a. Widespread from east to west etc. (23 taxa):

All the taxa listed here are primarily *caatinga* elements. They represent less than 28% of the taxa included in Area 3, the remainder falling into three parallel geographical and/or ecological categories (see Nos. 3b/c/d).

3a(i). Widespread north to south (5 taxa, Map 19)

*Tacinga inamoena*, *Cereus albicaulis*, *C. jamacaru* subsp. *jamacaru*, *Pilosocereus gounellei* subsp. *gounellei*, *Melocactus zehntneri*.

The taxa included here are amongst the cacti that are most characteristic of the *caatinga* and *agreste* of North-eastern Brazil, *T. inamoena* also ascending into the *campos rupestres*. *Cereus jamacaru* ranges further than any of the others included here, reaching W Maranhão, entering the Atlantic forest in NE Brazil and penetrating the South-eastern *campos rupestres* as far as the region of Diamantina, MG. The distribution of the endemic *C. albicaulis* is somewhat peculiar, since it occurs mainly in *caatinga* associated with the Serra do Espinhaço and Chapada Diamantina in the southern half of its range, but expands into sandy areas in SE Piauí, NW & NE Bahia, S Pernambuco etc., finally reaching the Serra da Ibiapaba (N Piauí & NW Ceará). Its sister species is *C. mirabella*, with a complementary range west and south (Map 34), and is one of the few cacti restricted to *cerrado* (eastern part).

Map 19 (next page). Distribution pattern 3a(i), represented by *Tacinga inamoena* [★, W, S and E records only], *Cereus albicaulis* [○], *C. jamacaru* subsp. *jamacaru* [▲, W, S and E records only], *Pilosocereus gounellei* subsp. *gounellei* [Δ] and *Melocactus zehntneri* [■]. Eastern Brazil. NB. In this and some subsequent maps, if two different taxa are recorded from the same site, symbols have been moved slightly away from their true positions in order that they can be distinguished.
Map 20. Distribution pattern 3a(ii): 

- Pilosocereus flavipulvinatus [□]
- P. pachycladus subsp. pernambucoensis [●]
- P. piauhyensis [▲]
- P. chrysostele [★]
3a(ii). Northern caatingas (S Piauí, N Bahia, Alagoas & Pernambuco northwards) (5 taxa, Maps 20 & 21A)

Pilosocereus flavipulvinatus, P. pachycladus subsp. pernambucoensis, P. piauhyensis, P. chrysostele, Discocactus bahiensis.

The above taxa are amongst the few caatinga elements with a significant part of their range north of the core area of Eastern Brazil. P. flavipulvinatus, which ranges beyond the limit of the caatingas as far as Carolina (W Maranhão), is the sister taxon of the P. pentaedrophorus / P. glaucochrous species pair from Nos. 3c(ii) & 3d(i). P. chrysostele and P. piauhyensis are relatives of the southern endemic, P. multicostatus (see 3d(ii) below).

3a(iii). Central-Southern caatingas from S Piauí, S Ceará, S Paraíba southwards (13 taxa):

3a(iiiia). Wide-ranging in the central-southern caatingas (7 taxa, Maps 21B–22D):

Tacinga funalis†, Arrojadoa penicillata†, A. rhodantha†, Pilosocereus tuberculatus†, P. pachycladus subsp. pachycladus†, Harrisia adscendens†, Leocereus bahiensis† [extends somewhat beyond the caatingas in W Bahia].

Except for Leocereus bahiensis and Pilosocereus pachycladus subsp. pachycladus, which have more western distributions beginning in the Chapada Diamantina (Maps 21B/21C), all of the above taxa are restricted to the caatinga and, together with those listed for category Nos. 3a(i)&(ii), are the most important cactus species of the caatingas generally. Although falling reasonably within the widespread category defined here, in detail the distribution of Leocereus is unlike that of any other and is hard to characterize in terms of its preferred vegetation type, being a plant of ecotones between mostly higher altitude caatinga.

Maps 21A–21D (next page). Distribution pattern 3a(ii) represented by (A) Discocactus bahiensis (?) = poorly localised records; and 3a(iiiia), represented by (B) Pilosocereus pachycladus subsp. pachycladus, (C) Leocereus bahiensis and (D) Harrisia adscendens. E Brazil (B–D core area).
Maps 22A–22D. Distribution pattern 3a(iii)a, represented by (A) Tacinga funalis, (B) Arrojadoa penicillata, (C) Arrojadoa rhodantha and (D) Pilosocereus tuberculatus. E Brazil (core area).
cerrado and campo rupestre. *Pilosocereus tuberculatus* is perhaps an example of an erratically distributed relict species (see Supplement 1), whose range (Map 22D) fits neatly inside Köppen’s semi-arid climatic zone (Cavalcanti Bernardes 1951). Like *Cereus albicaulis*, it is found on light sandy substrates or dunes (referred to the Cipó soil series) and both species appear to be characteristic of a distinct type of **caatinga** identified as no. 5 by Andrade-Lima (1981: 159). The disjunct occurrences of *Tacinga funalis, Arrojadoa penicillata* and *Harrisia ascendens* in sand-dunes west of the Rio São Francisco (Maps 21D, 22A & 22B) could represent range extensions during the drier periods of the Pleistocene, when the river’s flow is hypothesized to have ceased (Tricart 1985: 210) and with it a potential barrier to dispersal.

3a(iiiib). *Bahian caatingas, surrounding the Chapada Diamantina* (2 taxa, Map 23)

**Pereskia bahiensis†, Stephanocereus** (subg. **Stephanocereus†**) **leucostele‡.**

Both species are widespread and typical elements of the Bahian **caatingas** located around all sides of the East Brazilian Highlands, including the Chapada de Maracás. On present knowledge, they do not range southwards into Minas Gerais or, apparently, northwards into Pernambuco or Piauí. They also avoid the drier NW and NE parts of Bahia.

3a(iiiic). *Southern caatingas (Cent./S Bahia & N Minas Gerais)* (4 taxa, Maps 24A–24D)

**Pereskia aureiflora‡, Brasilicereus phaeacanthus‡, Coleocephalocereus** (subg. **Simplex‡**) **goebelianus‡, Melocactus ernestii** subsp. **longicarpus‡.**

These four species are typical elements on, or associated with gneiss/granite outcrops (inselbergs) or derived substrates in the southernmost **caatingas**, outside of the semi-arid climatic zone as defined by Köppen (Cavalcanti Bernardes 1951). *Coleocephalocereus goebelianus* and *Melocactus ernestii* subsp. **longicarpus** are absent from NE Minas Gerais (east of the Serra do Espinhaço), where they are replaced by sister taxa (see category Nos. 3d(ii/iii) below). *Brasilicereus phaeacanthus* has its much rarer sister species in No. 4c(iiia).
Map 23. Distribution pattern 3a(iib), represented by *Pereskia bahiensis* [●] and *Stephanocereus leucostele* [□]. Eastern Brazil (core area).
3b. Caatingas (and mata seca on southern limestone outcrops) in the middle and upper drainage of the Rio São Francisco (cent. Minas Gerais to W & cent.-N Bahia / SW Pernambuco) and adjacent SE Piauí (20 taxa)

All except 2 of the taxa listed below are endemic to this region (11 are endemic to Bahia alone), giving it a very characteristic cactus flora and suggesting that it may have been a refugium for such drought resistant taxa during past periods of greater humidity and/or cooler conditions. It should be noted that all 3 species of Facheiroa are endemic here, with one in each of the subdivisions (i)–(iii). The non-endemic Tacinga saxatilis subsp. saxatilis, so far as is known, extends beyond the core area only to NW Minas Gerais. Other floristic connexions in terms of sister species include a link with the western Chaco and its margins (ie. Quiabentia) and those with the immediately adjacent floras of NW Minas Gerais, Goiás and S Tocantins, via vicariant sister taxa or potential sister taxa of Pilosocereus floccosus subsp. floccosus, P. densiareolatus and Micranthocereus dolichospermaticus (see Supplement 1 for details). These vicariants could represent evidence of past caatinga expansions westwards, as discussed by Prado (1991). Pereskia stenantha and Pilosocereus gounellei subsp. zehntneri replace their respective allies, Pe. bahiensis and Pil. g. subsp. gounellei, which have extensive ranges to the north and east (Area category No. 3a). Both of these endemics are relatively widespread, but many of the others are restricted either to central-northern or S Bahia (south or east of the curving course of the Rio São Francisco), or to western Bahia and northern Minas Gerais on both sides of the São Francisco on Bambuí limestone, eg. Pilosocereus densiareolatus and Melocactus levitestatus (cf. Andrade-Lima 1977). Most of the endemics are found only on one of various rock types, eg. the widespread

Maps 24A–24D (next page). Distribution pattern 3a(iiic), represented by (A) Pereskia aureiflora, (B) Brasilicereus phaeacanthus, (C) Coleocephalocereus goebelianus and (D) Melocactus ernestii subsp. longicarpus. Eastern Brazil (core area).
limestone (numerous taxa, including two endemic species-groups in *Melocactus*) or
gneiss/granite (*Melocactus deinacanthus*, a taxonomically isolated species), but some, eg.
*Quiabentia zehntneri* and *Pilosocereus gounellei* subsp. *zehntneri*, are less specific,
inhabiting gneiss/granite or sandstones also. West of the river on soils derived from limestone
the cactus flora is rather different, since most of the widespread *caatinga* species (from
category Nos. 3a) are lacking, the chief exceptions being *Cereus jamacaru*,
*Pilosocereus pachycladus* and *Arrojadoa rhodantha*.

The following subdivisions are recognized, noting that Nos. 3b(ii)/(iii) conform to the
limits between Köppen's semi-arid and hot/humid climates (Cavalcanti Bernardes 1951):

3b(i). *Widespread in the caatingas of the middle part of the Rio São Francisco drainage* (2
taxa, Maps 25A & 25B)

*Pilosocereus gounellei* subsp. *zehntneri*, *Facheiroa squamosa*.

*Facheiroa squamosa* is restricted to crystalline rocks or sandstones, whereas its
south-western congener, *F. cephaliomelana* (see 3b(iii)), occurs only on limestone, and a
third, more poorly understood species, *F. ulei*, is found on non-calcareous rocks in central-
northern Bahia (see below). The range of both taxa included here is somewhat disjunct
between their northern and southern occurrences (subdivisions 3b(ii) and 3b(iii)), which
probably in part reflects a lack of suitable habitat, there being extensive intervening areas of

Maps 25A–25D (next page). Distribution pattern 3b(i), represented by (A) *Pilosocereus gounellei*
subsp. *zehntneri* and (B) *Facheiroa squamosa*; and pattern 3b(ii), represented by (C) *Melocactus azureus* subsp. *azureus* [o] & subsp. *ferreophilus* [■] and *M. pachyacanthus* subsp. *pachyacanthus*
[●] & subsp. *viridis* [●] and (D) *Facheiroa ulei* [o] and *Discocactus zehntneri* subsp. *zehntneri*
[■]. Eastern Brazil (core area).
3b(ii). *Caatingas of central-northern Bahia* (6 taxa, Maps 25C & 25D)

*Melocactus azureus* (2 subsp.)†, *M. pachyacanthus* (2 subsp.)†, *Facheiroa ulei*†,

*Discocactus zehntneri* subsp. *zehntneri*.

The *Melocactus* spp. included here, which represent a species-group endemic to this area, are found on outcrops of limestone in valleys draining into the Rio São Francisco system (Rio Jacaré & Rio Salitre) and dissecting the Chapada Diamantina area (cf. Area No. 3c), but clearly belong to this subdivision, being absent from such outcrops further east. The latter comment also applies to *Facheiroa ulei*, which occurs on sandstones and similar substrates and appears to interrupt the range of its more widespread congener, *F. squamosa*.

Most of the taxa included here are threatened with extinction due to extensive modification of their habitat by agriculture and the great Represa de Sobradinho dam-lake.

3b(iii). *Southern caatingas and other dry forests (on islands of limestone) of the Rio São Francisco / Rio das Velhas drainage (western & central-southern Bahia to central Minas Gerais)* (12 taxa, Maps 26A–27D):


Most of the species included here are rock-dwellers. The two *Melocactus* each represent a monotypic species-group endemic to this area — *M. deinacanthus* being restricted

Maps 26A–26D (next page). Distribution pattern 3b(iii), represented by (A) *Pereskia stenantha*, (B) *Quiabentia zehntneri*, (C) *Tacinga saxatilis* subsp. *saxatilis* [c] & subsp. *estevesii* [w] and (D) *Pilosocereus densiareolatus*. Eastern Brazil (core area).
to an isolated outcrop of gneiss. The most widespread taxon is *Cereus jamacaru* subsp. *calcirupicola*, which is found in the middle and upper drainage of the Rio São Francisco, in both the south-western caatingas and on limestone islands in cerrado further south, reaching the region immediately north of Belo Horizonte (Map 27A). It occasionally occurs on substrates other than limestone, straying into the South-eastern campos rupestres in the region of the Serra do Cabral. It ranges beyond the core area westwards into Central-western Brazil (Goiás and perhaps further west and north), mainly on calcareous outcrops. In the southern part of its range it is often found in association with *Pilosocereus floccosus* subsp. *floccosus* (Map 27B), a taxon normally thought of as associated with the campos rupestres, but actually a plant of *mata seca*.

3c. Northern campos rupestres, East Brazilian Highlands (Chapada Diamantina and northern part of Serra do Espinhaço, BA/MG — see Map 10) (17 taxa, Maps 28A–29D)

It should be noted that the term Chapada Diamantina as employed here extends this area somewhat farther northwards than the definition implied in Bandeira (1995), including parts of the municípios of Sento Sé, Umburanas, Campo Formoso and Jacobina, whose highlands are ± continuous with those to the south. All of the taxa included here are endemic to Eastern Brazil and only one has a close link with an extra-Brazilian cactus flora. Included are some morphologically rather unusual cacti, such as the *Stephanocereus* and *Arrojadoa* spp. and *Melocactus paucispinus*, which have evolved specialized habit forms in keeping with their environment and/or pollinators. Despite the availability of suitable...
habitats, it is curious that the genus *Discocactus* is absent from all but the northernmost part of this area (where the *caatinga* has its strongest influence), which is in stark contrast to the ecologically similar Area No. 4c (below), where the genus is well-represented.

In terms of distribution area, the taxa included here display the full spectrum from widespread within either one of the two subdivisions recognized (eg. *Micranthocereus purpureus*, *Arrojadoa dinae* subsp. *dinae*), to those known from single localities (eg. *Micranthocereus streckeri*, *Cipocereus pusilliflorus*), but only the first-listed below are known from both subdivisions. Map 28C shows the ranges of 3 characteristic species: *Pilosocereus glaucochrous*, restricted to ‘*caatinga de altitude*’; *Rhipsalis floccosa* subsp. *oreophila*, found on rocks and as an epiphyte in pockets of perhumid cloud forest (*mata de neblina*), and *Discocactus zehntneri* subsp. *boomianus*, a plant of northern habitats including flat rocks, gravel and sand. The remainder comprise typical *campo rupestre* elements (including ‘*cerrado de altitude*’). *Arrojadoa dinae* has a probable sister-species in NE Goiás.

3c(i). *Chapada Diamantina & Northern Serra do Espinhaço (BA/MG)* (2 taxa)

**Rhipsalis floccosa** subsp. *oreophila*‡, **Melocactus paucispinus**‡.

The distribution of both taxa is rather disjunct on present knowledge, but suggests that they may be expected to occur at other sites where their specific ecological preferences are catered for.

Maps 28A–28D (next page). Distribution pattern 3c, represented by (A) *Cipocereus pusilliflorus* [■] and *Stephanocereus luetzelburgii* [○], (B) *Arrojadoa bahiensis* [■], *A. dinae* subsp. *dinae* [○] & subsp. *eriocaulis* [▲] and *A. sp. nov.* (?) cf. *dinae* (NE Goiás — outside core area) [*], (C) *Rhipsalis floccosa* subsp. *oreophila* [○], *Pilosocereus glaucochrous* [■] and *Discocactus zehntneri* subsp. *boomianus* [▲] and (D) *Melocactus oreas* subsp. *cremnonphilus* [○], *M. paucispinus* [■] and *M. glaucescens* [▲]. Eastern Brazil (core area).
3c(ii). Chapada Diamantina (BA) (9 taxa)

Stephanocereus (subg. Lagenopsis) lutzelburgii†, Arrojadoa bahiensis†, Pilosocereus
glaucocrhrous†, Micranthocereus purpureus†, M. flaviflorus†, M. streckeri†§,
Melocactus oreas subsp. cremnophilus†, M. glaucescens†§, Discocactus zehntneri subsp.
boominianus†.

As can be seen from the above list the Chapada Diamantina has a significant number
of endemic Cactaceae, although it should be noted that all of these are restricted to its eastern
segment, generally east of 42°W. They are mostly allopatric or ecological-vicariant sister taxa
of species from the adjacent caatingas at lower elevations (cf. Pilosocereus pentaedrophorus,
Area No. 3d(i), Stephanocereus leucostele, No. 3a(iv)) or from the campos rupestres further
south (Serra do Espinhaço, S Bahia & Minas Gerais, Areas 3c(iii) & 4c below). S.
lutzelburgii and Micranthocereus purpureus range through most of the area (ie. from Mun.
Jacobina in the north to Mun. Rio de Contas in the south), while Arrojadoa bahiensis is
found only in its southern half. Then, except for the single-site endemic, Micranthocereus
streckeri, the remaining taxa are restricted to the northern part of the area, which
interdigitates with category No. 3b(ii).

3c(iii). Northern Serra do Espinhaço (Bocaiúva MG – Caetité BA) (6 taxa)

Arrojadoa dinae (2 subspp.)†, Cipocereus pusilliflorus†§, Micranthocereus violaci-
florus†, M. albicephalus†, M. polyanthus†.

This mountain region is separated from the broader ranges to its north and south by
areas of only moderate elevation and is itself generally lower, and as a consequence probably

Map 29 (next page). Distribution pattern 3c, represented by Micranthocereus violaciflorus [★], M.
albicephalus [●], M. purpureus [○], M. polyanthus [△], M. flaviflorus [▲] and M. streckeri [†].
drier, being surrounded by *caatinga* on all sides. The flora exists as a complex patchwork of small areas of *campo rupestre* and *cerrado*, and their ecotones with *caatinga*, the latter ascending high up the west-facing slopes. Of the five species listed here the first is the most widespread and ecologically most tolerant, being found on very sandy *cerrado* (where subsp. *eriocaulis* forms well-developed subterranean stem tubers functioning like xylopodia) as well as on more stony *campo rupestre* and *caatinga* ecotone substrates (Map 28B). *Cipocereus pusilliflorus* is the only member of its genus found outside the South-eastern *campos rupestres* of Area category No. 4c and is related to *C. minensis* and *C. bradei* from that area.


All except two of the taxa listed here are currently thought to be endemic to the core area of Eastern Brazil and comparison with category 3b (above) suggests that the East Brazilian Highlands, comprising the Serra do Espinhaço and Chapada Diamantina, have been an important barrier isolating the cactus flora of the Rio São Francisco drainage from that further east. Thus, in the east we have *Pseudoacanthocereus* and *Espostoopsis*, while the genera *Facheiroa* and *Discocactus*, characteristic of the Rio São Francisco valley, are lacking.

Some of the species listed below are elements of the now much depleted part of the *caatinga* biome that grades into the *agreste*, especially *Pseudoacanthocereus brasiliensis*, *Pilosocereus pentaedrophorus* and *P. catingicola*, while others also found partly associated with this transitional vegetation are characteristic of the granitic/gneissic outcrops found in many parts of this region.
3d(ia). *Widespread eastern taxa and those restricted to E/NE Bahia and Paraíba/Pernambuco* (10 taxa, Maps 30A–31D)

*Tacinga palmadora*, Pseudoacanthocereus brasiliensis†, Pilosocereus catingicola subsp. catingicola†, *P. pentaedrophorus* subsp. *pentaedrophorus†*, Melocactus ernestii subsp. ernestii, *M. bahiensis* subsp. *bahiensis†*, *M. lanssensianus*†, *M. concinnus†*, *M. violaceus* subsp. *ritteri†*, Espostoopsis dybowskii†.

Four of the taxa included here — *Tacinga palmadora*, *Pilosocereus pentaedrophorus* subsp. *pentaedrophorus*, *Melocactus ernestii* and *M. bahiensis* subsp. *bahiensis* — are more widespread, extending northwards into Pernambuco or beyond. In contrast *Melocactus violaceus* subsp. *ritteri* is found on isolated areas of quartz sand/gravel on the eastern slope of the Chapada Diamantina at Jacobina and further south at Rui Barbosa (BA), while *M. lanssensianus* is a local, cleistogamous endemic of uncertain status from the region of Garanhuns (PE), which can be associated with other, very similar plants from elsewhere in that state and from neighbouring Paraíba. The distribution of the Bahian endemic, *Espostoopsis*, is markedly disjunct (2 small areas c. 400 km apart) and is presumably indicative of its relict status (Map 31D). *Pseudoacanthocereus brasiliensis* is the only (and at best doubtful) representative of tribe Echinocereeae in Eastern Brazil (Map 31A). It seems to be a plant characteristic of the agrestes or more humid caatingas and, like *Pilosocereus pentaedrophorus*, ranges only within Köppen's hot/humid zone, avoiding the semi-arid climate (cf. Cavalcanti Bernardes 1951). The last-mentioned has recently been reported from the coastal restinga vegetation in NE Bahia (N of Salvador), but is otherwise a typical element of the caatinga-agrestes (Map 30B).

Maps 30A–30D (next page). Distribution pattern 3d(ia), represented by (A) *Tacinga palmadora*, (B) *Pilosocereus pentaedrophorus* subsp. *pentaedrophorus*, (C) *Melocactus ernestii* subsp. *ernestii* (? = reports to be localised/verified) & (D) *M. bahiensis* subsp. *bahiensis*. E Brazil (B/D core area).
3d(ib). Restricted to the E & SE caatingas-agrestes / and associated campos rupestres from the Rio Paraguaçu drainage (BA) southwards (6 taxa, Maps 32A–32D)

Tacinga werneri‡, Pilosocereus pentaedrophorus subsp. robustus‡, Melocactus oreas subsp. oreas‡, M. bahiensis subsp. amethystinus‡, M. conoideus‡§, M. salvadorensis‡.

Tacinga werneri, Pilosocereus pentaedrophorus subsp. robustus and Melocactus bahiensis subsp. amethystinus are southern relatives of taxa in category No. 3d(ia). M. salvadorensis replaces the more widespread M. zehntneri (see No. 3a(i), above) in southern and eastern Bahia (Map 32D), except for a small area to the east of Brumado where they are sympatric.

3d(ii). SE caatingas-agrestes of NE Minas Gerais (Rio Jequitinhonha drainage and watersheds with Rio Pardo and Rio Mucuri) (7 taxa, Maps 33A–33D)

Tacinga braunii‡, Pilosocereus azulensis‡§, P. floccosus subsp. quadricostatus‡, P. magnificus‡, P. multicostatus‡, Coleocephalocereus subg. Buiningia‡ (C. aureus & C. purpureus§).

The cactus flora of this relatively small region is extremely interesting, not only because of the variety of unusual cactus endemics it has, but also for the absence (or only marginal presence) of certain widespread caatinga/agreste Cactaceae, while other 'indicator' species, with which they are normally associated, are present and common (especially those from Nos. 3a & 3d(ia/ib) above). In many cases these absent or marginally present cacti are replaced by vicariant sister taxa or species from the same infrageneric group, eg. Tacinga

Maps 31A–31D (next page). Distribution pattern 3d(ia), represented by taxa with a more restricted range than those in Maps 30A–30D: (A) Pseudoacanthocereus brasiliensis, (B) Pilosocereus catingicola subsp. catingicola, (C) M. lanssensis [△, △ = records of questionable identity], M. concinnus [©] and M. violaceus subsp. ritteri [■] and (D) Espostoopsis dybowskii. Eastern Brazil (core area).
funalis by T. braunii, Pilosocereus pachycladus by P. magnificus, P. catingicola by P. azulensis, and Coleocephalocereus subg. Simplex (C. goebelianus) by C. subg. Buiningia. A particularly good example of this is provided by Pilosocereus pentaedrophorus (3d(ia/ib), above) and its relative P. floccosus subsp. quadricostatus, which are allopatric except in the small zone of contact between these two caatinga areas (Maps 32B/33B), near the borders of the Municípios of Taiobeiras and Águas Vermelhas (see the 'Biomas' map for Minas Gerais in Costa et al. 1998: 21). An instance of a more disjunct distribution pattern is that of the species group to which Pilosocereus multicostatus belongs (Map 33C), its nearest relatives being P. piauhyensis and P. chrysostele of the distant Northern caatingas, ie. from SE Piauí and Pernambuco northwards (see No. 3a(ii), above — Map 20). While there can be no doubt that parts of the middle Rio Jequitinhonha valley have typical caatinga vegetation, the aforementioned species composition and endemism of Cactaceae suggest that this region has been somewhat isolated from the main caatingas area further north and west during a substantial period in its history. It is a key area for the attention of conservationists.

The ranges of most (60 out of 83, ie. c. 72%) of the cactus species from Area No. 3 can be characterized in terms of three geographical/ecological subdivisions, running in parallel from SSW to NNE, and broadly corresponding to the major river and mountain systems. To summarize, these are: (3b) the middle and upper parts of the Rio São Francisco drainage, with 20 taxa, the majority caatinga elements; (3c) the campos rupestres etc. on primarily crystalline rocks and sandstones of the East Brazilian Highlands (Chapada Diamantina & northern Serra do Espinhaço), with 17 taxa; and (3d) the complex of caatingas-agrestes,

Maps 32A–32D (next page). Distribution pattern 3d(ib), represented by (A) Tacinga werneri, (B) Pilosocereus pentaedrophorus subsp. robustus, (C) Melocactus oreas subsp. oreas [o] and M. conoideus [■] and (D) M. bahiensis subsp. amethystinus [■] and M. salvadorensis [o]. Eastern Brazil (core area).
campos rupestres etc. eastwards and north-eastwards from within or to the east of the latter mountain system, with 23 taxa.

In terms of phytogeography it is worth noting that area category No. 3b has links with the immediately adjacent parts of Central-western Brazil — *Cereus jamacaru* subsp. *calcirupicola*, *Micranthocereus dolichospermaticus* / *M. estevesi*, *Pilosocereus densiareolatus* / *P. diersianus* and *P. floccosus* / *P. albisumnum* — or further afield, eg. *Facheiroa* has possible relatives in the east Bolivian *Yungasocereus* Ritter and *Vatricania Backeberg* (= *Espostoa* Britton & Rose), and includes one genus associated with the distant western Chaco (*Quiabentia*). In contrast, No. 3c is almost without links beyond the E Brazilian areas and subdivisions that surround it, whereas the more species-rich category No. 3d has the most distant links, including the Caribbean, northern South America and the central Andes.

The southern part of the Caatingas / Northern campos rupestres area is particularly rich in species and there are instances of high levels of sympatry. For example, climbing eastwards into the Serra Geral east of Monte Azul (MG) it is possible, including epiphytes, to find at least 16 cactus species over a distance of less than 2 kilometres, and in southern Bahia the caatinga may often have 10 or more sympatric cactus species. However, from the limits of Bahia northwards the diversity of Cactaceae diminishes rapidly and it is significant that none of the 3 caatinga species of the widespread neotropical genus *Pereskia* appears to range outside of Bahia and northern Minas Gerais. There are no cacti endemic to the extensive northern caatingas in Paraiba, Rio Grande do Norte, Ceará and northern Piauí and only 5 species can be said to be ± restricted to this area (see No. 3a(ii), above, Maps 20/21A). This

Maps 33A–33D (next page). Distribution pattern 3d(ii), represented by (A) *Tacinga braunii*, (B) *Pilosocereus azulensis* [■] and *P. floccosus* subsp. *quadricostatus* [○], (C) *P. magnificus* [○] and *P. multicoostatus* [■] and (D) *Coleocephalocereus aureus* [○] & *C. purpureus* [■]. E. Brazil (core area).

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perhaps suggests that either the northern caatingas are younger than the dry areas further south, or that they have experienced stronger forces of extinction in the past, or that they lack the diversity of habitats and refugia created by the combination of the Rio São Francisco valley, the East Brazilian Highlands and more humid ecotonal region towards the coastal Atlantic Forest. It is certainly curious that some rather widespread southern caatinga species, with distribution patterns around or between the East Brazilian Highlands and the agrestes, in Bahia and northern Minas Gerais, have not spread farther north, examples being Pereskia bahiensis and Pseudoacanthocereus brasiliensis. It is possible that the lower rainfall zone along the Rio São Francisco valley (and NE Bahia) have halted their expansion northwards.

<table>
<thead>
<tr>
<th>Caatinga area</th>
<th>Endemic/characteristic Cactaceae</th>
</tr>
</thead>
<tbody>
<tr>
<td>3a(ii). Northern caatingas: MA, PI, CE, RN, PB, PE, AL, northern BA</td>
<td>Pilosocereus flavipulvinatus, P. pachycladus subsp. pernambucoensis, P. piaubhyensis, P. chrysothele, Discocactus bahiensis</td>
</tr>
<tr>
<td>3a(iii). Central-southern caatingas: PI [part], PB [part], PE, AL, BA, SE, MG</td>
<td>Pereskia aureiflora, P. bahiensis, Tacinga funalis, Brasilicereus phaeacanthus, Stephanocereus leucostele, Arrojadaoa penicillata, A. rhodantha, Pilosocereus tuberculatus, Coleocephalocereus goebelianus, Melocactus ernestii subsp. longicarpus, Harrisia adscendens</td>
</tr>
<tr>
<td>3b. Caatingas of the Rio São Francisco drainage (MG, BA, PE) and adjacent south-eastern PI</td>
<td>Pereskia stenantha, Quiabentia zehntneri, Tacinga saxatilis, Pilosocereus gounellei subsp. zehntneri, P. densiarooolatus, Micranthocereus dolichospermaticus, Melocactus deinacanthus, M. levistatus, M. azureus, M. pachyacanthus, Discocactus zehntneri subsp. zehntneri, Facheiroa (3 spp.)</td>
</tr>
</tbody>
</table>

Table 4.4. Geographical subdivision of the caatingas dominion based on the distribution of Cactaceae
4. Cerrados and South-eastern campos rupestres (Minas Gerais) [Map 10, west of line A-B & south of line B-C] (28 taxa; 17% of the total)

As in the case of the Caatingas and Northern campos rupestres (Area No. 3), this region is well-defined in terms of endemic cactus taxa, including the genus *Uebelmannia* (3 spp. & 2 heterotypic subspp.), an ecologically highly specialized group with no close relatives and apparently relictual. Also notable is *Cipocereus*, a peculiar member of tribe Cereae, which is represented by 4 endemic species plus one heterotypic subspecies. A characteristic non-endemic genus found only in Area No. 4 within Eastern Brazil is *Arthrocerus* (3 spp. + 2 subspp.). The genera of cacti that occur in common with Area No. 3 are all represented by different species, although in some cases the southern species are actually sisters or probable sister taxa of those from further north, eg. *Brasilicereus phaeacanthus* [No. 3a(iiiic)] & *B. markgrafii* [4c(iiia)] and *Cereus albicaulis* [3a(iiia)] and *C. mirabella* [4a]. Table 4.5 summarizes the principal differences between the Northern and South-eastern campos rupestres in terms of Cactaceae (excluding a few very narrow endemics).

<table>
<thead>
<tr>
<th>Campo rupestre areas within E Brazil</th>
<th>Characteristic taxa of Cactaceae</th>
</tr>
</thead>
</table>

Table 4.5. Cactaceae defining the Northern and South-eastern campo rupestre areas (¹ = taxon also found in adjacent vegetation types — especially caatinga — of Area No. 3).

Map 34 (next page). Distribution pattern 4a: *Cereus mirabella* [? = record of doubtful identity].
The geography of cactus taxa within this southern area is very far from being random and a series of well-defined patterns of distribution and endemism can be recognized. Two exceptions to the line delimiting this Area on Map 10 should be noted. The first is provided by a narrow zone of cerrado located on the east side of the Rio São Francisco in central-southern Bahia, where Pilosocereus aureispinus is endemic (its relatives in the P. AURISETUS Group are all Cerrado / South-eastern campo rupestre taxa). The second is a similarly located disjunct record of Discocactus heptacanthus subsp. catingicola (see No. 4b, below).

4a. Widespread (cerrados) (Map 34)

Cereus mirabella.

On present knowledge C. mirabella has a markedly disjunct distribution, including the Rio Doce / Rio Jequitinhonha watershed (W of Água Boa, MG — the type locality), central-northern Minas Gerais (vicinity of Mirabela and Varzelândia), western Bahia (Barreiras westwards) and western Maranhão (near Carolina). It is assumed to be a relict species, the major part of whose range is within Eastern Brazil, mostly in sandy phases of the cerrado. Its sister species is C. albicaulis, with a parallel range further east in the caatingas.

4b. Western cerrados (including those immediately east of the Rio São Francisco in central-southern Bahia) (3 taxa, Maps 35A & 35B)

Pilosocereus machrisii, P. aureispinus‡, Discocactus heptacanthus subsp. catingicola‡
[incl. 1 record in caatinga vegetation on gravelly river terraces E of the Rio São Francisco].

Pilosocereus aureispinus, from isolated cerrados east of the Rio São Francisco, is the sister species of P. vilaboensis from Goiás (Zappi 1994: 126–129), while the other two species are wide-ranging in Central-western Brazil and eastern Paraguay. P. machrisii, which is found only on rock outcrops, is the sister species of P. auriisetus [category No. 4c(i)].
spite of it having received the epithet *catingicola*, the subspecies of *Discocactus heptacanthus* is usually found in the *cerrados* and ecotonal areas.

4c. **South-eastern campos rupestres and associated sandy/gravelly cerrados (Map 10, south of line B–C)** (24 taxa)

Nearly all the taxa listed here are endemic to the core area of Eastern Brazil and none of the species restricted to this type of habitat is common to that of comparable No. 3c (Chapada Diamantina and N Serra do Espinhaço), where there are only 17 taxa, although some genera are shared. The absence of various non-endemic genera and species groups characteristic of adjacent areas, viz. *Tacinga, Harrisia, Leocereus, Coleocephalocereus, Melocactus* and *Facheiroa*, is particularly worthy of note. From the conservation standpoint it is important to point out that Area No. 4c has by far the highest number of single-site endemics in Eastern Brazil (7 out of 24 taxa). The following categories are recognized:

4c(i). **Widespread taxa** (3 taxa, Maps 35C & 35D)

*Cipocereus minensis* subsp. *minensis*, *Pilosocereus aurisetus* subsp. *aurisetus*, *Discocactus placentiformis*.

The *Discocactus* and *Pilosocereus* have somewhat differentiated regional forms in each of the following subdivisions. These have been named by Braun & Esteves Pereira (see Supplement 1), but are not as clearly distinct as those given formal recognition here.
4c(ii). Northern part of area (16 taxa):

4c(iia). Municipios of Grão Mogol, Botumirim & Cristália (Rio Jequitinhonha drainage) (5 taxa, Maps 36A–36D)

Pilosocereus fulvilanatus subsp. fulvilanatus‡, Discocactus pseudoinsignis‡, D. horstii‡§, Micranthocereus auriazureus‡§, Brasilicereus markgrafii‡.

This subdivision is at the border with Area No. 3, and the above taxa can be found sympatric with, or in close proximity to Tacinga inamoena, Arrojadoa dinae, Melocactus bahiensis and M. concinnus, which are characteristic members of the Caatingas / Northern campos rupestres flora. Pilosocereus fulvilanatus, whose northern relatives are all caatinga taxa, is the sister species of P. ulei, from the dry coastal forest at Cabo Frio, eastern Rio de Janeiro (Zappi 1994), which potentially marks a southward expansion of caatinga-like vegetation during the Pleistocene (Ab'Saber 1974, Araújo in Davis et al. 1997: 373). Brasilicereus markgrafii is considered to be a plesiomorphic relict.

4c(iib). Serra do Cabral and lower W slopes of Serra do Espinhaço (Rio São Francisco drainage) (5 taxa, Maps 37A–37D)

Cipocereus bradei‡, Pilosocereus fulvilanatus subsp. rosae‡§, P. aurisetus subsp. aurilanus‡, Arthrocereus rondonianus‡, Uebelmannia pectinifera subsp. horrida‡§.

All the taxa listed here have sister taxa elsewhere in No. 4c.

4c(iic). Diamantina & E to the Serra Negra / Serra do Ambrósio (5 taxa, Maps 38A–38D)

Cipocereus crassisepalus‡, Uebelmannia‡ (3 spp. + 1 heterotypic subsp.).

The Cipocereus and the 2 species from Uebelmannia subg. Uebelmannia (endemic to this subdivision) are restricted to the abundant deposits of quartz sands and gravels found eastwards from Diamantina.
Maps 36A–36D. Distribution pattern 4c(iiia), represented by (A) *Pilosocereus fulvilanatus* subsp. *fulvilanatus*, (B) *Discocactus pseudoinsignis* [○] and *D. horstii* [▲], (C) *Micranthocereus auriazureus* and (D) *Brasilicereus markgrafii*. Eastern Brazil (core area).
4c(iii). Southern part: Serra do Cipó southwards (6 taxa, Map 39)

*Cipocereus laniflorus*, § C. *minensis* subsp. *pleurocarpus*, *Arthrocereus glaziovi*†, *A. melanurus* (3 subspp. [2 subspp.‡§]).

Giulietti & Pirani (1988: 65) note that Hensold regards the most primitive forms of *Paepalanthus* subg. *Xeractis* (Eriocaulaceae) as being from the southern and eastern Serra do Espinhaço. This observation can also be applied to *Cipocereus*, whose taxa with most plesiomorphies are *C. laniflorus* (Serra do Caraça), *C. minensis* subsp. *pleurocarpus* (Serra do Cipó) and *C. crassisepalus* (E of Diamantina). The 3 subspecies of *Arthrocereus melanurus* are each located in a different drainage system (ie. Rio São Francisco, Rio Grande and Rio Paraíba do Sul).

The relationships of the East Brazilian Highlands' cactus flora (including the *campos rupestres*, sensu stricto, plus 'cerrado de altitude' and humid montane forest) with other vegetation zones are quite varied, although most do not extend much beyond the core area. They include significant links with the *caatinga* flora, contrary to what is stated in general terms by Giulietti *et al.* in Davis *et al.* (1997: 400). These links are summarized in Table 4.6.

Taking together all the species of Cactaceae confined to *campo rupestre* and associated vegetation (eg. *cerrado de altitude, mata de neblina*), ie. most taxa from categories Nos. 3c and 4c, plus those from 3d(i), there is a total of 42 taxa, or more than one quarter (26%) of the cacti of Eastern Brazil, all but one of these being endemic to the core area. These include the endemic genera *Cipocereus* (5 spp.) and *Uebelmannia* (3 spp.), and the subgenera *Micranthocereus* subg. *Micranthocereus* (4 spp.), *M. subg. Austrocephalocereus* (3 spp.) and

Maps 37A–37D (next page). Distribution pattern 4c(iiib), represented by (A) *Cipocereus bradei*, (B) *Pilosocereus fulvilanatus* subsp. *rosae* [■] and *P. aurisetus* subsp. *aurilanatus* [○], (C) *Arthrocereus rondonianus* and (D) *Uebelmannia pectinifera* subsp. *horrida*. Eastern Brazil (core area).
Stephanocereus subg. Lagenopsis (1 sp.). Making the same analysis for species found only in the caatinga-agreste, we have a total of 58 taxa or 36%, of which 49 (c. 31%) are endemics

<table>
<thead>
<tr>
<th>E Brazilian Highland area / substrate or vegetation</th>
<th>Other area</th>
<th>Linking taxon/taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>widespread / humid montane forest &amp; rocks</td>
<td>Mata atlântica / mata de planalto</td>
<td>Rhipsalis russellii</td>
</tr>
<tr>
<td>E slopes from Itamarandiba (MG) to Jacobina (BA) / rocks &amp; gravels</td>
<td>E caatingas-agrestes</td>
<td>Melocactus oreas, M. ernestii subsp. ernestii, M. bahiensis, M. concinnus</td>
</tr>
<tr>
<td>E edge of Highlands: Serra da Areia (MG), Rui Barbosa &amp; Jacobina (BA), Serra da Itabaiana (SE) / quartz sand &amp; gravel</td>
<td>coastal restinga from RN to RJ</td>
<td>Melocactus violaceus, s.l.</td>
</tr>
<tr>
<td>From Grão Mogol (MG) northwards / arenitic rocks, sands &amp; gravels</td>
<td>SW caatingas (BA) &amp; planalto central, on limestone</td>
<td>Micranthocereus</td>
</tr>
<tr>
<td>N Chapada Diamantina, region of Morro do Chapéu northwards / arenitic rocks, sands &amp; gravels</td>
<td>caatingas of Rio São Francisco</td>
<td>Discocactus zehnmeri</td>
</tr>
<tr>
<td>Chapada Diamantina &amp; N Serra do Espinhaço, rocks, sands &amp; gravels</td>
<td>central-southern caatingas</td>
<td>Stephanocereus, Arrojadoa</td>
</tr>
<tr>
<td>Chapada Diamantina / perhumid montane forest</td>
<td>Mata atlântica (BA, ES, MG)</td>
<td>Rhipsalis baccifera subsp. hileiabaiana, Hatiora salicornioides</td>
</tr>
<tr>
<td>SE campos rupestres, between Grão Mogol and Augusto de Lima / arenitic rocks</td>
<td>coastal rocks, Cabo Frio, RJ</td>
<td>Pilosocereus fulvilanatus / P. ulei species pair</td>
</tr>
<tr>
<td>SE campos rupestres, Diamantina &amp; Serra do Cabral to Serra do Cipó / rocks &amp; gravels</td>
<td>W cerrados, on diverse rocks</td>
<td>PILOSOCEREUS AURISETUS Group</td>
</tr>
<tr>
<td>SE campos rupestres, Serra do Cabral (MG) southwards / rocks</td>
<td>Chapada dos Guimarães, MT</td>
<td>Arthrocereus</td>
</tr>
</tbody>
</table>

Table 4.6. Principal links between the E Brazilian Highlands and other areas (based on Cactaceae).

Maps 38A–38D (next page). Distribution pattern 4c(jic), represented by (A) Cipocereus crassisepalus, (B) Uebeimannia buiningii, (C) U. gummifera and (D) U. pectinifera subsp. pectinifera [o] & subsp. flavispinus [★]. Eastern Brazil (core area).
of the core area of Eastern Brazil. Thus, the number of endemic Cactaceae restricted to either 
**campo rupestre** (26%) or **caatinga-agreste** (31%) in Eastern Brazil is not remarkably 
different and accounts for c. 57% of the total. However, it should not be forgotten that there 
are some important taxa that occur in both vegetation types (eg. *Tacinga inamoena, 
Melocactus bahiensis, Leocereus bahiensis*), as well as a few that have an even wider 
ecological tolerance. The taxa found in neither **campo rupestre** nor **caatinga-agreste**, are 
from either the more humid forests, their included rock outcrops and coastal sand-dunes 
(Area No. 2), or the **cerrados**, and amount to c. 26% of the total, only 7% being endemic to 
the core area.

To summarize, these figures indicate that, although one might have expected the great 
majority of Cactaceae of Eastern Brazil to be from the extensive **caatingas**, in point of fact 
less than half occur there, and the representation of cactus taxa in the **campos rupestres** 
appears to be nearly as important, yet the area they occupy is relatively much smaller. Taxa 
that can be regarded as the best overall markers of each vegetation type include, for the 
**caatinga-agrestes**: *Brasilicereus phaeacanthus, Pilosocereus gounellei, sens. lat.* and *P. 
pachycladus, sens. lat.* (see Map 40, noting that both *Pilosocereus* species occasionally stray 
into the **campos rupestres**); for the **campos rupestres**: *Arthrocereus, Cipocereus* and 
*Micranthocereus* subg. *Micranthocereus* & subg. *Austrocephalocereus* (see Map 41); for the 
Atlantic Forest and included rock outcrops (Area No. 2, see Map 14A): *Pereskia aculeata 
and P. grandifolia* (Maps 14B & 16A); and for the **cerrados**: *Cereus mirabella, Discocactus 
heptacanthus* and *D. placentiformis* (see Maps 34, 35B & 35D).

Map 39 (next page). Distribution pattern 4c(iii), represented by *Cipocereus laniflorus [+]*, *C. 
minensis* subsp. *pleurocarpus [□], Arthrocereus glaziouii [★]* and *A. melanurus subsp. melanurus 
[○], subsp. magnus [■] & subsp. odorus [▲]. Eastern Brazil (core area).
4.6. Reproductive and dispersal strategies

While distribution patterns may be heavily influenced by geographic, climatic, edaphic and temporal factors, the range of a taxon will also be dependent, to a greater or lesser extent, on its reproductive ability and dispersal strategies. As far as can be determined, all of the cactus taxa native of Eastern Brazil reproduce by means of seeds, only very few also employing vegetative means. The chief examples of the latter are in the Opuntioideae, where the jointed stem-segments are frequently capable of being detached, transported and then forming roots upon contact with the ground. A few of the epiphytic and scrambling taxa in tribes Rhipsalideae and Hylocereeae may also indulge in a limited amount of vegetative propagation, but this is unlikely to spread the plant much beyond adjacent branches of the tree in which it originally established itself. Table 4.7, below, lists taxa in systematic order noting, where possible, the observed, reported or presumed dispersal vectors, principal habitat type(s) and a categorization of geographical range within specified habitat type(s) in E Brazil into either 'widespread', 'restricted' or 'single site'. The 'Formal Taxonomic Treatment' (Supplement 1) should be consulted for data on size, morphology and dehiscence of fruit and seed.

Map 40 (next page). Distribution records of all taxa restricted to caatinga-agreste [●], particularly noting Brasiliocereus phaeacanthus [■], Pilosocereus gounellei, sens. lat. [○] and P. pachycladus, sens. lat. [▲], and indicating the approximate limits of the caatinga biome. Eastern Brazil.

Map 41 (page 337). Distribution records of all taxa restricted to campo rupestre, sens. lat. [●] (but excluding pure cerrado elements), noting Micranthocereus (subg. Micranthocereus and subg. Austrocephalocereus) [○], Cipocereus [○] and Arthrocereus [▲]. Eastern Brazil (core area).
<table>
<thead>
<tr>
<th>TAXON</th>
<th>DISPERSAL VECTOR</th>
<th>HABITAT</th>
<th>RANGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pereskia aculeata</td>
<td>mammal</td>
<td>Mata atlântica, s.l.</td>
<td>widespread</td>
</tr>
<tr>
<td>P. grandifolia ssp. grandifolia</td>
<td>ground-feeding mammal (wild boar?)</td>
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<td>&quot;</td>
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<tr>
<td>P. grandifolia ssp. violacea</td>
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<td>P. bahiensis f</td>
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<td>P. aureiflora f</td>
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<td>Quaibentia zehnneri f</td>
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<td>Tacino funeal f</td>
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<tr>
<td>T. (Opuntia) wernersi f</td>
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<td>T. (Opuntia) saxatilsis ssp. estevensi f</td>
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<td>Pseudoeocanthocereus brasiliensis</td>
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<td>L. (Opuntia) inamoena f</td>
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| *C. fimunenis...
| **Espostoaopsis dybowskii** | bat & bird |  |
| Arthrocereus melanurus ssp. melanurus | bat, other mammal & bird | campo rupestre |
| A. melanurus ssp. magnus |  |  |
| A. melanurus ssp. odoratus |  |  |
| A. rondonianus |  |  |
| A. glaziouii |  |  |
| Discocactus zehntneri ssp. zehntneri | ant | castinga |
| D. zehntneri ssp. boiomiana |  | campo rupestre |
| D. bahiensis | ant (●) & water | castinga |
| D. heptacanthus ssp. catingicina | ant | cerrado |
| D. pleomeiformis | (●) | campo rupestre/cerrado |
| D. pseudoinsignis |  | cerrado |
| D. horstii |  | campo rupestre/cerrado |
| Uebelmannia buiningii | ant? |  |
| U. gummifera |  |  |
| U. pectinifera ssp. pectinifera | ant? | campo rupestre |
| U. pectinifera ssp. flavispina |  |  |
| U. pectinifera ssp. horrida |  | single site |

Table 4.7. Seed dispersal vectors of species and subspecies of Cactaceae in Eastern Brazil, with details of habitat and extent of range within that habitat type. **Key:** † = taxon endemic to the total area studied, ● = taxon endemic to core area. Actual observations of presumed vectors at work are indicated by (●). Some infraspecific taxa are not distinguished from their respective species, where their entries would otherwise be identical and repetitive.

**Diversity of dispersal strategies**

Amongst the range of observed or probable dispersal strategies demonstrated by the cacti of Eastern Brazil, the rarest appear to be those involving wind or water — *Micranthocereus dolichospermaticus* (W. Barthlott, pers. comm.), *Pilosocereus gounellei* (Zappi 1994) and *Discocactus bahiensis*. However, it is likely that in each case zoochory is still part of the initial stages of dispersal, enabling the seeds to escape from the fruit and/or wool of the cephalium or stem apex. Wind dispersal of the seeds of *M. dolichospermaticus* from its elevated cephalium is a strategy matched by associated species of the bromeliaceous genus *Encholirium*, both taxa needing to disperse their seeds across deeply fissured, karstic limestone outcrops. However, it may be doubted whether this strategy alone is capable of achieving dispersal over longer distances, and at least *M. dolichospermaticus* is known to have a rather limited range, occurring on only a small number of outcrops within a region where such habitats are relatively abundant. *Pilosocereus gounellei* is very widely distributed, perhaps because its fruits are attractive to bats and other vectors (large wasps have been observed flying away bearing funicular pulp with seeds attached), but its buoyant
seeds may be adapted for local dispersal during flash-floods, which affect the impermeable, flat rocky substrates the species tends to frequent. The same strategy for local dispersal may apply to the much rarer *Discocactus bahiensis*, which has been observed on a low-lying river flood plain subject to occasional inundation.

Bats, birds, lizards and ants are almost certainly the commonest seed vectors for E Brazilian cacti, with non-flying mammals being of lesser significance and linked to species with larger fruits and seeds. The most interesting amongst the latter vectors is that suggested by the behaviour of 3 species of *Pereskia* (the P. grandifolia Group), *Brasiliopuntia brasiliensis* and *Pseudoacanthocereus brasiliensis*. In these the fruits seem to ripen only once they have fallen to the ground, turning yellow or reddish and then smelling strongly of pineapple, just like the ripe infructescences of ground-dwelling species of *Bromelia*, with which they are often associated. Here it is hypothesized that such taxa are (or were formerly) dispersed by peccaries, within whose historic range they are included, and this could explain the wide distribution achieved by *Brasiliopuntia*, *Pseudoacanthocereus* and the 5 species of the *Pereskia grandifolia* Group across South America, via the Amazon basin, cerrado and/or dry seasonal forest environments. In the much altered caatingas of the present day, where the peccary is either extinct or very rare, the fallen fruits of *P. bahiensis* and *P. stenantha* are eaten by man’s cattle and good crops of pereskia seedlings can be observed germinating amongst recently deposited cow-pats. Two climbing or epiphytic taxa of Hylocereaeae (*Hylocereus* & *Epiphyllum*), wide-ranging in the neotropics, produce large succulent fruit that may be of interest to monkeys, which have been observed feeding in forest where *E. phyllanthus* was fruiting (bats are also possible vectors here).

Bats are assumed to be important seed vectors for the great majority of Brazilian columnar cacti with fleshy fruit (Taylor & Zappi 1989: 22; Locatelli et al. 1997) and this role is certainly well known in relation to the famous North American Sahuaro cactus, *Carnegiea*
gigantea, and other cereoid cacti from the Northern Hemisphere (Dobat & Peikert-Holle 1985). It seems reasonable to assume that the distances fruit-eating bats regularly travel are not likely to be a limiting factor in the expansion of range for such columnar species, and the substantial distributions attained by genera such as Pilosocereus in the Americas presumably reflect this. Birds may play a similar role (eg. Cereus jamacaru) and are likely also to be important vectors for the many smaller-fruited, epiphytic Rhipsalideae (Lepismium, Rhipsalis, Hatiora & Schlumbergera), whose ranges vary from 'widespread' to 'single site' (Table 4.7). Some of these taxa have very sticky fruit pulp and are assumed to be dispersed by birds in a manner similar to mistletoes (Viscum spp.), but small monkeys ('sagulis') have also been reported eating their fruits in South-Eastern Brazil (herbarium label data).

Lizards have been frequently observed upon Melocactus plants, eating the watery fruit, and are assumed to be effective local dispersal agents (Taylor 1991a, Figueira et al. 1993, 1994). However, it is improbable that this genus has achieved its currently extensive, yet discontinuous, neotropical range by this means alone and dispersal over longer distances by birds is presumed to have occurred (Taylor 1991a). Lizards may also consume the fruits of other cacti that grow close to the ground or which are not so densely covered in sharp spines as to render them inaccessible (however, dead lizards impaled on the spines of Melocactus have been observed on more than one occasion!). Pilosocereus arrabidae fruits have been seen being eaten by these vectors by Daniela Zappi (pers. comm.).

Ants are frequently attracted to the funicular pulp in which all cactus seeds are embedded, but generally do not appear to penetrate the often leathery pericarp of the fruit on their own and are probably less effective or unable to transport larger seeds. However, the small-seeded genera, Coleocephalocereus and Discocactus, have dehiscent fruit, the former opening by means of a basal pore, the latter by lateral fissures, and each type has been observed in the process of being raided by ants, which were carrying seeds away.
Furthermore, *Discocactus bahiensis* plants have been observed recently growing in the centre of old ants’ nests. Both genera are characterized by erratic occurrence, being abundant in some suitable habitats yet curiously absent from others, suggesting the possibility that longer distance dispersal is less effective and may rely on birds (or in the former case, also bats).

While it has been possible to make observations in habitat of a few taxa, and speculate on rather more, in relation to their dispersal vectors, there remain some species for which it is difficult to be sure how dispersal might be achieved. These include the opuntioids, *Quiabentia zehntneri*, *Tacinga funalis* and *T. braunii*, whose fruits are scarcely either conspicuously coloured, fragrant or juicy/fleshy at maturity. While *Quiabentia* may indulge in vegetative propagation on a local scale, this can hardly explain the present range of either the genus or its Brazilian species, unless this was once much more continuous than it is today, or was achieved over a long time scale. The same remark applies, to a lesser degree, to the above-mentioned *Tacinga* species, but careful studies of these, and of Brazilian cacti in general, are clearly desirable.

**Conclusions on the influence of dispersal strategies on distribution patterns**

Study of Table 4.7 suggests that dispersal strategies do have a significance for the interpretation of distribution patterns, but that this is probably much less important than other, even if interrelated, climatic and edaphic factors. While, as noted occasionally above, the range and frequency of certain taxa may well be explained by such strategies, many closely related taxa, with presumably similar or identical dispersal vectors, differ markedly in the range they have attained, suggesting that other habitat factors, climatic history or the age of the taxon itself have come into play. This is assumed to be the case with the disjunct occurrences of *Harrisia adscendens*, *Arrojadoa penicillata* and *Tacinga funalis* to the west/north-west of the Rio São Francisco, none of these displaying dispersal strategies, such
as very sticky fruit pulp enabling epizoochory, which could facilitate the extension of range over longer distances. The points made in this paragraph can also be applied to pollination vectors, which are briefly discussed under the heading of Conservation (Chapter 5). Pollinators are clearly of considerable importance, since extant knowledge suggests that the family is largely self-incompatible (Ross 1981, Boyle 1997).
Chapter 5

CONSERVATION OF THE CACTACEAE OF EASTERN BRAZIL

5.1. Why conserve the cacti of Eastern Brazil?

There are various arguments to be advanced in support of the conservation of the Cactaceae of Eastern Brazil. Perhaps the strongest, however, is the degree of biological uniqueness these plants represent in terms of endemic genera and species. This can be expressed both in terms of the family in Brazil and in the Americas as a whole, to which the Cactaceae is all but endemic (save only for Rhipsalis baccifera, which ranges from the neotropics into the paleotropics). Brazil has a total of 37 native genera of Cactaceae (ie. c. 30% out of a New World total of c. 120), of which 28 or 75% are found in Eastern Brazil, 12 (32%) of these being Brazilian endemics native in Eastern Brazil. Of the 28 genera from the Eastern region, 7 (25%) are endemic to it and the remaining 5 Brazilian endemics have the major parts of their ranges and nearly all of their biological diversity in the Eastern region as well. The 28 native cactus genera of Eastern Brazil comprise 128 species, of which 115 (90%) are endemic to Brazil and 87 (68%) are endemic to the Eastern region. If heterotypic subspecies are added to the total for Eastern Brazil, then we have 161, of which 122 (76%) are endemic. Taking the family as a whole, 3 out of the 4 subfamilies occur in E Brazil, and the largest of these, the Cactoideae, includes about 9 tribal groups. One such is Cereeae, whose 10 genera all occur in Brazil, 3 being endemic to
the Eastern region (*Brasilicereus, Cipocereus* & *Stephanocereus*) and a further 5 having most of their diversity in the region. Another, larger tribe are the Trichocereeeae, with 7 genera in Eastern Brazil, 4 of these being endemic to the region (*Leocereus, Facheiroa, Espostoopsis* & *Uebelmannia*). The taxonomic isolation, remarkable morphology and ecology of *Uebelmannia* make the strongest of biological arguments for its conservation and the preservation of its habitats.

While it may be legitimate to analyse the above cactus diversity in isolation, it is more environmentally relevant to consider the ways in which its loss might impact the overall ecology of the habitats the plants occupy and sometimes co-dominate. We know too little of the overall ecology of cacti in Eastern Brazil to be able to cite specific cases, but at least in parts of the *caatinga, campo rupestre*, drier phases of the *Mata atlântica* and coastal *restinga* there exist communities where the loss of cacti could certainly affect the survival of their pollinators and seed vectors, and *vice versa*. Perhaps the most vulnerable of higher animal groups in this respect are bats, which visit columnar cacti for nectar, pollen and fruit (Zappi 1994, Ruiz *et al.* 1997, Locatelli *et al.* 1997, Petit 1999). In some of these communities the cacti flower and fruit for much of the year, providing an ongoing food resource even when other vegetation is seasonally dormant or suffering from drought. Another group reliant on cactus nectar as an energy source, at least in some of the driest areas, are the hummingbirds, and in particular those which locate their territories amongst populations of *Melocactus, Arrojadoa* and *Tacinga*, which like some columnar cacti tend to flower for a significant part of the year (Taylor 1991a, Taylor & Zappi 1996, Raw 1996, Locatelli & Machado 1999a). In the case of *Melocactus*, the subsequent and regular production of juicy fruits is an important water resource for lizards (Figueira *et al.* 1993, 1994), which locally disperse the seeds. Besides these organisms, there are other birds, lepidopterans (Locatelli *et al.* 1997, Locatelli & Machado 1999b), bees (Schlindwein & Wittmann 1997), ants and terrestrial mammals that interact with Brazilian cacti in various
ways (see Chapter 4.6), not to mention the important roles played by other plants. These are many and various, ranging, for example, from the carnaúba palm (*Copernicia prunifera*) in flooded forests in northern Piauí and Ceará, upon which *Pilosocereus gounellei* is often epiphytic, to great trees in the Atlantic Forest supporting many epiphytes belonging to the tribe Rhipsalideae. And while birds may need cacti as a source of energy, they can also be a source of nesting material, the author having seen birds collecting the cephalium wool of *Micranthocereus purpureus* for this purpose. The same is reported by Schulz & Machado (2000: 63), involving *Pilosocereus aurisetus* and a hummingbird.

The numerous locality records for cacti in Eastern Brazil assembled for the present study may in future enable assessments of the well-being of diverse vegetation types to be made and guide those who have the power to create reserves, as environments inevitably deteriorate further. Few, if any, cacti found in Eastern Brazil appear to increase significantly when habitat disturbance occurs (*Quiabentia zehntneri* being a possible exception), but it is probable that a more complete knowledge of the ecology of cactus habitats will permit the identification of indicator species amongst members of the family. This would seem a real possibility in the case of certain Rhipsalideae, whose presence, diversity and abundance in parts of the Atlantic Forest should be a reliable indicator of its primary or secondary status, since these epiphytes seem only to occur on mostly large trees of considerable antiquity.

Another compelling argument in favour of cactus conservation in Eastern Brazil is their economic potential, if used sustainably, both at the local level and for international trade. They are already employed for a variety of purposes locally, whether as substitute livestock fodder in times of drought, for their delicious fruit, for making ‘cactus candy’ or planted to form living, impenetrable fences (especially *Cereus jamacaru*). The frequent attributions of medicinal value made by locals in relation to cacti mostly lack any kind of scientific insight at present, but in other countries these plants are frequently used in
alternative medicine and some are still cultivated commercially for extraction of drugs, eg. *Selenicereus* (see Backeberg 1966: pl. between pp. 10–11). While they are already recognized for their potential in amenity horticulture in Brazil, where an established nursery industry exports large volumes to Europe, the USA and beyond, more could be made of native species from Eastern Brazil. Some are especially attractive as seedlings and certainly marketable, provided their production does not rely on a constant supply of seeds or plants from the wild, but employs artificial propagation. A further area of commerce that native cacti have a role to play in is that of the ever-increasing trend for ‘eco-tourism’. There are enough cactophiles in the world to make it worthwhile for specialised tour companies to arrange bespoke holidays for aficionados to visit the more spectacular habitats, once again given that the object is to photograph, video and observe, but not to collect, in nature! Such tours have operated in Mexico for some years now and, if properly policed, can heighten public awareness of the value of nature conservation.

Cacti are also important to preserve for purely aesthetic and cultural reasons. The Xique-xique, Mandacaru and Palmatória (*Pilosocereus gounellei, Cereus jamacaru* & *Tacinga palmadora*, resp.) frequently appear on the signs of restaurants and bars in the Brazilian Nordeste, where they form a part of the folklore, as well as providing names for numerous villages and towns. Their vernacular nomenclature is extensive, interesting and sometimes quite entertaining for those with knowledge of Brazilian Portuguese and, as such, is listed for each species/subspecies in the ‘Formal Taxonomic Treatment’ (Supplement 1). Cacti are frequently planted as decorative symbols of the region in village and town squares and sometimes allowed to remain in the fields when other vegetation has been cleared during agricultural development. Last, but not least, it is hard to forget the Brazilian passer-by in a remote part of Minas Gerais, who upon noticing my interest in a large planted *Cereus* flowering by the roadside, warmly offered the comment, “É Mandacaru da Bahia! — Quer uma muda?” [... Do you want a cutting?].
5.2. Present status of the environment and conservation of cacti in Eastern Brazil

The following background information has been updated from the relevant Brazilian elements in the chapter on South America in the IUCN Species Survival Commission’s Cactus & Succulent Specialist Group Action Plan, by Taylor et al. (see Oldfield 1997). Since then an important official report recording the levels of habitat destruction in Brazil has also been published (Brasil 1998: 49 etc). In terms of East Brazilian cactus species, special conservation concerns include endemic taxa from the genera Discocactus (6 spp., 5 endemic), Uebelmannia (endemic, 3 spp.) and Melocactus (M. conoideus, M. deinacanthus, M. glaucescens, M. paucispinus), which are ‘Critically Endangered’, ‘Endangered’ or ‘Vulnerable’ (sensu IUCN 1994) and have been placed in Appendix I of CITES (Convention on Trade in Endangered Species of fauna & flora) to afford them protection from the export trade since 1992 (Taylor 1991c). Most of these ‘Appendix I’ plants and equally threatened taxa in the genera Cipocereus, Arthrocereus and Espostoopsis are known from only one or very few localities, where the populations number between less than ten to at most a few thousand individuals. Discocactus placentiformis, D. horstii, D. pseudoinsignis, D. zehntneri subsp. boomianus, Melocactus glaucescens, M. paucispinus (all except the first being known from between only 1 and 5 small sites each) and all Uebelmannia species (U. buiningii being ‘Critically Endangered’, cf. Braun & Esteves Pereira 1988) are threatened in part by trade, via regular collection of plants for seed production, or of seeds, for wholesale export in large quantities. Discocactus bahiensis and Melocactus deinacanthus (the latter with only a single population) are more seriously threatened by agricultural development, and both the former and D. zehntneri subsp. zehntneri have had their ranges and numbers significantly reduced by inundation from the Represa de Sobradinho, a huge dam lake created in the 1970s on the Rio São Francisco (Bahia/Pernambuco). Repeated commercial collecting was only partly responsible for the decline of Melocactus conoideus at its type locality above the expanding city of Vitória da Conquista, southern Bahia, a species that remains ‘Critically Endangered’
due to the extraction of the quartz gravel in which it grows (Taylor 1992b). The tall columnar species, *Micranthocereus dolichospermaticus* (from karstic Bambuí limestone outcrops of difficult access in SW Bahia), has attractive young seedlings appreciated by the international horticultural trade and may be in danger from the practise of felling mature individuals to facilitate the collection of seed. Export of seed is not controlled for CITES Appendix II species such as this, which deserves further investigation in habitat to determine if it should be proposed for Appendix I listing.

The driest zone of Eastern Brazil, namely the *caatinga* (Area 3, see Chapter 4) and its ecotones with Atlantic Forest to the east (*agreste*), dry forests to the south (in Minas Gerais & Espírito Santo) and savannas (*cerrados*) to its west, represents a severely disturbed ecosystem (Andrade-Lima 1981), which has been subject to forest clearance for agriculture and fuelwood over more than two centuries (Lleras in Davis *et al.* 1997: 395). Over half of the energy needs in North-eastern Brazil are met by plant biomass (Brasil 2000: 10). Desertification in its northern part has recently begun to accelerate at an alarming rate, as reports in the popular press testify and are currently stimulating government action towards grand irrigation schemes (Gusmão 1999). Sadly, this is driven more by an understandable desire to further exploit the land than to conserve its remaining biodiversity. Nevertheless, many cacti have probably suffered less than most other plants as a consequence of their frequent occurrence on rock outcrops unsuitable for cultivation or livestock grazing. Thus, species of *Coleocephalocereus*, various *Pilosocereus* and some *Melocactus* (eg. *M. ernestii, M. oreas*), have significant populations in places dominated by gneiss/granite inselbergs, which are probably at less risk from habitat modification, unless situated near expanding towns. Of those cacti that are not mainly restricted to rock outcrops, the least threatened are those which seem able to regenerate when their forest habitat is cut over. These include *Cereus jamacaru, Pereskia grandifolia, P. bahiensis* and *P. stenantha*, and all are also conserved by their use in the form of impenetrable livestock hedges and fences surrounding
homesteads, both within and sometimes outside their natural ranges. A few very widely
distributed endemic cacti, which inhabit little-utilised or sufficiently diverse habitats, are
probably not at risk, even though their numbers may have dropped significantly, eg.
Facheiroa squamosa, Harrisia adscendens, Leocereus bahiensis, Tacinga inamoena,
Pilosocereus gounellei subsp. gounellei and P. pachycladus, sens. lat. However, other,
mostly wide-ranging species that are mainly found growing in the soil of the caatinga-
agreste, or on exposed rocks more or less level with the floor of the surrounding thorn forest,
have suffered considerable reductions in their distributions and abundance through forest
clearance. Endemic species affected in this way, whose ranges now appear to be strongly
fragmented, include Arrojadoa penicillata, A. rhodantha, Brasilicereus phaeacanthus,
Cereus albicaulis, Coleocephalocereus goebelianus, Melocactus salvadorensis, M.
zehnneri, Pereskia aureiflora, Pseudoacanthocereus brasiliensis, Pilosocereus catingicola,
sens. lat., P. floccosus subsp. quadricostatus, P. flavipulvinatus, P. glaucochrous, P.
pentaedrophorus, sens. lat., Stephanocereus leucostele, Tacinga palmadora, T. braunii and
T. funalis. Although most of these are unlikely to become seriously threatened in the
immediate future, regular monitoring is essential if some are not to become ‘Endangered’ in
the longer term. Of more urgent concern are taxa, such as Melocactus azureus subsp.
azureus and M. pachyacanthus, sens. lat., which have smaller ranges and are restricted to
local low-lying outcrops of limestone in the Rio São Francisco valley (Area 3b(ii)), whose
vegetation gets destroyed when the surrounding caatinga forest is cleared for cultivation.
These taxa are here assessed as ‘Endangered’ or ‘Critically Endangered’ on the basis of their
known populations, but further field studies are needed in the remoter parts of northern
Bahia, where additional and less disturbed habitats could exist, although as time goes on this
seems less likely. Even if cacti found on raised rock outcrops within the caatinga are
generally at less risk from agricultural development etc., some, and particularly those close
to roads or human settlements, are at risk from the quarrying of stone for building materials.
Those found only on limestone outcrops and probably most at risk are *Facheiroa cephaliomelana*, sens. lat., *Melocactus azureus* subsp. *ferreophilus*, *M. levistatus*, *Micranthocereus dolicho-spermaticus*, *Pilosocereus densiareolatus*, *P. floccosus*, *P. gounellei* subsp. *zechneri*, *Tacinga saxatilis* subsp. *saxatilis* & *estevesii*), all of which inhabit the Rio São Francisco valley (Area 3b). Other rocks, such as gneiss, granite and other crystalline formations are also quarried and, if this should take place at the site(s) of one of the very local taxa, extinction could be sudden (eg. *Coleocephalocereus purpureus*, *Espostoopsis dybowskii*, *Tacinga werneri*). *Tacinga werneri* is already threatened at one of its localities through granite quarrying (near Rui Barbosa, Bahia) and the other species mentioned are each known from only 1 or 2 restricted areas in the Eastern *caatinga-agrestes* (Area 3d).

Examples of the few and mostly relatively small protected areas (WCMC 1992, Brasil 1998: 66–91) within the vast ‘*Caatinga dominion*’ (Andrade-Lima 1981) are, as follows: ‘Parque Nacional Serra de Capivara’ (includes *Pilosocereus piauhyensis*) and ‘Parque Nacional Sete Cidades’ (both in Piauí state), ‘Parque Nacional de Ubajara’ (Ceará), ‘Estação Ecológica de Seridó’ (Rio Grande do Norte), ‘Reserva Ecológica do Raso da Catarina’ (NE Bahia), the ‘Áreas de proteção ambiental’ known as ‘Serra de Baturité’ (Ceará) and ‘Gruta dos Brejões / Vereda do Romão Gramacho’ (Bahia — includes *Melocactus azureus*, *fide* M. Machado, *in litt.*, 13.04.2000), ‘Estação Ecológica Federal de Aiuaba’ (Ceará) and the ‘Estação Experimental do IPA’, Caruaru (PE). These can offer protection to only few and mostly widespread species, since, unfortunately, there are currently no significant protected areas in the southern part of the *caatinga* zone (ie. Areas 3a(iii) & 3b(iii) in cent-S Bahia and N Minas Gerais), where a very high species diversity and endemism is matched by a most disturbing level of habitat destruction (mainly for agriculture and charcoal production). One of the most important areas needing protection amongst the southern *caatinga-agrestes* is the middle section of the Rio Jequitinhonha valley.
(ie. Area 3d(ii), between the towns of Araçuaí and Jacinto) in north-eastern Minas Gerais, where a remarkably rich assortment of cacti exists, including many endemic and potentially threatened cactus species (Taylor & Zappi 1992a). Another promising site for protection, with a comprehensive range of southern caatinga cacti, including the rare Espostoa dybowskii, is situated to the east of the village of Porto Alegre, on the north bank of the Rio de Contas drainage, Mun. Maracás, Bahia (Area 3d(ia)). Other sites need to be identified for the conservation of taxa characteristic of the deep soils and ‘Bambuí’ limestone outcrops in the middle section of the valley of the São Francisco River (especially for columnar Cactaceae in Area 3b(iii)). One such would be the massive raised outcrop south of the town of Iuiú on the east bank of the river (SW Bahia), which has two very local endemics restricted to the rock itself (Facheiroa cephaliomelana subsp. estevesii and Tacinga saxatilis subsp. estevesii). Other sites should be found on the west side of the river, where further endemics, such as the aforementioned Micranthocereus dolichospermaticus and Facheiroa cephaliomelana subsp. cephaliomelana, are located.

The East Brazilian Highlands, with their mosaic of campo rupestre and cerrado vegetation (Giulietti & Pirani 1988, Zappi & Taylor 1994: 77), represent the least modified of the environments in Eastern Brazil (ie. Areas 3c, 3d & 4c). However, they have much greater concentrations of threatened species than the caatingas-agrestes just discussed, and many are of extremely local occurrence and therefore potentially at considerable risk. Widespread and mostly common, non-threatened exceptions include Cipocereus minensis subsp. minensis, Melocactus bahiensis, M. concinnus, Pilosocereus aurisetus subsp. aurisetus, Micranthocereus purpureus and Stephanocereus luetzelburgii, the latter two endemic to the extensive uplands of the Chapada Diamantina, Bahia, and also found within its national park (‘Parque Nacional Chapada Diamantina’, Mucugê–Lencóis, Area 3c(ii)).

Utilization of the campos rupestres is generally limited to cattle grazing, with associated burning to induce re-growth of edible pasture, and local extraction of some plants,
eg. Eriocaulaceae (dried flower export trade — a serious conservation issue), orchids and *Vellozia* spp. (Harley in Stannard 1995: 35–37, Giulietti *et al.* in Davis *et al.* 1997: 403), and there is also limited disturbance caused by small-scale mining for gold and precious stones. In certain areas tourism, including eco-tourism, is becoming popular due to the spectacular scenery. Some parts where *cerrado* vegetation is more abundant are being cut over for the production of charcoal and later converted into *Eucalyptus* plantations, especially in Minas Gerais, where this activity is one of the factors threatening *Uebelmannia* species and *Cipocereus crassisepalus* (Area 4c(iic). The burning for cattle grazing does affect some native populations of cacti, but the regular collection of plants, and nowadays more especially of seed, of certain rare cacti may be cause for greater concern. In addition to some of the CITES Appendix I taxa noted above, the following *campo rupestre/cerrado* cacti are known from only one or two small populations, or at best have a very localized range which does not include any kind of designated protected area: *Arrojadoa dinae* (especially the rare variant, subsp. *eriocalis*), *Arthrocerceus rondonianus*, *Brasilicereus markgrafii*, *Cipocereus bradei*, *C. crassisepalus*, *C. laniflorus*, *C. pusilliflorus*, *Melocactus violaceus* subsp. *ritteri*, *Micranthocereus albicephalus*, *M. auriazureus*, *M. polyanthus*, *M. streckeri*, *M. violaciflorus*, *Pilosocereus aurisetus* subsp. *aurilanatus* and *P. fulvilanatus*, sens. lat. Similarly restricted taxa located within protected areas are rather few: *Arrojadoa bahiensis* (partly inside the ‘Parque Nacional Chapada Diamantina’, Bahia), *Cipocereus minensis* subsp. *pleurocarpus* (partly within the ‘Parque Nacional da Serra do Cipó’, Minas Gerais) and *Arthrocerceus melanurus* subsp. *magnus* (‘Parque Estadual de Ibitipoca’, MG). If extended slightly to its west, the ‘Parque Nacional Chapada Diamantina’ would include a second population of the remarkable *Arrojadoa bahiensis*. The Serra da Piedade (Mun. Caeté, Minas Gerais) is not a designated protected area, but benefits from some protection as a site of religious significance, which has a population of *Arthrocerceus glaziovii*, a specialized species generally restricted to rocks very rich in iron (known as *canga*), many of
its former habitats having disappeared through ore extraction. A peculiar and specialized cactus, found in the sandy *cerrados* bordering on the *caatinga* and *campo rupestre* zones, from western Maranhão to central-eastern Minas Gerais (Area 4a), is *Cereus mirabella*. It is widespread, but of erratic occurrence, and much of the habitat in the southern part of its range is being destroyed by charcoal producers, so its status needs to be monitored carefully.

Locations within Areas 3c & 4c, where new protected areas have been suggested to assist the conservation of the above listed rarities (Taylor in Oldfield 1997, Costa *et al.* 1998), including the earlier discussed CITES Appendix I taxa, are as follows: the sandstone outcrops 20–25 km west of Morro do Chapéu (Bahia), the southern end of the Serra Chapada and associated *cerrado* (27–28 km W of Seabra, BA), the quartzitic outcrops at Brejinho das Ametistas (S Bahia), the Serra Geral c. 12–15 km east of Monte Azul (Minas Gerais), the Serra Geral with white sand *cerrado* 12 km east of Mato Verde (MG), the Serra do Cabral (MG), the western slopes of the Serra de Minas east of Santa Bárbara (Mun. Augusto de Lima, MG), one or more sites for *Uebelmannia* in the vicinity of Diamantina (MG) and likewise for the same genus in the Serra Negra, between Itamarandiba and Rio Vermelho (MG), and the Serra do Caraça (Mun. Santa Bárbara, MG), home of the remarkable *Cipocereus laniflorus*.

Of great concern, in general terms, is the Brazilian Atlantic Forest. This comprises the coastal rainforest (*Mata atlântica* in its strictest sense) and sandy littoral dunes (*restingas*) of North-eastern Brazil and their extensions southwards, where the former broadens and merges with the *planalto* forests of South-eastern Brazil. This more or less humid area, which has a high alpha-diversity of epiphytic cacti from the tribe Rhipsalideae (cf. Ibisch *et al.* 1996), is represented by only a small fraction of the original forest — Myers *et al.* (2000: Table 1) state that only 7.5% of the original primary forest remains. Endemic Rhipsalideae include the horticulturally and economically important genera *Schlumbergera* and *Hatiora*. A few very widespread or regionally common taxa, such as the epiphytic *H.*
saliicornioides, Lepismium cruciforme, L. houletianum, L. warmingianum, Rhipsalis floccosa, R. teres, R. elliptica and R. cereuscula, and the non-epiphytes Brasiliopuntia brasiliensis, Opuntia monacantha, Cereus fernambucensis, Pilosocereus arrabidae and P. brasiliensis are here regarded as at 'Lower Risk', but the remaining Brazilian endemic species are of conservation concern to varying degrees. For example, the wide-ranging but erratically occurring, restinga taxa, Melocactus violaceus subsp. violaceus & margaritaceus, and other coastal cacti, are threatened at various points in their ranges by ever-expanding tourism, urban and agricultural developments (sugarcane/pineapple). At least one extensive population of M. violaceus subsp. margaritaceus and a few plants of Pilosocereus catingicola subsp. salvadorensis (syn. P. rupicola) are, however, currently offered some protection in the 'Estação Ecológica da Serra de Itabaiana', apparently the only effectively managed reserve of its kind in the state of Sergipe. The flora of southern Espírito Santo is poorly understood and its habitats severely altered, but can count a recently described species of Christmas Cactus, Schlumbergera kautskyi (known from only 2 small sites), and the remarkable, red-flowered Rhipsalis hoelleri, as yet not localized with certainty. Other species, represented by disjunct populations or forms, are Hatiora salicornioides f. cylindrica, Rhipsalis cereoides, R. pilocarpa and Schlumbergera microsphaerica (the last within the boundaries of the 'Parque Nacional do Caparaó', which straddles the border with the state of Minas Gerais). Another protected area in this state, which merits investigation, is the 'Reserva Biológica Federal de Nova Lombardia' (in the município of Santa Teresa).

Destruction of the Atlantic Forest has been greatest in North-eastern Brazil, where very little remains (Wayt Thomas in Davis et al. 1997: 364) and, therefore, our knowledge of the flora is correspondingly fragmentary. To judge from the number of taxa known from only one or two records, it is quite possible that epiphytic Cactaceae from here have become extinct before discovery and description. In Paraíba and Pernambuco remnants of
this forest include that termed as ‘brejos’, on higher land far away from the coast, where
the watersheds are an important resource for the human populations living below them.
Such forests have recently been studied and catalogued (Rodal et al. 1998, Sales et al.
1998) as part of an Anglo-Brazilian project, supported by the U.K. Government’s Darwin
Initiative and the Royal Botanic Gardens, Kew (‘Plantas do Nordeste’ programme), with
great emphasis being placed on the need to preserve these floristic refuges which, inter
alia, include disjunct northern populations of cactus epiphytes, such as Lepismium
cruciforme and Rhipsalis crispata. A protected area including one of these brejos is the
‘Reserva Biológica Federal da Serra Negra’, Pernambuco, which includes a population of
the monotypic Brasiliopuntia brasiliensis. Further south, in coastal Bahia (up to 100 km
inland), between the capital Salvador and Teixeira de Freitas, where annual rainfall is
generally in excess of 1750 mm, there are occasional records of various species of
Rhipsalideae, indicating a once rich centre of diversity, including Hatiora salicornioides f.
cyldrica, Rhipsalis paradoxa subsp. septentrionalis (‘Endangered’), R. baccifera subsp.
hileiabaiana, R. russellii (‘Vulnerable’) and R. oblonga. With so little forest remaining,
post 1971, when road BR 101 was completed, it seems reasonable to assume that all of
these are threatened to a significant extent, even if some may benefit from protection in
local reserves, such as the ‘Reserva Biológica Federal de Una’ (south of Ilhéus, BA) and
‘Parque Nacional de Monte Pascoal’ (N of Itamaraju, BA) — other, smaller protected
areas are described by Wayt Thomas in Davis et al. (1997: 367). Table 5.1 lists brejo
forests in NE Brazil (see Map 10) including notable cacti, with dates of most recent
collections. Unfortunately, it is likely that many of these are now much altered or
destroyed. Those brejos that survive merit regular monitoring (Rodal et al. 1998).

Also part of the Brazilian Nordeste, is the Archipelago of Fernando de Noronha, a
Federal Environment Protection area. These Atlantic islands are home to at least one
endemic cactus, Cereus insularis (a close relative of the Brazilian coastal C.
femambucensis), which seems adequately protected at present. A second, putative species, or perhaps a form of the preceding, is *C. ridleii*, which has not been seen since its original collection in the 1950s and may now be extinct (Braun 1990), if, indeed, it is distinct (see Supplement 1). The locations of protected areas that potentially assist the conservation of threatened Cactaceae of Eastern Brazil are indicated on Map 42.

<table>
<thead>
<tr>
<th>Brejo locality (state)</th>
<th>Cactaceae (date of most recent record), notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Serra de Baturité (Ceará)</td>
<td><em>Rhipsalis baccifera</em> subsp. <em>baccifera</em> (1979)</td>
</tr>
<tr>
<td>N slope of Chapada do Araripe (Ceará)</td>
<td><em>Pereskia grandifolia</em> subsp. <em>grandifolia</em> (1971)</td>
</tr>
<tr>
<td>Poção (Pernambuco)</td>
<td><em>Pereskia aculeata</em> (1991)</td>
</tr>
<tr>
<td>Caruaru (Pernambuco)</td>
<td><em>Rhipsalis crispata</em> (1970), <em>R. floccosa</em> (1971) — these species records urgently need re-confirmation in habitat</td>
</tr>
<tr>
<td>Serra Negra, Inajá (Pernambuco)</td>
<td><em>Brasiliopuntia brasiliensis</em> &amp; <em>Rhipsalis lindbergiana</em> (1995)</td>
</tr>
<tr>
<td>Serra do Cumanati (Pernambuco)</td>
<td><em>Rhipsalis floccosa</em> (1969) — this <em>brejo</em> may have been destroyed, since it does not figure in Rodal et al. (1998)</td>
</tr>
<tr>
<td>Mata Grande (Alagoas)</td>
<td><em>Brasiliopuntia brasiliensis</em> (1974)</td>
</tr>
<tr>
<td>Rui Barbosa (Bahia)</td>
<td><em>Pereskia aculeata</em> (1973), <em>Brasiliopuntia brasiliensis</em> (1978)</td>
</tr>
<tr>
<td>Monte Verde, Itabera (Bahia)</td>
<td><em>Pereskia aculeata</em> (1973)</td>
</tr>
<tr>
<td>Jaguaquara (Bahia)</td>
<td><em>Pereskia aculeata, Brasiliopuntia brasiliensis, Rhipsalis russellii</em> (all 1915) — <em>brejo</em> assumed to have been destroyed</td>
</tr>
<tr>
<td>Venceslau Guimarães (Bahia)</td>
<td><em>Hatiora salicornioides f. cylindrica</em> (1993) — in protected area</td>
</tr>
<tr>
<td>Juçári/Jussari (Bahia)</td>
<td><em>Rhipsalis paradoxa</em> subsp. <em>septentrionalis</em> (before 1966)</td>
</tr>
</tbody>
</table>

Table 5.1. *Brejo* forests in North-eastern Brazil with notable Cactaceae and their most recent collection dates. Precise localities are given under materials cited for the above in Supplement 1.
5.3. Criteria for the identification of priority taxa

The internationally agreed process for assessing the level of threat of extinction to living organisms is that established by IUCN, whose latest system aims, as far as is possible, to provide an objective means of determining Categories of Threat, or 'Red List Categories' (IUCN 1994). The principal categories employed in the IUCN system are 'Extinct (EX)', 'Extinct in the Wild (EW)', 'Critically Endangered (CR)', 'Endangered (EN)', 'Vulnerable (VU)' and 'Lower Risk (LR)'. The series of standard criteria that lead to their determination should be stated when an assessment is published, in order that the category can be easily verified or reassessed in the future, as circumstances change. The Categories CR, EN & VU are defined by any one of 5 sets of criteria, which are of a consistent type throughout, but differ in degree for each Category. These criteria can be summarised as follows:

A) Population reduction within 10 years or 3 generations, whichever is the longer (the % reduction varying from 80% for Category CR, to 50% for EN and 20% for VU, and capable of being observed/estimated/inferred in various ways).

B) Extent of occurrence/occupancy estimated to be less than a given area (100/10 km$^2$ for CR, 5000/500 km$^2$ for EN, 20000/2000 km$^2$ for VU) in combination with any two of a range of further criteria, eg. severe fragmentation and/or numbers of populations, decline of populations, fluctuations of numbers of individuals etc.).

C) Population [ie. total population] estimated to number less than a given number of mature individuals (250 for CR, 2500 for EN, 10000 for VU) and differing percentages of further decline over various periods of time are predicted, depending on population structure).

D) Population estimated to number less than a given number of mature individuals (50 for CR, 250 for EN, 1000 for VU) or, for VU alone, the area of occupancy is acutely restricted (< 100 km$^2$) or located at less than 5 sites.
E) Quantitative analysis indicates the possibility of extinction in the wild is a given %
with a varying number of years or generations, whichever is the longer (ie. 50% within
10 years / 3 generations for CR, 20% within 20 years / 5 generations for EN, and 10%
within 100 years for VU).

It is a relief to be able to report that the present study has not identified any Cactaceae
native of Eastern Brazil that belong in either the ‘Extinct’ or ‘Extinct in the Wild’
categories, but, unfortunately, there is no shortage of taxa whose assessments place them in
the remaining categories. The last of the categories listed above (LR) is divisible into a
series of subcategories as follows: ‘Conservation Dependent (cd)’ for taxa where current
conservation action (eg. within a protected area) is avoiding an increase in the risk of
extinction; ‘Near Threatened (nt)’ for taxa that are not benefiting from protection as above
and are close to qualifying as VU; ‘Least Concern (lc)’ for taxa that do not qualify for
either of the above LR subcategories; and ‘Data Deficient (DD)’ where there is inadequate
information to make a direct or indirect assessment of its risk of extinction based on
geographical distribution and/or population status. This last subcategory applies to 4 out of
the 161 taxa covered in the present study, while a further 3 and most natural hybrids have
not been assessed, ie. these are referred to as ‘Not Evaluated (NE)’. The assessments made
in this study are recorded under each taxon in the ‘Formal Taxonomic Treatment’
(Supplement 1) and are based on the total range of the taxon, whether or not it is endemic
to Eastern Brazil as defined here.

The standard methodology embodied in the published IUCN system is not being
questioned here. However, as noted by Farjon & Page (1999) for conifers, its application
can result in rather long lists of equally threatened taxa, suggesting that further
prioritisation is desirable if the limited resources currently applied to nature conservation
are not to be spread too thinly. Farjon & Page (1999: 28) have devised a novel additional

* ‘Occurrence’ referring to the total geographical area, ‘occupancy’ to the area of specific habitat in which
the taxon is found; eg. a species may occur in a large area within the caatinga zone, but actually occupy only
isolated limestone outcrops of much smaller area within that zone.
formula for achieving such a prioritisation, which has proved eminently capable of being applied here. This formula calculates a score based on the Category of Threat, where arbitrarily assigned values of CR=4, EN=3, VU=2 and LR=1, are multiplied by the sum of 3 other criteria, namely ‘Phylogenetic Distinction’, ‘Ecological Importance’ and ‘Genetic Diversity’, whose ranges of values are given below. The resulting total score effectively short-lists and prioritises between taxa with the same IUCN rating, as can be seen for the cacti of Eastern Brazil in Table 5.2. The Farjon & Page criteria are defined as follows:

*Phylogenetic distinction* (PD). This is a measure of the relative taxonomic isolation of an organism and recognises that not all taxa of the same rank are equal. Thus, if the taxon is representative (a) of a monotypic genus, it scores 4; (b) of a species or infraspecific rank of a small genus (2–5 species) or monotypic infrageneric rank within any genus, it scores 3; (c) of a species of a larger genus (>5 species*), it scores 2; and (d) of an infraspecific rank of a species of a larger genus, it scores 1.

*Ecological importance* (EI). This was devised with forest conifers in mind, but can be applied equally to cacti, which are also woody and frequently take the place, or are an important component of arborescent vegetation in dryland ecosystems. Here, if a taxon is co-dominant in a distinct vegetation type, it scores 2; if it is only a more minor constituent of the vegetation, it scores 1. (Farjon & Page, l.c., give a score of 3 to what they call ‘keystone species of a biotic community’, but none of the cacti treated here seems to fall into this category, although some of the arborescent cereoids arguably come close and those found elsewhere in the Americas would definitely qualify, eg. some Mexican Pachycereeeae.)

* Farjon & Page, l.c., divide small and larger genera on the basis of ‘2–5’ versus ’>6’ species, leaving genera with exactly 6 species in limbo. The author is grateful to Aljos Farjon (pers. comm., 30.11.99) for clarifying that the stated ’>6’ should be read as >5 species.
Genetic diversity (GD). This criterion distinguishes between taxa known to be unusually rich in regional diversity, often expressed in high levels of morphological variation or varied ecological adaptation, from those whose genetic diversity is less. This is the most subjective of the Farjon & Page additional criteria, at least if based only on morphological and ecological assessments, because it is known from modern studies of conservation genetics that taxa which appear to be variable may have low levels of measurable genetic diversity and vice versa. However, since it will be many years before the population genetics of the cacti of Eastern Brazil have been properly investigated in the laboratory, use of this criterion remains justifiable as the best option available. Taxa displaying genetic diversity within and/or between regional populations receive a score of 2 (eg. Uebelmannia gummifera and Espostoopsis dybowskii), less diverse taxa scoring 1 (eg. Melocactus violaceus subsp. ritteri) — see Supplement 1 for details in each case.

The short-list formula is, therefore, calculated as follows: IUCN category of threat (score 1–4) × (PD [score 1–4] + EI [score 1–2] + GD [score 1–2]); see Table 5.2 (below).

<table>
<thead>
<tr>
<th>Conservation short-list score (see Formal Taxonomic Treatment, Supplement 1) / shared priority order / taxon / (state codes)</th>
<th>IUCN Category (criteria)/ CITES App.†</th>
<th>Area (Table 5.3 qv)</th>
<th>References to protected area proposals and other recommendations</th>
</tr>
</thead>
<tbody>
<tr>
<td>24</td>
<td>1. Espostoopsis dybowskii (BA)</td>
<td>EN (B1/2bce) / App. II</td>
<td>3d(ia)</td>
</tr>
<tr>
<td></td>
<td>1. Melocactus deinacanthus (BA)</td>
<td>CR (B1/2c) / App. I</td>
<td>3b(iii)</td>
</tr>
<tr>
<td></td>
<td>2. C. pusilliflorus (MG)</td>
<td>CR (D) / App. II</td>
<td>3c(iii)</td>
</tr>
<tr>
<td>4. <em>Melocactus conoideus</em> (BA)</td>
<td>CR (B1/2c) / App. I</td>
<td>3d(ib)</td>
<td>Adequate protection for a recently designated site is needed (see below).</td>
</tr>
<tr>
<td>4. <em>M. pachyacanthus</em> subsp. <em>pachyacanthus</em> (BA)</td>
<td>CR (A2c) / App. II</td>
<td>3b(ii)</td>
<td>Conservation <em>ex situ</em> may be the only option available.</td>
</tr>
<tr>
<td>15</td>
<td>5. <em>Cipocereus minensis</em> subsp. <em>pleurocarpus</em> (MG)</td>
<td>EN (B1/2c) / App. II</td>
<td>4c(iii)</td>
</tr>
<tr>
<td>5. <em>Arthrocereus melanurus</em> subsp. <em>magnus</em> (MG)</td>
<td>EN (C2b) / App. II</td>
<td>4c(iii)</td>
<td>Included within the 'Parque Estadual do Ibitipoca'.</td>
</tr>
<tr>
<td>5. <em>A. melanurus</em> subsp. <em>odorus</em> (MG)</td>
<td>EN (B1/2c) / App. II</td>
<td>4c(iii)</td>
<td>Part of range incl. in 'Parque Nacional Serra do Cipó'.</td>
</tr>
<tr>
<td>5. <em>Discocactus bahiensis</em> (BA/PI/CE)</td>
<td>EN (A1ac) / App. I</td>
<td>3a(ii)</td>
<td>A site is recommended for protection here (see below).</td>
</tr>
<tr>
<td></td>
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<td>---</td>
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<td>---</td>
</tr>
<tr>
<td>7. Schlumbergera kautskyi (ES)</td>
<td>EN (B1/2c) / App. II</td>
<td>2d(ii)</td>
<td>Sites are recommended for protection here (see below).</td>
</tr>
<tr>
<td>7. Arrojadoa bahiensis (BA)</td>
<td>VU (D2) / App. II</td>
<td>3c(ii)</td>
<td>Probably not a high priority for further protection, but see discussion below relating to Melocactus paucispinus.</td>
</tr>
<tr>
<td>7. A. dinae subsp. dinae (BA/MG)</td>
<td>VU (B1/2c) / App. II</td>
<td>3c(iii)</td>
<td>Taylor in Oldfield (1997): 144, prop. 105(e).</td>
</tr>
<tr>
<td>7. C. fluminensis subsp. decumbens (MG)</td>
<td>EN (B1/2c) / App. II</td>
<td>2d(i)</td>
<td>Costa et al. (1998): 67, prop. E7?</td>
</tr>
<tr>
<td>7. Melocactus azureus subsp. azureus (BA)</td>
<td>EN (B1/2bcd) / App. II</td>
<td>3b(ii)</td>
<td>Conservation within the ‘Área de Proteção Ambiental’ (APA): ‘Gruta dos Brejões / Vereda do Romão Gramacho’ is best option for this taxon.</td>
</tr>
<tr>
<td>7. M. pachyacanthus subsp. viridis (BA)</td>
<td>CR (B1/2a–c/ C2a/D) / App. II</td>
<td>3b(ii)</td>
<td>Conservation ex situ may be the only option available.</td>
</tr>
<tr>
<td>7. M. paucispinus (BA)</td>
<td>EN (B1/2ce) / App. I</td>
<td>3c(i)</td>
<td>Taylor in Oldfield (1997): 144, prop. 105(c). A second site is recommended for protection here (see below).</td>
</tr>
<tr>
<td>7. M. violaceus subsp. ritteri (BA)</td>
<td>CR (B1/2c) / App. II</td>
<td>3d(ia)</td>
<td>Sites are recommended for protection here (see below).</td>
</tr>
<tr>
<td>7. Discocactus zehntneri subsp. zehntneri (BA)</td>
<td>EN (B1/2b–d) / App. I</td>
<td>3b(ii)</td>
<td>Requires further field studies to determine conservation options.</td>
</tr>
<tr>
<td>8. Rhipsalis russellii (BA/MG/ES?)</td>
<td>VU (B1/2b–e) / App. II</td>
<td>1b</td>
<td>Part of range incl. within ‘Parque Nacional Chapada Diamantina’ (nr Mucugê, BA) and, possibly, ‘Parque Nac. de Monte Pascoal’ (SE Bahia).</td>
</tr>
</tbody>
</table>
10 (cont.)

<table>
<thead>
<tr>
<th>No.</th>
<th>Taxon Name (Abbreviation)</th>
<th>Threat Category</th>
<th>Score</th>
<th>Reference(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>8.</td>
<td>R. pilocarpa (MG/ES)</td>
<td>VU (B1/2a–d) / App. II</td>
<td>2d(ii)</td>
<td>See site recommended for Schlumbergera kautskyi here.</td>
</tr>
<tr>
<td>8.</td>
<td>Micranthocereus flaviflorus (BA)</td>
<td>VU (B1/2c) / App. II</td>
<td>3(c(ii)</td>
<td>Taylor in Oldfield (1997): 144, prop. 105(b).</td>
</tr>
</tbody>
</table>

| 9.  | Melocactus azureus subsp. ferreophilus (BA) | EN (B1/2c–e) / App. II | 3b(ii) | Conservation *ex situ* may be the only option available. |

Table 5.2. ‘League-table’ of conservation priorities for taxa short-list scores ranging from 24 to 9. The above 51 taxa represent approximately one third of the 154 Cactaceae native to Eastern Brazil scored in this exercise (omitting 4 taxa scored as ‘Data Deficient’ and 3 that were ‘Not Evaluated’ from the total of 161). The full range of scores was from 24 down to 3 and it is important to stress that many of the remaining 103 taxa scored also merit conservation action. **Key to IUCN Categories of Threat codes.** CR = Critically Endangered, EN = Endangered, VU = Vulnerable. † = Convention on International Trade in Endangered Species (CITES): trade in wild-collected CITES Appendix I taxa is prohibited, while those in CITES App. II and artificially propagated App. Itaxa may be traded under export and import licences issued by national management authorities.

More sophisticated uses of phylogenetics and population genetics for assessing conservation priorities are discussed by Linder (1995), in relation to the Southern African

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* According to Marlon Machado (in litt., 20.05.2000) an official reserve at Grão Mogol, called ‘Parque Estadual da Serra do Barão’, had been created when he visited the town in May 1999.
orchid genus, *Herschelia*, but such methods require a considerably more detailed knowledge of relationships and biology/ecology than is currently available for most Brazilian cacti.

### 5.4. Conservation hotspots

The above short-listing process can also be used to identify geographical areas of high priority for attention by conservationists, these nowadays commonly being referred to as ‘hotspots’ (Reid 1998, Myers *et al.* 2000). Here (Table 5.3), the short-list scores of the top

<table>
<thead>
<tr>
<th>Priority hot-spots (sum of taxon scores from Table 5.2)</th>
<th>Endemics (no. × score)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A). Second order Area subdivisions</strong></td>
<td></td>
</tr>
<tr>
<td>1 (93). South-eastern <em>campos rupestres</em> (MG): Southern part [4c(iii)]</td>
<td>1×20, 1×18, 3×15, 1×10</td>
</tr>
<tr>
<td>2 (84). SE <em>campos rupestres</em> (MG): Diamantina eastwards [4c(iic)]</td>
<td>1×20, 3×18, 1×10</td>
</tr>
<tr>
<td>3 (66). SE <em>campos rupestres</em> (MG): Serra do Cabral etc. [4c(iib)]</td>
<td>1×20, 1×15, 1×12, 1×10, 1×9</td>
</tr>
<tr>
<td>3bis (66). Northern <em>campos rupestres</em>: N Serra do Espinhaço [3c(iii)]</td>
<td>1×20, 1×18, 1×16, 1×12</td>
</tr>
<tr>
<td>4 (62). Rio São Francisco <em>caatingas</em>: southern <em>caatingas</em> etc. [3b(iii)]</td>
<td>1×24, 1×15, 1×14, 1×9</td>
</tr>
<tr>
<td>5 (61). Rio São Francisco <em>caatingas</em>: cent.-northern Bahia [3b(ii)]</td>
<td>1×16, 3×12, 1×9</td>
</tr>
<tr>
<td>6 (54). Northern <em>campos rupestres</em>: Chapada Diamantina (BA) [3c(ii)]</td>
<td>2×16, 1×12, 1×10</td>
</tr>
<tr>
<td>7 (48). Eastern <em>caatingas-agrestes / campos rupestres</em> [3d(iia)]</td>
<td>1×24, 2×12</td>
</tr>
<tr>
<td>8 (38). SE <em>campos rupestres</em> (MG): Grão Mogol etc. [4c(iia)]</td>
<td>1×16, 1×12, 1×10</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>B). First order Area subdivisions</strong></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1 (291). South-eastern <em>campos rupestres</em> (Minas Gerais) [4c]</td>
<td>3×20, 4×18, 1×16, 4×15, 2×12, 5×10, 1×9</td>
</tr>
<tr>
<td>2 (132). Northern <em>campos rupestres</em> (BA/MG) [3c]</td>
<td>1×20, 1×18, 3×16, 3×12, 1×10</td>
</tr>
<tr>
<td>3 (123). Rio São Francisco <em>caatingas</em> (BA/MG) [3b]</td>
<td>1×24, 1×16, 1×15, 1×14, 3×12, 2×9</td>
</tr>
<tr>
<td>4 (102). Eastern <em>caatingas-agrestes / campos rupestres</em> [3d]</td>
<td>1×24, 2×16, 3×12, 1×10</td>
</tr>
<tr>
<td>5 (34). Southern subhumid/humid forest and inselbergs (MG/ES) [2d]</td>
<td>2×12, 1×10</td>
</tr>
</tbody>
</table>

Table 5.3. ‘League-table’ of principal conservation area hot-spots based on a summation of the scores presented in Table 5.1. Key. BA = Bahia, MG = Minas Gerais, ES = Espírito Santo.
51 priority taxa have been summed according to the geographical area patterns they are characteristic of (Chapter 4), giving a prioritised list of these area subdivisions, which can be analysed at different scales of area. This indicates that the South-eastern campos rupestres (Area category No. 4c) are by far the most important for attention by conservationists and land managers. This subdivision is followed by 3 with very similar scores: 2\textsuperscript{nd} the Northern campos rupestres (3c), 3\textsuperscript{rd} the Caatingas of the Rio São Francisco (3b) and 4\textsuperscript{th} the Eastern caatingas-agrestes / campos rupestres (3d), each of whose scores are comparable, but less than half the value of the first-named area. Nevertheless, they include taxa of key conservation importance. In last place, in terms of Cactaceae, comes the Atlantic Forest, whose present state of destruction is so great that all remaining areas merit immediate preservation. Unfortunately, cactus diversity can only play a small role in the biological and other arguments in support of this obvious need.

Reid (1998: 278–279) discusses the different approaches to defining hotspots. For example, using a complementarity method and starting, in this case, with the area containing the highest scores of endemic and threatened taxa and successively adding immediately adjacent areas with the next highest scores (see Table 5.3, part A), we get a result close to that indicated above in Table 5.3, part B, namely 3 out the 4 subdivisions of the South-eastern campos rupestres [ie. 4c(iii)+(iib)+(iic)] whose combined score would be 253. To these could then be added the adjacent part of the Northern campos rupestres [subdivision 3c(iii)], raising this score to 319. Leaving these aside and starting with the next highest scoring areas outside of the South-eastern campos rupestres we get (Table 5.3, part B) two closely adjacent pairs comprising nos. 3bis+4 (66+62 = 128) and nos. 5+6 (61+54 = 115). However, even if these are restricted to the minimal areas required to include the distributions of the most threatened taxa they hold, the resultant areas requiring protection are massive and probably unrealistic. A solution to this difficulty is to adopt an inventory based on small arbitrarily defined units of area, such as that employed in north-
eastern Mexico by Gómez-Hinostrosa & Hernández (2000). Another approach is to first identify the main biogeographic regions and then attempt to protect a realistic percentage of habitat in each. Then, Table 5.3, part B, already identifies 5 such regions within each of which a more restricted and manageable reserve could be designated. These would ideally be sited so as to include as many of the highest scoring taxa listed in Table 5.2 as possible.

5.5. Priority actions recommended

Since the late 1970s when eminent Brazilian botanists, such as Dârdano de Andrade-Lima (1981) and Nanuza de Menezes (in many verbal presentations), drew attention to the levels of modification and threats being suffered by the caatingas and campos rupestres, only relatively few and mostly very small protected areas have been created in the more than one million square kilometres of land surface in which these major ecosystems are represented in Eastern Brazil. The various federal and state reserves offering protection to Cactaceae have been mentioned already, but many more are needed, as has been indicated by recent symposia and studies conducted by international, governmental and non-governmental interests (Oldfield 1997, IBAMA 1997, Costa et al. 1998), in which the present author participated. The most encouraging development of recent times is the evolution of various legal instruments that offer Brazilian municipalities and citizens tax credits in return for the setting aside for conservation reasons of natural areas they oversee or own (cf. Costa et al. 1998). In addition to these, Brazilian cactus enthusiasts are attempting to persuade municipal authorities to establish local protected areas and take pride in the rare taxa and unusual habitats that they were probably unaware of until very recently. Such developments are to be greatly applauded and, none more so, than the remarkable achievement represented by the publication of the comprehensive report, entitled 'Biodiversidade em Minas Gerais' (Costa et al. 1998). This places the collective knowledge of conservation priorities for the state of Minas Gerais on a level that all other
Brazilian states from the area covered in this study need to emulate. It is only to be hoped that the recommendations in this ground breaking report will be actioned by the authorities empowered to do so, and especially, since the present study identifies by far the greatest concentration of conservation priority taxa as endemics of Minas Gerais (see Tables 4.1, 5.2 & 5.3). The same aspirations apply to the need for protected areas and associated actions detailed in the IUCN-SSC Cactus & Succulents Action Plan (Oldfield 1997). The following additional actions are recommended here:

- **Establishment of local reserves / protected areas** (A1 = taxon in CITES App. I):

  1. For the first listed taxon with the highest priority in Table 5.2, *Espostooptis dybowskii*, in the Município of Jaguarari, northern Bahia, to complement that recommended for its southern populations (Oldfield 1997: 143) and to protect it from urban expansion.

  2. For the equally high scoring *Melocactus deinacanthus* (A1), known for certain from only one locality (‘Morro da Barriguda, Juá’) on a small, isolated gneissic outcrop in Mun. Bom Jesus da Lapa (at the border of Mun. Riacho de Santana), southern Bahia, to protect it from agricultural activities including depredations by livestock.

  3. A reserve for *Melocactus conoideus* (A1), above Mun. Vitória da Conquista, Bahia, has recently been designated, but needs better enforcement, since habitat destruction caused by gravel extraction and urban expansion continue (M. Machado, in litt., 20.05.2000).

  4. For *Discocactus bahiensis* (A1), in an area of former flood plain of the Rio São Francisco, near Rodeadouro, WSW of Juazeiro, northern Bahia. More than half of this population was recently destroyed by the construction of an embanked asphalt road, but healthy plants remain at the western edge of the former site dominated by *Mimosa tenuiflora* bushes.

  5. For *Schlumbergera kautskyi*, at mountain sites (inselbergs) in Mun. Domingos Martins (Pico da Pedra Azul) and Mun. Alfredo Chaves (São Bento de Urânia), Espírito Santo, from which region a range of other rare Rhipsalideae is also reported: *Rhipsalis pacheco-leonis* subsp. *catenulata*, *R. cereoides*, *R. sulcata*, *R. burchellii*, *R. pilocarpa* and, perhaps, *R. hoelleri*. This region is being developed as a high cost residential and tourism area.
6. For *Melocactus paucispinus* (A1), at its sites around the Pico das Almas, Mun. Rio de Contas / Érico Cardoso (Água Quente), Chapada Diamantina, Bahia. Inclusion of the Pico das Almas itself would also protect a population of the remarkable *Arrojadoa bahiensis*.

7. For *Melocactus violaceus* subsp. *riteri*, at its two sites near to the towns of Jacobina and Rui Barbosa, Bahia, to protect it from urban expansion and general habitat disturbance.

- **Establishment of ex situ gene banks to enable future re-introductions, if Extinction in the Wild should occur:**

1. Specifically for *Melocactus azureus* subsp. *ferreophilus* and *M. pachyacanthus* (2 subspp.), whose known habitats are in imminent peril of destruction and hold wild populations that are highly fragmented or numbering only tens of individuals. It is desirable that projects for the cold storage of seeds in one or more seed banks (Dickie *et al.* 1990, Yang 1999), supplemented by *ex situ* gene banks of living plants under controlled conditions of pollination (to avoid hybridisation), are established. However, this should not detract from any efforts to conserve wild populations, if sufficiently intact habitats can be protected.

2. The above actions are equally applicable to many of the taxa discussed in this chapter, as well as others in the 'Formal Taxonomic Treatment' (Supplement 1), where it is difficult to identify secure protected areas, or where there is a severe risk of catastrophic reduction in genetic diversity. In the latter case, seed banking may provide an effective insurance, if collecting programmes are carefully designed.

- **Monitoring of wild populations**

Regular monitoring of the status in the wild of many of the taxa documented in the 'Formal Taxonomic Treatment' (Supplement 1) is essential, whether or not these are currently rated as threatened (eg. those listed in Table 5.1, above). Many taxa presently assessed as 'Lower Risk' are likely to become 'Vulnerable' in due course and could become yet more seriously threatened shortly thereafter, if timely conservation actions are not triggered.

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Maps 42 & 43 (pages 371 & 372): 42, location of protected areas (sensu lato) that potentially assist the conservation of threatened Cactaceae of Eastern Brazil (NB. Fernando de Noronha in the Atlantic Ocean); 43, location of the 19 single site endemic taxa (see Table 4.1 and Supplement 1).
Chapter 6

CONCLUSIONS

This study has been mainly one of critical inventory, attempting to bring order to a complex group of plants that, prior to the 1990s, were poorly understood in terms of their relationships and geographical extent. Having come so far it is time to draw conclusions from the work of inventory and describe the spin-offs from it — a better understanding of the history of discovery, of phytogeography and of conservation priorities.

Eastern Brazil is a vast tropical area known to be rich in cactus diversity and endemism. Early explorers could document little of this due to the difficulty cacti presented for the preservation and description of living and museum specimens, not to mention the inaccessibility of so many of the most biodiverse Brazilian cactus habitats prior to the mid-twentieth century. Most taxa now known were discovered in the past 100 years, the majority being named and classified by horticulturists, whose activities greatly distorted the number of botanically justifiable entities and their geographical range. Even so, many 'good' taxa do have rather restricted ranges and in an area of c. 2M km² extensive field excursions have been essential for the determination of generic and specific limits and adequate documentation of distribution and ecological data. In combination with herbarium and literature studies the outcome has been the
recognition of 30 genera, 134 species and 43 heterotypic subspecies, and the completion of identification guides to all of these. From this base of information a number of clear conclusions can be drawn:

1. Level, origin and significance of high endemism. In Eastern Brazil cactus biodiversity is concentrated in Bahia and Minas Gerais — each having > 90 taxa and 30 or more state endemics (Table 4.1). The most likely explanation for this is greater complexity and discontinuity of habitats, leading to isolation of taxa and increased speciation, but past forces of extinction, climate history and the age of the different environments must also be key factors. Prado (1991) accepts the view that the caatingas are an old environment, dating from the late Tertiary period. This he believes is confirmed by the high levels of endemism in families such as the Cactaceae, from which he cites examples, although in the light of a better taxonomic understanding not all of these now hold true (eg. Arrojadoa and Stephanocereus, while endemic to E Brazil, are not restricted to the caatingas). Indeed, the present study suggests that endemism in the caatinga Cactaceae is considerably higher than he could have been aware (given the poor state of published knowledge available to him). This is detailed in Chapter 4, under Area category no. 3 (see also Table 4.4). Whether high endemism can be upheld as an indicator of age is clearly debatable (consider, for example, the case of the flora of Hawaii, which is rich in endemics but of recent origin) and other evidence, such as the presence of dry environments elsewhere in South America during the Tertiary, may be more telling (Burnham 1995, Burnham & Graham 1999: 557). Whatever the explanation, of equal significance is the high endemism of Cactaceae in the
campos rupestres, which occupy a tiny area when compared with the caatingas that surround or adjoin them. The campos rupestres may also be old environments, whose floras have been protected from climatic fluctuations and contain at least some elements dating from the Tertiary (Harley in Stannard 1995: 33–34). Knowledge of the Cactaceae as a whole strongly implies that a substantial part of the cactus endemism in both vegetation types is autochthonous, ie. it has evolved in situ (eg. much of tribe Cereeae), rather than being a derivative of another flora, such as the Atlantic Forest, whose contribution must be smaller than Rizzini (1979) supposed. The high cactus diversity in Bahia and Minas Gerais, compared to the relative impoverishment of the family in the Northern caatingas, may suggest that the northern areas lacked the refuges provided by the diverse terrain in the two southern states, which could have offered protection during Pleistocene climatic fluctuations, when drought intensified (Tricart 1985).

2. Phytogeography and historical migration routes. Cactus phytogeography lends support to recent hypotheses on historical plant migration routes involving dry seasonal forest formations in South America. Amongst the origins and routes discussed by Prado (1991: Fig. 8.3) for the flora of the caatingas, the following are supported by examples from the Cactaceae of the caatinga-agrestes and adjacent dry phases of the Mata atlântica etc. of Eastern Brazil: (i) the Caribbean islands and coastal regions of northern South America ('Guajira province'), via a trans-Amazonian route; (ii) the same region and/or dry valleys of the central Andes, via a western route including the 'Pleistocene Arc'; (iii) N South America or beyond, via a 'pincers movement' (ie. via both trans-Amazonian and Andean
routes; (iv) foothills of the eastern Andes (including the ‘Piedmont’ and W Chaco) and Misiones nucleus, via the ‘Pleistocene Arc’; (v) the Atlantic Forests of Brazil; and (vi) the *cerrados* of Central-western Brazil. Some of the clearest examples supporting routes (i)–(vi) are summarized below in Table 6.1. It should be noted that here it is not necessarily the origin of the *caatinga* flora that is being elucidated, rather that the *caatinga* is one of the nodes for migration routes, which may either have brought taxa to it, or from it to other dry areas. When more phylogenies are available for Cactaceae, like those recently obtained for *Pereskia* and *Harrisia*, it may be possible to determine the directions of these radiations. A further point to note is that Prado’s routes should not be seen as mutually exclusive, since, for example, (i), (ii) and (iv) are essentially subsets of (iii). Nevertheless, for ease of comparison his list has been followed in the table below.

<table>
<thead>
<tr>
<th>Region / migration route (Map refs)</th>
<th>Vicariant taxa / ranges (country codes [± Brazilian state codes]: E Brazilian vegetation types)</th>
<th>Notes</th>
</tr>
</thead>
</table>
| (i) Caribbean & ‘Guajira province’, via Amazonia (see Maps 5 & 6) | (1) *Pereskia guamacho* (CO,VE) & allies (Caribbean): *P. aureoflora* (S *caatingas-agrestes*) 
(2) *Pseudoacanthocereus sicariguensis* (CO,VE): *P. brasiliensis* (E *caatingas-agrestes*) 
(3) *Cereus hexagonus* (CO,VE,GY,GF,SR,RR[PA]): *C. jamacaru* (caatingas-agrestes) 
(4) *Harrisia* subg. *Harrisia* (Caribbean): *H. ascendens* (caatingas) | (1) & (3) were examples in Prado, l.c.; (1) & (4) are now confirmed by molecular evidence. NB. *Pseudoacanthocereus* has only 2 species |
| (ii) Ibid., via dry cent. Andean valleys and the ‘Pleistocene Arc’ (see Map 2) | (1) *Prorocereus* (CO,VE,EC,PE,BO,RY,AR,RR[MS,SP,PR]): *Brasilicereus* (S *caatingas-agrestes* & adjacent campos rupestres) | Relationship needs to be confirmed by molecular data |
| (iii) N South America and beyond, via both (i) and (ii) above | (1) *Hylocereus setaceus* complex (MX,BE,CO,EC,PE,BO,RY,AR,GF,SR,RR[PA,MS,PR], / caatingas & Mata atlântica) | See Chap. 3.2 & Supplement 1 for notes on this complex |

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3. Palaeoclimatic evidence. In addition to his discussion of migration routes for species of dry seasonal forests in South America, Prado (1991: 232–239) considered palaeoclimates and particularly the Pleistocene fluctuations, when the *caatingas* and similar dry forests appear to have expanded (12–18,000 years BP). He presents evidence that the northern *caatinga* area expanded westwards into Maranhão and thence northward, forming a corridor along a route including the Monte Alegre / Faro area (region of Santarém, Pará) and north of the Amazon River to the Roraima/Guyana area, potentially linking ultimately with the dry areas in present day northern South America (‘Guajira province’). Such a route seems plausible on the basis of the known distribution of the as yet inadequately resolved *Cereus jamacaru* / *C. hexagonus* taxonomic complex, *C. jamacaru* subsp. *jamacaru* ranging north-westwards at least as far as the limits of Eastern

| (iv) Via the 'Pleistocene Arc', from the floristic nodes it connects (see Maps 3, 5 & 7) | (1) *Pereskia sacharosa* & *P. nemorosa* (BO,AR,PY,BR[MT,MS,RS]: remainder of P. GRANDIFOLIA Group (Mata atlântica & S caatingas) <br> (2) *Quaiabentia verticillata* (BO,PY,AR): *Q. sehntneri* (SW caatingas) <br> (3) *Brassiliopuntia brasiliensis* (PE,BO,AR,PY / caatingas-agrestes & dry phases of Mata atlântica) <br> (4) *Cereus* subg. *Ebneria* (BO,AR,PY,BR[MT,MS,RS]): C. subg. *Mirabella* (caatingas & adjacent E Brazilian cerrados) <br> (5) *Harrisia* subg. *Eriocereus* (BO,AR,PY,UY,BR[MS]): *H. adscendens* (caatingas) | Molecular evidence has *Harrisia* spp. and the western pereskias as basal or potentially basal within their respective groups. <br> NB. *Quaiabentia* has only 2 species |
| (v) Brazilian Atlantic Forest (see Maps 13, 14A, 16A, 23, 26A & 31B) | (1) *Pereskia grandifolia* (BR[CE,PE,MA,ES,RJ,SP,SC]): *P. bahiensis* & *P. stenantha* (Bahian & SW caatingas) <br> (2) *Pilosocereus catingicola* subsp. *salvadorensis* (BR[RN,PB,PE,AL,SE,BA]): *P. catingicola* subsp. *catingigola* (Bahian caatingas-agrestes) | Molecular evidence indicates *Pe. grandifolia* subsp. *violacea* as basal to the caatinga taxa |
| (vi) Central-western Brazilian cerrados | (1) *Discocactus heptacanthus*, s.l. (PY,BO,BR[MS,MT,GO,TO,PI,BA,MG]): *D. bahiensis* & *D. sehntneri* (N caatingas & adjacent N campos rupestres) | See Chap. 3.2 & Supplement 1 |

Table 6.1. Cactus evidence in support of historical migration routes to and from the caatingas etc., as proposed by Prado (1991).
Brazil (see Map 19). Equally significant is *Pilosocereus flavipulvinatus*, which also ranges to the western border of Maranhão, reaching Carolina (see Map 20). Furthermore, Zappi (1994: 69) suggests that this species provides a link to the related *P. oligolepis*, known only from the Roraima/Guyana region and the northernmost member of the large and otherwise endemic E Brazilian *P. PENTAEDROPHORUS* Species Group. Do the present ranges of *P. flavipulvinatus* and *P. oligolepis* represent remnants of a Pleistocene expansion of the caatingas? If so, then it is possible that the presence of *Tacinga inamoena, Melocactus zehntneri* and *Leocereus bahiensis* on rock outcrops in the *cerrados* of westernmost Bahia, and of *Pilosocereus ulei* at Cabo Frio, Rio de Janeiro (Araújo in Davis *et al.* 1997: 373) are also remnants representative of former *caatinga* expansions (Maps 19 & 21C). Similarly, the disjunct occurrences of *Tacinga funalis, Arrojadoa penicillata* and *Harrisia adscendens* in sand-dunes west of the Rio São Francisco (NW Bahia) could represent historical range extensions during these Pleistocene fluctuations, when the river is believed to have dried up in its middle section (Tricart 1985: 210). These are not taxa that are likely to have been long-distance dispersed into this area (see Chap. 4.6 & Table 4.7).

4. **Analysis of distribution patterns.** Within Eastern Brazil > 94% of taxa are ± restricted to one of 3 major vegetation-area categories: (1) *Mata atlântica* 25%, (2) *Caatingas* & Northern *campos rupestres* 51.5%, and (3) *Cerrados* & Southeastern *campos rupestres* 17%. Significantly, the *campos rupestres* are divisable into two areas on the basis of cactus diversity, having slightly more in common with the vegetation types that surround them, ie. *caatinga* or *cerrado*, than with
each other, although the distinctions between them also owe much to their very
different suites of endemics. In contrast to what has been stated in general floristic
terms (Giulietti et al. in Davis et al. 1997: 400), the Northern campos rupestres do
show significant floristic links with the caatingas, at least with reference to
Cactaceae. Of taxa included in the Caatingas & Northern campos rupestres,
> 70% belong to one of three major geographical-ecological areas, ranged west to
east. These correspond closely with topographic phenomena and to the origins of
the taxa displaying extra-Brazilian phytogeographical links. A very significant
assemblage of caatinga cacti is found in north-eastern Minas Gerais, in the middle
drainage of the Rio Jequitinhonha (between Salinas, Araçuaí, Pedra Azul, Padre
Paraíso and Jacinto), where a mixture of widespread, locally endemic-vicariant
and isolated endemic taxa imply that this restricted area may have been cut off
from the main caatinga zone to the north for substantial periods of time. While it
falls outside of the North-eastern Region of Brazil, this is an important stronghold
for caatinga cacti, which should be urgently considered as part of an overall
strategy for the conservation of this biome and its biodiversity.

5. Conservation. While the study of plant diversity and geography is a rewarding
academic activity, it is the author's conviction that such investigation should, as
far as possible, lend support to the conservation and sustainable use of the
environment and its included species. To this end the conservation status of most
taxa has been determined using information gathered for the taxonomic inventory
and by applying IUCN 1994 'Red List Categories' combined with Farjon & Page
criteria ('phylogenetic distinction', 'ecological importance', 'genetic diversity').
This has enabled the compilation of prioritised shortlists of Critically Endangered, Endangered and Vulnerable taxa, and of Area hotspots, both intended as guidance to conservationists, planners and land managers. Whilst this has shown the South-eastern *campos rupestres* to be of the greatest concern in terms of threatened taxa, because so many of these are of highly restricted occurrence, it is equally important to stress that many of the widespread taxa of the *caatingas* and *Mata atlântica* are also suffering severe reductions in range and implied genetic diversity (cf. Brasil 1998: 49, Tab. 2-17). In a country with the size and economic momentum of Brazil, where sources of fossil fuel are very limited, it is difficult for the wood of the *caatinga* to be sustainably harvested. With it disappear the shade and protective nurse plants for the vulnerable seedlings of cacti, a plant group that figures large in the local culture of the Nordeste. Loss of these and the rest of biodiversity soon follow, as can desertification. However, it is pleasing to note that Brazilian legislators have been evolving legal instruments to facilitate and offer incentives towards the creation of reserves and protected areas at many different levels — national, state, municipal and private. Furthermore, Brazil is replete with official and non-governmental organizations and pressure groups, whose effectiveness doubtless varies. Nevertheless, when these can be brought together and synergistic activity involving informed individuals results, the outcome can be impressive, as a recently published compendium on conservation of biodiversity in Minas Gerais demonstrates (Costa et al. 1998). It is hoped that the present work will be a further small push in the right direction.
Chapter 7

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7.1. Bibliography and references


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(1991c). [Submission to the Republic of Brazil’s CITES Management Authority (IBAMA), via the CITES Secretariat, Lausanne, Switzerland, proposing the inclusion of *Discocactus, Uebelmannia* and 4 species of *Melocactus* in Appendix I of the Convention on International Trade in Endangered Species of fauna & flora.]


--- (ined. [1996]). Cladistic analysis of 25 taxa representative of major elements of Rhipsalideae (Cactaceae), based on 29 morphological characters and utilising PAUP3 with Adams consensus tree.


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Appendix 1

DATA ON THE SCIENTIFIC DISCOVERY AND DESCRIPTION OF THE CACTACEAE OF EASTERN BRAZIL

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<th>TAXA (IN SYSTEMATIC ORDER)</th>
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<td><strong>M. zebrinieri</strong></td>
<td>1915, BA, Rose &amp; Russell</td>
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<td>1977; PE, Horst</td>
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<td><strong>M. glaucescens</strong></td>
<td>1967; BA, Horst</td>
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<td><strong>M. concanans</strong></td>
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<td><strong>M. paucispinus</strong></td>
<td>1981, BA, Heimen et al.</td>
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<td><strong>F. cephalomelana ssp. esteviae</strong></td>
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<td><strong>F. squamosa</strong></td>
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<td><strong>A. melanurus</strong></td>
<td>1964, MG, Ritter</td>
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<td><strong>A. glaziou</strong></td>
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<td><strong>D. plecosistoma</strong></td>
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<td><strong>D. horstii</strong></td>
<td>1972, MG, Horst</td>
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<td><strong>U. pectinifera</strong></td>
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subsp. floccosus 20:10b
subsp. quadricostatus 20:11
fulvianatus 20:11a
subsp. fulvianatus 20:11b
var. rosea 20:11b

gaturianensis 20:18

subsp. gaturianensis 20:18
glaucescens 20:13

subsp. glaucescens Rizz. & Mattos (92) 20:13

subsp. glaucescens 20:13

glaucochrous 20:9

gounellei 20:2
subsp. gounellei 20:2a
subsp. zehntneri 20:2b
var. zehntneri 20:2b

hapalacanthus 20:14
jaurensis 20:14

lewoccephalus 20:14
indianus 20:14
indianus 18:2
letzelburgii 20:14
machrisil 20:13
magnificus 17:4
minensis 20:18
mucosiflorus 20:17
multicostatus 20:17

occultiflorus see below 20 (20 x 12a ?) 20:12a

oreus 20:12

subsp. pachycladus 20:12a
subsp. pernambucoensis 20:12b
parvus 20:14

pentaedrophorus 20:8a
subsp. pentaedrophorus 20:8b
subsp. robustus 20:8b

pernambucoensis 20:12b
var. caesius 20:12b
var. montealoi 20:12a

pleurocarpus 20:18
subsp. gaturianensis 20:18
subsp. mucosiflorus 17:4b

pseudopilocereusarrabidae 20:5
atraflavispinus 20:12a
aurilanus 20:15b
aurisetus 20:15
azureus 20:12a

aziurea P. V. Heath 20:12a
bradsi 17:3

coleonensis 20:7
var. robustispinus 20:7

eatingicola 20:3
chrysoastele 20:19
cuyahensis 20:14
densiareolatus 20:20
flavipulvinatus 20:10
flocoscus 20:11
fulvianatus 20:18

var. gaturianensis 20:18
glaucens 20:9
glaucodrhorus 20:9
gounellei 20:2
hapalacanthus 20:3b

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jauruensis 20:14
jauruensis 20:14
luetzelburgii 18:2
machrisii 20:14
magnificus 20:13
mucoisflor us 20:18
multicosatus 20:17
oreus 20:12
pachycladus 20:14
parus 20:8
pentaedrophorus 20:12b
pernambucensis 20:12b
pernambucoensis var. caesius var. montealtai
piauhyensis polyedrophorus
pustilbaccatus quadricostatus
robutus 20:3a
rupicola 20:3b
ruschianus 20:3b
salvadorensis 20:3b
sergipensis splendidus
superbus 20:12a
var. gacapaensis var. lanosior var. regius
superfloccosus 20:2b
tuberculatus 20:1
werdermannianus var. densilanatus var. diamantinensis
zehntneri
QUIABENTIA
zehntneri
RHIPSALIS
alboareolata 12:11
alternata 12:6
anceps 11:3
baccifera 12:12
subsp. baccifera subsp. hileiaibaiana
brevibarbis
burchellii capilliformis
campos-portoana cavernosa
cassuha cassuthopsis
cassuthoides
cassuthoides
cereoides cereuscula chloropetera clavata
clavata Lützelb. clavellina
cribrata (Lem.) N.E. Brown
crissa (Lem.) N.E. Brown
cribrata sensu K. Schum.
crispat a
cripimarginata cruciformis
densiareolata elliptica
floccosa subsp. floccosa
subsp. oreophila
subsp. pulvinigera
gonocarpa gracilis heteroclada
hoelteri houletiana
var. regnellii
houlletii juengeri
knichtii lindbergiana linearis
macahensis macroprocen sig maricaensis
mulleri
monteazulensis myosurus
oblonga pacheco-leoni
pacheco-leonis superfloccosus
paradoxa subsp. catenulata
subsp. septentrionalis
var. cattenuata
penduliflora
penduliflora sensu K. Schum.
piilocarpa platycarpa Lützelb.
prismatic a
pulchra pulvinigera
radicans ramossissima
regnellii
rhombus sensu Löfgren
robusta Lützelb.
russellii saglions
salicornoides salicornoides
var. cylindrica var. villigera
salicornoides
squamulosa
sulcata teres
f. capilliformis
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f. heteroclada
f. prismatica
tetragona
virgata
vollii
warmingiana
Rhodocactus grandifolius
SCHLUMBERGERA
kautskyi
microsphaerica
f. obtusangula
f. parvula
subsp. candida
obtusangula
opuntioides
truncata subsp. kautskyi
var. kautskyi
SELENICEREUS
anthonyanus*
see 8
rizzinnii
setaceus
Siccoocactus dolichoespermaticus
STEPHANOCEREUS
leucostele
luetzelburgii
3
TACINGA
atropurpurea
var. zehntnerioides
braunii
funalis
subsp. atropurpurea
var. atropurpurea
inamoena
luetzelburgii
palmadora
xquipa
saxatilis
subsp. estvesei
subsp. saxatilis
werneri
zehntneri
Trichocereus campos-portoi
damazioi
damazioi sensu Werderm.
glaevii
UEBELMANNIA
ammothrophus (nom. nud.)
anthoensis (nom. nud.)
buingii
buingiana (orth. var.)
see sub 30:3c
centeteria
cineria (nom. nud.)
crebrisina (nom. nud.)
flavisina
var. longisina (nom. nud.)
gummifer
subsp. meninensis
var. gigantea (nom. nud.)
var. rubra
horrida (nom. nud.)
meninensis
var. antenaensis (nom. nud.)
var. rubra
pectinifera
subsp. crebrisina (nom. nud.)
subsp. flavisina
subsp. horrida
subsp. pectinifera
var. crebrisina (nom. nud.)
var. elegans (nom. nud.)
var. heteracantha (nom. nud.)
var. horrida
var. multicostata
var. pseudopectinifera
pseudopectinifera (nom. nud.)
warstii
Zehntnerella chaetacantha
var. montealtoi
polygona
squamulosa
Zygocactus candidus
obtusangulus
opuntioides
var. rubra
30:2
horrida (nom. nud.)
30:2
meninensis
30:2
var. antenaensis (nom. nud.)
30:2
var. rubra
30:3
pectinifera
30:3b
subsp. crebrisina (nom. nud.)
30:3b
subsp. flavisina
30:3c
subsp. horrida
30:3a
subsp. pectinifera
30:3b
var. crebrisina (nom. nud.)
30:3
var. elegans (nom. nud.)
30:3
var. heteracantha (nom. nud.)
30:3
var. horrida
30:3c
var. multicostata
30:3a
var. pseudopectinifera
30:3a
pseudopectinifera (nom. nud.)
30:3b
warstii
26:3
Zehntnerella chaetacantha
26:3
var. montealtoi
26:3
polygona
14:2
squamulosa
14:2
Zygocactus candidus
14:2
obtusangulus
opuntioides
14:3
Appendix 3

CHECKLISTS OF CACTACEAE FROM ADJACENT BRAZILIAN REGIONS

The states for species of restricted occurrence are indicated by means of 2-letter codes; otherwise the taxon is known or expected to occur in all states included in the Region, those with a dagger (†) being endemic to the region or area indicated in the heading to the list. (Map 1, Chapter 4, indicates the division of Brazil into Regions, the ‘Grandes Regiões’, and its caption explains the standard 2-letter abbreviations for the names of their constituent states.) The most up-to-date published list of the Cactaceae native to Brazil as a whole is that provided by the present author in Hunt (1999a).
Northern Brazil (15 spp.):
Cereus hexagonus (syn. C. perlucens, Pilocereus perlucens)
C. sp. nov.† (TO: Mun. Palmas, limestone)*
Disocactus amazonicus (Wittia amazonica, Wittiocactus amazonicus) (AM)
Epiphyllum phyllanthus
Melocactus estevesiš† (RR)
M. neryi (AM,RR,RO?)
M. smithii (syn. M. roraimensis, Echinocactus amazonicus?) (RR)
Micranthocereus (subg. Siccobaccatus) estevessiš (TO)
Pilosocereus flexibilispinus† (TO)
P. oligolepis (RR)
P. machrisii (PA)
Pseudorhipsalis ramulosa (AC)
Rhipsalis baccifera subsp. baccifera
Hylocereus cf. setaceus (PA, RR)
Selenicereus wittii (Strophocactus wittii) (AM)

Central-western Brazil (28 spp.):
Arrojadoa sp. nov. (?), cf. dinae† (GO)
Arthrocereus spinosissimus (MT)
Brasiliopuntia brasiliensis (MT)
Cereus adelmarii† (MT)
C. hildmannianus (syn. C. bicolor?) (MT)
C. jamacaru subsp. calcirupicola (GO,†?)
C. kroenleinii (MT,MS)
C. saddianus† (MT)
C. spegazzinii (syn. Monvillea spegazzinii) (MS) ©
Cleistocactus baumannii subsp. horstii (MT,MS) ©
Discocactus heptacanthus (many synonyms!)
Echinopsis hammerschmidtii (MT,MS)
Epiphyllum phyllanthus
Frailea cataphracta (syn. F. matoana) (MS)
Gymnocalycium anisitsii (MS)
G. marsoneri (MS)
Harrisia balansae (syn. H. guelichii, Eriocereus guelichii, Cereus balansae) (MS) ©
Hylocereus setaceus (MS,MT)
Micranthocereus (subg. Siccobaccatus) estevessiš (GO)
Opuntia cf. quimilo (MS)
O. sp. indet. (O. elata?) (MS)
Pereskia aculeata (GO)
P. scharzara (MS,MT) ©
Praecereus euchlorus subsp. euchlorus (syn. Monvillea alticostata, ‘M. cavendishii’) (MS) ©
Pilosocereus diersianus† (GO)
P. machrisii (many synonyms)

Southern Brazil and the parts of South-eastern Brazil not included in the core area of Eastern Brazil (92 spp.):
Cereus aethiops (RS)
C. hildmannianus (sens. lat.)
C. mirabella (MG)
Discocactus heptacanthus (MG)
Echinopsis calochlora (RS)
E. eyriesii (RS)
E. oxygona (RS)
E. rhodotricha (RS)
Epiphyllum phyllanthus
Frailea albicolumnarist (RS)
F. castanea (RS)
F. cataphracta (RS)
F. curvispinis† (RS)
F. gracillima (RS)
F. horstiiš† (RS)
F. lepida† (RS)
F. mammifera (RS)
F. perumbilicata† (RS)
F. phaeodisca (RS)
F. pumila (RS)
F. pygmaea (RS)
Gymnocalycium buenekiš† (RS)
G. denudatum (RS)
G. horstiiš† (RS)
G. uruguyense (RS)
Hatoria eplhpiloides† (SP,RJ)
H. gaertneriš† (PR,SC,RS)
H. herminiae† (SP)
H. rosea† (PR,SC,RS)
H. salicornioides (PR,SP,RJ,MG)
Hylocereus setaceus (PR,SP,RJ,MG)
Lepismium cruciforme
L. houlletianum
L. umbrosum
L. warmingianum
Micranthocereus (subg. Siccobaccatus) estevessiš (MG)
Opuntia monacantha (syn. O. arachavactae)
Parodia alacriportana† (RS,SC)
P. buiningii (RS)
P. caespitosa (RS)
P. concinna (RS)
P. crassigibbaš† (RS)
P. crassispina (RS)
P. erinacea (RS)
P. graessneriš† (RS,SC)
P. hasselbergii† (RS,SC)
P. herteri (RS)
P. horstiiš† (RS)
P. limeninghausi s.l. (syn. P. schumanniana, P. warasii, P. claviceps etc) (RS)

* Seen in the nursery of the Jardim Botânico de Brasilia, July 2000. Rootstock said not to be tuberous; stems creeping over rocks, elongate cylindric, 2 cm diam., plain green, not glaucous; ribs 4-6(-8), low; spines brownish with pale tips, centrals 1(-4), to 12 mm, radials 6, shorter. Flowers and fruit unknown.
P. vilaboensis (syn. P. rizzoanus) † (GO)
Rhipsalis russellii (GO,MT)
[© = cited as Chaco element in Prado (1991)]
P. magnifica† (RS)
P. mammulosa (RS)
P. neohorstii† (RS)
P. ottonis
P. scopo (RS)
P. succinea† (RS)
Pereskia aculeata
P. grandifolia (SP)
P. nemorosa (RS)
Pilosocereus albissimmus† (cf. P. floccosus) (MG)
P. brasiliensis (RJ)
P. machrisii (MG, SP)
Præcereus euchlorus subsp. euchlorus (SP,PR)
Rhipsalis baccífera subsp. shaferi (SP)
R. burchellii† (SP,PR)
R. campos-portoana
R. cereoides (RJ)
R. cercuscula
R. clavata (SP,RJ)
R. dissimilis† (SP,PR)
R. elliptica
R. ewaldiana† (RJ)

R. floccosa (sspp. floccosa & pulvinigera)
R. grandiflora† (RJ,SP,PR)
R. lindbergiana (RJ,SP)
R. mesembryanthemoides† (RJ)
R. neves-armondii†
R. olivifera† (SP,RJ)
R. orminoi† (RJ)
R. pacheco-leonis (subsp. pacheco-leonist†) (RJ)
R. pachyptera†
P. paradoxa (subsp. paradoxt†)
R. pentaptera† (RJ)
R. pilocarpa
R. pulchra (MG,SP,RJ)
R. puniceodiscus†
R. teres
R. trigona† (SP,PR,SC)
Schlumbergera microsphaerica (RJ)
S. opuntioides (SP,RJ)
S. orssichiana† (SP,RJ)
S. russelliana† (RJ)
S. truncata† (RJ)
Tacinga saxatilis (subsp. saxatilis) (MG)