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UNRESTRICTED

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TAXONOMY AND PHYTOGEOGRAPHY
OF THE CACTACEAE OF
EASTERN BRAZIL

Thesis for the award of 'Doctor of Philosophy'

Life Sciences

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ABSTRACT

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 sertão³
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
E 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* born in the *caatinga* region, at the town of Exu, northern Pernambuco, where there is a museum about his life

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’), ie. 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, JPB, L, M†, MAC, MBM, MBML, MEXU, MG, MO, NY†, P (loan only), PEUFR, 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 1986, Lewis 1987).

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.

Dates	Areas visited	Main purpose of excursion	Collaborator(s)
Oct. 1988 – Feb. 1989	Minas Gerais, Bahia, coastal São Paulo	Collecting material for 'Flora of the Pico das Almas' and related projects	A. M. Giulietti, N. L. de Menezes, D. C. Zappi
July 1989	Bahia, N Minas Gerais	Collecting material for D. C. Zappi's revision of <i>Pilosocereus</i>	D. C. Zappi
Jan.–Feb. 1990	cent. & SW Ceará, SE Piauí, E Maranhão, N Bahia, NW & cent. Pernambuco	As above	D. C. Zappi
May 1990	coast of E Rio de Janeiro & S Espírito Santo	Assisting D. C. Zappi give Cactaceae course at Univ. Federal, Vitória, ES	O. J. Pereira & D. C. Zappi
Dec. 1990	NE & SE Minas Gerais, W Espírito Santo	Collecting material for 'Cacti of Eastern Brazil' project	D. C. Zappi
Jan.–Feb. 1991	Bahia, E Goiás, N Minas Gerais, Sergipe, Alagoas, S Pernambuco	As above	D. C. Zappi & U. Eggli
April 1992	N & E Bahia	Noting/photographing additional distribution records	D. C. Zappi
Feb. 1995	E Bahia, E Alagoas, cent.-N Pernambuco, E & S Paraíba, N Piauí, NW Ceará	As above	a) A. M. Carvalho (BA) b) R. Lyra-Lemos (AL) c) M. F. Agra & E. A. Rocha (PE/PB) d) J. B. da Silva (PI/CE)
Aug. 1998	NE Bahia (by bus), E Sergipe	Determine identity of <i>Pilocereus rupicola</i> Werdermann (Serra da Itabaiana, Sergipe)	M. L. Santos (SE)
March – April 2000	W Pernambuco, N & W Paraíba, S Rio Grande do Norte, S Ceará, SE Piauí, N Bahia	Noting/photographing additional distribution records. Testing phytogeographical hypotheses	E. A. Rocha & P. Griffiths

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, eg. *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 *M. ellemeetii* 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 WIED-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 Bambuí 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 20th 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 *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 *caatinga* species are amongst the many significant discoveries made by Ule: *Pereskia bahiensis*, *Stephanocereus leucostele*, *Arrojadoa penicillata*, *A. rhodantha*, *Pilosocereus catingicola*, *P. pachycladus* (the earliest definite record, but named much later), *P. piauhyensis*, *Melocactus ernestii*, *Harrisia adscendens* (see above), *Facheiroa ulei* and *F. squamosa*. He also made the first collection of the most widespread of the Chapada Diamantina's *campo rupestre* cacti, *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 finalis*, *Pseudoacanthocereus brasiliensis*, *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 DYBOWSKI, the discoverer of the remarkable *Epostoopsis 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 Espírito 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 wernerii*, *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 Zeppel 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, *Uebemannia 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

employed ignored regional variation and resulted in a plethora of weakly defined microspecies, many of which have since been dumped into synonymy or down-graded in rank by the studies of the present author and collaborators (Taylor 1980, 1981, 1982, 1991a; Taylor & Zappi 1990, 1991, 1997; Taylor in Hunt 1992b, 1999; Zappi 1994). Nevertheless, Ritter can lay claim to having discovered at least 20 distinct taxa between 1959 and 1965, although he was not always the first person to name these (Ritter 1979): *Tacinga saxatilis*, *Rhipsalis floccosa* subsp. *oreophila* (*R. monteazulensis*), *Cereus mirabella* (*Mirabella minensis*), *Cipocereus crassisepalus*, *C. pusilliflorus*, *Arrojadoa dinae*, *Pilosocereus floccosus* subsp. *quadricostatus*, *P. aurisetus* subsp. *aurilanatus*, *P. multicostatus*, *Micranthocereus albicephalus*, *Coleocephalocereus buxbaumianus* subsp. *flavisetus*, *C. fluminensis* subsp. *decumbens*, *C. aureus*, *Melocactus ernestii* subsp. *longicarpus*, *M. bahiensis* subsp. *amethystinus*, *M. levitestatus*, *M. concinnus*, *M. violaceus* subsp. *ritteri* (*M. macrodiscus* var. *minor*), *Facheiroa cephaliomelana*, *Arthrocereus melanurus* subsp. *odorus*.

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. *buxbaumianus*, *C. purpureus*, *Melocactus conoideus*, *M. deinacanthus*, *M. azureus* (2 subspp.), *M. pachyacanthus*, *M. lanssensianus*, *M. glaucescens*, *Discocactus zehntneri* subsp. *boomianus*, *D. heptacanthus* subsp. *catingicola*, *D. pseudoinsignis*, *D. horstii*, *Uebemannia buiningii*, *U. pectinifera* (3 subspp.). 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 Rhipsalideae 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. *estevensis* and *Facheiroa cephaliomelana* subsp. *estevensis*), 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 pachecoleonis* subsp. *catenulata*, *R. cereoides*, *R. sulcata*, *R. clavata*, *R. pilocarpa* and *Schlumbergera kautskyi*. The following year Countess Beatrix ORSSICH 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 Hylocereeae 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 Ceroideae (correctly Cactoideae), an arrangement which has remained little changed until

very recently (*Maihuenia* (Weber) Schumann, which he placed in Pereskioideae, 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 (Pachycereeae 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 Trichocereeae; 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 opuntiod 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, recognising 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 *Astrocephalocereus*, which modern authors now agree should be subsumed in *Micranthocereus*, according to the type species he cited for

the former (*Cephalocereus purpureus* Gürke), 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 cephalioid structures, ie. *Arrojadoa*, *Stephanocereus*, *Micranthocereus*, *Astrocephalocereus*, *Coleocephalocereus* and *Pilosocereus*. The only Brazilian exception to this was *Facheiroa*, which was subsumed into the Andean genus *Epostoa* 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, *Pseudacanthocereus* 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 (Supput 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 (eg. 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 Cereeae (Taylor & Zappi 1989), *Melocactus* (Taylor 1991a), *Pilosocereus* (Zappi 1994), tribe Rhipsalideae (Barthlott & Taylor 1995) and *Uebemannia* (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.

E Brazilian genus	IOS Consensus status	Comments / justification
PERESKIOIDEAE Schumann: 1. <i>Pereskia</i> Mill. 1754	Unanimously accepted since 1986	Earliest generic name in subfamily, though potentially paraphyletic as currently circumscribed (Table 2.2)
OPUNTCIOIDEAE Schumann:		
2. <i>Quiabentia</i> Britton & Rose 1923	Sunk into <i>Pereskiopsis</i> 1986 & 1990; recognised by Hunt (1992b, 1999a)	Seed anatomy (Stuppy submitted) supports separation from <i>Pereskiopsis</i>
3. <i>Tacinga</i> Britton & Rose 1919	Unanimously accepted 1986 & 1990, but only in original circumscription (<i>sens. str.</i>) including 2 spp.	Recognized in an expanded sense here for 6 spp., based on seed anatomy and floral similarities (Taylor & Stuppy submitted)
4. <i>Brasiliopuntia</i> (Schumann) A. Berger 1926	Sunk into <i>Opuntia</i> / 1986 & 1990	Recognized here based on seed- and pollen-morphology (lacks reticulate exine of <i>Opuntia sens. str.</i>) and unique, autapomorphic habit and behaviour (Taylor & Stuppy submitted)
5. <i>Nopalea</i> Salm-Dyck 1850	Sunk into <i>Opuntia</i> / 1986 & 1990	Recognized here based on pollen-morphology (lacks reticulate exine of <i>Opuntia sens. str.</i>) and floral differences
6. <i>Opuntia</i> Mill. 1754	Unanimously accepted since 1986 with <i>sens. lat.</i> circumscription	Earliest generic name in subfamily, here recognized <i>sens. str.</i> for taxa with unique autapomorphic reticulate pollen exine and sensitive stamens
CACTOIDEAE (HPE clade)– Hylocereeae:		
7. <i>Hylocereus</i> Britton & Rose 1909	Unanimously accepted 1986 & 1990, employing circumscription adopted by Hunt (1967)	Circumscription expanded here to include <i>Selenicereus</i> sect. <i>Salmdyckia</i> Hunt, based on trigonous stem-morphology and taxa with transitional floral/fruit characters, supported by gene sequence data (Wallace ined.)
8. <i>Selenicereus</i> Britton & Rose 1909	Unanimously accepted 1986 & 1990, with its circumscription adjusted in 1990 in line with Hunt (1989)	Circumscription adjusted here, as indicated above
9. <i>Epiphyllum</i> Haw. 1812	Unanimously accepted since 1986	Earliest generic name in tribe

CACTOIDEAE (HPE clade?) –Echinocereeae(?)		
10. <i>Pseudoacanthocereus</i> Ritter 1979	Included in <i>Acanthocereus</i> in 1986 & 1990, and by Hunt (1992b) with a note about its probable distinctness. Recognised by Taylor <i>et al.</i> (1992) and by Hunt (1999a)	Fruit- and seed-morphology (Taylor <i>et al.</i> 1992) unique within the HPE clade and sister group as yet unidentified
CACTOIDEAE–Rhipsalideae:		
11. <i>Lepismium</i> Pfeiffer 1835	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)	Circumscription employed here defined on the basis of plesiomorphic stem- and fruit-morphology character states, as detailed in Barthlott (1987) and Barthlott & Taylor (1995). Brazilian elements shown to be a monophyletic group on the basis of gene sequence data (Wallace ined.), but genus becomes paraphyletic if some Andean taxa are included
12. <i>Rhipsalis</i> 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. <i>Hatiora</i> 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 (<i>Hatiora</i> subg. <i>Hatiora</i>) on the basis of phylogenetic analyses, but genus becomes paraphyletic if taxa referable to <i>Rhipsalidopsis</i> Britton & Rose are included. See also Chapter 3.1
14. <i>Schlumbergera</i> 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
CACTOIDEAE (BCT clade)– Cereeae:		
15. <i>Brasilicereus</i> Backeberg 1938	Included in <i>Monvillea</i> Britton & Rose 1920 in 1986, but accepted by a minority of IOS WP members in 1990, following recommendations in Cereeae paper by Taylor & Zappi (1989); accepted by Hunt (1992b, 1999a)	Defined on the basis of a unique combination of vegetative and floral features within the BCT clade (cereoid habit, short-tubed flowers with glabrous but scaly pericarpel, stamens inserted in 2 series and indehiscent fruits bearing brownish, not blackish, perianth remains)
16. <i>Cereus</i> Mill. 1754	Unanimously accepted since 1986	Earliest generic name in the tribe

17. <i>Cipocereus</i> Ritter 1979	Lumped with <i>Pilosocereus</i> in 1986, then accepted (incl. <i>Floribunda</i> Ritter) by a minority of IOS WP members in 1990, following recommendations in Cereeae paper by Taylor & Zappi (1989); accepted by Hunt (1992b, 1999a)	Distinguished from other Cereeae by its blue-waxy, globose, indehiscent fruits with translucent funicular pulp and persistent, erect, blackened perianth remains in combination with small seeds
18. <i>Stephanocereus</i> A. Berger 1926	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)	Present circumscription reflects presumed homology between the two included species in respect of juvenile to adult developmental stages and reproductive structures (cephalia, flowers & fruit). It differs from other Cereeae in these same characteristics (Taylor & Zappi 1989)
19. <i>Arrojadoa</i> Britton & Rose 1920	Unanimously accepted since 1986	Earliest generic name amongst a closely related group of genera including nos. 17 & 18, amongst which it has derived pollen characters (Taylor & Zappi 1989)
20. <i>Pilosocereus</i> Byles & Rowley 1957 [<i>Pilocereus</i> Schumann 1894 nom. illeg.]	Unanimously accepted 1986 (incl. <i>Cipocereus</i>) and then with present circumscription in 1990	Differentiated from other Cereeae by its depressed-globose, dehiscent fruits (Taylor & Zappi 1989, Zappi 1994).
21. <i>Micranthocereus</i> Backeberg 1938	Sunk into <i>Arrojadoa</i> in 1986, but accepted by a majority of IOS WP members in 1990, following papers by Taylor & Zappi (1989) and Braun & Esteves Pereira (1990).	Since 1990 its circumscription has followed that of Ritter (1968, 1979) and Taylor & Zappi (1989), including <i>Austrocephalocereus</i> Backeberg 1938, which the 1986 IOS report accepted as distinct. Probably close to <i>Pilosocereus</i> , but with small, hummingbird-syndrome flowers and indehiscent fruit
22. <i>Coleocephalocereus</i> Backeberg 1938	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 <i>Melocactus</i> by Taylor & Zappi (1989). Accepted by Hunt (1992b, 1999a)	Present acceptance assumes that the presence of fruits dehiscent by a small basal pore is a sound autapomorphy, distinguishing the genus from both its presumed sister group, <i>Melocactus</i> , and other Cereeae (cf. Taylor 1991a: 18)
23. <i>Melocactus</i> Link & Otto 1828	Unanimously accepted since 1986	Highly derived within Cereeae, with autapomorphic non-chlorophyllous terminal cephalium and distinctive fruit, pollen and seeds (Taylor & Zappi 1989, Taylor 1991a)
CACTOIDEAE (BCT clade)– Trichocereeae:		
24. <i>Harrisia</i> Britton & Rose 1908	Unanimously accepted since 1986 in the broad sense including <i>Eriocereus</i> Riccobono (1909)	Distinctive for its seed-anatomy (Barthlott & Hunt in press); circumscription supported by gene sequence data (Wallace 1995, 1997)

25. <i>Leocereus</i> Britton & Rose 1920	Accepted less than unanimously by IOS WP members in 1986 (when it was hinted that <i>Arthrocereus</i> 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 & Zappi (1990)	Fruit- and seed-morphology unique within the BCT clade and sister group as yet unidentified. Position awaits confirmation based on molecular data.
26. <i>Facheiroa</i> Britton & Rose 1920	Accepted less than unanimously by IOS WP members in 1986 & 1990; accepted by Hunt (1992b, 1999a)	Sister group within tribe at present uncertain and its position remains to be elucidated with molecular data
27. <i>Epsotoopsis</i> Buxbaum 1968	Maintained as a synonym of <i>Austrocephalocereus</i> 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 & Zappi (1989); accepted by Hunt (1992b, 1999a)	In stem and habit characters this plant strongly resembles the Andean genus, <i>Epsotooa</i> Britton & Rose, but has naked flowers and polycoplate 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
28. <i>Arthrocereus</i> A. Berger 1929	Tentatively referred to <i>Leocereus</i> 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)	Close to the very large and complex genus, <i>Echinopsis</i> Zucc., but differing in its pollen (Leuenberger 1976) and indehiscent fruits. Molecular evidence is needed to confirm its generic status or otherwise
29. <i>Discocactus</i> Pfeiff. 1837	Unanimously accepted since 1986	Assumed to be the sister group of the much larger <i>Gymnocalycium</i> Pfeiff. ex Mittler 1844, but distinguished by having 12–15-colporate (vs 3-colporate) pollen (Leuenberger 1976) and the presence of a terminal cephalium — a parallelism with <i>Melocactus</i>
30. <i>Uebelmannia</i> Buining 1967	Accepted less than unanimously by IOS WP members in 1986, then unanimously in 1990; accepted by Hunt (1992b, 1999a)	Apparently a member of the BCT clade, but presently without obvious allies and thought to be an isolated relict

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

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.

Subfamily	Characters / molecular markers
PERESKIOIDEAE Schumann (<i>Pereskia</i> only)	Woody, with essentially non-succulent stems bearing broad, functional, scarcely succulent leaves and unbarbed spines; seeds of 'common ancestral centrospermous type' (Barthlott & Hunt 1993); pollen 3–15-colporate. Has no shared cpDNA restriction site changes with the putatively basal Maihuenoioideae (<i>Maihuenia</i> only), but may be paraphyletic in respect of Cactoideae (Wallace 1995: 9)
OPUNTIOIDEAE Schumann	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 <i>accD</i> , ORF 512, from the large single copy portion of cpDNA (Wallace, pers comm.)
CACTOIDEAE	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)-colporate. Has autapomorphic c. 700 base-pair deletion from the chloroplast encoded gene <i>rpoC1</i> intron (Wallace & Cota 1996)

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 Hylocereeae, 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 *rpl16* intron and *rbcL* markers, *fide* Wallace): the so-called Hylocereeae-Pachycereeae-Echinocereeae clade (HPE, also includes Leptocereeae *pro parte* and *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 (*Hylocereus*, *Epiphyllum* etc.) to which should probably be added the similar if enigmatic *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 *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 *rpl16* 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 *n*-alkanes of *Cereus*, *Pilosocereus* and *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 Cereeae here, but has aberrant, scaly flowers and potentially might represent the Browningieae component of BCT or belong to the Trichocereeae Buxbaum. The presumed Trichocereeae component is 7 genera, of which *Leocereus*, *Epostoopsis* and *Uebelmannia* are each aberrant in different ways and their inclusion in the tribe is provisional at present. Unlike the naked-flowered Cereeae this tribe is characterised by pericarpels/flower-tubes ± clothed in hair-spines and/or sometimes spines or bract-scales, although *Epostoopsis* has almost naked flowers.

The remaining major clades of Cactoideae recognizable on molecular evidence, that are absent from Eastern Brazil, are the Cacteae (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.

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

PACHYCEREEAE Buxbaum: 4 subtribes <i>Pterocereus</i> , <i>Escontria</i> , <i>Pachycereus</i> , <i>Stenocereus</i> , <i>Carnegiea</i> , <i>Neobuxbaumia</i> , <i>Cephalocereus</i> , <i>Myrtillocactus</i> etc. Erect columnar-cereoid taxa with woody tissues organized into discrete rods and diverse flowers with spiny, bristly, scaly or woolly pericarps	These form a significant part of the HPE clade, to which must be added the relevant parts of Buxbaum's Leptocereeae and Hylocereeae, and the Echinocereeae (q.v.)	Buxbaum included <i>Pilosocereus</i> p.p. (tribe Cereeae) in <i>Cephalocereus</i> .
BROWNINGIEAE Buxbaum <i>Browningia</i> , <i>Castellanosia</i> etc. Erect columnar-cereoid taxa with densely scaly tubular flowers	Part of <i>Browningia</i> <i>sens. lat.</i> belongs to the BCT clade, but recent reports suggest that <i>Castellanosia</i> is part of the HPE clade (Hunt 2000)	
CEREEAE Salm-Dyck <i>Jasminocereus</i> , <i>Stetsonia</i> , <i>Praecereus</i> , <i>Cereus</i> *, <i>Pseudopilocereus</i> [<i>Pilosocereus</i> p.p.]*, <i>Stephanocereus</i> *, <i>Coleocephalocereus</i> *, <i>Brasilicereus</i> * Erect columnar-cereoid taxa, bearing ± naked, tubular, mostly nocturnal flowers and ± naked fruit	With the exception of <i>Jasminocereus</i> , which belongs with <i>Armatocereus</i> 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 <i>Stetsonia</i> Browningioid?	The positions of the putative sister taxa, <i>Praecereus</i> and <i>Brasilicereus</i> , await clarification on the basis of molecular markers. Are they Cereeae?
TRICHOCEREEAE Buxbaum: 4 subtribes <i>Echinopsis</i> , <i>Haageocereus</i> , <i>Espostoa</i> , <i>Facheiroa</i> *, <i>Astrocephalocereus</i> (incl. <i>Espostoopsis</i>)*, <i>Leocereus</i> *, <i>Arthrocereus</i> *, <i>Cleistocactus</i> , <i>Oreocereus</i> , <i>Matucana</i> , <i>Micranthocereus</i> *, <i>Arrojadoa</i> *, <i>Rebutia</i> etc. Erect columnar-cereoid to low-growing taxa, bearing long-tubed flowers with bract-scales and/or spines/hair-spines on the pericarpel, tube and fruit	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-Trichocereeae were misplaced in the Notocacteae. <i>Samaipaticereus</i> (Leptocereeae) and <i>Harrisia</i> (Hylocereeae <i>sensu</i> Buxb.) belong here (Wallace 1997)	The position of <i>Leocereus</i> remains to be clarified on the basis of molecular markers
NOTOCACTEAE Buxbaum: 5 subtribes <i>Corynocactus</i> , <i>Astrocactus</i> , <i>Eriosyce</i> , <i>Eulychnia</i> , <i>Copiapoa</i> , <i>Parodia</i> , <i>Frailea</i> , <i>Uebelmannia</i> *, <i>Astrophytum</i> , <i>Gymnocalycium</i> , <i>Sulcorebutia</i> [= <i>Rebutia</i> p.p., see above], <i>Discocactus</i> *, <i>Melocactus</i> * etc. Mostly globular-stemmed, ribbed or tuberculate cacti, bearing diurnal short-tubed flowers with mostly scaly and/or bristly and woolly pericarps; many unique seedcoat characters	Notocacteae in its strictest sense (<i>Astrocactus</i> , <i>Eriosyce</i> , <i>Parodia</i> <i>sens. lat.</i> and <i>Frailea</i>) 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 (<i>Corynocactus</i>), <i>Copiapoa</i> and Cacteae (<i>Astrophytum</i>)	The Notocacteae as now defined are recognizable on the basis of floral characters (woolly pericarpel with bristles above) in combination with unique seedcoat morphology
ECHINOCEREEAE Buxbaum <i>Bergerocactus</i> , <i>Echinocereus</i> . Low-growing, shortly cereoid cacti bearing diurnal flowers with areolate-spiny pericarps	Not recognizable as a discrete entity on molecular data, being an integral part of the large HPE clade and close to <i>Stenocereus</i> (Pachycereeae)	Echinocereeae will likely prove to be the oldest name for the HPE clade
CACTEAE: 4 subtribes <i>Echinocactus</i> , <i>Sclerocactus</i> , <i>Thelocactus</i> , <i>Turbinicarpus</i> , <i>Lophophora</i> , <i>Strombocactus</i> , <i>Ariocarpus</i> , <i>Ferocactus</i> , <i>Escobaria</i> , <i>Mammillaria</i> , <i>Coryphantha</i> etc. Mostly globular-stemmed, ribbed or tuberculate cacti, bearing diurnal short-tubed flowers with naked, scaly and/or woolly pericarps	Well-defined major clade strongly supported by molecular and other data when the North American <i>Astrophytum</i> is included from Buxbaum's Notocacteae.	The majority of taxa are characterized by a suite of apomorphic seedcoat characters that sets them apart from all other cacti

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.

Chapter 3

TAXONOMIC CONCEPTS AND SYNOPSIS OF E BRAZILIAN CACTACEAE

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 unwearying 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, i.e. 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 character[s]' (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, eg. 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

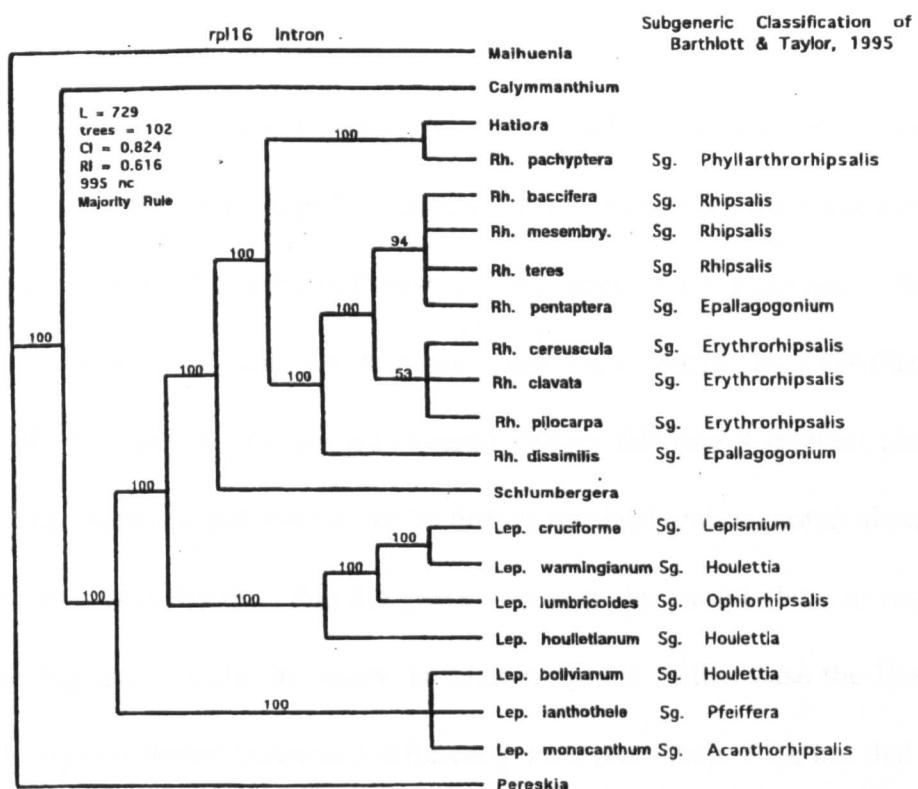


Figure 1. Cladogram of Rhipsalideae with *Maihuenia* (Maihuenoideae), *Calymmanthium* (Cactoideae) and *Pereskia* (Pereskioideae) as outgroups, based on gene sequence analysis of the *rpl16* intron of ribosomal protein L16 (© 1996, R. Wallace, Iowa State Univ., USA).

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 & Bitrich 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 *Espositopsis dybowskyi* and *Brasiliopuntia brasiliensis* do not give an immediate clue as to their relationship, although the

Strict

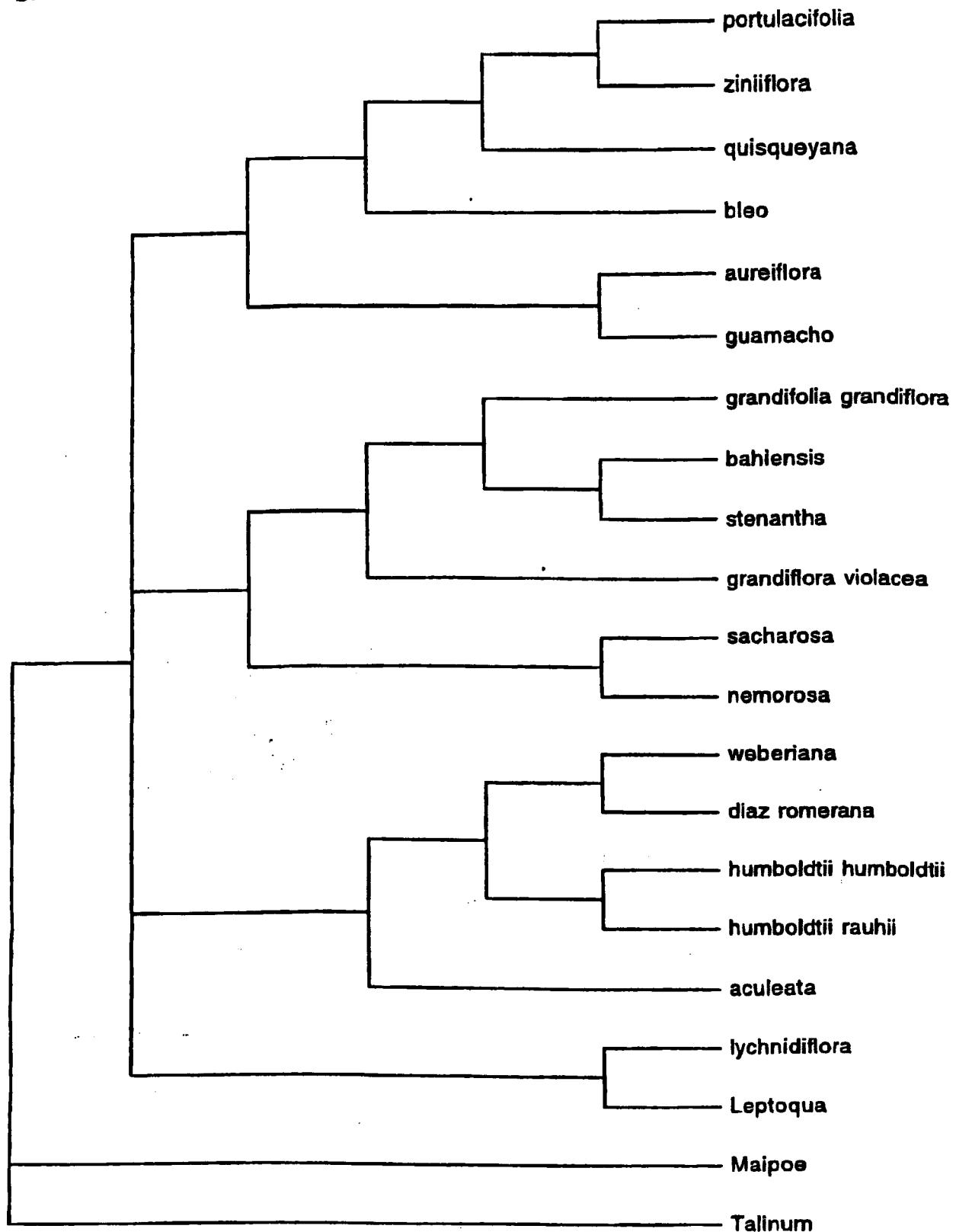


Figure 2. Cladogram of *Pereskia* taxa (Pereskioideae) with *Leptocereus* ('Leptoqua', Cactoideae); *Maihuenia* ('Maipoe', Maihuenoideae) and *Talinum* (Portulacaceae) are outgroups; based on gene sequence analysis of the *rpl16* intron of ribosomal protein L16. *Pereskia* comprises 4 unresolved clades, 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

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 ascendancy 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, eg. *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, eg. 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. fulvilanatus*. 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. fulvilanatus* 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 (eg. *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 (eg. 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 Cereeae.

- *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 Cereeae. In *Cereus*, the vegetatively very similar *C. jamacaru* 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. jamacaru* 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* (Cereeae) and *Discocactus* (Trichocereeae) are highly convergent, both being low-growing plants bearing (uniquely in Cactaceae) 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*).

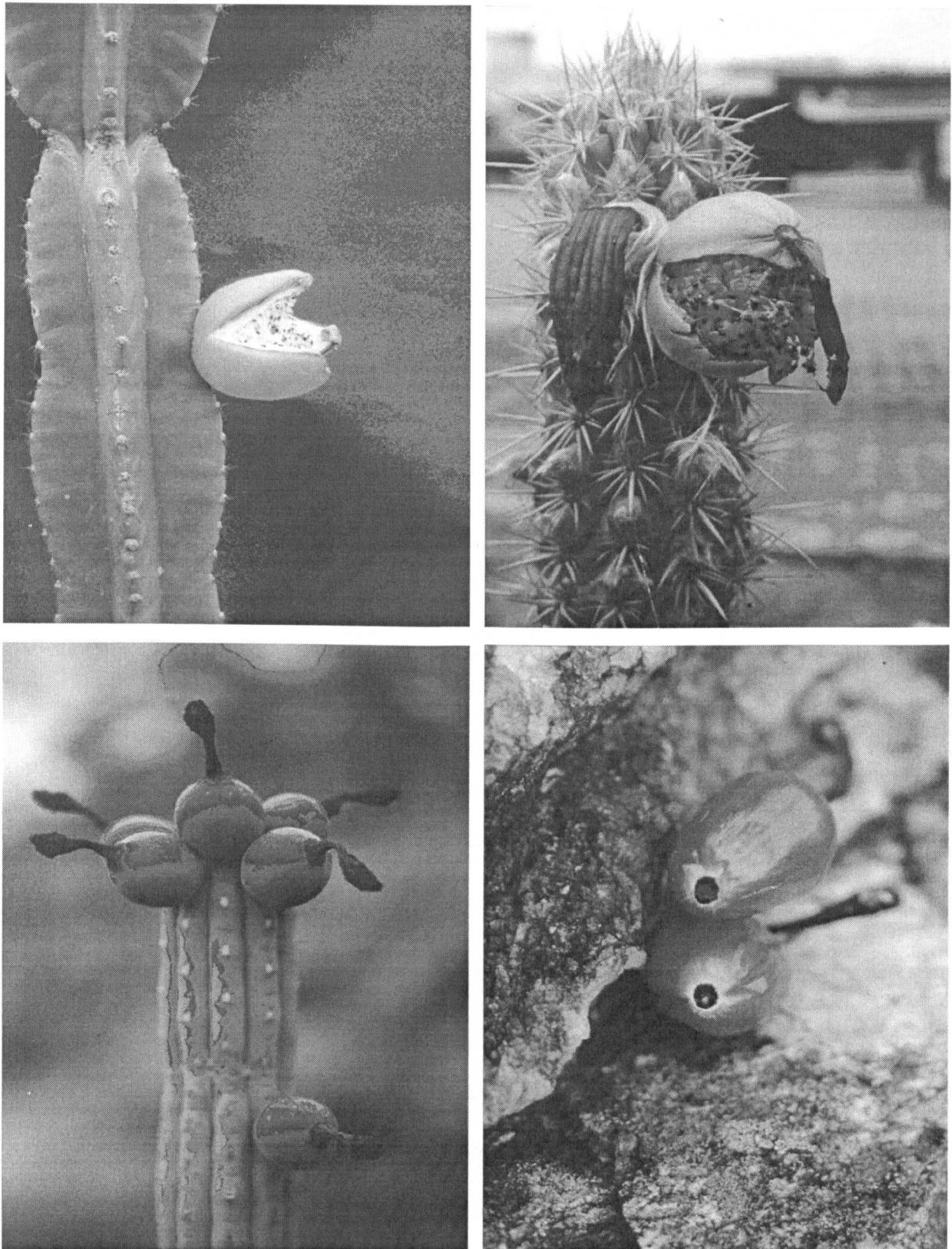


Plate 1. Examples of fruit diversity in tribe Cereeae. 1.1 (top left), *Cereus hildmannianus* (ovoid, apically dehiscent, perianth remains deciduous); 1.2 (top right), *Pilosocereus gounellei* (depressed-globose, subapically/laterally dehiscent, perianth remains persistent); 1.3 (bottom left), *Cipocereus 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, e.g. 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
1. Actively growing stems leafless or with only minute scale-like leaf primordia	7
2. Spines not microscopically barbed, not becoming strongly attached if allowed to penetrate the skin; glochids lacking; seed with black testa visible	1. Pereskia
2. Spines microscopically barbed, very difficult to detach if allowed to penetrate the skin, or true spines lacking and glochids present (at least on older stem-segments or the trunk); seed encased in a pale and sometimes fibrous/hairy funicular envelope (Opuntioideae)	3
3. Leaves broad (SW Bahia & Cent.-N Minas Gerais)	2. Quiabentia
3. Leaves awl-shaped (widespread)	4

4. Tree to 4 m or more with dimorphic stems, comprising a cylindric indeterminate leader shoot and flattened determinate lateral segments, the ultimate thin and leaflike, 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
5. Stamens and perianth spreading, the former sensitive, closing around the style when touched, the latter patent but never strongly reflexed, at least partly yellow; (pollen exine reticulate)	6. Opuntia
5. Stamens erect, clustered around the style, not sensitive; perianth erect, spreading or strongly reflexed, greenish, deep pinkish, red or purplish, or orange-yellow and plants not exceeding 50 cm; (pollen exine not as above)	6
6. Stamens long-exserted and perianth-segments erect, not spreading; spineless and with few glochids (introduced/cultivated)	*5. 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	8
7. Flowers < 8 cm long, or 8–10 cm and tube bract-scales naked in their axils or lacking or minute	15
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: <i>caatinga-agreste</i>)	10. Pseudoacanthocereus
8. Fruit not as above; seed blackish	9
9. Stems flat, trigonous or 3-winged	10
9. Stems with > 3 wings/ribs	13
10. Pericarpel and flower-tube bearing conspicuous spines/bristles or broad-based bract-scales; perianth > 15 cm diam.	11
10. Pericarpel and flower-tube with inconspicuous, narrow-based bract-scales, minute spines and/or trichomes only, or expanded perianth < 15 cm diam.	12

11. Stems trigonous or 3-winged	7. Hylocereus
11. Stems flattened	*8. Selenicereus
12. Epiphyte or garden plant with mostly flattened stems	9. Epiphyllum
12. Terrestrial with mostly trigonous or 3-winged stems	16. Cereus p.p.
13. Perianth remains cleanly abscissing from young fruit or persistent and strongly blackened	16. Cereus p.p.
13. Perianth remains not as above (blackening somewhat only if attacked by fungi)	14
14. Fruit > 5 cm, dehiscent; seeds 3–4 mm (Bahia northwards: <i>caatinga</i>)	24. Harrisia
14. Fruit 1–5 cm, indehiscent; seeds 1–2 mm (Minas Gerais: <i>campo rupestre</i>)	28. Arthrocereus
15. Epiphytic, or epilithic on coastal rocks, in <i>Mata atlântica</i> 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
15. Terrestrial, or epilithic in <i>caatinga</i> / <i>campo rupestre</i> and/or stems and flowers not as above	19
16. Flowers ± zygomorphic, tube to 8 mm long or more (S Espírito Santo & SE Minas Gerais)	
	14. Schlumbergera
16. Flowers actinomorphic, tube lacking or < 3 mm long	17
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 acrotonic), old and diseased stems separating from the plant at the joints between segments	18
17. New stem-segments arising only at base or singly from the sides of older segments (branching basi- to mesotonic), not separating at the segment joints when old or diseased	11. Lepismium
18. Flowers whitish or not strongly coloured, or developed laterally on stem-segments of ± indeterminate growth; plant ± pendent	12. Rhipsalis
18. Flowers bright yellow or orange, from composite areoles at the apex of ultimate or penultimate segments of strictly determinate growth; plant ± erect	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	20
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	23
20. Flowers yellowish, diurnal (central Minas Gerais)	30. Uebelmannia
20. Flowers not as above (widespread)	21
21. Flowers to 4 cm long, tubular, deep magenta-pink to red at least without, diurnal to crepuscular	22
21. Flowers > 4 cm long, salverform, whitish, nocturnal	29. Discocactus
22. Flowers from a cephalium	23. Melocactus
22. Flowers from the stem apex, true cephalium lacking (Chapada Diamantina, Bahia: <i>A. bahiensis</i>)	
	19. Arrojadoa p.p.
23. Pericarpel and tube clothed in conspicuous bract-scales and/or wool and bristle-spines	24
23. Pericarpel and tube ± naked, bract-scales lacking, minute or very widely spaced	27
24. Fruit with red or purplish pulp when ripe, spiny at first; stems to 2 cm diam.	25. Leocereus
24. Fruit with white or translucent pulp, spineless, or if spiny then stem > 2 cm diam.	25
25. Pericarpel and tube bearing areoles and bristle-spines; fruit covered in an intensely blue waxy bloom (Cent.-S Minas Gerais)	17. Cipocereus p.p.
25. Pericarpel and tube with bract-scales but lacking bristle-spines; fruit not as above (widespread)	26
26. Flowers shortly funnelform, at least 4 cm diam. at full anthesis; seed 2–3 mm	15. Brasilicereus
26. Flowers tubular, to 2.5 cm diam. at full anthesis; seed to c. 1.5 mm	26. Facheiroa
27. Fruit depressed-globose (rarely globose), 2–6 cm diam., bursting open laterally or apically due to pressure from the expanding funicular pulp; stems never regularly segmented (widespread)	
	20. Pilosocereus
27. Fruit not as above, or < 2 cm diam.; stems various	28

28. Stems segmented, with bristly/woolly ring cephalia at the joints and apex of distal stem-segments	29
28. Stems not as above; cephalium, if present lateral and ± continuous or elongate-terminal	30
29. Flowers green without, 8–10 cm long (Bahia, <i>caatinga</i>)	18. Stephanocereus subg. Stephanocereus
29. Flowers deep pink to bright red without, < 4 cm long (widespread)	19. Arrojadoa p.p.
30. Mature plant bottle-shaped, the upper part narrowed into a terminal chlorophyllous cephalium (Bahia, Chapada Diamantina)	18. Stephanocereus subg. Lagenopsis
30. Mature plant not as above	31
31. Flower-bearing areoles not differing markedly from those on purely vegetative stems and/or fruit covered in blue wax (Minas Gerais)	17. Cipocereus p.p.
31. Flower-bearing areoles ± modified or comprising a lateral cephalium; fruit not as above	32
32. Fruit clavate, sometimes laterally compressed, > 11 mm diam., deep pink to red, expelled from within the deeply sunken lateral cephalium when ripe and with a small basal pore allowing ants to enter (plants of naked gneiss/granite inselbergs of SE Brazil; <i>C. goebelianus</i> 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
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: <i>caatinga</i>)	27. Espostoaopsis
33. Stem tissues highly mucilaginous and perianth-segments coloured, at least without (Minas Gerais & Bahia: <i>campo rupestre</i>), or plant a glaucous, single-stemmed column (W of Rio São Francisco, Bahia: <i>Bambuí</i> limestone)	21. Micranthocereus

PERESKIOIDEAE Schumann

This subfamily comprises only one genus following the removal of *Maihuenia* (S Chile & S Argentina: Patagonia) to the Maihuonioideae 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

Gard. dict. abr. ed. 4 (1754). Type: *Pereskia aculeata* 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. <i>aculeata</i> |
| 1. Erect shrubs or trees, spines always straight, spreading, never paired-recurved; flower yellow, pink, magenta, orange or red | 2 |
| 2. Flower bright yellow; fruit globose, 1–3-seeded | 5. <i>aureiflora</i> |
| 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 (<i>Mata atlântica</i> , s.l.)	
	2. grandifolia
3. Leaves ovate to broadly elliptic-obovate; lateral veins 5–7; seeds 4–5.5 mm (<i>caatinga</i>)	4
4. Flowers with campanulate to urceolate perianth; flower-buds orange; perianth-segments reddish pink, erect, recurving at apex only, stamens and style enclosed	4. stenantha
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.

1. **Pereskia aculeata** Miller, Gard. dict., ed. 8 (1768). Lectotype (Leuenberger 1986): Dillenius, Hort. eltham.: t. 227, fig. 294 (1732).

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).

2. *Pereskia grandifolia* Haworth, Rev. pl. succ.: 85 (1819). Neotype (Leuenberger 1986): ‘raised from seed collected by Bowie & Cunningham in 1816 in the neighbourhood of Rio de Janeiro’, drawing by T. Duncanson, 11 June 1824 (K).

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.

2b. subsp. *violacea* (*Leuenberger*) N. P. Taylor & Zappi in *Cactaceae Consensus Initiatives* 3: 7 (1997). Holotype: Brazil, Minas Gerais, Mun. Santana do Riacho, Serra do Cipó, 19°21'S, 43°36'W, 23 Sep. 1981, *F. C. F. Silva* 89 (HRB; B, iso.).

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

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.

3. *Pereskia bahiensis* *Gürke* in Monatsschr. Kakt.-Kunde 18: 86 (1908). Type (Leuenberger 1986: 119): Brazil, Bahia, ‘Calderão’ [Caldeirão, Mun. Maracás], Oct. 1906, Ule 7050 (HBG, lecto.; L, lectopara.).

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).

4. *Pereskia stenantha* *Ritter*, Kakt. Südamer. 1: 21, figs 3–4 (1979). Holotype: Brazil, Bahia, Caitité, Ritter 1251 (U, not found). Lectotype (Leuenberger 1986: 123): Ritter, l.c., fig. 3 (1979).

Southern Rio São Francisco *caatinga* element: *caatinga*, 450–750 m, valley of the Rio São Francisco, western and central-southern Bahia and central-northern Minas Gerais. Endemic to the core area of Eastern Brazil. Map 26A.

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.).

5. **Pereskia aureiflora** Ritter, Kakt. Südamer. 1: 22, fig. 5 (1979). Holotype: Brazil, Minas Gerais, Itaobim, Ritter 1413 (U, not found). Lectotype (designated here): Ritter, l.c., fig. 5 (1979).

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 Maihuonioideae, 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 southwestern 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

Cact. 1: 39 (1919). Type: *Tacinga funalis* 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 4
2. Stamens exserted (cultivated) **Nopalea cochenillifera*
2. Stamens included (Eastern *caatinga-agrestes*) 3
3. Fruit greenish to reddish or purple outside, to 3 cm, funicular pulp yellowish 4. *palmadora*
3. Fruit greenish white, sometimes with faint pink shades, 4–5.5 cm, funicular pulp bright pink 3. *werneri*
4. 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) 5
4. 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*) 6
5. Joints spineless (present in some areoles of *T. ×quipa*); areoles well spaced, 10–20 mm apart 6. *inamoena*
5. Joints with minute spines; areoles congested, 1–14 mm apart 5. *saxatilis*
6. All stem-segments perfectly cylindric; flowers green to purplish (S to NW Bahia & W Pernambuco) 1. *funalis*
6. Ultimate stem-segments ± flattened; flowers green (Rio Jequitinhonha valley, NE Minas Gerais) 2. *braunii*

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. *zehntnerioides*, as described, seem to be of somewhat intermediate colour. More collections and observations during its late winter (August/September) flowering period are needed.

2. *Tacinga braunii* E. Esteves Pereira in Kakt. and. Sukk. 40: 134–135 (1989). Holotype: Brazil, Minas Gerais, surroundings of the Rio Jequitinhonha, P. J. Braun 864 (ZSS).

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.

3. *Tacinga wernerii* (Eggli) N. P. Taylor & Stuppy [◊] in Succulent Pl. Res. 6: 00 (2001). Holotype: Brazil, Bahia, Mun. Jequié, N. P. Taylor et al. 1555 (CEPEC; HRCB, K, ZSS, isos.).

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. wernerii* and *T. inamoena*, has been observed near Pedra Azul, Minas Gerais.

4. *Tacinga palmadora* (Britton & Rose) N. P. Taylor & Stuppy [◊] in Succulent Pl. Res. 6: 00 (2001). Holotype: Brazil, Mun. Jaguarari, Barrinha, 7 June 1915, Rose & Russell 19787 (US).

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.

5. *Tacinga saxatilis* (Ritter) N. P. Taylor & Stuppy [◊] in Succulent Pl. Res. 6: 00 (2001). 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

[◊] 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) **5a. subsp. saxatilis**

1. Areoles very densely disposed, 1–6 mm apart; perianth-segments lanceolate (Mun. Iuiú, S Bahia)

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* × *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.).

Southern Rio São Francisco *caatinga* element: on exposed Bambuí limestone outcrops in *caatinga*, c. 500–550 m, east of the Rio São Francisco, Mun. Iuiú, southern Bahia. Endemic to Bahia. Map 26C.

♀ New name not accepted by the author in this thesis

6. *Tacinga inamoena* (*K. Schumann*) N. P. Taylor & Stuppy[◊] in Succulent Pl. Res. 6: 00 (2001).

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

Widespread Eastern Brazil element: usually on rocks (including inselbergs) or very stony ground, open *caatinga* and *campo rupestre*, c. 100–1550 m, from the middle drainage of the Rio Jequitinhonha (MG) northwards to northernmost Piauí, and westwards on sandstone outcrops in the *cerrado* of western Bahia. Endemic to Eastern Brazil. Amongst the commonest of cacti from the region. 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 ‘*Opuntia rubescens*’ [sensu Schumann (1890), non DC.], Glaziou 14865, which is *Tacinga braunii* (q.v.), immediately precedes that for *T. inamoena* (Gl. 14864) and both species grow together in the valley of the Rio Jequitinhonha, north-eastern Minas Gerais, where *T. braunii* is endemic. It seems probable, therefore, that the type of *T. inamoena* came from north-eastern Minas Gerais, where it reaches its southern limit.

Braun & Esteves Pereira (1989: 272) remark that *Opuntia* [*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 *T. inamoena* has spineless stem-segments as in *T. funalis* and *T. braunii*, but, like those species, its abundant fine glochids demand that it be treated with appropriate respect and handled only with forceps.

[◊] New name not accepted by the author in this thesis

Forms with stems bearing occasional spines are usually to be referred to the following hybrid:-

Tacinga ×quipa (F. A. C. Weber) N. P. Taylor & Stuppy [†] in *Succulent Pl. Res.* 6: 00 (2001).

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

[*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

4. BRASILIOPUNTIA (K. Schumann) A. Berger

Entwicklungslien Kakt.: 94 (1926). Type: *Cactus brasiliensis* Willd.

A very distinct, highly specialized, monotypic, arborescent genus, which is allied to *Opuntia sensu stricto* on the basis of seed-morphology/anatomy (Stuppy 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

Santo (rare to the west of the Chapada Diamantina and Serra do Espinhaço); semi-humid forests of extra-Amazonian Brazil; Atlantic drainage of Andes eastwards (Peru, Bolivia, northern Argentina, Paraguay). Map 12A.

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, ie. *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.).

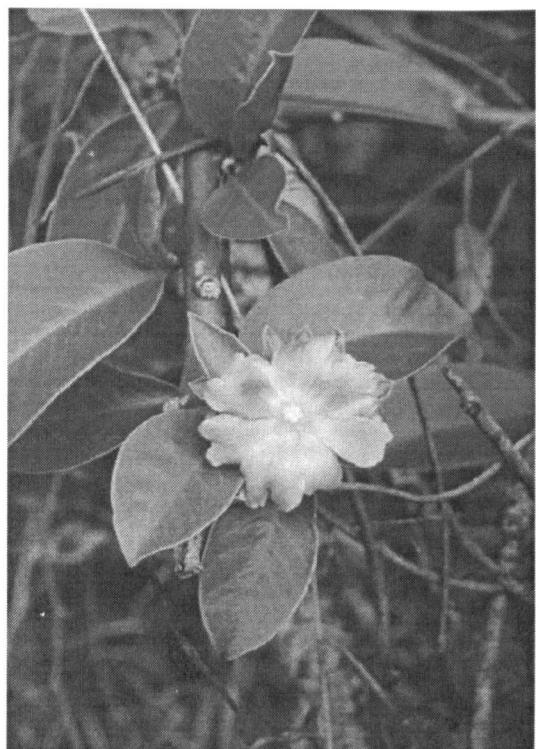


Plate 2. Diversity of Cactaceae in Eastern Brazil. 2.1 (top left), example of Pereskioideae: *Pereskia bahiensis*; 2.2–2.4, examples from Opuntioideae: 2.2 (bottom left), *Brasiliopuntia brasiliensis* (Caruaru, Pernambuco), 2.3 (top right), *Tacinga inamoena* (Tacima, Paraíba), 2.4 (centre right), *T. funalis* (cult., Desert Bot. Museum, Tucson, USA); 2.5 (bottom right), example from Cactoideae-Hylocereeae: *Hylocereus setaceus* (fruit, Itarana, Espírito Santo). [2.2 & 2.5 © D Zappi]

*5. NOPALEA Salm-Dyck

Cact. Hort. Dyck. 1849: 63–64 (1850). Lectotype: *Cactus cochenillifera* L.

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:

*1. **Nopalea cochenillifera** (*Linnaeus*) Salm-Dyck, Cact. Hort. Dyck. 1849: 64 (1850).

Lectotype (Howard & Touw 1982: 173): Dillenius, Hortus elthamensis: t. 297, fig. 383 (1732).

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

Gard. Dict. Abr. ed. 4: [unpaged] (1754). Type (cf. Leuenberger 1993): *Cactus opuntia* L. (= *O. ficus-indica* (L.) Mill.).

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. <i>dillenii</i>
1. Areoles spineless or with few or dark brownish spines; segments obovate, elliptic or rhomboid	2
2. Segments dark green; fruits proliferating	1. <i>monacantha</i>
2. Segments generally somewhat glaucous; fruits never proliferating (cultivated)	*3. <i>ficus-indica</i>

1. *Opuntia monacantha* Haworth, Suppl. pl. succ.: 81 (1819). Type: Lesser Antilles, Barbados, *fide* Haworth, not extant. Neotype (designated here): Brazil, Santa Catarina, Mun. Itajaí, Praia Brava, beach, above high-water mark, 18 July 1966, Hunt 6363 (K).

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 unequivocally based on a collection from Barbados (Lesser Antilles), whence only *O. dillenii* (Ker-Gawler) Haw. is currently recorded as native (Howard 1989). In order to maintain its use for the plant now widely associated with Haworth's name, a Brazilian neotype has been designated above. This assumes that the provenance data given by Haworth were erroneous, or that *O. monacantha* as now understood had been introduced to Barbados by the early years of the 19th Century. In any case, Haworth's brief and unsatisfactory diagnosis does not agree with *O. dillenii* and so neotypification or rejection are the only realistic options open. The above action seems marginally preferable to taking up the next available, well-typified name, *O. urumbeba* (Vell.) Steudel, which unfortunately has never been used, even though its

epithet repeats the distinctive, vernacular name for the plant. The name *Cactus monacanthos* Willd. (1814) was cited by Haworth with a question mark as a possible synonym of his *Opuntia monacantha*. This indication of doubt rules out any consideration of Haworth's name as a combination based on that of Willdenow, which 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-eastern 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 Physiognomiae): t. VII (1841).

*2. *Opuntia dillenii* (Ker-Gawler) Haworth, Suppl. pl. succ.: 79 (1819). Lectotype (Benson 1969: 126): Edwards Bot. Reg. 3: t. 255 (1818).

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).

*3. **Opuntia ficus-indica** (*Linnaeus*) *Miller*, Gard. Dict. ed. 8: no. 2 (1768). Neotype (Leuenberger 1991: 625): ‘*Cactus articulato-prolifer, articulis ovatis-oblongis: spinis setaceis.* Lin. Spec. plant. 468. 16’ (S, n.v.).

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 tricolporate; 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

1996). The tribes and their generic composition adopted here is that employed by Barthlott & Hunt (1993) modified on the basis of unpublished cladistic analyses, derived from 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

in Contr. U.S. Nat. Herb. 12: 428 (1909). Type: *Hylocereus triangularis* (L.) Britton & Rose (*Cactus triangularis* L.).

Including *Selenicereus* sect. *Salmdyckia* D. Hunt (1989) (*Mediocactus* Britton & Rose, excl. typ.).

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. *Salmdyckia* 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. *Salmdyckia* 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**

1. Hylocereus setaceus (*Salm-Dyck*) N. P. Taylor [†] **comb. ined.** Type: assumed not to have been preserved. Neotype (designated here): Pfeiffer & Otto, Abbild. Beschr. Cact. 1: t. 16 (1839).

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

in Contr. U.S. Nat. Herb. 12: 429 (1909).

Including *Cryptocereus* Alexander; *Selenicereus* sect. *Cryptocereus* (Alex.) D. Hunt (1989).

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

Only the following Mexican plant is encountered in Eastern Brazil:

**Selenicereus anthonyanus* (Alexander) D. Hunt in Bradleya 7: 93 (1989), native of southern Mexico, is the cactus most frequently cultivated as a house plant (in pots and hanging baskets) in Eastern Brazil. It is

more rarely planted outdoors, where it has been observed climbing trees in a semi-naturalized state in South-eastern Brazil, outside the area treated here. It resembles the following genus in its vegetative state (especially the Mexican *Epiphyllum anguliger*), but has flowers with a stouter, much shorter tube and bristly pericarpel.

9. EPIPHYLLUM Haworth

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

1. ***Epiphyllum phyllanthus* (Linnaeus) Haworth**, l.c. (1812). Lectotype (Leuenberger 1997):
Dillenius, Hortus elthamensis: t. 64, fig. 74 (1732).

Widespread neotropical element: epiphyte in *Mata atlântica*, *caatinga-agreste*, *mata do planalto*, *mata ciliar* and *cerrado*, near sea level to at least 1300 m, ± common throughout the more humid parts of Eastern Brazil; Neotropics from Central America southwards. It is the most widespread cactus species in Eastern Brazil.

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

Kakt. Südamer. 1: 47 (1979). Type: *P. brasiliensis* (Britton & Rose) Ritter.

Literature: Taylor, Zappi & Eggli (1992).

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

1. **Pseudoacanthocereus brasiliensis** (Britton & Rose) Ritter, l.c. Type: Brazil, Bahia, Mun. Marcionílio Sousa, Machado Portella, 1915, Rose & Russell 19903 (US, lecto. designated here; NY, lectopara.).

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 RHIPSALIDEAE DC.

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

11. LEPISMIUM Pfeiffer

in Allg. Gartenz. 3: 314–315 (1835). Lectotype: *Lepismium commune* Pfeiffer (= *L. cruciforme* (Vell.) Miq.).

Literature: Barthlott (1987); Barthlott & Taylor (1995: 44).

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

1. Lepismium houletianum (*Lemaire*) Barthlott in Bradleya 5: 99 (1987); Barthlott & N. P. Taylor, ibid. 13: 49, plate 7 (1995). Type: Brazil, *Houlet*, s.n. (assumed not to have been preserved). Neotype (Barthlott & Taylor 1995: 46): Gürke, Blühende Kakt. 2: t. 111 (1909).

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

1995: 46): Minas Gerais, Caldas, 18 Oct. 1854, *Lindberg* 511 (S; BR & MO lectoparas. numbered '611').

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.

3. *Lepismium cruciforme* (*Vellozo*) Miquel in Bull. Sci. phys. nat. Néerl.: 49 (1838). Type: not extant. *Typ. cons.* (Taylor 1994, Greuter *et al.* 2000: 385): Brazil, Rio de Janeiro, Vellozo, Fl. flum., Icones 5: t. 29 (1831).

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

De fruct. sem. plant. 1: 137, t. 28 (1788). Type: *R. cassutha* Gaertner (= *R. baccifera* (J. S. Mueller) Stearn).

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

Literature: Barthlott (1987), Barthlott & Taylor (1995: 48).

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 Espírito Santo)	19. hoelleri
1. Flower not red and/or flower-buds not erumpent; stems various	2
2. Stems flat, angled, winged, strongly to weakly ribbed or terete with ± raised podaria subtending ± fleshy scale leaves (or cylindric and smooth but with conspicuously erumpent flower-buds exposing floccose areoles after the fall of the fruit); flower-buds etc. 1–many per lateral areole	3
2. Stems perfectly terete or only the shortest, ultimate segments somewhat angled; scale leaves minute, not fleshy or soon scarious; flower-buds etc. 1 per lateral areole or flowers terminal	11
3. Flower-buds conspicuously erumpent from sunken, often very woolly areoles that were absent, hidden by scale-leaves or minute prior to flower development, solitary	4
3. Flower-buds not erumpent or only so on close inspection, the areoles not more obviously woolly after flowering, or flowers 2 or more per areole, at least on the older stem-segments	7
4. Stem-segments of indeterminate growth, branching often only subacrotonic, with numerous discontinuous ribs (S Espírito Santo)	7a. pacheco-leonis subsp. catenulata
4. Stem-segments of determinate growth, branching acrotonic from terminal composite areoles, terete, angled or with low ± continuous ribs	5
5. Stem-segments terete, not ribbed, but sometimes with raised podaria subtending the scale-leaves (widespread)	5. floccosa
5. Stem-segments ribbed or angled	6
6. Stems weakly 5-ribbed (S Espírito Santo)	9. sulcata
6. Stems 3–4-angled in cross-section, the angles discontinuous and not forming ribs (widespread)	6a. paradoxa subsp. septentrionalis
7. Fruit white or faintly tinged pink in part; stems mostly flat	8
7. Fruit entirely pink to red or purplish; stems flat or 3–4(–5)-angled/winged	9
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)	3. oblonga

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**
9. Stems mostly erect, to 25(–30) mm wide, 3–5-angled (S Espírito Santo) **8. cereoides**
10. Flowers/fruits 1–5 per areole, flower 12–20 mm diam., yellowish, fruit globose to oblong **2. elliptica**
10. Flowers/fruits (1–)3–9 per areole, flower to 8.5 mm diam., whitish, fruit globose **1. russellii**
11. Flowers < 8 mm long, with 4–7, patent to reflexed perianth-segments visible from within **12**
11. Flowers > 8 mm long, campanulate, with 8–15 concave perianth-segments visible from within **14**
12. All stems of ± indeterminate growth, not forming composite areoles at apex; flowers and fruits always lateral (widespread) **10. lindbergiana**
12. Higher order stem-segments of determinate growth, forming composite areoles at apex; flowers/fruits both lateral and terminal **13**
13. Pericarpel shorter than perianth; fruit globose to shortly barrel-shaped, to c. 5 × 4 mm; flowers/fruit mostly lateral (S Minas Gerais) **11. teres**
13. Pericarpel as long or longer than perianth both in bud and at anthesis; fruit ovoid, c. 7 × 6 mm; flowers/fruit mostly from the terminal composite areoles (Bahia & Pernambuco northwards) **12. baccifera**
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 **16. clavata**
14. Basal and higher order extension shoots of indeterminate growth present and > 12 cm long, other stem-segments usually decreasing in size towards distal parts of plant; stamens yellow, red or purplish at base **15**
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**
15. Stems clearly differentiated into long extension shoots and much shorter secondary segments, some < 7 cm long and all with terminal composite areoles; flowers terminal on the higher order stem-segments **16**
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**

17. Stems clothed in semi-adpressed, bristle-like spines; fruit bristly	18. <i>pilocarpa</i>
17. Stems and fruit naked	18
18. Flower 20–25 × 20 mm; fruit globose-ovoid, c. 10 mm long; plant flowering when < 1 m long	14. <i>burchellii</i>
18. Flower c. 15 × 12 mm; fruit truncate, c. 6 mm long; plant attaining 2 m before flowering	15. <i>juengeri</i>

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.

1. *Rhipsalis russellii* Britton & Rose, Cact. 4: 242 (1923). Type (Barthlott & Taylor 1995: 60): Brazil, Bahia, Mun. Jaguaquara [Toca da Onça], 27–29 June 1915, Rose & Russell 20106 (NY, lecto.; US, lectopara.).

Widespread humid forest / *campo rupestre* element: epilithic or epiphytic, *campo rupestre*, *mata de brejo* and *Mata atlântica* and their ecotones with *caatinga-agreste*, 50–1050 m, from the Chapada Diamantina and Serra do Espinhaço eastwards, Bahia, Minas Gerais and (?) 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 & Taylor 1995: 60): São Paulo, Sorocaba, *Mosén* 3630 (S).

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.

3. *Rhipsalis oblonga* Löfgren in Arch. Jard. Bot. Rio Janeiro 2: 36–37, t. VIII (1918). Type: Brazil, Rio de Janeiro, Ilha Grande, 1915, Löfgren & Rose (holo. not found at SP, RB or R; material at US is *R. elliptica* / *R. goebeliana* Backeb.; material at NY is dated 1917). Lectotype (Barthlott & Taylor 1995: 61): Löfgren, l.c., t. VIII (1918).

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.

4. *Rhipsalis crispata* (Haworth) Pfeiffer, Enum. cact.: 130 (1837); Britton & Rose, Cact. 4: 245, fig. 232, t. XXXV fig. 3 (1923). Type: Brazil, not known to have been preserved. Neotype (Barthlott & Taylor 1995: 61): Brazil, São Paulo, Mun. Rio Claro, Fazenda São José, edge of lake, 1991, A. Cardoso in Zappi 249, cult. N. P. Taylor, 10 Jan. 1994 (K, in spirit).

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*

eximum 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. *Epallagonium* Schumann (including Subg. *Trigonorhipsalis* A. Berger and Subg. *Goniorhipsalis* Schumann) (nos. 5–9): stems ± angled to ribbed or terete with raised podaria, never flattened (except in the first shoot of seedlings of no. 5 and very rarely in shade forms of no. 8); all adult stem-segments determinate, except in *R. pacheco-leonis*; flower-buds 1 per areole (except in *R. cereoides*), strongly erumpent and the pericarpel 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,

Mun. Ilhéus, grounds of CEPLAC, 3 Mar. 1974, C. Erskine 164, cult. Royal Botanic Gardens, Kew, 11 Nov. 1992 (K, in spirit).

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.

5b. subsp. *oreophila* N. P. Taylor & Zappi in Cactaceae Consensus Initiatives 6: 7 (1998).

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:

5c. subsp. *pulvinigera* (Lindberg) Barthlott & N. P. Taylor in Bradleya 13: 55 (1995). Lectotype (Barthlott & Taylor, l.c.): Gartenflora 38: 184, fig. 34 (1889).

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.

6. *Rhipsalis paradoxa* (*Salm-Dyck ex Pfeiffer*) *Salm-Dyck*, Cact. Hort. Dyck. 1849: 228 (1850).

Type: Brazil, assumed not to have been preserved. Neotype (Barthlott & Taylor 1995: 57): Lemaire in Hort. Univ. 2: t. 50 (1840).

Only the following heterotypic subspecies is found in Eastern Brazil:

6a. subsp. *septentrionalis* N. P. Taylor & Barthlott in Bradleya 13: 57 (1995). Holotype: Brazil, E Bahia, Mun. Juçari, 250 m, [before 1966], Martins in coll. Brieger, Piracicaba, SP, cult. R. B. G. Kew accn. no. 1966.48946, 18 Nov. 1991 (K in spirit; iso. dried).

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.

7. *Rhipsalis pacheco-leonis* Löfgren in Arch. Jard. Bot. Rio Janeiro 2: 38 (1918) ('pacheco-leoni'). Type: region of Cabo Frio, 1915, Campos-Porto & Rose (not found at RB or SP). Lectotype (Barthlott & Taylor 1995: 59): Rio de Janeiro, Iguaba Grande, 1915, Rose /& Campos-Porto] 20707 (US).

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

7a. subsp. *catenulata* (Kimnach) Barthlott & N. P. Taylor in Bradleya 13: 59 (1995). Holotype: Rio de Janeiro, Mun. Nova Friburgo, 2000 feet below Sansão, 1976, Fowlie s.n. (HNT, US, iso.).

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).

8. *Rhipsalis cereoides* (Backeberg & Voll) Backeberg, Kakteen Pflanzen Samen 1927–1937, 10 Jahre Kakteenforschung [cat.]: 39 (1937–1938). Type: Brazil, Voll, assumed not to have been preserved. Neotype (Barthlott & Taylor 1995: 61): Rio de Janeiro, Mun. Maricá, Itaipu-Açu, Apr. 1936, Voll & Brade s.n. (RB 10258).

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).

9. *Rhipsalis sulcata* F. A. C. Weber in Bois, Dict. hort.: 1046 (1898). Type: cultivated material of unknown wild origin, assumed not to have been preserved (P, not found). Neotype (Barthlott & Taylor 1995: 60): cult. New York Bot. Gard., Mar. 1912 (fls), received from Simon, ex Muséum [Nat. d'Histoire Naturelle] Paris [where Weber worked], in 1902 (NY).

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.

10. *Rhipsalis lindbergiana* K. Schumann in Martius, Fl. bras. 4(2): 296 (1890). Type: based on various syntypes (B†). Lectotype (Barthlott & Taylor 1995: 63): K. Schumann, l.c., t. 53 (1890).

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 *Hiléia 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.

11. *Rhipsalis teres* (*Vellozo*) Steudel, Nom., ed. 2, 2: 449 (1841). Type: not extant. Lectotype (Barthlott & Taylor 1995: 64): Brazil, Rio de Janeiro, Ilha de Santa Cruz, Vellozo, Fl. flum. Icones 5: t. 30 (1831).

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:

11a. f. *capilliformis* (F. A. C. Weber) Barthlott & N. P. Taylor in Bradleya 13: 65 (1995). Type: Brazil, cult. Hort. Chantin, not known to have been preserved. Neotype (Barthlott & Taylor, l.c.): Rio de Janeiro, Serra dos Órgãos, 1966, Hunt 6510 (K, neo. & isoneo.).

Southern humid forest element: epiphyte or lithophyte in *Mata atlântica*, to 1600 m, Minas Gerais and Espírito 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.

12. *Rhipsalis baccifera* (J. S. Mueller) Stearn in Cact. J. (Croydon) 7: 107 (1939). Lectotype (cf. Barthlott & Taylor 1995): J. S. Mueller, Ill. syst. sex. Linnaei. class IX. ord. 1, t. 29 (1770–77).

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, l.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 subspp. *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. *shafieri* (Britton & Rose) Barthlott & N. P. Taylor is known from the state of São Paulo, where it has been collected in Mun. Campinas.

12b. subsp. *hileiabaiana* *N. P. Taylor & Barthlott* in Bradleya 13: 63 (1995). Holotype: Brazil, Bahia, Mun. Ilhéus, 7 Aug. 1983, *J. L. Hage & H. S. Brito* 2113 (CEPEC; K, MBM, HRB isos.).

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

13. *Rhipsalis pulchra* Löfgren in Arch. Jard. Bot. Rio Janeiro 1: 75–76, t. 5 (1915). Holotype: Brazil, Serra da Mantiqueira, *O. A. Derby* 4394 in Comm. Geogr. Geol. S. P. 8834 (SP; US, iso.).

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.

14. *Rhipsalis burchellii* Britton & Rose, Cact. 4: 225 (1923). Lectotype (Barthlott & Taylor 1995: 69): São Paulo, Mun. São Paulo, Jabaquara, 15 Aug. 1915, Rose & Russell 20857 (US; NY, K, lectoparas).

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. cibrata* (Lemaire) N. E. Brown (*Hariota cibrata* 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).

15. *Rhipsalis juengeri* Barthlott & N. P. Taylor in Bradleya 13: 69, 72, pl. 29 & 30 (1995).

Holotype: origin unknown, cult., Bot. Gard. Univ. Bonn, Germany, accn. No. 01700, Mar. 1995 (BONN).

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 (nº 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. ormindoai* N. P. Taylor & Zappi (1997), from the adjacent parts of Rio de Janeiro, to take into account.

16. *Rhipsalis clavata* F. A. C. Weber in Rev. Hort. (Paris) 64: 429 (1892). Type: Brazil, Rio de Janeiro, Petrópolis, 1886, Binot, probably a living plant (assumed not to have been preserved).

Neotype (Barthlott & Taylor 1995: 72): l.c., Teresópolis, Granja Comari, 11 Feb. 1964, Castellanos 24569 (GUA).

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.

18. *Rhipsalis pilocarpa* Löfgren in Monatsschr. Kakt.-Kunde 13: 52 (Apr. 1903) and in Revista Centr. Sci. (Campinas) 1903(4): 188 (July 1903); N. P. Taylor in Bot. Mag. 14: 125–129, tab. 320 (1997). Type: Brazil, São Paulo, Mun. Itu, forests of Ipanema and Itu, cult. Hort. Bot. São Paulo, Feb. 1903, *Löfgren* (not found at SP, RB or R). Lectotype (Barthlott & Taylor 1995: 69): Löfgren, l.c. 55, illus. (April 1903).

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*, *Epallagonium*, *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.

19. *Rhipsalis hoelleri* Barthlott & N. P. Taylor in Bradleya 13: 50, plate 9 (1995). Holotype: Brazil, Espírito Santo, (?) Mun. Domingos Martins, 1987, *Orssich* s.n., cult. Univ. Bonn, Germany, accn. no. 04841 (BONN).

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

in Stand. Cycl. Hort. Bailey 3: 1433 (1915). Type: *Hatiora salicornioides* (Haw.) Britton & Rose.

Literature: Barthlott & Taylor (1995, 1996) [including *Rhipsalidopsis* 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. epiphyloides* (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.

1. Hatiora salicornioides (*Haworth*) *Britton & Rose* in Stand. Cycl. Hort. Bailey 3: 1433 (1915). Type: ‘Ind. Occident.’ (assumed not to have been preserved). Neotype (Barthlott & Taylor 1995: 73): ‘Brazil [Rio de Janeiro], Messrs Bowie & Cunningham, Duncanson del.’, water colour illustration (K).

Disjunct humid forest element: epiphytic or lithophytic, *Mata atlântica*, *mata de brejo*, *mata de grotao* 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*) Süpplie (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

in Rev. Hort. (Paris), ser. 4, 7: 253 (1858). Type: *S. epiphyloides* Lem. (= *S. russelliana* (Hook.) Britton & Rose).

Including *Epiphyllanthus* A. Berger (1905).

Literature: Hunt (1969), Barthlott & Rauh (1975), Barthlott & Taylor (1995: 74), Taylor & Zappi (1995).

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. <i>microsphaerica</i>
1. Terminal segments orbicular to obovate or truncate in outline, laterally compressed	2
2. Joints almost unarmed, but margins toothed; flowers scarcely zygomorphic	1. <i>kautskyi</i>
2. Joints covered in areoles with pungent, very thin spines; flowers strongly zygomorphic	3. <i>opuntioides</i>

1. *Schlumbergera kautskyi* (*Horobin & McMillan*) *N. P. Taylor* in *Bradleya* 9: 90 (1991); *McMillan & Horobin* in *Succulent Pl. Res.* 4: 23–26, plates 3.1–3.3 (1995). Holotype: Brazil, Espírito Santo, Mun. Domingos Martins, 900 m, May 1986, *R. Kautsky* in *Rauh* 67558, cult. Univ. Bonn, Germany (BONN).

Southern humid forest (inselberg) element: lithophytic on inselbergs, rarely epiphytic, *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.

2. *Schlumbergera microsphaerica* (*K. Schumann*) *Hövel* in *Kakt. and. Sukk.* 21: 186 (1970); *Heath* in *Calyx* 2(2): 64 (1992); *McMillan & Horobin* in *Succulent Pl. Res.* 4: 27, plates 6.1–6.4 (1995). Type: Brazil, Rio de Janeiro, *Glaziou* s.n. (B†). Neotype (Taylor 1991b; Heath, l.c.): *Arch. Jard. Bot. Rio de Janeiro* 2: t. 5, fig. B (1918).

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

The name *S. microsphaerica* must be used in preference to the more familiar *S. obtusangula* (Schumann) D. Hunt, since the former, as *Epiphyllanthus microsphaericus*, was the name

accepted by Britton & Rose (1923: 181), the first authors to treat these two equally priorable names as synonyms.

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

The distribution of *S. microsphaerica* is markedly disjunct between the localities cited above and its *locus classicus* on Itatiaia, by some 350 kilometres. Living plants from these two areas should be compared in view of the distances involved.

3. Schlumbergera opuntioides (Löfgren & Dusén) D. Hunt in Kew Bull. 23: 260 (1969);
McMillan & Horobin in Succulent Pl. Res. 4: 26–27, plates 3.4, 3.5, 5.1 & 13.6 (1995).
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.

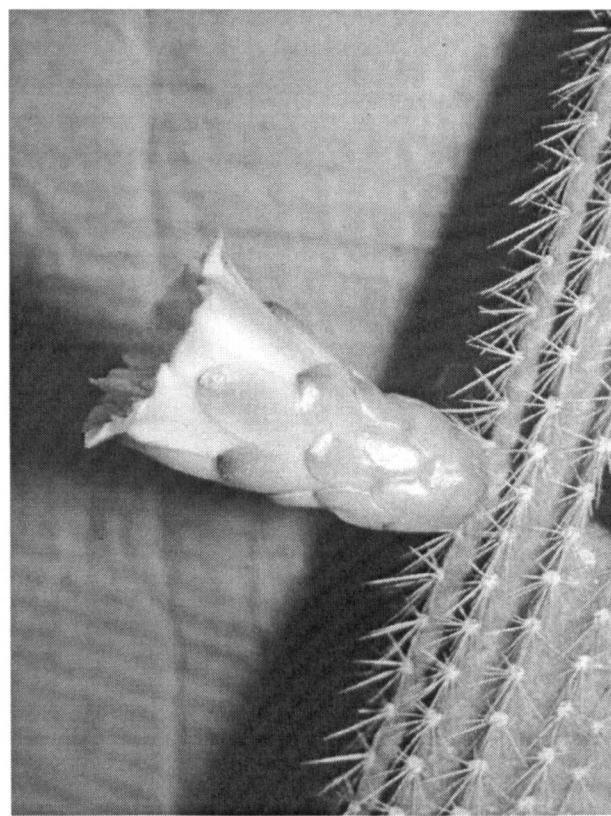
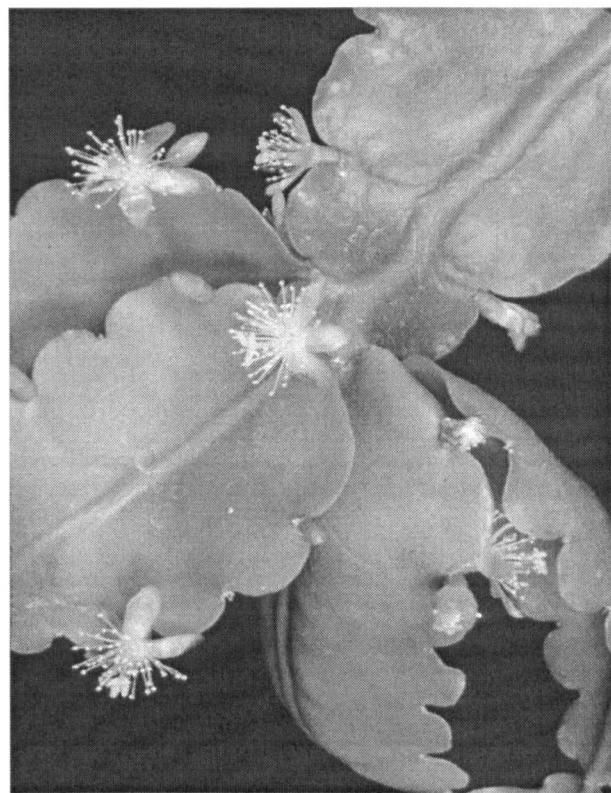


Plate 3. Diversity of Cactaceae in Eastern Brazil. 3.1 (top left), example from Cactoideae-Echinocereeae (?): *Pseudoacanthocereus brasiliensis* (Itinga, Minas Gerais); 3.2–3.3, examples from Cactoideae-Rhipsalideae: 3.2 (top right), *Rhipsalis crispata* (neotype collection), 3.3 (bottom left), *R. lindbergiana* (near São João da Sapucaia, Minas Gerais); 3.4 (bottom right), example from Cactoideae-Cereeae (?): *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

Blätt. Kakteenforsch. 1938: 20 (1938). *Cereus* subg. *Brasilicereus* (Backeb.) P. J. Braun (1988). Type: *Brasilicereus 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) **1. phaeacanthus**
1. Stem solitary or poorly branched at base; flowers with acute to acuminate bract-scales; pericarpel < 2× wider than long; stems 1.5–2.0 cm diam.; hilum-micropylar region forming an angle of 60° with the long-axis of seed (*campo rupestre / carrasco*, near Grão Mogol, MG) **2. markgrafii**

1. Brasilicereus phaeacanthus (Gürke) Backeberg in Blätt. Kakteenforsch. 1938: 20 (1938).

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.

2. *Brasilicereus markgrafii* Backeberg & Voll in Arch. Jard. Bot. Rio de Janeiro 9: 155 (1949 publ. 1950); Hofacker & P. J. Braun in Kakt. and. Sukk. 49: 267–268, illus. (1998). Holotype: Brazil, Minas Gerais, Grão Mogol, Nov. 1938, *Markgraf et al.* s.n. (RB 65043).

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.

16. CEREUS Miller

Gard. Dict. Abr., ed. 4 [unpaged] (1754).

Including *Mirabella* Ritter (1979); *Cereus* subg. *Mirabella* (Ritter) N. P. Taylor (1992).

Literature: Taylor (1992a: 17, 25).

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. <i>Cereus</i>) | 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. <i>Mirabella</i>) | 5 |
| 2. Fruit (when undamaged) opening from apex into c. 3 segments (S Minas Gerais) | 6. <i>hildmannianus</i> |
| 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 (<i>caatinga/agreste</i> and on limestone etc. in other ecosystems, NE Brazil to cent. Minas Gerais)	5. <i>jamacaru</i>
3. Semi-decumbent or low shrub, 0.5–4.0 m; fruit pinkish red (coastal sand & rocks) or yellow (gneiss/granite outcrops in <i>Mata atlântica</i> , W Espírito Santo, S edge of Minas Gerais & N Rio de Janeiro)	4
4. Ribs 3–5; flowers 14–25 cm (mainland Brazil)	3. <i>fernambucensis</i>
4. Ribs 5–9; flowers c. 13 cm (Fernando de Noronha)	4. <i>insularis</i>
5. Ribs (2–)3–5(–6), acute; wood yellow beneath the bark (<i>caatinga</i> , Piauí, Pernambuco, N & S Bahia to cent.-N Minas Gerais)	2. <i>albicaulis</i>
5. Ribs (3–)4–6, rounded; wood whitish beneath the bark (<i>cerrado</i> & <i>cerrado-caatinga</i> ecotone, SW Maranhão, W Bahia, N & cent.-E Minas Gerais)	1. <i>mirabella</i>

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 neotyped *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*).

1. *Cereus mirabella* N. P. Taylor in Bradleya 9: 85 (1991), ibid. 10: 21, fig. F (1992). Holotype: Brazil, Minas Gerais, c. 15 km W of Água Boa, Ritter 1238 (U).

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.

2. *Cereus albicaulis* (Britton & Rose) Lützelburg, Estud. Bot. Nordeste 3: 111 (1923, publ. 1926); N. P. Taylor in Bradleya 10: 24, plate III (1992). Type: Brazil, Bahia, Barrinha, 1915, Rose & Russell 19808 (US, lecto. designated here; NY, lectopara.).

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).

3. *Cereus fernambucensis* Lemaire, Cact. gen. nov. sp.: 58 (1839). Type: ‘patria est Fernambuco’ [Pernambuco = Recife]; not known to have been preserved. Now extinct within Mun. Recife. Neotype (designated here): Brazil, Pernambuco, Mun. Jaboatão dos Guararapes, Candeias, by the sea, 20 Feb. 1990, Zappi 228 (HRCB).

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

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

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

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).

3b. subsp. *sericifer* (*Ritter*) N. P. Taylor & Zappi in Cactaceae Consensus Initiatives 3: 7 (1997).

Holotype: Brazil, Rio de Janeiro, Três Rios, 1965, *Ritter* 1410 (U).

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 Paraíba drainage). Endemic to South-eastern Brazil. Map 16B.

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

4. *Cereus insularis* Hemsley, Voy. Challenger, Bot. 1(2): 16 (1884). Type: Brazil, Fernando de Noronha (St Michael's Mount), Moseley s.n. (K, lectotype designated here; BM, lectopara.).

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. fernambucensis*, 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 been seen recently in habitat (Braun 1990) and so its true nature seems likely to remain a mystery for the time being.

5. *Cereus jamacaru* *De Candolle*, Prodr. 3: 467 (1828), *nom. cons.* Holotype (Taylor & Zappi 1992c): Brazil, Bahia, Mun. Curaçá, 7 Jan. 1991, *Taylor et al.* 1369 (CEPEC; HRCB, K, ZSS isos.), *typ. cons.* (Greuter *et al.* 2000: 387).

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

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.

5b. subsp. *calcirupicola* (Ritter) N. P. Taylor & Zappi in Cactaceae Consensus Initiatives 3: 7 (1997). Holotype: Brazil, Montes Claros, 1959, Ritter 1011 (U).

Caatinga / mata seca Rio São Francisco (Rio das Velhas, MG) element: on ± forest-covered limestone (Bambuí) 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*.

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

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* subspp. *fernambucensis* and *sericifer*, with whose ranges it slightly overlaps, and from the related but allopatric *C. jamacaru*. All three species exist as spineless forms and when these are cultivated outside their natural range their identification can be very difficult unless ripe fruits are present.

C. hildmannianus may be widespread in drier phases of the semi-humid and humid, subtropical and tropical planalto forests north and east of the Chaco in central and south-eastern South America, and has a potentially much more extensive synonymy than that tentatively given 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 Cereeae, 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

Kakt. Südamer. 1: 54 (1979); N. P. Taylor & Zappi in Bradleya 7: 16–17 (1989). Type: *C. pleurocarpus* Ritter (= *C. minensis* (Werderm.) 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-morphology (including seedlings); likewise nos. 3–5. However, natural hybridization between nos. 2 and 4 has been observed (Taylor & Zappi 1989).

1. Ribs 4–7, triangular in section; areoles with dense felt and long hairs; central spines larger than radials (C. CRASSISEPALUS Group)	2
1. Ribs > 8, rounded in section; areoles with short, brown or white felt, long hairs absent; central and radial spines alike or upper areoles unarmed (C. MINENSIS Group)	3
2. Areoles contiguous; flowers and fruits bearing areoles with spines and long hairs (Serra do Caraça, MG)	
1. <i>laniflorus</i>	
2. Areoles distinct; flowers and fruits naked (Diamantina MG, eastwards & north-eastwards)	2. <i>crassisepalus</i>
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. <i>bradei</i>
3. Stems 2.5–5.0 cm diam., densely spiny; transverse folds absent; epidermis grey-green or bright green	4
4. Plants highly mucilaginous, to c. 50 cm tall; flowers small, < 2 cm, diurnal; fruits to 1.3 cm diam., pinkish, with a translucent waxy bloom (W slope of Serra Geral, northern Minas Gerais)	5. <i>pusilliflorus</i>
4. Plants not very mucilaginous, to > 50 cm tall; flowers > 4 cm, nocturnal; fruits > 2 cm diam., dark blue-black covered in a pale blue waxy bloom, or whitish	5
5. Flower blue outside, tube smooth, glabrous; perianth-segments patent to reflexed at anthesis; fruits not ridged, smooth (Serra da Bocaina, Grão Mogol & Serra do Cabral, southwards, disjunctly, to Serra do Caraça & Itabirito, MG)	4a. <i>minensis</i> ssp. <i>minensis</i>
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. <i>minensis</i> ssp. <i>pleurocarpus</i>

1. *Cipocereus laniflorus* N. P. Taylor & Zappi in Cactaceae Consensus Initiatives 3: 7 (1997).
Holotype: Brazil, Minas Gerais, Mun. Santa Bárbara, Serra do Caraça, c. 1800 m, 11 Sep. 1990,
Zappi et al. 240 (SPF; HRCB, BHCB, isos.).

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.

2. *Cipocereus crassisepalus* (*Buining & Brederoo*) Zappi & N. P. Taylor in Bradleya 9: 86 (1991). Holotype: Brazil, Minas Gerais, Diamantina, 500–1000 m, Horst & Uebelmann 169 (U).

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.

3. *Cipocereus bradei* (*Backeberg & Voll*) Zappi & N. P. Taylor in Bradleya 9: 86 (1991). Type: Brazil, Minas Gerais, Diamantina, Brade s.n. (apparently not preserved). Lectotype (designated here): Backeberg & Voll, in Blätt. Kakt.-Forsch. 1935 (1): [p.3], photograph (1935).

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

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

4. *Cipocereus minensis* (Werdermann) Ritter, Kakt. Südamer. 1: 57 (1979). Type: Minas Gerais, June 1932, Werdermann 3992 (B†). Lectotype (designated here): Werdermann, Bras. Säulenkakt.: 112, photograph captioned ‘*Cereus minensis* Werderm.’ (1933).

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 Caraça 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*.

4b. subsp. *pleurocarpus* (Ritter) N. P. Taylor & Zappi in Bol. Bot. Univ. São Paulo 12: 48 (1990, publ. 1991). Holotype: Brazil, Minas Gerais, Serra do Cipó, Nov. 1964, Ritter 1327 (U).

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.

5. *Cipocereus pusilliflorus* (Ritter) Zappi & N. P. Taylor in Bradleya 9: 86 (1991). Holotype: Brazil, Minas Gerais, Monte Azul, Jan. 1964, Ritter 1232 (U).

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

Entwicklungsli. Kakt.: 59, 97 (1926). Type: *Stephanocereus leucostele* (Gürke) A. Berger (*Cereus leucostele* Gürke).

Including *Coleocephalocereus* subg. *Lagenopsis* F. Buxbaum (1972); *Stephanocereus* subg. *Lagenopsis* (F. Buxbaum) N. P. Taylor & Eggli (1991).

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 (<i>caatinga</i> surrounding the East Brazilian Highlands of N to S Bahia) | 1. <i>leucostele</i> |
| 1. Bottle-shaped, to 1.5 m, rarely more, with subapical flowers on a continuous, elongate, terminal, chlorophyllous cephalium (<i>campo rupestre</i> , Chapada Diamantina, central Bahia) | 2. <i>luetzelburgii</i> |

1. **S. leucostele** (Gürke) A. Berger, Entwicklungsli. Kakt.: 59, 97 (1926). Holotype: Brazil, Bahia, Mun. Maracás, 'Calderão', Ule 2 (B).

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

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*).

2. *S. luetzelburgii* (Vaupel) N. P. Taylor & Eggli in Bradleya 8: 91 (1991). Type: Brazil, Bahia, Serra das Almas [Pico das Almas], July 1913, Lützelburg 22 (B, holo., n.v.).

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

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

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

Literature: Taylor & Zappi (1996).

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**
 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: Caitité 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**
 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**

1. Arrojadoa bahiensis (*P. J. Braun & E. Esteves Pereira*) *N. P. Taylor & Eggli* in Kew Bull. 49(1): 98 (1994); *N. P. Taylor & Zappi* in Curtis's Bot. Mag. 13: 72–75, t. 291 (1996). Type: Bahia, 'Chapada Diamantina', *E. Esteves Pereira* 337 (UFG 13007, holo., n.v.).

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*.

2. Arrojadoa dinae *Buining & Brederoo* in Kakt. and. Sukk. 24: 99–101 (1973). Holotype: Bahia, Brazil, Mun. Urandi, 900 m, *Horst & Uebelmann* 399 (U).

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. beataeae* P. J. Braun & E. Esteves Pereira and *A. heimenii* van Heek & Strecker) appear to be disjunct, being interrupted by the following subspecies.

2b. subsp. eriocaulis (*Buining & Brederoo*) N. P. Taylor & Zappi in Cactaceae Consensus Initiatives 3: 7 (1997). Holotype: Brazil, Minas Gerais, Mun. Mato Verde, 900 m, Horst & Uebelmann 349 (U).

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.

3. *Arrojadoa penicillata* (Gürke) Britton & Rose, Cact. 2: 171 (1920); N. P. Taylor & Zappi in Curtis's Bot. Mag. 13(2): 75–78, tab. 292 (1996). Type: Brazil, Bahia, Mun. Maracás, 'Calderão', 1906, Ule 7052 (B, holo. in spirit, HBG, iso., K, photo.).

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.

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

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:

BAHIA: Mun. Palmas de Monte Alto / Mun. Guanambi, road BR 030, 31 Mar. 1984, 14°14'S, 43°1'W, J.E.M. Brazão 303 (HRB, K photo).

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

A. albiflora Buining & Brederoo in Succulenta 54: 21–27 (1975). Holotype: Brazil, Bahia, Mun. Urandi, 1070 m,

Horst 401 (U).

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 Caetité (Bahia) and east of Monte Azul (Minas Gerais).

3 × 4: *Arrojadoa penicillata* × *Arrojadoa rhodantha*

Caatinga in the drainage of the Rio Paraguaçu 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

in Cact. Succ. J. Gr. Br. 19: 66–69 (1957). Type: *P. leucocephalus* (Poselger) Byles & Rowley.

Including *Pseudopilocereus* F. Buxbaum (1968).

Literature: Zappi (1994).

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 candelabiform, 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. <i>Gounellea</i>) | 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. <i>Pilosocereus</i>) | 3 |
| 2. Treelike, with a well-defined trunk, not branching near base; ribs 4–7; flower-bearing areoles without long trichomes | 1. <i>tuberculatus</i> |
| 2. Shrublike, without a well-defined trunk, branching near base; ribs (8–)10–15; flower-bearing areoles with abundant, silky, long trichomes enveloping the flowers | 2. <i>gounellei</i> |

3. Treelike or shrubby, branching above the base; vascular cylinder strongly to moderately woody	4
3. Shrubby, branching only at base when undamaged; vascular cylinder weakly woody	18
4. Apical, subapical and flower-bearing areoles without long hairs (at least in habitat)	5
4. Apical, subapical and flower-bearing areoles with long hairs	7
5. Epidermis blue, covered in wax	8. pentaedrophorus
5. Epidermis greyish, pale or olive-green, not strongly waxy	6
6. Spines brown to greyish, opaque; flower-buds acute; flower opening wide, $6\text{--}7 \times 4\text{--}5$ cm, tube straight (<i>restinga</i> , SE Brazil & S Bahia)	5. arrabidae
6. Spines golden to greenish yellow; flower-buds obtuse; flower narrow, $5.8\text{--}6.0 \times 3.5\text{--}3.7$ cm, tube curved (<i>caatinga</i> and littoral zone, Ceará, Piauí and S Maranhão)	7. flavipulvinatus
7. Epidermis rough, green to grey-green, not covered in wax	10. floccosus
7. Epidermis smooth, frequently bluish or covered in wax	8
8. Areoles continuous, difficult to isolate from one another	9
8. Areoles > 2 mm apart, distinct	10
9. Flower-bearing areoles with scarce, white long hairs; young spines golden, flexible	13. P. magnificus
9. Flower-bearing areoles with abundant dark yellow to reddish brown long hairs; spines dark brown to blackish	11. fulvilanatus
10. Spines golden, translucent	11
10. Spines brownish, reddish or blackish, opaque	15
11. Long hairs not more abundant on flower-bearing areoles than on the vegetative areoles; flower-tube narrow, curved, pinkish or reddish without	9. glaucochrous
11. Long hairs more abundant on the flower-bearing areoles; tube \pm straight, broad at apex, greenish, brownish or dark purplish brown	12
12. Ribs 5–12; central spines thicker and longer than the radials; stem epidermis blue	
12. Ribs > 12 ; central spines delicate, nearly indistinguishable from the radials, stem epidermis green or bluish	13. pachycladus ssp. pachycladus
13. Fertile part of stem with golden bristles to 3–4 cm and few long hairs; ribs (15–)18–26	19. multicostatus
13. Fertile part of stem without or with few bristles, long hairs white, silky; ribs 13–19	14

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 (Bambuí 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-vorticillate; 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
23. Flowers curved, > 5 cm, flower-buds obtuse before anthesis (SE Piauí northwards)	18. <i>piauhensis</i>
23. Flowers straight, < 5 cm, flower-buds acute before anthesis (NE Minas Gerais)	17. <i>multicostatus</i>

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

1. Pilosocereus tuberculatus (Werdermann) Byles & Rowley in Cact. Succ. J. Gr. Brit. 19(3): 69 (1957). Type: Brazil, Pernambuco, 1932, Werdermann (B†). Lectotype (Zappi 1994): l.c., Serra Negra, '900 m', Mar. 1932, Werdermann, Bras. Säulenkakt.: photograph, p. 21 (1933).

Central-southern *caatinga* element: in dense or sparse *caatinga* vegetation, on fine, white or reddish, sandy soil (especially of the Cipó series), c. 200–790 m, 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 (nº 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 aggressor.

2. *Pilosocereus gounellei* (F. A. C. Weber) Byles & Rowley in *Cact. Succ. J. Gr. Brit.* 19: 67 (1957). Type: Brazil, Pernambuco, *Gounelle* s.n. (P†). Neotype (Zappi 1994): Brazil, Paraíba, São Gonçalo [Várzea de Souza], Jan. 1936, *P. Lützelburg* 26921 (M; K, photo.; IPA).

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).

2b. subsp. zehntneri (*Britton & Rose*) Zappi in Succulent Pl. Res. 3: 43 (1994). Type (Zappi, l.c.): Brazil, Bahia, district of Chique-Chique [Mun. Xique-Xique], Serra de Tiririca, Nov. 1917, Zehntner s.n. (US, lecto.; NY, lectopara.).

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

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*.

3. *Pilosocereus catingicola* (Gürke) Byles & Rowley in Cact. Succ. J. Gr. Brit. 19: 66 (1957).

Lectotype (Zappi 1994): Gürke in Monatsschr. Kakt.-Kunde 18: 55, photograph ‘*Cereus catingicola* Gürke in den sandigen Gebieten der Catinga bei Bahia [de São Salvador] nach einer von Herrn E. Ule aufgenommenen Photographie’.

This species is divided in two subspecies:

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

3a. subsp. *catingicola*

1. Branches 3.5–6.0(–8.0) cm diam., ribs (5–)6–12, spines slender, 2–10 mm (Bahia northwards from Salvador to

Rio Grande do Norte and inland as far as cent.-S Pernambuco)

3b. subsp. *salvadorensis*

3a. subsp. *catingicola*

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 neotyped.

3b. subsp. *salvadorensis* (Werdermann) Zappi in *Succulent Pl. Res.* 3: 55 (1994). Holotype: not extant (B†). Lectotype (Zappi, l.c.): Brazil, Bahia, between Bolandeiras and São Salvador, Apr. 1932, Werdermann, Bras. Säulenkakt.: 37, photograph (1933).

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 Paraíba, 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.

4. *Pilosocereus azulensis* N. P. Taylor & Zappi in *Cactaceae Consensus Initiatives* 3: 8 (1997).
Holotype: Brazil, Minas Gerais, Mun. Pedra Azul, 16°3'S, 41°14'W, 20 Oct. 1988, *Taylor & Zappi* in Harley 25220 (SPF; K, iso.).

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.

5. *Pilosocereus arrabidae* (Lemaire) Byles & Rowley in Cact. Succ. J. Gr. Brit. 19: 66 (1957).

Lectotype (Zappi 1994): Brazil, Rio de Janeiro, Vellozo, Fl. flum., Icones 5: t. 18 (1831).

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 caatingas of the Rio São Francisco valley.

6. Pilosocereus brasiliensis (*Britton & Rose*) Backeberg, Die Cact. 4: 2423 (1960). Type (Zappi 1994): Brazil, Rio de Janeiro, Mun. Rio de Janeiro, Corcovado, 10 July 1915, *Rose & Russell* 20190 (US, lecto.; NY, lectopara.).

Two subspecies are recognized as follows:

- | | |
|---|---------------------------------------|
| 1. Branches dark green; ribs 4–5 | 6a. subsp. <i>brasiliensis</i> |
| 1. Branches greyish green to glaucous; ribs (4–)5–7 | 6b. subsp. <i>ruschianus</i> |

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.

6b. subsp. *ruschianus* (*Buining & Brederoo*) Zappi in *Succulent Pl. Res.* 3: 64 (1994).

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.

7. *Pilosocereus flavipulvinatus* (*Buining & Brederoo*) Ritter, *Kakt. Südamer.* 2: 707 (1980).

Holotype: not extant. Lectotype (Zappi 1994): Brazil, Piauí, Simplício Mendes, c. 350 m, Buining & Brederoo in *Succulenta* 58: 138, photograph (iconotype) (1979).

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.

8. *Pilosocereus pentaedrophorus* (Cels) Byles & Rowley in Cact. Succ. J. Gr. Brit. 19: 67 (1957). Type: not extant. Neotype (Zappi 1994): Brazil, Bahia, Mun. Serrinha, 16 km N of town on road BA 409 towards Conceição do Coité, 14 July 1989, Zappi 120 (SPF; HRCB, isoneo.).

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 Ituaçu, 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*.

9. *Pilosocereus glaucochrous* (Werdermann) Byles & Rowley in *Cact. Succ. J. Gr. Brit.* 19: 67 (1957). Type: Brazil, Bahia, near Morro do Chapéu, Serra do Espinhaço, 'c. 1000 m', Apr. 1932, Werdermann (B†). Lectotype (Zappi 1994): Werdermann, Bras. Säulenkakt.: 102, photograph (1933).

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.

10. *Pilosocereus floccosus* Byles & Rowley in Cact. Succ. J. Gr. Brit. 19: 67 (1957). Holotype:
Brazil, Minas Gerais, Diamantina, June 1934, A. C. Braude s.n. (RB).

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 semi-arid region of the Rio Jequitinhonha valley (Taylor & Zappi 1992a). This species is subdivided as follows:

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

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

10b. subsp. *quadricostatus*

10a. subsp. *floccosus*

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.

10b. subsp. *quadricostatus* (*Ritter*) *Zappi* in Succulent Pl. Res. 3: 86 (1994). Holotype: Brazil, Minas Gerais, Padre Paraíso (formerly Água Vermelha), 1965, *Ritter* 1342 (U).

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*

P. subsimilis Rizzini & Mattos-F. in Rev. bras. Biol. 46: 327 (1986). Holotype: Brazil, Minas Gerais, Itinga, 18 Dec. 1984, *Rizzini & Mattos* 41 (RB).

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*.

11. *Pilosocereus fulvilanatus* (*Buining & Brederoo*) *Ritter*, Kakt. Südamer. 1: 84 (1979).

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

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. <i>fulvilanatus</i> |
| 1. Branches to 5.5 cm diam.; ribs (5–)6–8; fruit green to brownish red | 11b. subsp. <i>rosae</i> |

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.

11b. subsp. *rosae* (*P. J. Braun*) Zappi in Succulent Pl. Res. 3: 100 (1994). Holotype: Brazil, Minas Gerais, Mun. Augusto de Lima, near Santa Bárbara, 6 km from road BR 135, west slopes of the Serra do Espinhaço, 800 m, 1982, Horst & Uebelmann 546 (ZSS; K, iso.).

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. fulvilanatus* sens. str. have led to its present position (Zappi 1994). It has a less robust habit, with branches less than 6 cm in diameter, and a tendency to develop a higher number of ribs (6–8) than in mature stems of subsp. *fulvilanatus* (4–6). Otherwise, the remaining characteristics of both taxa are very similar, and only the geographical separation on either side of the Serra do Espinhaço — the two taxa being found c. 170 km apart — justifies the acceptance of *P. rosae* as a very restricted western subspecies, which is so far known from only a single population, found near the village of Santa Bárbara, in the Município of Augusto de Lima, Minas Gerais.

12. *Pilosocereus pachycladus* Ritter, Kakt. Südamer. 1: 69–70, Abb. 5, 40–41 (1979).

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.

12b. subsp. *pernambucoensis* (*Ritter*) *Zappi* in Succulent Pl. Res. 3: 109 (1994). Holotype: Brazil, Pernambuco, Araripina, 1963, *Ritter* 1219 (U).

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, Paraíba, 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 coerulecent 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 piauhensis* Gürke (1907), which they combined as *Cephalocereus piauhensis* (Gürke) Britton & Rose (1920), and *Pilocereus piauhensis* (Gürke) Werdermann (1933). The type material of *Cereus piauhensis* 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. piauhensis*. 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.

13. *Pilosocereus magnificus* (*Buining & Brederoo*) Ritter, Kakt. Südamer. 1: 72–73, Abb. 1 (1979). Holotype: Brazil, Minas Gerais, Rio Jequitinhonha, 370 m, Horst & Uebelmann 224 (U).

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*.

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

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. PENTAEDROPHORUS 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*.

15. *Pilosocereus aurisetus* (Werdermann) Byles & Rowley in Cact. Succ. J. Gr. Brit. 19: 66 (1957). Type: Brazil, Minas Gerais, Serra do Cipó, Werdermann 3993 (B†). Lectotype (Zappi 1994): Werdermann, Bras. Säulenkakt.: 104, photograph ‘*Pilocer. aurisetus* Werd.’ (1933).

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*

1. 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 rupestris* element: quartzitic rock outcrops associated with *campo rupestris*, 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.

15b. subsp. *aurilanatus* (Ritter) Zappi in Succulent Pl. Res. 3: 123 (1994). Holotype: Brazil, Minas Gerais, Joaquim Felício, 1964, Ritter 1325 (U).

South-eastern *campo rupestris* (Serra do Cabral) element: locally co-dominant with other cacti on quartzitic rock outcrops, *campo rupestris*, 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. supthatianus* P. J.

Braun. The most striking feature of subsp. *aurilanatus* is its stouter, taller stems with dense, golden hairs on the flower-bearing areoles.

16. *Pilosocereus aureispinus* (*Buining & Brederoo*) Ritter, Kakt. Südamer. 1: 83–84 (1979).

Holotype: Brazil, Bahia, E of the Rio São Francisco, ‘Serra da Barriguda’, 450 m, s.d., *Horst & Uebelmann* 391 (U).

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*.

17. Pilosocereus multicostatus Ritter, Kakt. Südamer. 1: 79–80, Abb. 52 (1979). Holotype: Brazil, Minas Gerais, Mun. Itaobim, 1965, Ritter 1346 (U).

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.

18. Pilosocereus piauhyensis (Gürke) Byles & Rowley in Cact. Succ. J. Gr. Brit. 19(3): 67 (1957). Holotype: Brazil, Piauí, ‘Serra Branca’ [Mun. São Raimundo Nonato], Jan. 1907, Ule 09 (B; K, SPF, photos ex B).

Northern *caatinga* element: on arenitic/granitic rock outcrops associated with *caatinga*, c. 200–850 m, central-eastern Piauí, northern Ceará and northern Rio Grande do Norte. Endemic to North-eastern Brazil. Map 20.

Described by Gürke (1908) as *Cereus piauhensis*, 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 piauhensis* (Gürke) Britton & Rose, and later by Werdermann (1933), as *Pilocereus piauhensis* (Gürke) Werderm. Both authors had not seen living material of *P. piauhensis* 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. piauhensis* rather than *P. chrysostele*, are the lack of a cephalium, the slender flower-tube and the morphology of the dehiscent fruit. *P. piauhensis* occupies a crescent-shaped northern and western distribution zone peripheral to that of *P. chrysostele*.

19. *Pilosocereus chrysostele* (Vaupel) Byles & Rowley in Cact. Succ. J. Gr. Brit. 19: 66 (1957).
Type: not extant. Neotype (Zappi 1994): Brazil, Ceará, 'Serra do Cantim', June 1933, *Lützelburg* 23755 (M; K, photo.; IPA, isoneo.).

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.

20. *Pilosocereus densiareolatus* Ritter, Kakt. Südamer. 1: 73–74, Abb. 43 (1979). Holotype: Brazil, Minas Gerais, Montes Claros, 1959, Ritter 957 (U).

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*:

? *P. occultiflorus* P.J. Braun & E. Esteves Pereira in Cact. Succ. J. (US) 71: 310–315, figs 1–5, 7–9, tt. 1 & 2 (1999).
Type: Minas Gerais, W of Rio São Francisco, '400 m', E. Esteves Pereira 223 (UFG, holo. n.v., BONN, ZSS, iso.).

Braun & Esteves Pereira's recently described species is here regarded as a putative hybrid, with little hesitation, since its 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 candelabrum for *P. gounellei* subsp. *zehntneri* and erect for *P. densiareolatus*, whose spination is also denser and finer. The examination of the apex of the fruits has proved to be the best character to differentiate them: *P. densiareolatus* has a deeply sunken, pendent floral remnant, typical of subgenus *Pilosocereus*, while *P. gounellei* subsp.

zehntneri has fruits with rounded and superficially inserted floral remnants, characteristic of subgenus *Gounellea*.

Insufficiently known taxa

- 1) The following names refer to a taxon treated as *incertae sedis* here (cf. Zappi 1994: 103; Ritter 1979: 64–65): *Pilocereus glaucescens* A. Linke (1858); *Cephalocereus glaucescens* (A. Linke) Borg; *Pilosocereus glaucescens* (A. Linke) Byles & Rowley; *Pseudopilocereus glaucescens* (A. Linke) F. Buxbaum; ‘*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. und. 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 (\times *Pacherocactus* Rowley) and, separately, with *Myrtillocactus* Console (\times *Myrtgerocactus* 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 Cereeae, 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.

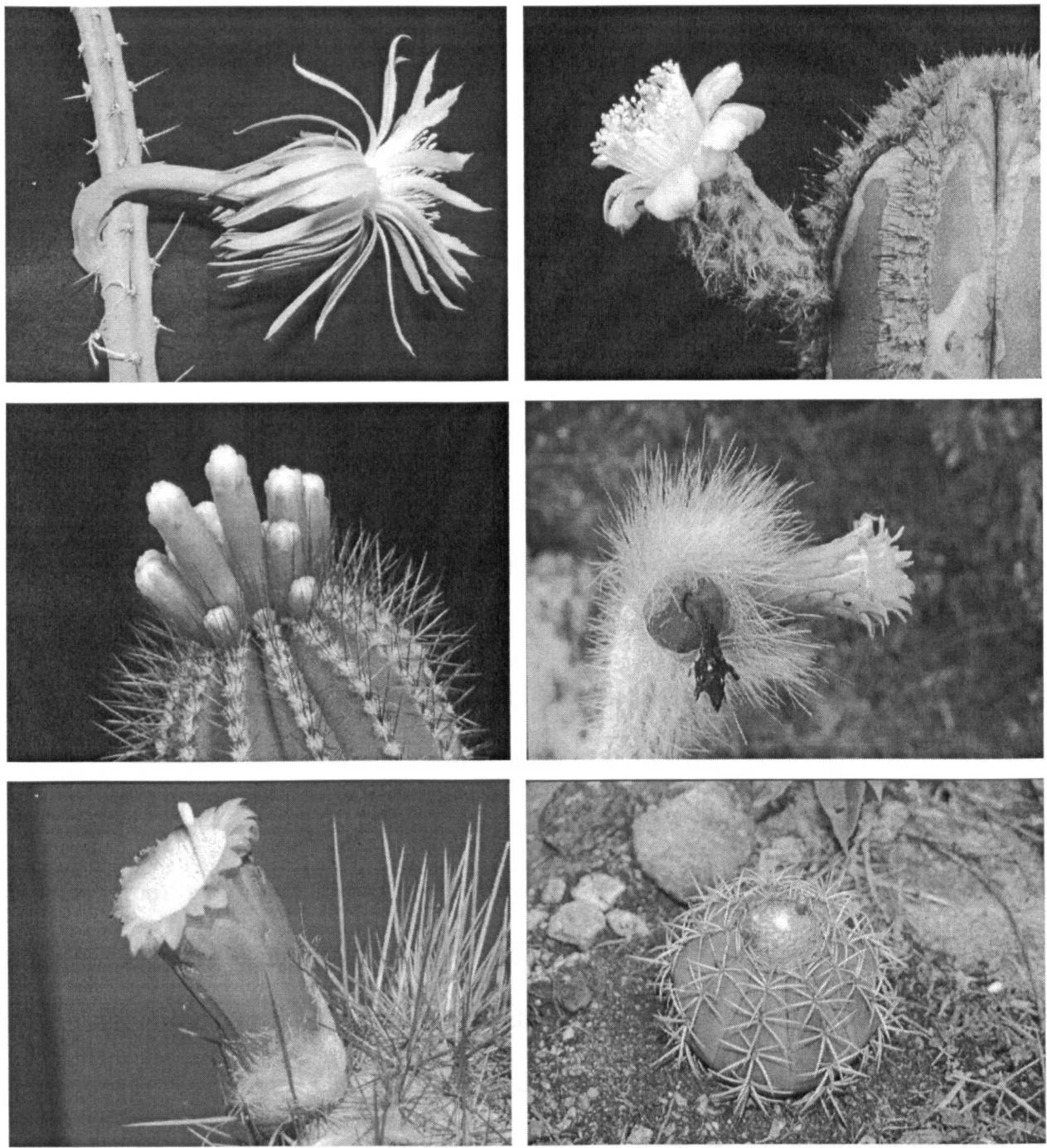


Plate 4. Diversity of Cactaceae in Eastern Brazil. 4.1–4.6, examples from Cactoideae-Cereeae: 4.1 (top left), *Cereus albicaulis* (near Nova Petrolina, Pernambuco), 4.2 (top right), *Cipocereus laniflorus* ('clonotype', cult. RBG Kew), 4.3 (centre left), *Arrojadoa bahiensis* (cult. RBG Kew, ex Mucugê, Bahia), 4.4 (centre right), *Stephanocereus leucostele* (Aracatu, Bahia), 4.5 (bottom left), *Pilosocereus pachycladus* (near Morro do Chapéu, Bahia), 4.6 (bottom right), *Melocactus cf. lanssensianus* (Mun. Tacima, Paraíba). [4.2–4.3 © RBG Kew; 4.5 © U Eggli; 4.6 © E Rocha]

21. MICRANTHOCEREUS Backeberg

in Blätt. Kakteenforsch. 1938(6): [22] (1938). Type: *M. polyanthus* (Werderm.) Backeb. Including *Austrocephalocereus* Backeberg (1938) and *Siccobaccatus* P. J. Braun & E. Esteves Pereira (1990); *Micranthocereus* subg. *Austrocephalocereus* (Backeberg) P. J. Braun & E. Esteves Pereira (1991a); *M. subg. Siccobaccatus* (P. J. Braun & E. Esteves Pereira) N. P. Taylor (1991b).

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. *zehntneri*) 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, <i>campos rupestres</i> , 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 orange-red with white to yellowish inner perianth-segments (N Bahia: Mun. Morro do Chapéu to Mun. Sento Sé)	7. flaviflorus
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*.

1. ***Micranthocereus violaciflorus* Buining** in Kakt. and. Sukk. 20: 129–130 (1969). Holotype: Brazil, Minas Gerais, ‘Chapada Diamantina’ [Mun. Grão Mogol, Serra da Bocaina], 24 June 1968, *Buining* in *Horst* 275 (U).

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

2. ***Micranthocereus albicephalus* (Buining & Brederoo) Ritter**, Kakt. Südamer. 1: 108 (1979).

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.

3. ***Micranthocereus purpureus* (Gürke) Ritter** in Kakt. and. Sukk. 19: 157 (1968); Buining in *Ashingtonia* 2: 28–29 (1975). Holotype: Brazil, Bahia, Serra do Sincorá, 1906, *Ule* 4 (B, n.v.).

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 Andaraí and Ituaçu.

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*.

4. ***Micranthocereus auriazureus* Buining & Brederoo** in Cact. & Succ. J. (US) 45(3): 120–123 (1973) ('*auri-azureus*'). Holotype: Brazil, Minas Gerais, Grão Mogol, 900–1000 m, 17–18 Aug. 1972, *Buining* in *Horst & Uebelmann* 346 ['348'] (U).

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*).

5. *Micranthocereus streckeri* van Heek & van Criel in Kakt. and. Sukk. 37: 102–105, with illus. (1986). Holotype: Brazil, Bahia, W of Seabra, van Heek & van Criel 85/250 (KOELN [‘Succulentarium’], n.v.).

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.

6. *Micranthocereus polyanthus* (Werdermann) Backeberg in Blätt. Kakteenforsch. 1938(6): [22] (1938). Holotype: Bahia, near Caitité, May 1932, Werdermann 3457 (B†). Lectotype (designated here): Werdermann in Fedde, Rep. Sp. Nov., Sonder-Beih. C, Lfg 11, t. 43 (1932).

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.

7. *Micranthocereus flaviflorus* *Buining & Brederoo* in Kakt. and. Sukk. 25: 25–27 (1974).

Holotype: Brazil, Bahia, Mun. Sento Sé / Umburanas, Serra do Curral Feio, 850 m, 22 July 1972, *Buining* in *Horst* 389 (U).

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.

8. *Micranthocereus dolichospermaticus* (*Buining & Brederoo*) *Ritter*, Kakt. Südamer. 1: 108 (1979). Holotype: Brazil, Bahia, W of Bom Jesus da Lapa, 460 m, *Horst & Uebelmann* 395 (U).

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

Blätt. Kakteenforsch. 1938(6): unpaged [22] (1938). Type: *C. fluminensis* (Miquel) Backeberg. Including *Buiningia* F. Buxbaum (1971); *Coleocephalocereus* subg. *Buiningia* (F. Buxbaum) P. J. Braun (1988).

Literature: Taylor (1991a: 17–19).

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. <i>goebelianus</i>
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. <i>buxbaumianus</i>
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. <i>fluminensis</i>
4. Flowers c. 19–35 mm; cephalium bristles dark brown and adpressed, not intermixed with wool; stem 12–34-ribbed	3. <i>pluricostatus</i>
5. Flowers yellow-green; seeds c. 1.35 mm; spines yellowish	5. <i>aureus</i>
5. Flowers magenta; seeds c. 1.75 mm; spines reddish brown	6. <i>purpureus</i>

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.

1. **Coleocephalocereus buxbaumianus** Buining in Succulenta 53: 28–33 (1974); Taylor in Bradleya 9: 17, *adnot.* (1991). Holotype: Minas Gerais, Mun. (?) Itambacuri, 1972, Horst 379 (U).

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.

1b. subsp. *flavisetus* (Ritter) N. P. Taylor & Zappi in Cactaceae Consensus Initiatives 3: 7 (1997). Holotype: Minas Gerais, Mun. Engenheiro Caldas, 1965, Ritter 1339 (U).

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

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 ‘isoetas 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.

2. ***Coleocephalocereus fluminensis* (Miquel) Backeberg** in Blätt. Kakteenforsch. 1938(6): unpaged [22] (1938); Taylor in Bradleya 9: 17, *adnot.* (1991). Type: not extant. Lectotype (designated here): Brazil, Rio de Janeiro, Vellozo, Fl. flumin., Icones 5: t. 20 (1831).

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. <i>fluminensis</i> |
| 1. Stem decumbent except at the inclined apex, to 6 cm diam. (NE Minas Gerais) | 2b. subsp. <i>decumbens</i> |

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*.

2b. subsp. *decumbens* (*Ritter*) N. P. Taylor & Zappi in Cactaceae Consensus Initiatives 3: 7 (1997). Holotype: Minas Gerais, Padre Paraíso ['Água Vermelha'], *Ritter* 1340 (U).

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 Paraíso (MG) and the Rio Doce in Espírito Santo (eg. municípios Nova Venécia 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.

3. Coleocephalocereus pluricostatus *Buining & Brederoo* in Krainz, Die Kakteen, Lfg. 46–47 (1971). Holotype: Minas Gerais, *Horst & Uebelmann* 245 (ZSS).

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:

4. Coleocephalocereus goebelianus (*Vaupel*) *Buining* in Kakt. and. Sukk. 21: 202–206 (1970); Ritter ex Backeb., Kakteenlex.: 92 (1966), nom. inval. (Art. 33.2). Type: Bahia, Serra das Almas,

Lützelburg 32 (B†). Neotype (designated here): Bahia, Mun. Ituaçu, c. 10 km S of town towards Tanhaçu, 18 Aug. 1988, *Eggli* 1195 (ZSS).

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 Maracás, 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 Espírito 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).

5. Coleocephalocereus aureus *Ritter* in Kakt. and. Sukk. 19: 158–160 (1968). Holotype: Minas Gerais, Itaobim, 1964, *Ritter* 1341 (U).

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.

6. Coleocephalocereus purpureus (*Buining & Brederoo*) *Ritter*, Kakt. Südamer. 1: 128 (1979). 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

in Verh. Ver. Beförd. Gartenb. Preuss. Staat. 3: 417 (1827), *nom. cons.* Type: *Cactus melocactus* L., *typ. cons.*

Literature: Taylor (1991a).

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 \times no. 9, 1b \times 13, 2a \times 9, 2a \times 10, 2a \times 12, 7b \times 10, 8a \times 10, 10 \times 13, 12 \times 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
1. Fruit red or pinkish magenta, at least at apex, to 45 mm long	12
2. Stem lacking mucilage; fruit length 1.5–2.0 \times diam.	3
2. Stem with at least some mucilage in the green cortical tissues or highly mucilaginous; fruit length 2 or more \times diam.	4
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)	5. <i>deinacanthus</i>
3. Lowermost radial spine \pm equal to or shorter than longest central spine; flower red, at least without; seed 1.35–1.75 mm, testa-cells almost flat (limestone, N Minas Gerais, W & cent.-S Bahia)	6. <i>levitestatus</i>
4. Fruit white, or white and very pale pink only at apex, or pale pink and seed with almost flat testa-cells	5
4. Fruit lilac-pink to pink; seed with testa-cells strongly convex at end opposite hilum	7
5. Central spine(s) $>$ 20 \times 1.5 mm (inland Bahia, limestone)	6
5. Central spine lacking or $<$ 20 \times 1.5 mm (coastal sand dunes)	15c. <i>violaceus</i> subsp. <i>margaritaceus</i>
6. Perianth-segments 0.7–1.7 mm wide; cephalium 7–9 cm diam., wool often conspicuous; fruit to 6 mm diam.	
	7. <i>azureus</i>
6. Perianth-segments 1.4–2.2 mm wide; cephalium 10 cm diam., with very dense fine bristles only; fruit 7–9.5 mm diam.	8. <i>pachyacanthus</i>
7. Stem pale bluish waxy-glaucous, at least when young	8
7. Stem always plain green	10
8. Flowers cleistogamous (Pernambuco & Paraíba)	11. <i>lanssensianus</i>
8. Flowers opening prior to fruit development	9

9. Stem 11–16 cm diam., pith chlorophyllous; ribs 8–12; areoles 13–20 mm apart on the ribs	13. concinnus
9. Stem to 25 cm diam., pith white; ribs 10–22; areoles 20–40 mm apart on the ribs	9. zehntneri
10. Spines (3–)4–6 per areole, largest 1.2–2.0 mm thick (cent. & S Bahia, 1100–1500 m)	14. paucispinus
10. Spines > 6 per areole or only 0.5–1.0 mm thick	11
11. Radial spines 5–10(–11), almost straight, 0.5–1.5 mm thick (<i>restinga</i> and sandy places inland, 0–1100 m)	
	15. violaceus
11. Radial spines (6–)7–11, ± curved, to 2.5 mm thick (inland, especially in the <i>caatinga</i>)	10. zehntneri
12. Fruit to 16 × 7 mm, dark red to base; cephalium white-woolly throughout, bristles hidden (Bahia: Mun. Morro do Chapéu)	11. glaucescens
12. Fruit to 45 × 12 mm, reddish to magenta at apex, paler below; cephalium with conspicuous bristles or white-woolly only at apex	13
13. Ribs ± rounded in cross-section (but edge often acute) or very low; stems depressed-globose to taller than broad	
	14
13. Ribs triangular in cross-section; stems broader than tall	17
14. Lowermost radial spine recurved at apex, to 35 mm, central spine 1, to 22 mm; stem hemispheric; ribs very low (Bahia: Mun. Vitória da Conquista)	4. conoideus
14. Lowermost radial spine straight or outcurved at apex, or > 35 mm, central spines > 1, > 22 mm, or stem and ribs not as above	15
15. Lowermost radial spine > 40 mm and < 1.5 mm thick, or stem taller than broad or lacking mucilage and/or flowers with pinkish, long-exserted stigma-lobes; ribs 9–16	16
15. Lowermost radial spine < 40 mm or > 1.5 mm thick; stem depressed to globose, with mucilage in the green cortical tissues; stigma-lobes white, scarcely exserted; ribs 8–12	3. bahiensis
16. Spines 9–14 per areole, lowermost radial 40–80 mm; stem to 15 × 18 cm	1. oreas
16. Spines (11–)14–21 per areole, lowermost radial 50–150 mm; stem to 45 × 35 cm	2. ernestii
17. Stem light greyish blue-green or quite glaucous; flower with c. 23 perianth-segments visible from above; spines usually < 40 mm (S & E Bahia)	9. salvadorensis
17. Stem pale to dark green; flower with 25–33 perianth-segments visible from above (rarely cleistogamous); spines to 60 mm (Pernambuco, Bahia & N Minas Gerais)	3. bahiensis

MELOCACTUS OREAS Group (nos. 1–4):

1. *Melocactus oreas* Miquel, Monogr. Melocacti: 113 (1840). Type: ‘Habitat circa Bahiam’ [Salvador] (assumed not to have been preserved). Neotype (Taylor 1991a: 24–25, illus.): Bahia, Mun. Santa Teresinha, Zappi 181A (K, photo.).

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 Paraguaçu, 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.

1b. subsp. *cremnophilus* (*Buining & Brederoo*) *P. J. Braun* in Bradleya 6: 95 (1988). Holotype: Bahia, Mun. Morro do Chapéu, *Horst* 223 (ZSS, apparently never deposited; U 531296, lectotype designated here).

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. Caetés, *Taylor & Zappi* 1627B, K, photos) requires further study (cf. *Taylor* 1991a).

2. *Melocactus ernestii* *Vaupel* in Monatsschr. Deuts. Kakt.-Ges. 30: 8 (1920); *Buining* in Krainz, Die Kakteen, Lfg 58 (1974). Type: Bahia, Mun. Barra da Estiva (?), *Ule* (photos, see *Vaupel*, l.c. and *Ule* 1908).

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.

2b. subsp. *longicarpus* (*Buining & Brederoo*) N. P. Taylor in Bradleya 9: 26 (1991). Holotype: Minas Gerais, Mun. Porteirinha, Horst 149 (U 531269).

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.

3. *Melocactus bahiensis* (Britton & Rose) Lützelburg, Estud. Bot. Nordeste 3: 111 (1926).

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 | 2 |
| 1. Central spine 1, to 25 mm, lowermost radial spine 22–32 mm (N Bahia) 3a(ii). subsp. <i>bahiensis</i> f. <i>acispinosus</i> | |
| 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) | 3 |
| 2. Ribs acute and triangular in cross-section; lowermost radial spine to 40 × 1.5 mm (S Bahia & N Minas Gerais) | |
| | 3b. subsp. <i>amethystinus</i> |
| 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. <i>bahiensis</i> f. <i>inconcinnus</i> |
| 3. Ribs 8–12, ± rounded, to 45 mm diam.; areoles to c. 8 mm; lowermost radial spine to 50 mm | |
| | 3a(i). subsp. <i>bahiensis</i> f. <i>bahiensis</i> |

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 Ituaçu.

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

3b. subsp. *amethystinus* (Buining & Brederoo) N. P. Taylor in Bradleya 9: 30 (1991). Holotype: Bahia, Mun. Caitité, Horst 270 (U 531291).

Eastern *caatinga* / Northern *campo rupestre* element: under and between shrubs on mainly crystalline (quartzitic/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.

4. *Melocactus conoideus* Buining & Brederoo in Krainz, Die Kakteen, Lfg. 55–56 (1973).

Holotype: Bahia, Mun. Vitória da Conquista, Horst 183 (U 531247).

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):

5. *Melocactus deinacanthus* Buining & Brederoo in Kakt. und. Sukk. 24: 217 (1973). Holotype: Bahia, Horst 153 (U 531251).

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):

6. *Melocactus levitestatus* Buining & Brederoo in Cact. Succ. J. (US) 45: 271 (1973). Holotype: Bahia, Mun. Bom Jesus da Lapa, Horst 397 (U 531285).

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):

7. *Melocactus azureus* *Buining & Brederoo* in Kakt. and. Sukk. 22: 101 (1971). Holotype: Bahia, [Mun. Juçara / 'Juassara' *fide* Uebelmann (1996)], 1968, Horst 256 (U, not found April 1989). Lectotype (Taylor 1991a): colour photograph in Buining & Brederoo, l.c.

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.

7b. subsp. *ferreophilus* (*Buining & Brederoo*) N. P. Taylor in Bradleya 9: 40 (1991). Holotype: Bahia, Mun. Barro Alto / Souto Soares, Horst 217 (U 531260).

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.

8. *Melocactus pachyacanthus* Buining & Brederoo in Kakt. and. Sukk. 27(1): 1, with illus. (1975) [vol. for 1976 but Heft 1 publ. Dec. 1975]. Holotype: Bahia, Mun. Ourolândia, Horst 407 (U 531288).

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.

8b. subsp. *viridis* N. P. Taylor in Bradleya 9: 40, pl. 16 (1991). Holotype: Bahia, Mun. América Dourada, *Taylor & Zappi* in Harley 27400 (CEPEC; SPF, K, isos.).

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):

9. *Melocactus salvadorensis* Werdermann in Notizbl. Bot. Gart. Berlin 12: 228 (1934). Type (syntypes): Bahia, Mun. Ipirá (Camisão) and Mun. São Félix / Muritiba, Bananeiras, 1932, Werdermann 3391, 3392 (both B†). Neotype (Taylor 1991a): Bahia, Bananeiras, Horst 301 (U 531290), illustrated in Krainz, Die Kakteen, Lfg 54 (1973).

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. oreas*, *M. ernestii* (both subspp.), *M. zehntneri* and, probably, *M. bahiensis* and *M. concinnus*. It occasionally hybridizes with *M. oreas* and *M.*

ernestii subsp. *ernestii*. It is easily confused with *M. zehntneri*, but has much darker, magenta fruit. Its pollination biology has been studied by Raw (1996).

10. *Melocactus zehntneri* (Britton & Rose) Lützelburg, Estud. Bot. Nordeste 3: 111 (1926).

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. ernestii*, *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. ernestii* (*q.v.*).

M. zehntneri varies greatly in stem size, shape and colour, in spine number, length, thickness and colour, and in the degree to which its flowers are exserted from the cephalium and thus able to expand. Its pollination biology has been studied by Locatelli & Machado (1999a).

11. *Melocactus lanssensianus* P. J. Braun in *Succulenta* 65: 26, 61–63 (1986). Holotype: Pernambuco, Mun. Caetés, 1977, Horst 474 (ZSS).

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).

12. *Melocactus glaucescens* Buining & Brederoo in *Cact. Succ. J. (US)* 44: 159, with illus. (1972). Holotype: Bahia, Mun. Morro do Chapéu, Horst 219 (U, not found Apr. 1989). Lectotype (Taylor 1991a): Buining & Brederoo, l.c. fig. 2.

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. ×albicephalus* 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).

13. *Melocactus concinnus* Buining & Brederoo in Kakt. and. Sukk. 23: 5–7 (1972). Holotype:
Bahia, Mun. Seabra, Horst 214 (U 531262).

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*.

14. *Melocactus paucispinus* G. Heimen & R. Paul in Kakt. and. Sukk. 34: 227–229, with illus. (1983). Holotype: Bahia, Mun. Seabra, *Heimen et al.* 81/149 (KOELN, n.v.).

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.

15. *Melocactus violaceus* Pfeiffer in Allg. Gartenz. 3: 313 (1835); Enum. Cact.: 45–46 (1837).
 Type (see Schumann 1897–98): Brazil, cult. Schelhase (B†). Neotype (Taylor 1991a): Brazil,
 Rio de Janeiro, D. Sucre 9186 (RB 192529).

Two of the 3 subspecies recognized here are endemic to the core area of Eastern Brazil:

1. Fruit lilac- to pale pink	2
1. Fruit white to very pale pink (NE Bahia, Sergipe & Alagoas)	15c. subsp. <i>margaritaceus</i>
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. <i>violaceus</i>
2. Flower c. 18–22 × 7–10 mm; spines 5–6; ribs 8–10 (Bahia inland: Jacobina & Rui Barbosa)	15b. subsp. <i>ritteri</i>

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.

15b. subsp. *ritteri* N. P. Taylor in Bradleya 9: 57 (1991). Holotype: Bahia, Mun. Rui Barbosa, Ritter 1209a (U 531256).

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*.

15c. subsp. **margaritaceus** *N. P. Taylor*, l.c., plate 19 (1991). Holotype: Sergipe, Mun. Santo Amaro das Brotas, *Rizzini & Mattos* (RB 215018).

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 *Epostoopsis* 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

in Bull. Torr. Bot. Club. 35: 561 (1908). Type: *H. gracilis* (Miller) Britton (*Cereus gracilis* Miller).

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 Corumbá, 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 Paraguaçu 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

Cact. 2: 108 (1920). Type: *L. bahiensis* 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 *Facheiroa squamosa* (Gürke) P. J. Braun & E. Esteves Pereira. For *Leocereus paulensis* Spegazzini, see *Coleocephalocereus fluminensis* (Zappi & Taylor 1992b).

1. *Leocereus bahiensis* Britton & Rose, Cact. 2: 108 (1920); N. P. Taylor & Zappi in Bradleya 8: 107–108 (1990). Type: Bahia, Serra do Tinga ['Tingga'], Zehntner 266 (US, lecto. designated here; NY, K, lectoparas.).

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

Cact. 2: 173 (1920); P. J. Braun & E. Esteves Pereira (1986–89). Type: *Facheiroa pubiflora* Britton & Rose (= *Facheiroa ulei* (Gürke) Werderm.).

Including *Zehntnerella* Britton & Rose (1920); *Facheiroa* subg. *Zehntnerella* (Britton & Rose) P. J. Braun & E. Esteves Pereira (1986).

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 *Epostoa* Britton & Rose). Buxbaum (1959) published *Epostoa* 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. <i>F. squamosa</i> |
| 2. Flowers to 3 × 2.8 cm; perianth-segments sometimes pinkish (Bambuí limestone outcrops of SW Bahia and cent.-N Minas Gerais) | 2. <i>F. cephaliomelana</i> |
| 2. Flowers 4–4.7 × 2 cm; perianth-segments white (cent.-N Bahia, non-calcareous rocks) | 1. <i>F. ulei</i> |

1. *Facheiroa ulei* (Gürke) Werdermann, Bras. Säulenakt.: 113 (1933); P. J. Braun & E. Esteves Pereira in Kakt. and. Sukk. 38: 26, Abb. 1 (1987); ibid. 39: 64 (1988). Holotype: Brazil, Bahia, Mun. Gentio do Ouro, Serra de Santo Inácio, 1907, Ule 12 (B, n.v.).

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.

2. Facheiroa cephaliomelana *Buining & Brederoo* in Kakt. and. Sukk. 26(6): 121–124 (1975).

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 Bambuí limestone outcrops from the same region, eg. *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 Bambuí 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).

2b. subsp. *estevesii* (P. J. Braun) N. P. Taylor & Zappi in Cactaceae Consensus Initiatives 3: 7 (1997). Holotype: Brazil, Bahia, E of the Rio São Francisco, [E of Malhada, Iuiú], July 1984, E. Esteves Pereira 186 (KOELN ['Succulentarium'], n.v.; UFG, K, isos.).

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.

3. *Facheiroa squamosa* (Gürke) P. J. Braun & E. Esteves Pereira in Kakt. und. Sukk. 40: 202 (1989). Holotype: Brazil, Piauí, Serra Branca [Mun. São Raimundo Nonato], Jan. 1907, Ule 10 (B; K, SPF photos ex B).

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

in Krainz, Die Kakteen, Lfg. 38–39 (July 1968). Type and only species: *E. dybowskii* (Roland-Gosselin) F. Buxbaum (*Cereus dybowskii* Roland-Gosselin).

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.

1. *Espostopsis dybowskii* (Roland-Gosselin) F. Buxbaum, l.c. (1968). Type: Brazil, N Bahia, Itumirim, Dybowski (living material), Casabianca (fls & frs), apparently not extant (cf. Kiesling 1986). Neotype (designated here): Brazil, Bahia, Mun. Jaguarari, 38 km N of Senhor do Bonfim on road BR 407, 15 July 1989, Zappi 125 (SPF; HRCB, ZSS isoneotypi; K, photos).

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.

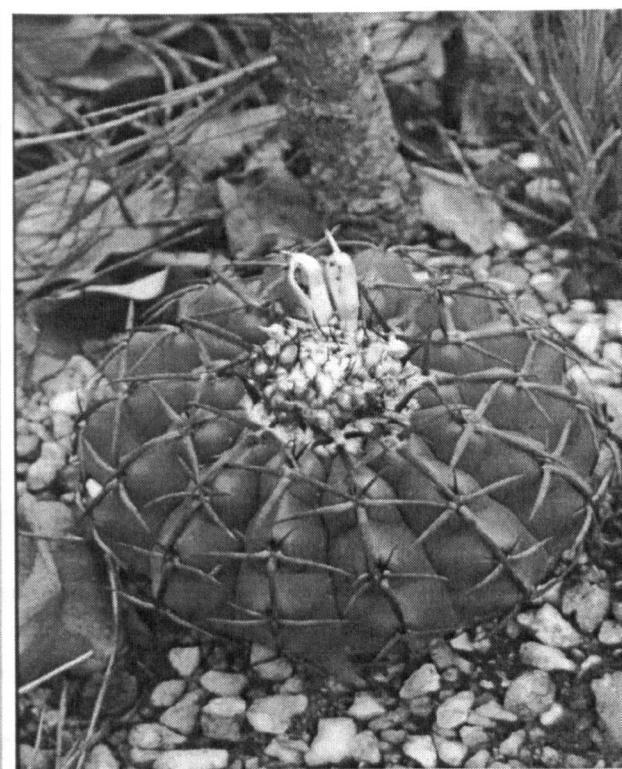
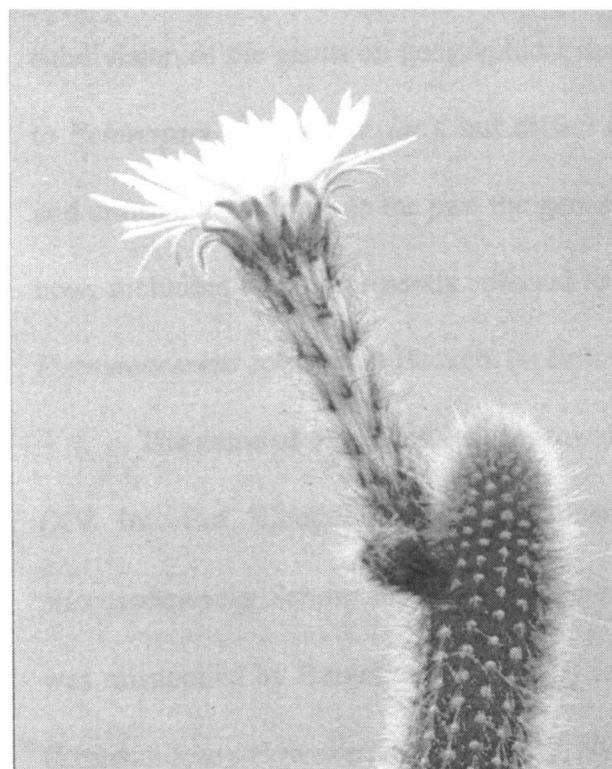
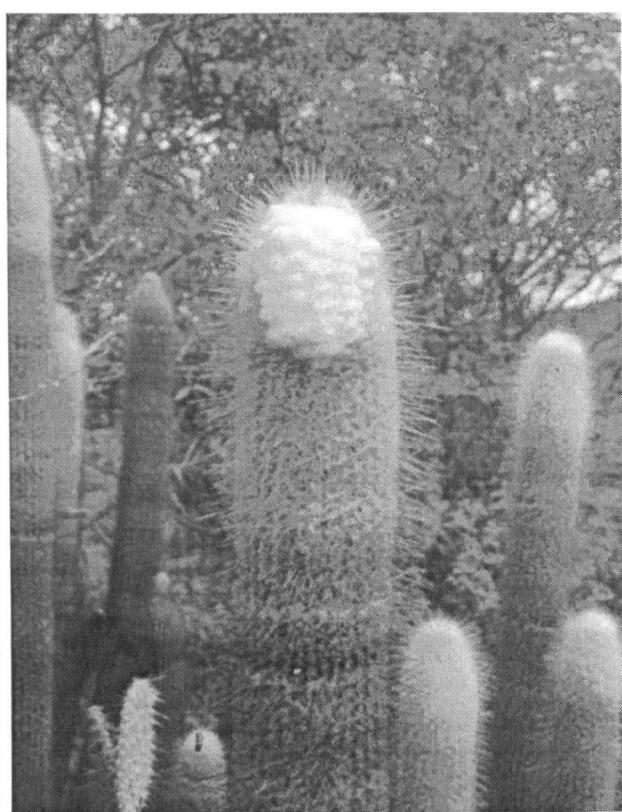
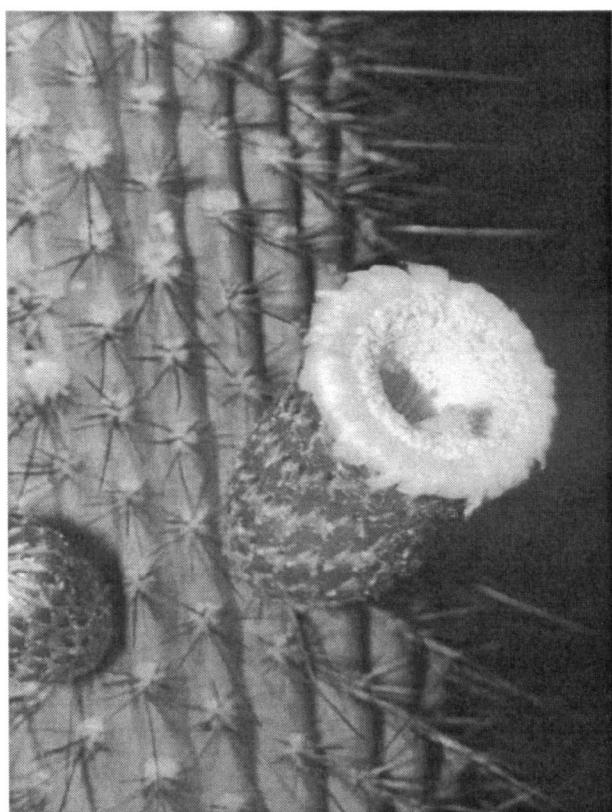


Plate 5. Diversity of Cactaceae in Eastern Brazil. 5.1–5.4, examples from Cactoideae-Trichocereeae: 5.1 (top left), *Facheiroa squamosa* (Mun. Curaçá, Bahia), 5.2 (top right), *Espostoa dybowskii* (E of Porto Alegre, Mun. Maracás, Bahia), 5.3 (bottom left), *Arthrocereus melanurus* (cult. R. Mottram, 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

Kakteen: 337 (1929), *nom. cons.*; F. Knuth, Den Nye Kaktusbog: 111 (1930). Type: Monatsschr. Kakt.-Kunde 28: illus. opp. p. 62 (1918), as '*Cereus damazioi*', *typ. cons.* (= *A. glaziovii* (K. Schum.) N. P. Taylor & Zappi).

Literature: Taylor (1991d, 1992a); Brummitt (1994).

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. A. rondonianus
1. Inner perianth-segments and anthers white or cream (Serra do Espinhaço and Serra da Mantiqueira)	2
2. Flower-tube ± naked, with only few areoles and hair-spines; stems usually decumbent to ascending, often segmented, sometimes very short to nearly spherical (usually on <i>canga</i> formation)	3. A. glaziovii
2. Flower-tube densely covered in areoles and conspicuous hair-spines; stems ± erect, not segmented (on substrates other than <i>canga</i>)	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): Brasilia, (?) 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:

1. Flowers 9–11.5 cm; pericarpel and tube densely covered in areoles with dark, ferrugineus, hair-spines; perianth-segments 23–40 mm (Rio Grande drainage, SW Minas Gerais)	1a. subsp. melanurus
1. Flowers 10–16 cm; pericarpel and tube covered in areoles with pale brown or pinkish, soft hair-spines; perianth-segments 40–60 mm	2
2. Plants with few or no basal branches, reaching 2 m or more, stout rootstock not visibly developed; ribs 12–19 (Serra do Ibitipoca, MG)	1b. subsp. magnus
2. Plants shrubby, branching freely at base, not > 1 m, stems slender; rootstock well-developed; ribs 9–12 (Rio São Francisco drainage, E foot of Serra do Cipó, MG)	1c. subsp. odorus

1a. subsp. melanurus

South-eastern *campo rupestre* (Rio Grande drainage) element: in sandy, gravelly and rocky places in *campo rupestre*, south-western Minas Gerais. Endemic to Minas Gerais. Map 39.

1b. subsp. *magnus* N. P. Taylor & Zappi in Cactaceae Consensus Initiatives 3: 7 (1997).

Holotype: Brazil, Minas Gerais, Mun. Lima Duarte, Parque Estadual do Ibitipoca, 27 July 1991, Zappi et al. 262 (SPF; CESJ, HRCB, K isos.).

South-eastern *campo rupestre* (Rio Preto / Rio Paraíba 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).

1c. subsp. *odoratus* (Ritter) N. P. Taylor & Zappi in Cactaceae Consensus Initiatives 3: 7 (1997).

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.

2. *Arthrocereus rondonianus* Backeberg & Voll in Cact. Succ. J. (US) 23: 120 (1951). Type:

Brazil, Minas Gerais, Diamantina [Serra do Cabral], 700 m (presumed not to have been preserved). Lectotype (designated here): Blätt. Kakteenforsch. 1935(4): [unpaged] (1935), illus. ‘*Arthrocereus rondonianus* Bckbg. et Voll n. sp.’; the same illustration also in Arch. Jard. Bot. Rio Janeiro 9: 158, fig. 1 (1949) and Backeberg, Die Cact. 4: 2110, Abb. 1990 (1960).

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.

3. *Arthrocereus glaziovii* (K. Schumann) N. P. Taylor & Zappi in Bradleya 9: 84–85 (1991).

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

in Allg. Gartenz. 5: 241 (1837). Type: *D. insignis* Pfeiffer (= *D. placentiformis* (Lehm.) Schumann).

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, tricolporate (vs. 12–15-colporate) 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
1. Radial spines > 8 per areole, to 1.5 mm thick; stems freely offsetting, or solitary and < 11 cm diam. 5
2. Exposed part of stem with only 3 areoles visible per rib; ribs not broken up by tubercles (N Bahia to Piauí and Ceará) 2. *bahiensis*
2. Exposed part of stem with > 3 areoles per rib and/or ribs tuberculate with deep sinuses between areoles 3
3. Seed 1.5–2.0 mm; fruit white or greenish, rarely pinkish red at apex; ribs 9–26, ± tuberculate; spines often flattened, > 1.5 mm thick 4
3. 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) 5. *pseudoinsignis*

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**

1. Discocactus zehntneri *Britton & Rose*, Cact. 3: 218 (1922); N. P. Taylor in Cact. Succ. J. Gr. Brit. 43: 40 (1981). Type: Bahia, Mun. Sento Sé, Zehntner in *Rose & Russell* 19779 (US, lecto. designated here).

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 \times 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 \times 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 – $30 \times < 1$ 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.

1b. subsp. *boomianus* (*Buining & Brederoo*) N. P. Taylor & Zappi in Bradleya 9: 86 (1991).

Holotype: Bahia, Mun. Morro do Chapéu, Horst 222 (U).

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.

2. *Discocactus bahiensis* Britton & Rose, Cact. 3: 220 (1922); Buining, Gen. Discocactus: 123–129 (1980). Holotype: Bahia, Zehntner in Rose 19783 (US).

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*.

3. **Discocactus heptacanthus (Rodrigues) Britton & Rose**, Cact. 3: 218 (1922); Taylor in Cact. Succ. J. Gr. Brit. 43: 38 (1981). Type: Brazil, Mato Grosso, near Cuiabá, Rodrigues (†, see Britton & Rose, l.c.). Lectotype (designated here): Rodrigues, Pl. Mato Grosso: t. 11 (1898).

Only the following subspecies occurs in Eastern Brazil:

3a. subsp. **catingicola (Buining & Brederoo) N. P. Taylor & Zappi** in Cactaceae Consensus Initiatives 3: 7 (1997). Holotype: W Bahia, Mun. São Desidério, Horst 392 (U).

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*.

4. *Discocactus placentiformis* (*Lehmann*) *K. Schumann* in *Engler & Prantl, Pflanzenfam.* 3(6a): 190 (1894). Type: ‘*Brasilia meridionali*’, apparently not preserved. Neotype (designated here): *Lehmann* in *Nov. Act. Nat. Cur.* 16(1): t. 16 (1832).

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, *Tabulae 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 Poções, Jequitáí, 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.

5. *Discocactus pseudoinsignis* N. P. Taylor & Zappi in Bradleya 9: 86 (1991). Holotype: Minas Gerais, Mun. Cristália, Zappi et al. in CFCR 12045 (SPF).

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.

6. *Discocactus horstii* Buining & Brederoo in Krainz, Die Kakteen, Lfg 52 (1973); Buining, Gen. *Discocactus*: 106–110 (1980). Holotype: Minas Gerais, Mun. Grão Mogol, Horst 360 (U).

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

in *Succulenta* 46: 159–163 (1967). Type: *U. gummifera* (Backeb. & Voll) Buining (*Parodia gummifera* Backeb. & Voll).

Literature: Nyffeler (1997, 1998); Schulz & Machado (2000).

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 $> 20 \times 15$ mm; fruit yellowish or greenish, inconspicuous; seeds with convex testa-cells (Subg. *Uebelmannia*)
 - 2
2. Ribs 15–22; stem cortex with mucilage cells but lacking ducts
 1. *buiningii*
2. Ribs 22–42; stem cortex with vertically arranged mucilage ducts
 2. *gummifera*

Subg. *Uebelmannia*

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

- 1. *Uebelmannia buiningii* Donald** in Nat. Cact. Succ. J. (UK) 23: 2–3 (1968); P. J. Braun & E. Esteves Pereira in Kakt. and. Sukk. 39: 2–3 (1988); van Heek & Strecker in ibid. 45: 234–235, illus. (1994). Holotype: Brazil, Minas Gerais, Mun. Itamarandiba, Serra Negra, Tromba d'Anta, 1966, 'c. 1000 m', Horst HU 141 (U; ZSS, iso.).

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.

- 2. *Uebelmannia gummifera* (Backeberg & Voll) Buining** in Succulenta 46: 159–160 (1967). Holotype: Brazil, Minas Gerais, Serra do Ambrósio [Mun. Rio Vermelho], 1938, Mello-Barreto s.n. (RB 64065).

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

Subg. *Leopoldohorstia* P. J. Braun & E. Esteves Pereira in Succulenta 74: 134 (1995).

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

- 3. *Uebelmannia pectinifera* Buining** in Nat. Cact. Succ. J. (UK) 22: 86–87 (1967). Holotype: Brazil, Minas Gerais, Mun. Couto de Magalhães de Minas, Feb. 1966, Horst HU 106 (U).

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. <i>pectinifera</i> |
| 1. Plants with green epidermis, white scaly plates absent; ribs (16–)18–29 | 2 |
| 2. Spines yellow, ascending, organized in rows following the edge of the rib; plants to 50 cm | 3b. subsp. <i>flavispina</i> |
| 2. Spines greyish, spreading, not organized in rows; plants to 100 cm | 3c. subsp. <i>horrida</i> |

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.

3b. subsp. *flavispina* (*Buining & Bredero*) P. J. Braun & E. Esteves Pereira in Succulenta 74: 135 (1995). Holotype: Brazil, Minas Gerais, Barão do Guaçuí, 1280 m, Horst & Uebelmann 361 (U).

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.

3c. subsp. *horrida* (*P. J. Braun*) *P. J. Braun & E. Esteves Pereira* in *Succulenta* 74: 135 (1995).

Holotype: Brazil, Minas Gerais, Mun. Bocaiúva, near Sítio, 1982, *Horst & Uebelmann* 550 (ZSS; K, iso.).

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, l.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).

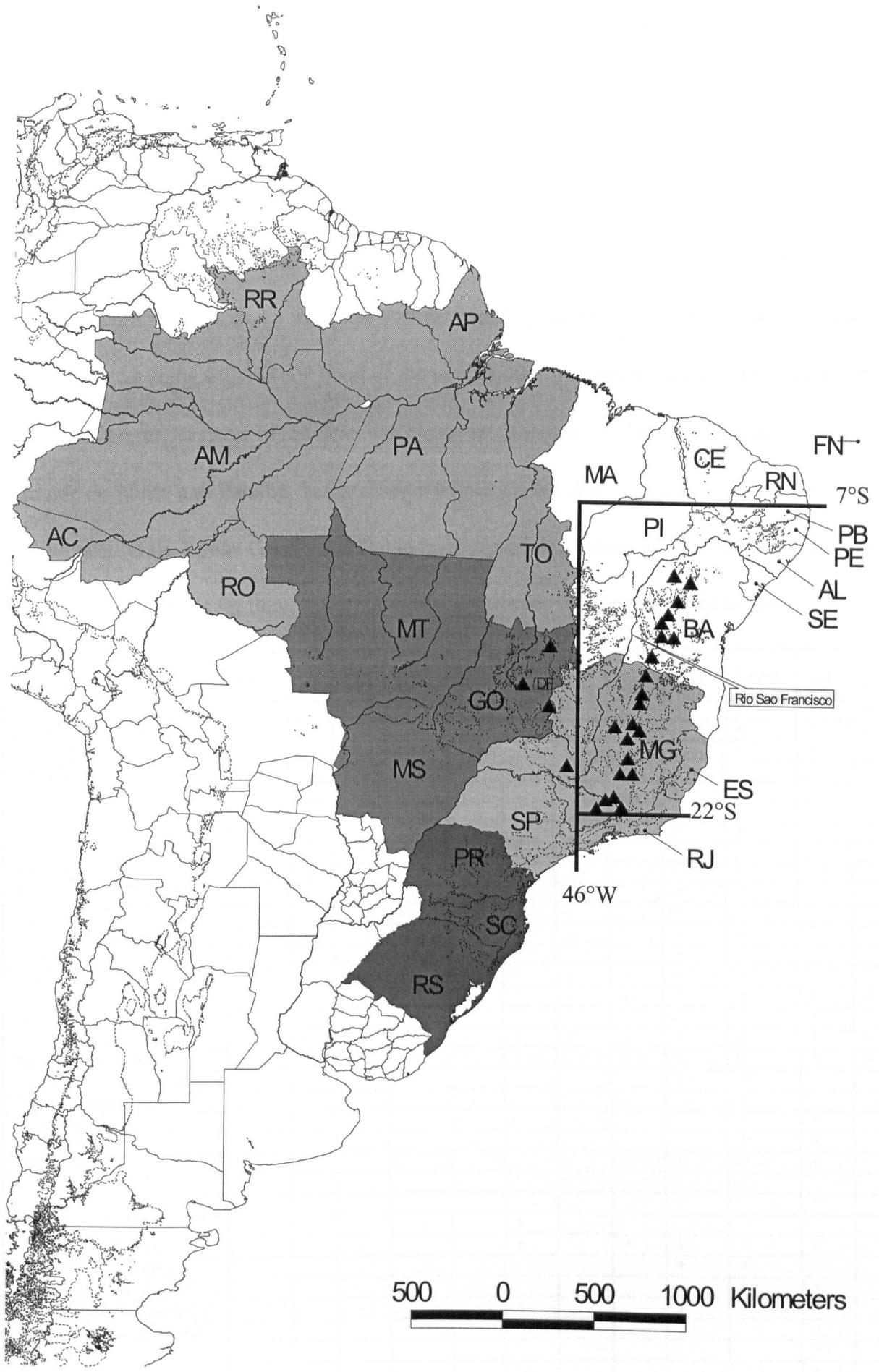
Perhaps the most interesting and potentially informative aspect of this study is to use the areas defined below as a model to compare with other floristically important plant groups found in Eastern Brazil, especially those with ecological preferences similar to Cactaceae, such as Araceae (eg. *Philodendron*, *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.

Map 1 (next page). Brazil, indicating the East Brazilian Highlands (—), principal *campo rupestre* areas (▲), limits of the main area (ie. 'Eastern Brazil' = unshaded area + box), limits of the core study area (box delimited by 7°S, 46°W & 22°S), Brazilian regions (Grandes Regiões, differently shaded) and states. *Key to state codes by region.* Northern Brazil: AC = Acre, AM = Amazonas, RO = Rondônia, RR = Roraima, AP = Amapá, PA = Pará, TO = Tocantins. Central-Western Brazil: MT = Mato Grosso, MS = Mato Grosso do Sul, GO = Goiás, DF = Distrito Federal. North-eastern Brazil (unshaded): MA = Maranhão, PI = Piauí, CE = Ceará, RN = Rio Grande do Norte, PB = Paraíba, PE = Pernambuco, FN = Fernando de Noronha, AL = Alagoas, SE = Sergipe, BA = Bahia. South-eastern Brazil: MG = Minas Gerais, ES = Espírito Santo, RJ = Rio de Janeiro, SP = São Paulo. Southern Brazil: PR = Paraná, SC = Santa Catarina, RS = Rio Grande do Sul.



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.

TAXON / STATE	MA	PI	CE	RN	PB	PE	AL	SE	BA	MG ¹	ES	RJ ²
<i>Pereskia aculeata</i>	+					+	+	+	+	+	+	+
<i>P. grandifolia</i> ssp. <i>grandifolia</i>	+?		+			+			+	+	+	+
<i>P. grandifolia</i> ssp. <i>violacea</i> †								c	+	+		
<i>P. bahiensis</i> †									+			
<i>P. stenantha</i> †									+	+		
<i>P. aureiflora</i> †									+	+		
<i>Quiabentia zehntneri</i> †									+	+		
<i>Tacinga funalis</i> †	±					+			+			
<i>T. braunii</i> †										+		
<i>T. wernerii</i> †									+	+		
<i>T. palmadora</i> †				+	+	+	+	+	+			
<i>T. saxatilis</i> ssp. <i>saxatilis</i>									+	+		
<i>T. saxatilis</i> ssp. <i>estevensis</i> †§									+			
<i>T. inamoena</i> †	+	+	+	+	+	+	+	+	+	+	+	+
<i>Brasiliopuntia brasiliensis</i>					+	+	+	+	+	+	+	+
<i>Opuntia monacantha</i>								c	c	+	+	
<i>Hylocereus setaceus</i>	±	+	+			+	+	+	+	+	+	+
<i>Epiphyllum phyllanthus</i>	+	+	+		+	+	+	+	+	+	+	+
<i>Pseudoacanthocereus brasili.</i> †									+	+		
<i>Lepismium houletteianum</i>										+		
<i>L. warmingianum</i>										+	+	
<i>L. cruciforme</i>						+				+	+	
<i>Rhipsalis russellii</i>									+	+	±	
<i>R. elliptica</i>										+		
<i>R. oblonga</i>									+		+	
<i>R. crispata</i>						+						
<i>R. floccosa</i> ssp. <i>floccosa</i>						+		+	+		+	
<i>R. floccosa</i> ssp. <i>oreophila</i> †								+	+			
<i>R. floccosa</i> ssp. <i>pulvinigera</i>									+	+		
<i>R. paradoxa</i> ssp. <i>septentrion.</i> †						+		+	+	+		
<i>R. pacheco-leonis</i> ssp. <i>catenul.</i>										+		
<i>R. cereoides</i>										+		
<i>R. sulcata</i> †§										+		
<i>R. lindbergiana</i>						+		+	+	+	+	
<i>R. teres</i>										+	+	
<i>R. baccifera</i> ssp. <i>baccifera</i>	+		+		+	+						
<i>R. baccifera</i> ssp. <i>hileiabaiana</i> †									+			

<i>R. pulchra</i>									+		
<i>R. burchellii</i>									±	+	
<i>R. juengeri</i>									+		
<i>R. clavata</i>									±	+	+
<i>R. cereuscula</i>					+			+	+		
<i>R. pilocarpa</i>								+	+		
<i>R. hoelleri</i> †§										+	
<i>Hatiora salicornioides</i>								+	+	+	+
<i>Schlumbergera kautskyi</i> †										+	
<i>S. microsphaerica</i>									+	±	
<i>S. opuntioides</i>									+		
<i>Brasilicereus phaeacanthus</i> †								+	+		
<i>B. markgrafii</i> †									+		
<i>Cereus mirabella</i>	+								+	+	
<i>C. albicaulis</i> †		+	+			+	±	+	+	±	
<i>C. fernambucensis</i> ssp. <i>fernambucensis</i>					+	+	+	+	+	+	+
<i>C. insularis</i> †											
									FN		
<i>C. jamacaru</i> ssp. <i>jamacaru</i> †?	+	+	+	+	+	+	+	+	+	c	c
<i>C. jamacaru</i> ssp. <i>calcirupicola</i>	±								+	+	
<i>C. hildmannianus</i>									+		
<i>Cipocereus laniflorus</i> †§									+		
<i>C. crassisepalus</i> †									+		
<i>C. bradei</i> †									+		
<i>C. minensis</i> ssp. <i>minensis</i> †									+		
<i>C. minensis</i> ssp. <i>pleurocarpus</i> †									+		
<i>C. pusilliflorus</i> †§									+		
<i>Stephanocereus leucostele</i> †									+		
<i>S. tuetzeliburgii</i> †									+		
<i>Arrojadoa bahiensis</i> †									+		
<i>A. dinae</i> ssp. <i>dinae</i> †									+	+	
<i>A. dinae</i> ssp. <i>eriocaulis</i> †									+		
<i>A. penicillata</i> †									+	+	
<i>A. rhodantha</i> †	+					+			+	+	
<i>Pilosocereus tuberculatus</i> †									+	+	
<i>P. gounellei</i> ssp. <i>gounellei</i> †	+	+	+	+	+	+	+	+	+	+	
<i>P. gounellei</i> ssp. <i>zehntneri</i> †									+	+	
<i>P. catingicola</i> ssp. <i>catingicola</i> †									+		
<i>P. catingicola</i> ssp. <i>salvadorensis</i> †					+	+	+	+	+	+	
<i>P. azulensis</i> †§?										+	
<i>P. arrabidae</i>									+	+	+
<i>P. brasiliensis</i> ssp. <i>brasiliensis</i>										+	
<i>P. brasiliensis</i> ssp. <i>ruschianus</i> †									+	+	+
<i>P. flavipulvinatus</i> †	+	+	+								
<i>P. pentaedrophorus</i> ssp. <i>pent.</i> †							+	+	+		
<i>P. pentaedrophorus</i> ssp. <i>robustus</i> †								+	+		
<i>P. glaucochrous</i> †									+		
<i>P. floccosus</i> ssp. <i>floccosus</i> †									+		
<i>P. floccosus</i> ssp. <i>quadricostatus</i> †									+		
<i>P. fulvilanatus</i> ssp. <i>fulvil.</i> †									+		
<i>P. fulvilanatus</i> ssp. <i>rosae</i> †§									+		
<i>P. pachycladus</i> ssp. <i>pachycl.</i>									+	+	
<i>P. pachycladus</i> ssp. <i>pernambuco</i> . †	+	+	+	+	+	+	+	+			
<i>P. magnificus</i> †										+	
<i>P. machrisii</i>		+							+		
<i>P. aurisetus</i> ssp. <i>aurisetus</i> †										+	
<i>P. aurisetus</i> ssp. <i>aurilanatus</i> †										+	
<i>P. aureispinus</i> †									+		
<i>P. multicostatus</i> †										+	
<i>P. piauhyensis</i> †		+	+	+							
<i>P. chrysostele</i> †			+	+	+		+	+			
<i>P. densiareolatus</i> †									+	+	
<i>Micranthocereus violaciiflorus</i> †										+	
<i>M. albicephalus</i> †									+	+	
<i>M. purpureus</i> †									+		
<i>M. auriazureus</i> †§										+	
<i>M. streckeri</i> †§									+		
<i>M. polyanthus</i> †									+		
<i>M. flaviflorus</i> †									+		
<i>M. dolichospermaticus</i> †									+		

<i>Coleocephalocer. buxb. ssp. b</i> †										+	+	
<i>C. buxbaum. ssp. flavisetus</i> †										+		
<i>C. fluminensis</i> ssp. <i>fluminensis</i>										+	+	+
<i>C. fluminensis</i> ssp. <i>decumbens</i> †										+		
<i>C. pluricostatus</i> †										+	+	
<i>C. goebelianus</i> †										+	+	
<i>C. aureus</i> †										+		
<i>C. purpureus</i> †§										+		
<i>Melocactus oreas</i> ssp. <i>oreas</i> †										+		
<i>M. oreas</i> ssp. <i>cremophilus</i> †							±			+		
<i>M. ernestii</i> ssp. <i>ernestii</i> †		±	±	+	+	±	+	+	+	+		
<i>M. ernestii</i> ssp. <i>longicarpus</i> †										+	+	
<i>M. bahiensis</i> ssp. <i>bahiensis</i> †						+				+		
<i>M. bahiensis</i> ssp. <i>amethystinus</i> †										+	+	
<i>M. conoideus</i> †§										+		
<i>M. deinacanthus</i> †§										+		
<i>M. levitestatus</i> †										+	+	
<i>M. azureus</i> ssp. <i>azureus</i> †										+		
<i>M. azureus</i> ssp. <i>ferreophilus</i> †										+		
<i>M. pachyacanthus</i> ssp. <i>pachy.</i> †										+		
<i>M. pachyacanthus</i> ssp. <i>viridis</i> †										+		
<i>M. salvadorensis</i> †										+		
<i>M. zehntneri</i> †	+	+	+	+	+	+	+	+	+	+		
<i>M. lanssesianus</i> †§?					±	+						
<i>M. glaucescens</i> †§										+		
<i>M. concinnus</i> †										+	+	
<i>M. paucispinus</i> †										+		
<i>M. violaceus</i> ssp. <i>violaceus</i>			+	+	+			+	+	+	+	+
<i>M. violaceus</i> ssp. <i>ritteri</i> †										+		
<i>M. violac.</i> ssp. <i>margaritaceus</i> †								+	+	+		
<i>Harrisia adscendens</i> †	±	+			+	+	+	+	+	+		
<i>Leocereus bahiensis</i> †	±	+								+	+	
<i>Facheiroa ulei</i> †										+		
<i>F. cephaliomelana</i> ssp. <i>c.</i> †										+	+	
<i>F. cephaliom.</i> ssp. <i>estevesii</i> †§										+		
<i>F. squamosa</i> †		+				+				+		
<i>Epsotoopsis dybowskii</i> †										+		
<i>Arthrocereus melanurus</i> ssp. <i>m.</i>										+		
<i>A. melanurus</i> ssp. <i>magnus</i> †§										+		
<i>A. melanurus</i> ssp. <i>odorus</i> †§										+		
<i>A. rondonianus</i> †										+		
<i>A. glaziovii</i> †										+		
<i>Discocactus zehntneri</i> ssp. <i>z.</i> †										+		
<i>D. zehntneri</i> ssp. <i>boormanianus</i> †										+		
<i>D. bahiensis</i> †	+	+				±				+		
<i>D. heptacanthus</i> ssp. <i>catingic.</i> †	+									+	+	
<i>D. placentiformis</i> †										+		
<i>D. pseudoinsignis</i> †										+		
<i>D. horstii</i> †§										+		
<i>Uebelmannia buiningii</i> †										+		
<i>U. gummifera</i> †										+		
<i>U. pectinifera</i> ssp. <i>pectinifera</i> †										+		
<i>U. pectinifera</i> ssp. <i>flavispina</i> †										+		
<i>U. pectinifera</i> ssp. <i>horrida</i> †§										+		
STATE	MA	PI	CE	RN	PB	PE	AL	SE	BA	MG ¹	ES	RJ ²
STATE ENDEMICS	0	0	0	0	0	1	0	0	30	36	3	0
TAXA SCORED +	8	16	15	11	15	33	14	19	91	96	33	11
SPECIES SCORED +	8	16	15	11	15	33	14	19	75	79	29	11

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/RJ² = 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 Espinhaço (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 Andaraí, 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.

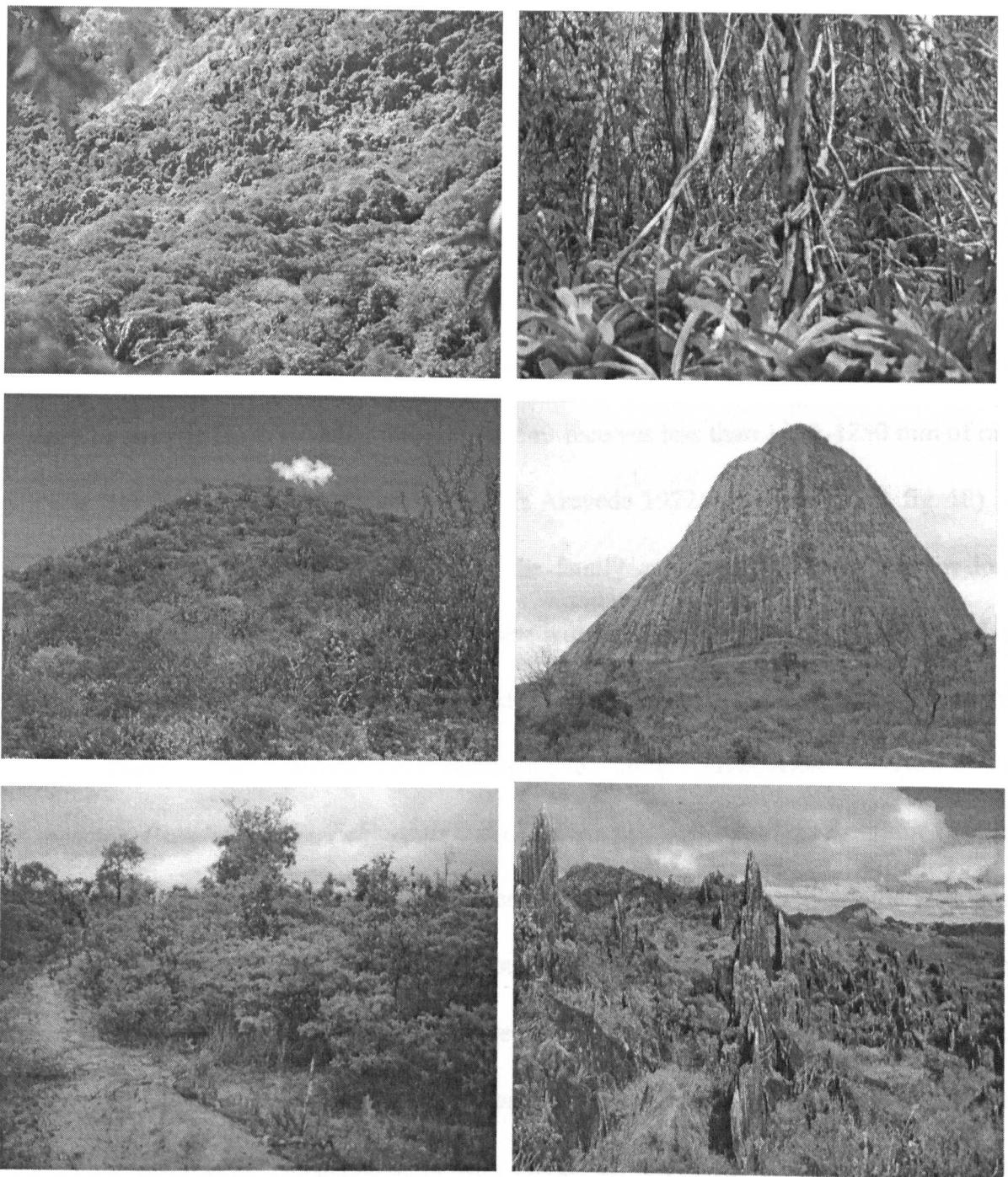


Plate 6. Habitat types. 6.1 (top left), Atlantic Forest / *Mata atlântica* (descent to Caraguatatuba, São Paulo); 6.2 (top right), *caatinga-agreste* (near Rui Barbosa, Bahia); 6.3 (centre left), shrubby *caatinga* (near Casa Nova, Bahia); 6.4 (centre right), inselberg in *caatinga-agreste* (Pedra Azul, 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 ‘isoietas 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, e.g. *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* (Maihuonioideae, 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-scendent 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. *Astrocephalocereus* (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.), *Epostoopsis* (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 *Espstoopsis* (see Area No. 3d(i), below) and its presumed relative, the central Andean genus, *Espstooa* — 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.



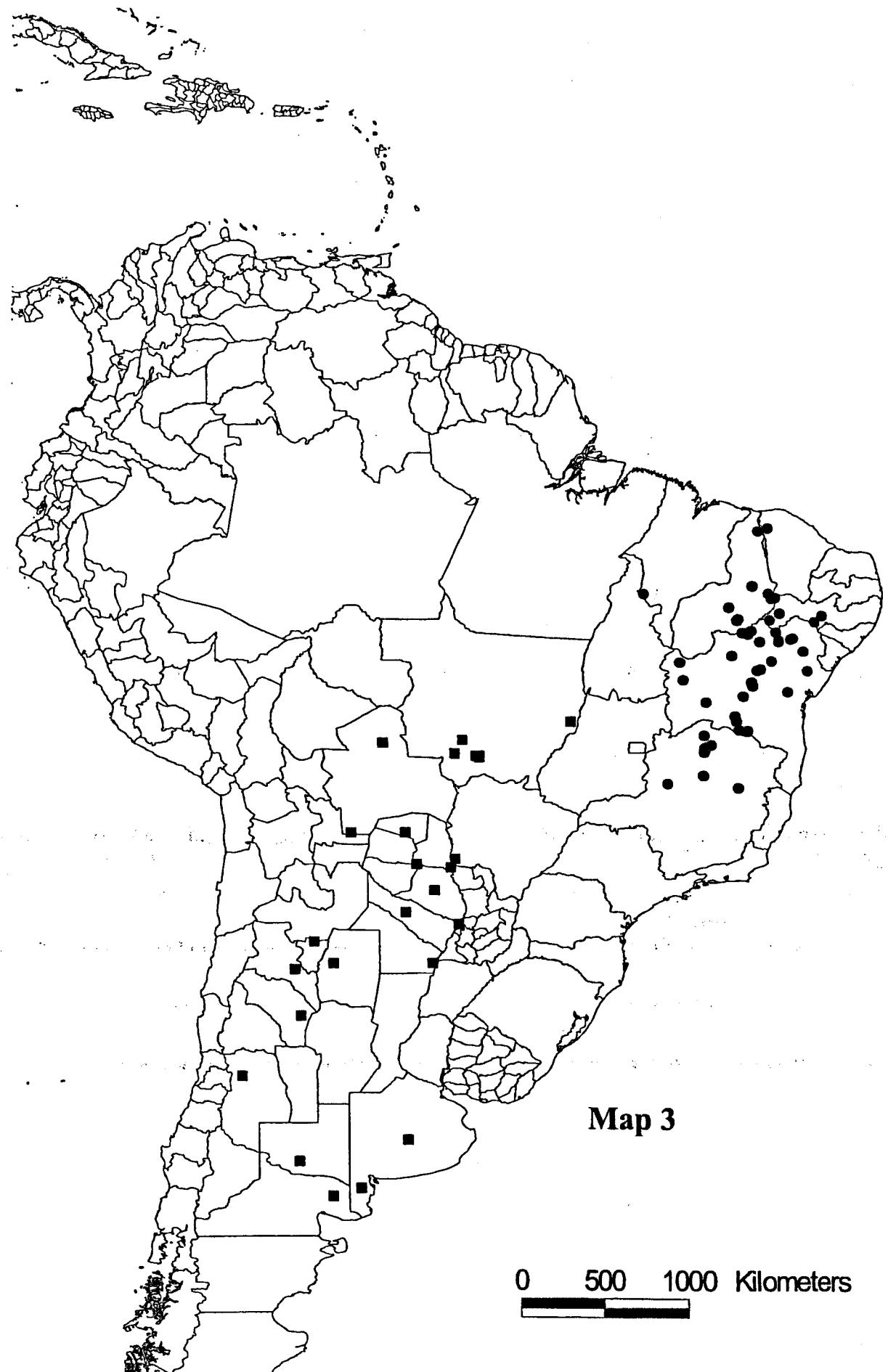
Map 2

0 500 1000 Kilometers

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(iiic) 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

Map 3 (next page). Distribution of *Cereus* subg. *Ebneria* [■] and subg. *Mirabella* [●]. S America.



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 *Quiabentia 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 heptacanthus*, *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

0 500 1000 Kilometers

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).



Map 5. Distribution of *Harrisia* subg. *Eriocereus* [▲] plus *H. adscendens* [●, Eastern Brazil] and subg. *Harrisia* [■]. Caribbean and South America.

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 *Pseudoeanthocereus*: *P. sicariguensis* [*] 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.

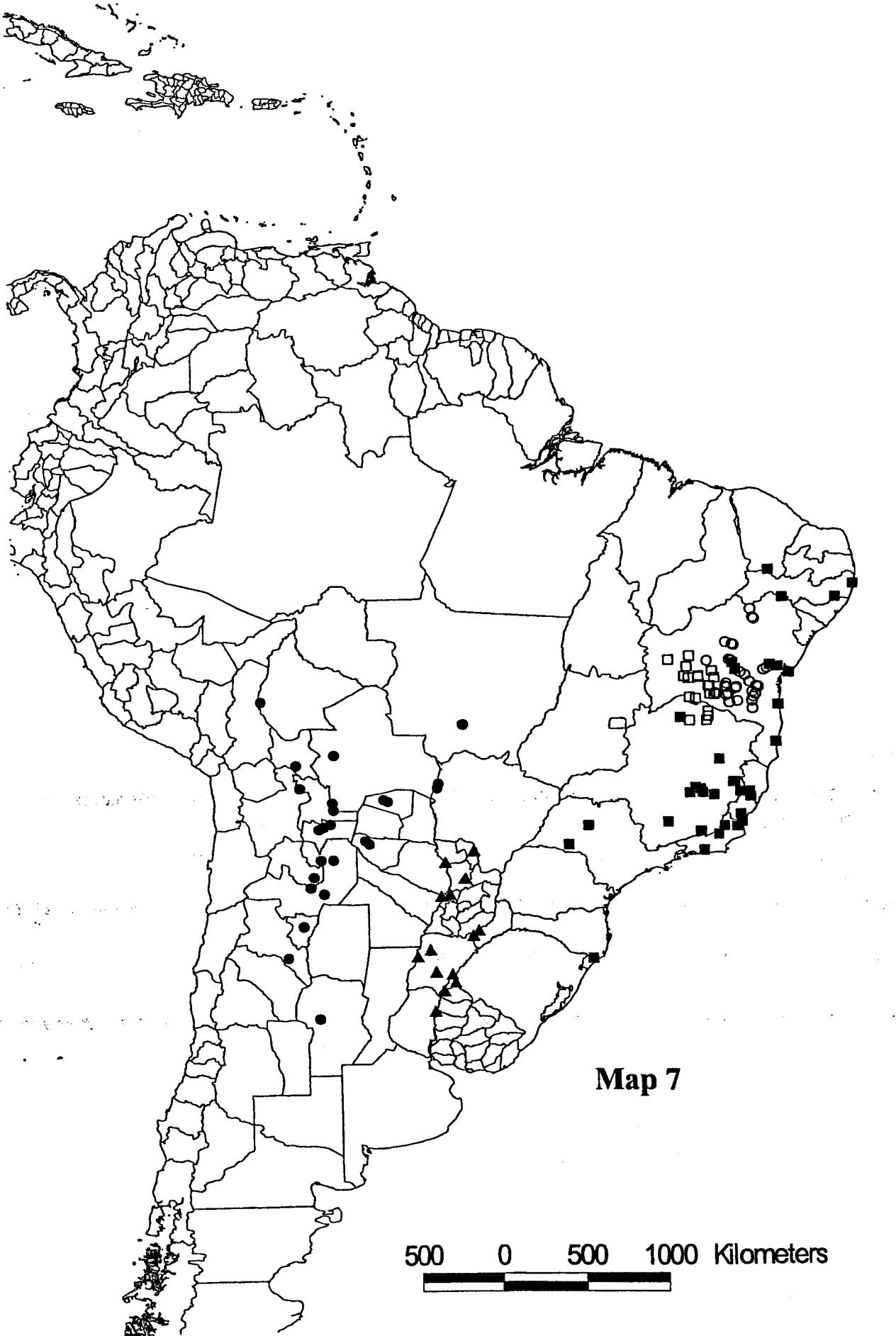
Distribution patterns and phytogeographical areas

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).

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.

1a. *Very widespread/non-specific in Areas 2–4* (2 taxa, Map 11)

Hylocereus setaceus, Epiphyllum phyllanthus.

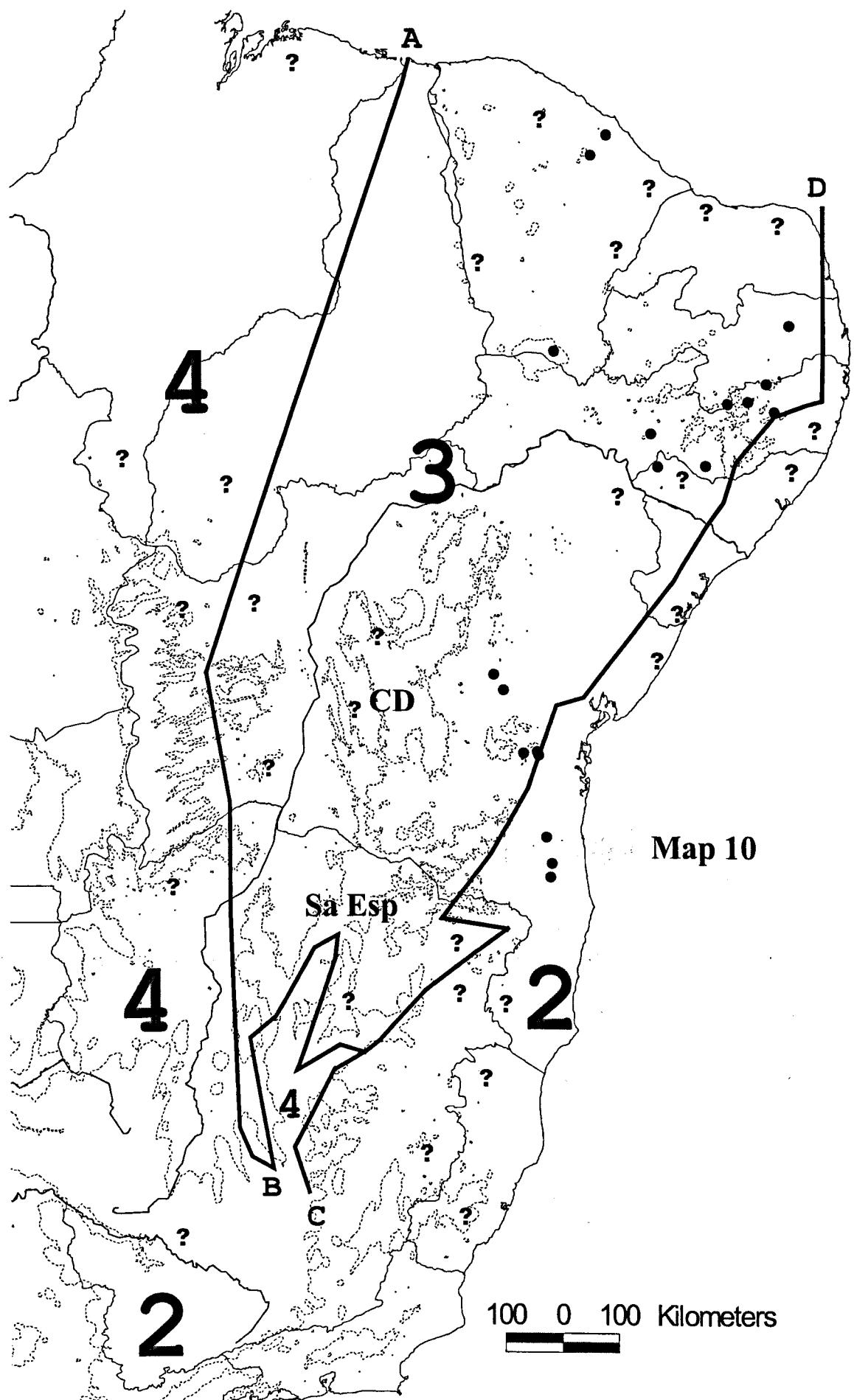
These are wide-ranging neotropical taxa of broad ecological tolerance, being strongly xerophytic epiphytes and lithophytes. They belong to tribe Hylocereeae, which phylogenetic research based on gene sequences (Wallace 1995 & pers. comm.) has shown to be amongst the most basal branches in the Cactoideae 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).

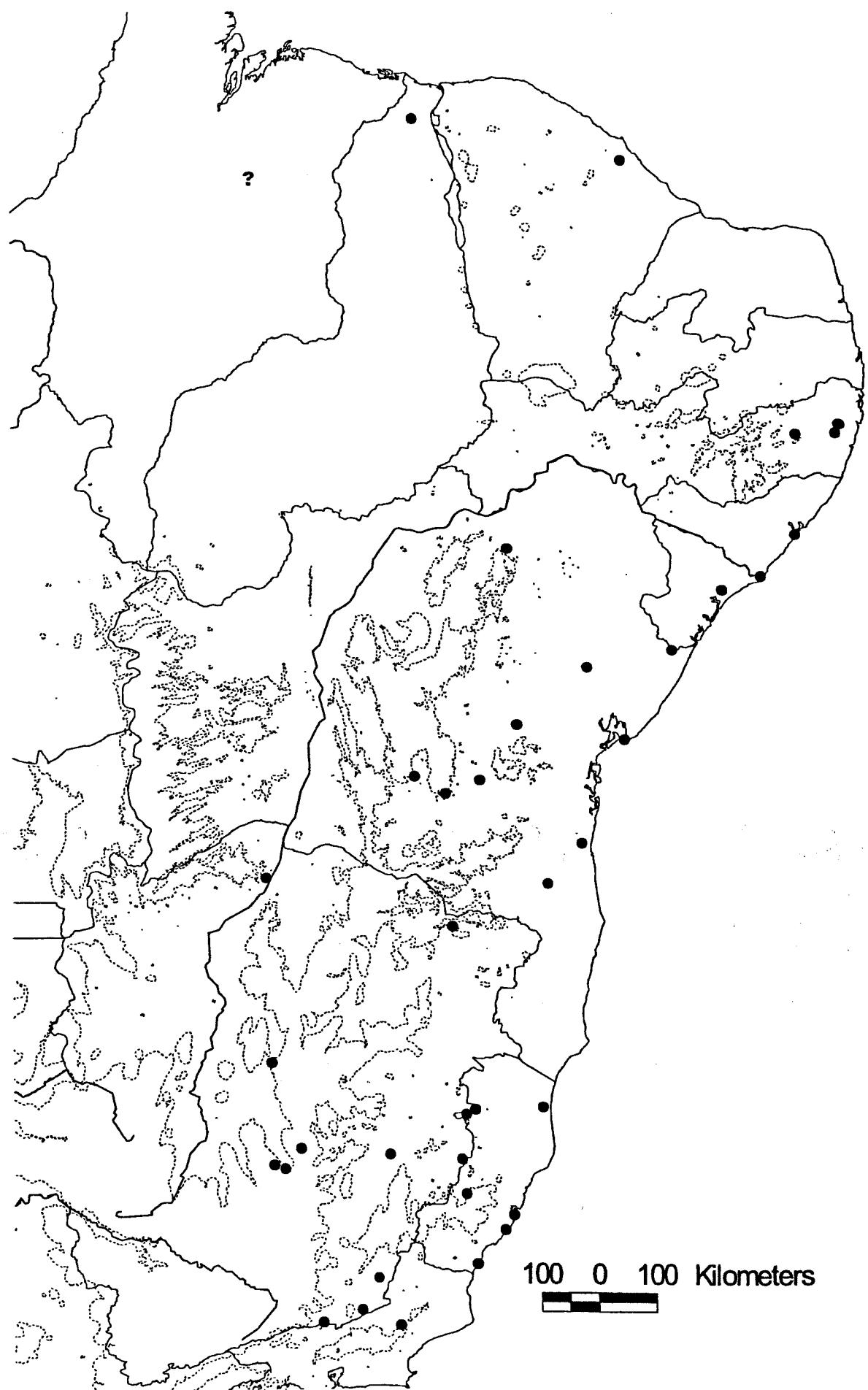
1b. *Ranging between Area No. 2 and No. 3 or No. 4, in restinga / Mata atlântica / mata de brejo / mata de neblina / campo rupestre / caatinga / agreste etc.* (7 taxa, Maps 12A–13)

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

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

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. *calcirupicola*, *Rhipsalis floccosa* subsp. *floccosa*, *R. paradoxa*, *Cipocereus laniflorus*, *Arthrocereus rondonianus*.



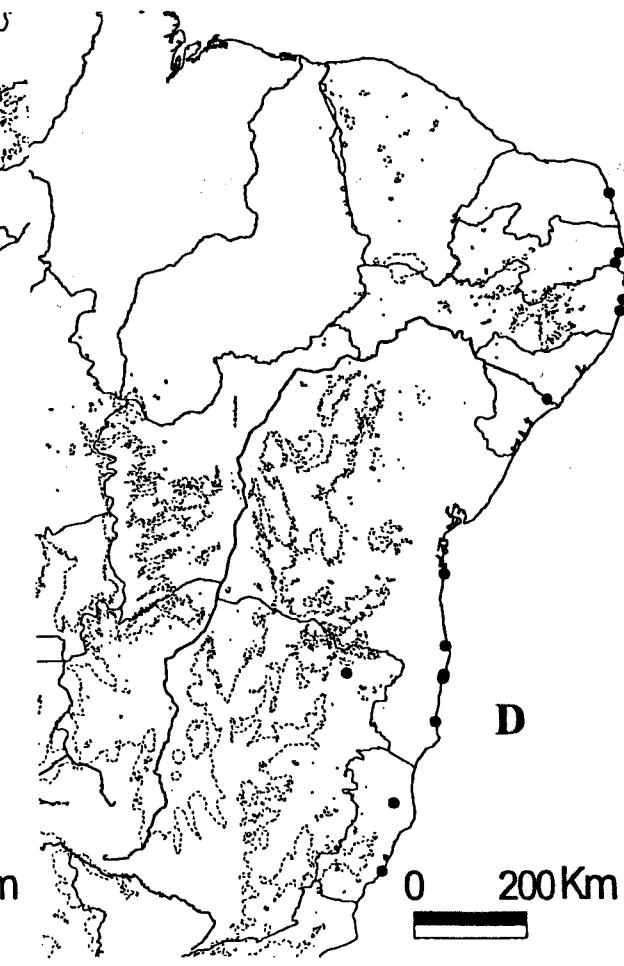
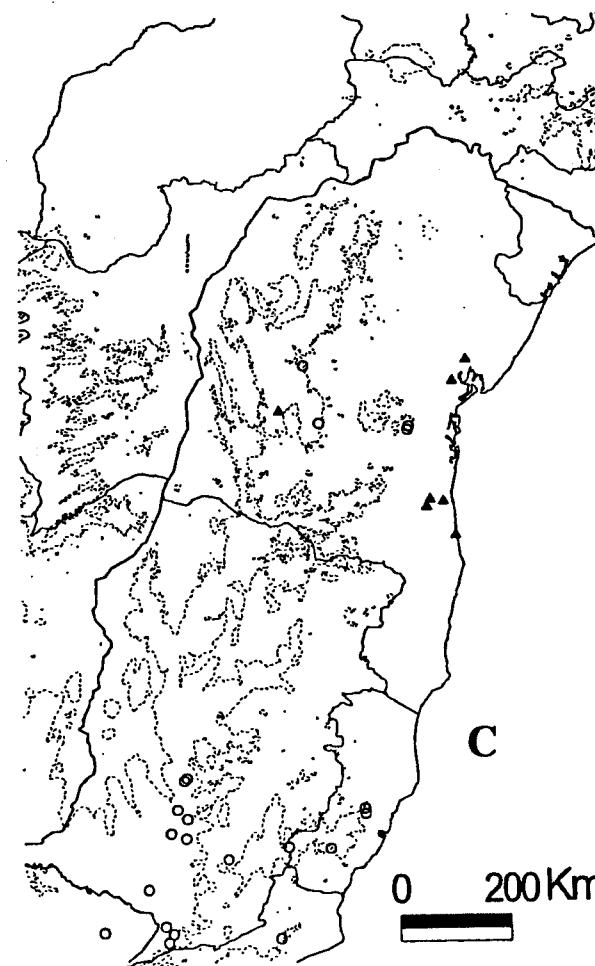
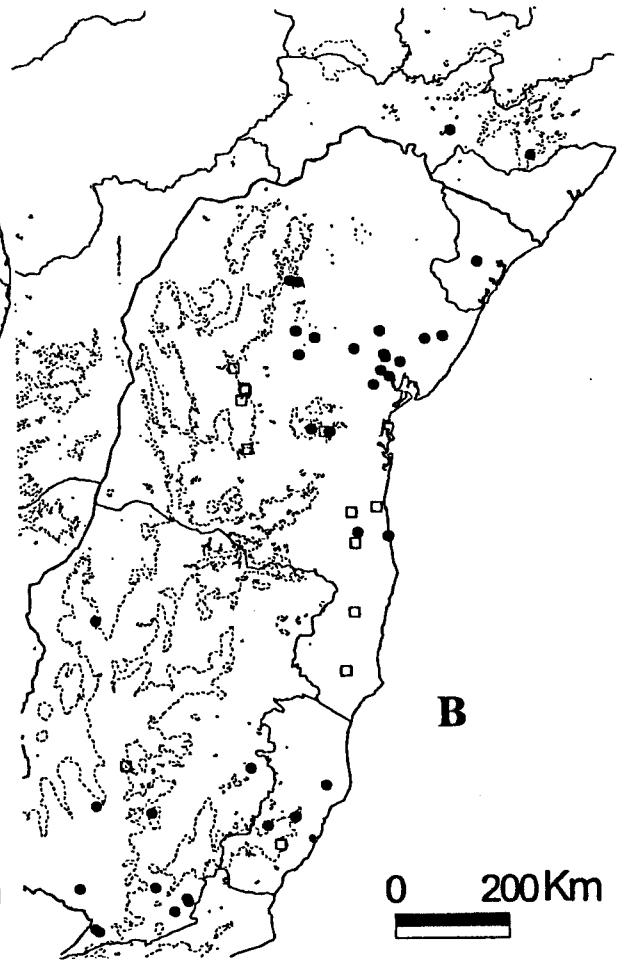
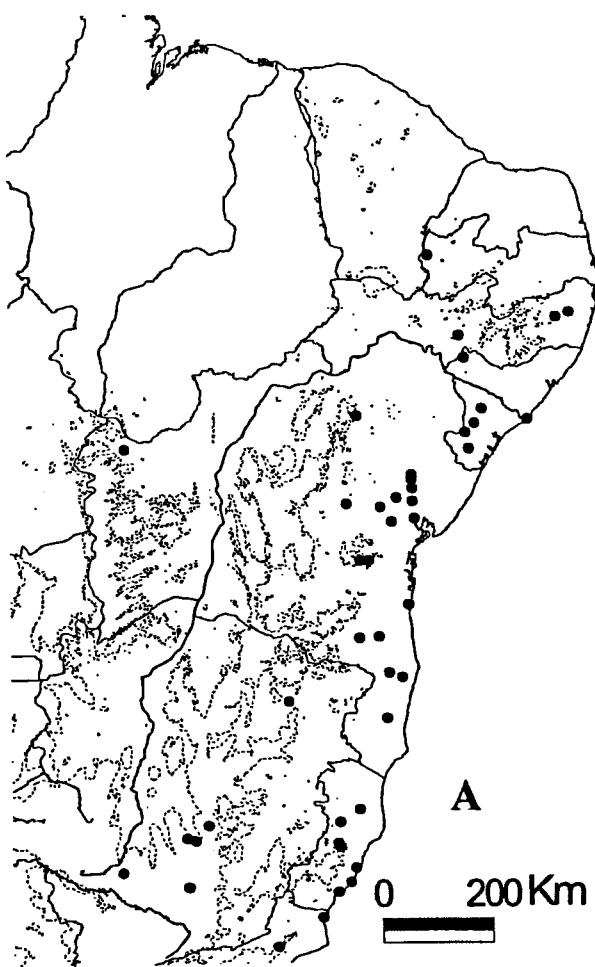


Map 11. Distribution pattern 1a, represented by *Hylocereus setaceus*. Eastern Brazil. [? = record whose identity requires confirmation]

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 *restinga / 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).

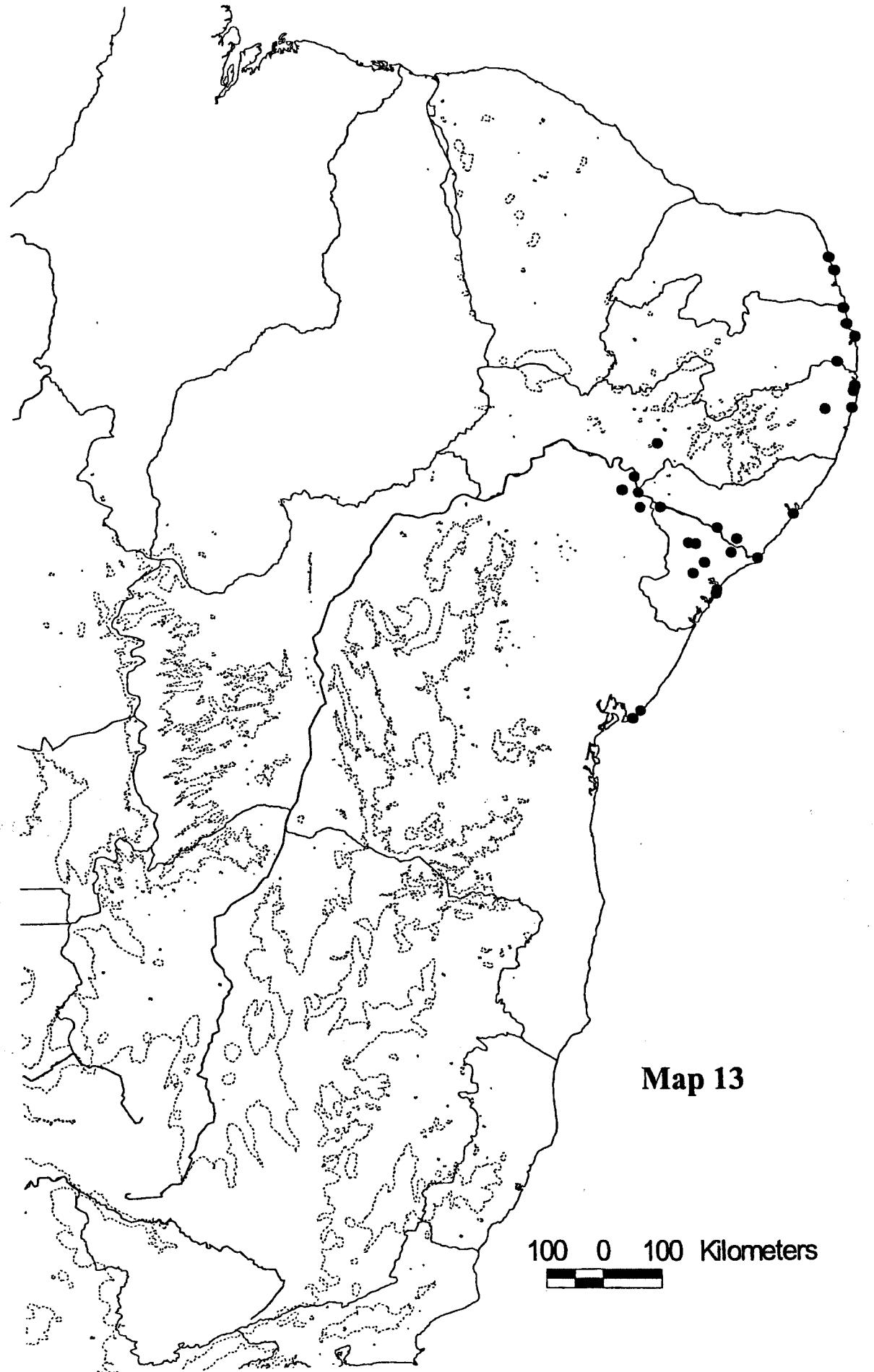
Maps 12A–12D (next page). Distribution pattern 1b, represented by (A) *Brasiliopuntia brasiliensis*, (B) *Rhipsalis russellii* [□] and *R. lindbergiana* [●], (C) *R. baccifera* subsp. *hileiabaiana* [▲] and *Hatiora salicornioides* [○] and (D) *Melocactus violaceus* subsp. *violaceus*. Eastern Brazil (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 *agreste* 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 erratically 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*.



Map 13

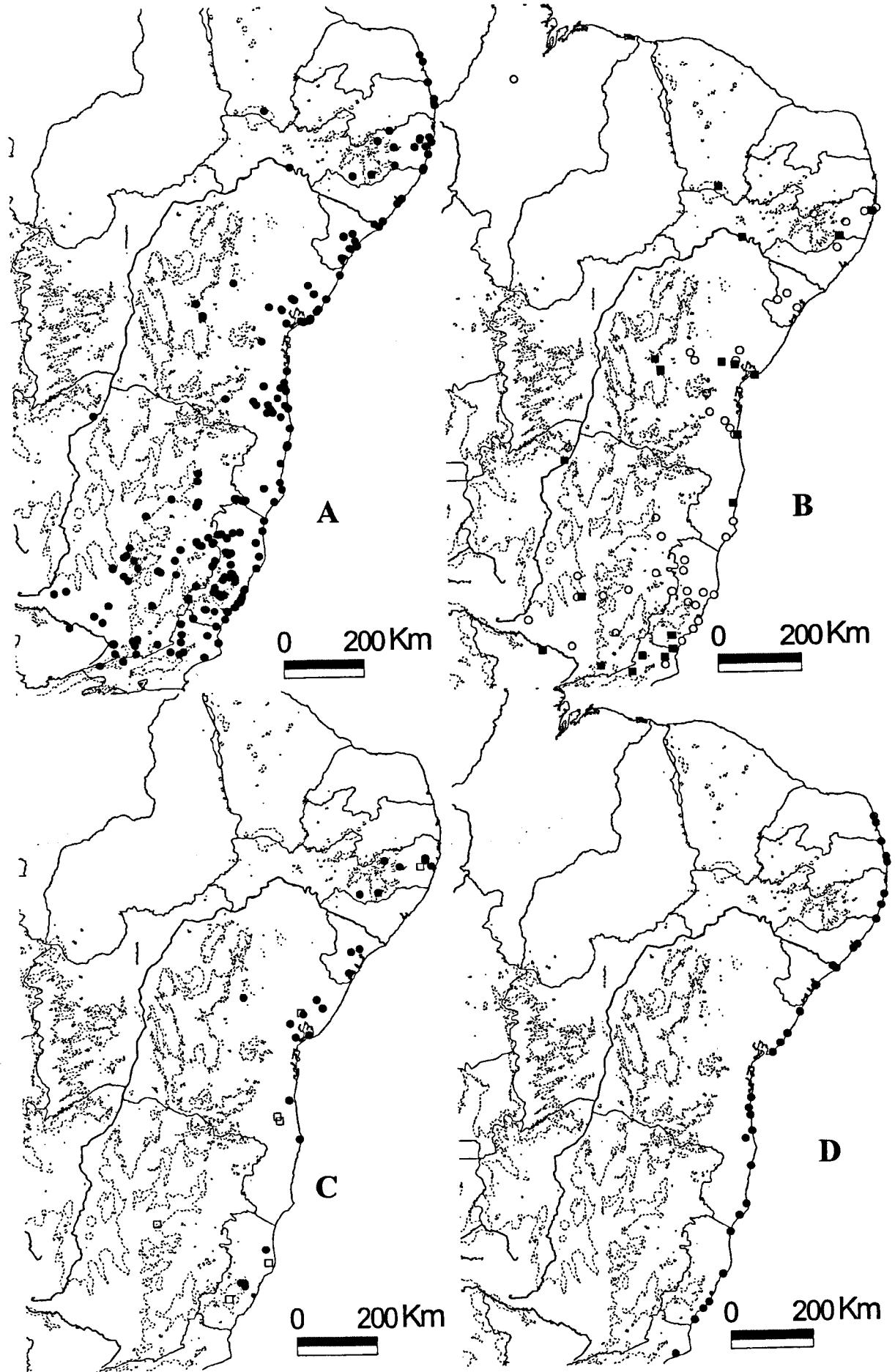
100 0 100 Kilometers

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 Paraguaçu (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 ‘isoetas 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

Maps 14A–14D (next page). (A) E Brazilian cacti restricted to *Mata atlântica* (incl. *brejo* forest); distribution pattern 2a, represented by (B) *Pereskia aculeata* [○] and *P. grandifolia* subsp. *grandifolia* [■], excl. cult. records, (C) *Rhipsalis floccosa* subsp. *floccosa* [●] and *R. paradoxa* subsp. *septentrionalis* [□] 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)

Pereskia aculeata, **P. grandifolia** subsp. *grandifolia*, **Lepismium cruciforme**, **Rhipsalis paradoxa** subsp. *septentrionalis*†, **R. floccosa** subsp. *floccosa*, **R. crispata**, **R. cereuscula**, **Cereus fernambucensis** subsp. *fernambucensis*.

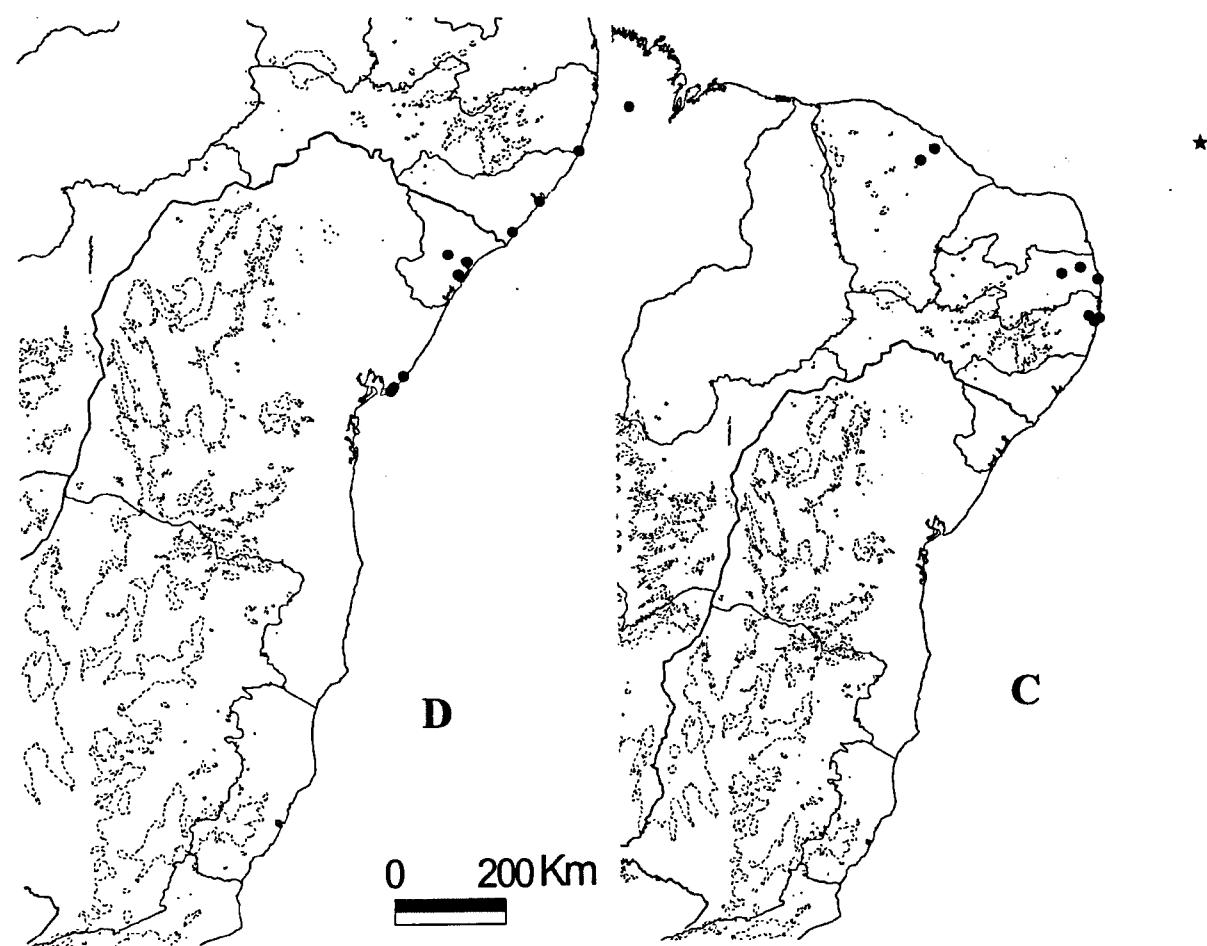
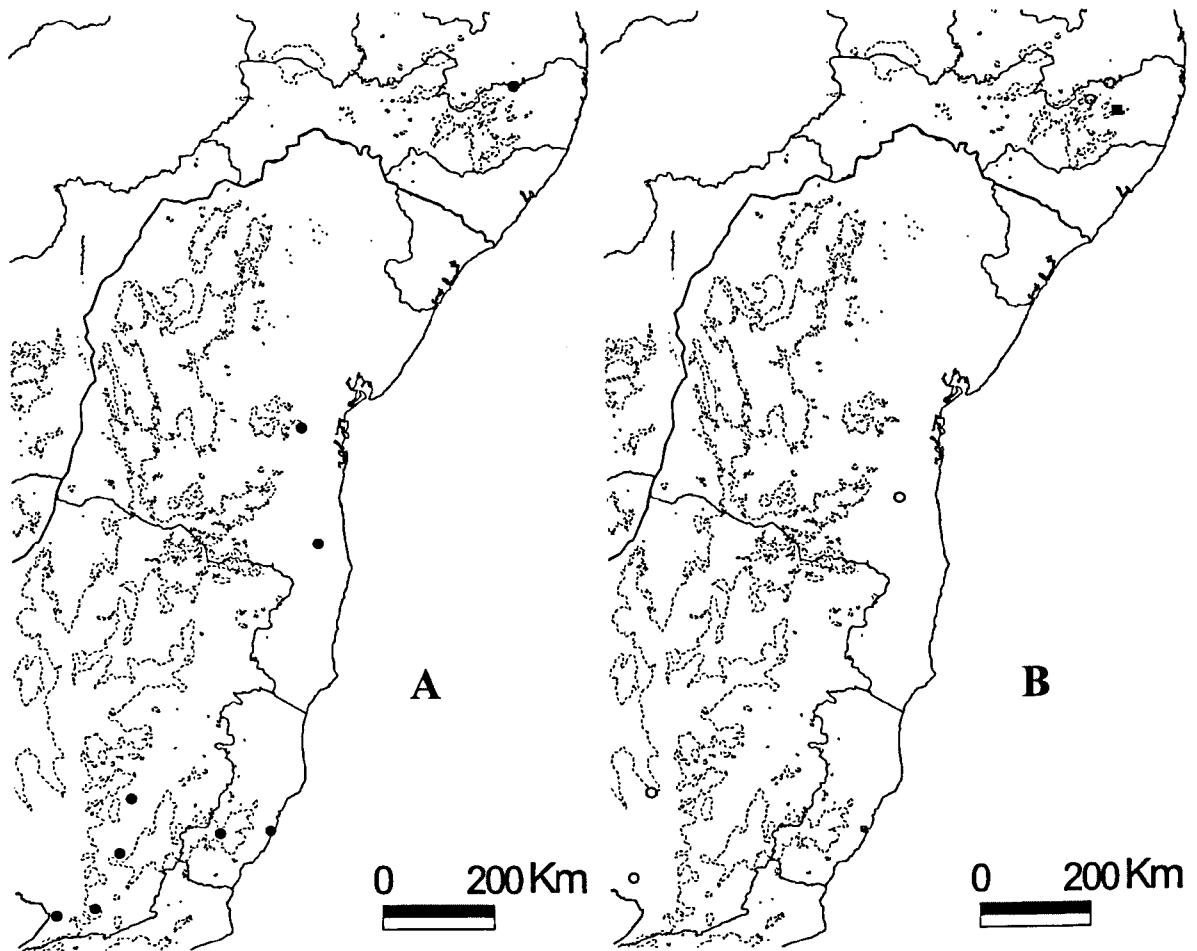
Pereskia aculeata is a scrambling shrub or semi-liana with a bimodal distribution in the E Caribbean / N South America (to Guyana) and SE South America (Leuenberger 1986). It inhabits scrubby *restinga* vegetation and gneissic outcrops of the *Mata atlântica*, reaching the edge of drier vegetation in 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 subspp.: 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

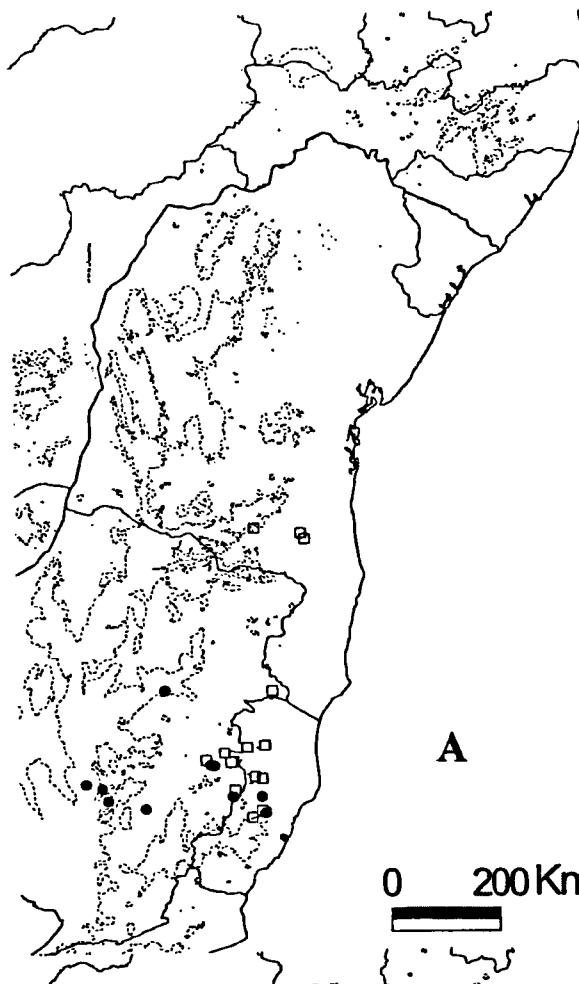
southern limit of 22°S), have extensive distributions in the drainage basins of the Rios Mucuri (MG/BA), Doce (MG/ES) and Paraíba do Sul (MG/RJ), with *Co. buxbaumianus* subsp. *flavisetus* reaching westwards to the watershed between the Rio Grande and Rio São Francisco (MG). These six, plus the more 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)

***Opuntia monacantha*, *Lepismium houletteianum*, *L. warmingianum*, *Rhipsalis elliptica*, *R. oblonga*, *R. floccosa* subsp. *pulvinigera*, *R. pacheco-leonis* subsp. *catenulata*, *R. cereoides*, *R. sulcata*†§, *R. teres*, *R. pulchra*, *R. burchellii*, *R. juengeri*, *R. clavata*, *R. pilocarpa*, *R. hoelleri*†§, *Schlumbergera kautskyi*†, *S. microsphaerica*, *S. opuntioides*, *Cereus hildmannianus*, *Pilosocereus arrabidae*, *P. brasiliensis* subsp. *brasiliensis*.**

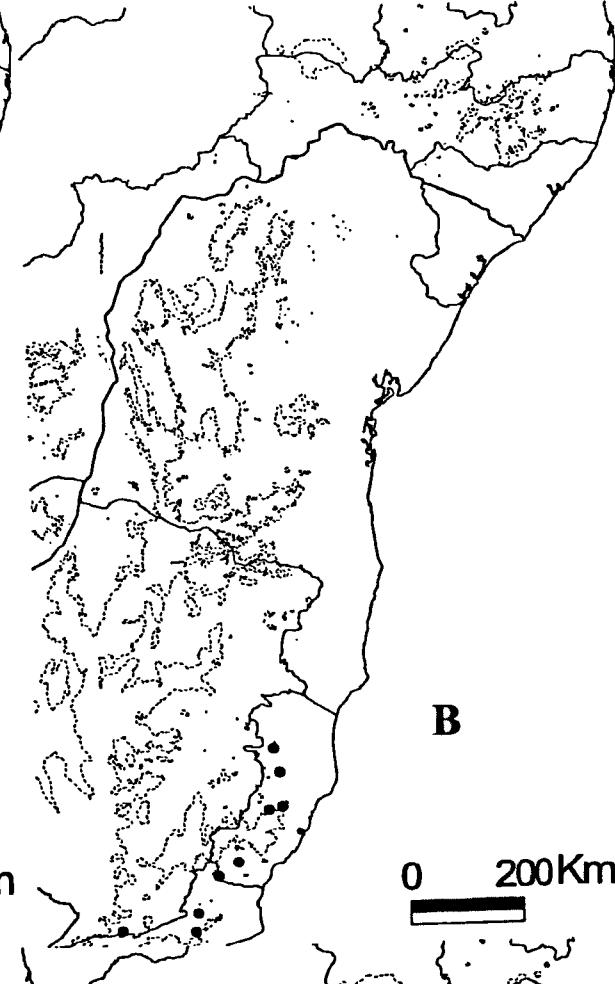
Of those included here, 10 are Rhipsalideae with the major part of their range outside the core area, ie. in South-eastern Brazil, or further afield, and are not, so to speak, 'typical'

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. buxbaumianus* subsp. *buxbaumianus* [Δ] & subsp. *flavisetus* [▲] and *C. pluricostatus* [★]. Eastern Brazil (core area).



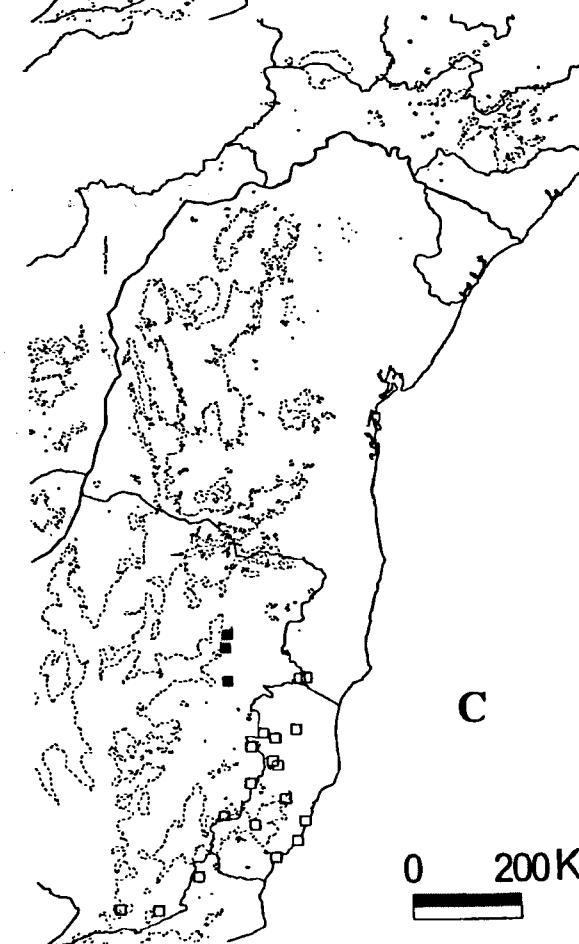
A

0 200 Km



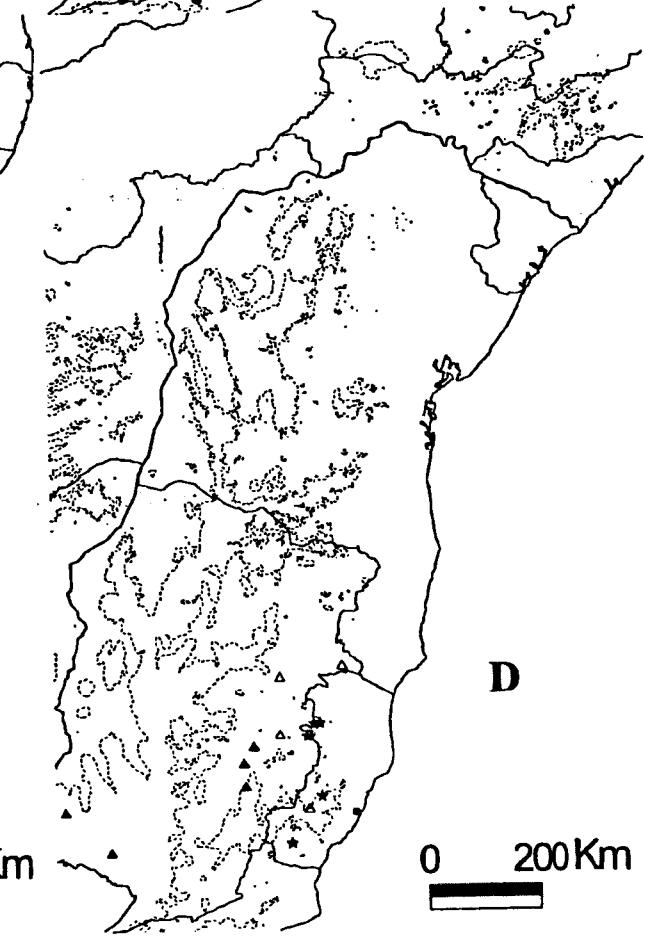
B

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C

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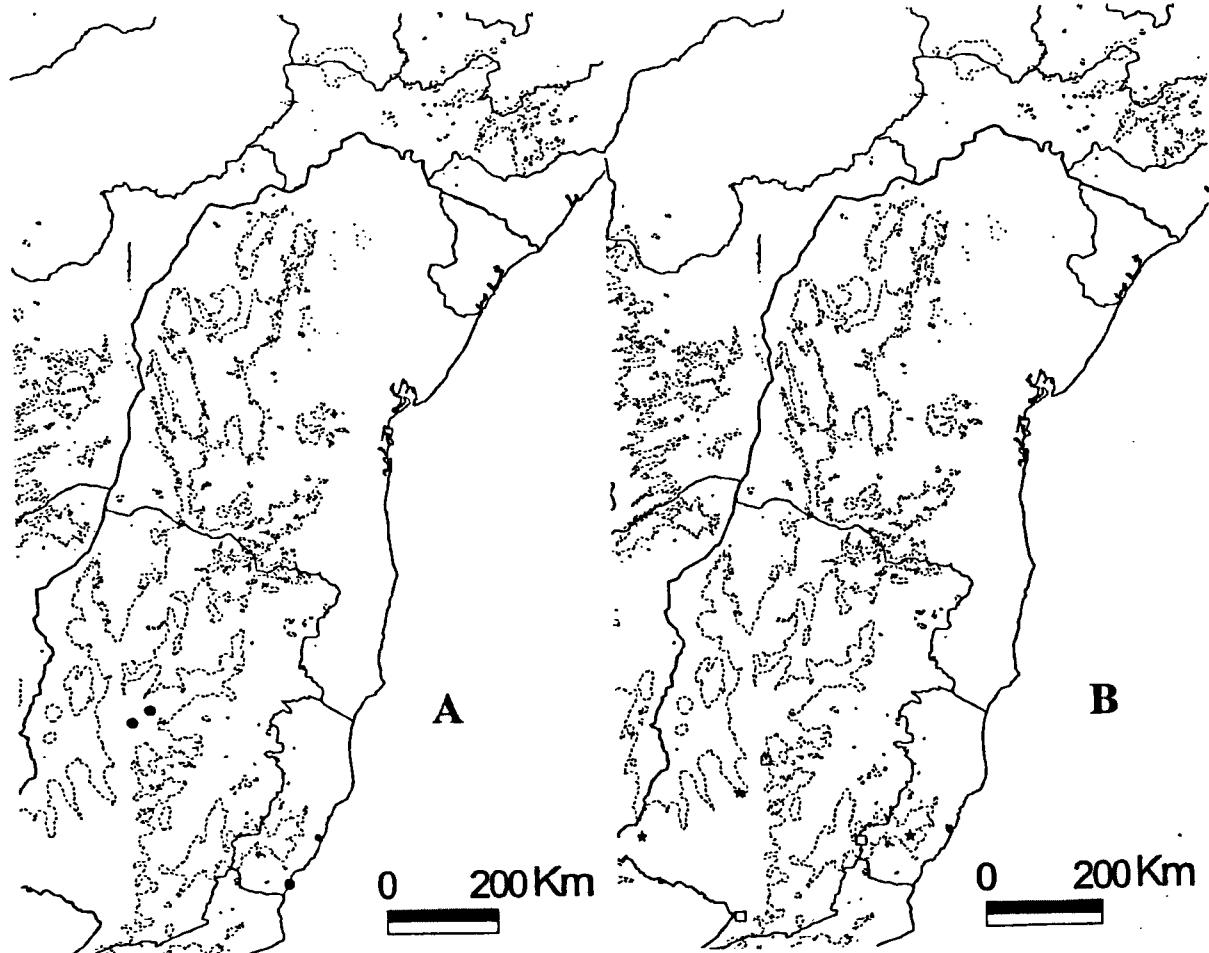
D

0 200 Km

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

Maps 17A–17D (next page). Distribution pattern 2d(ii), represented by (A) *Opuntia monacantha* excluding cultivated records, (B) *Lepismium houletteanum* [□] and *L. warmingianum* [●], (C) *Rhipsalis oblonga* [●] and *R. elliptica* [□], and (D) *Pilosocereus arrabidae* [●] and *P. brasiliensis* subsp. *brasiliensis* [★]. Eastern Brazil (core area).

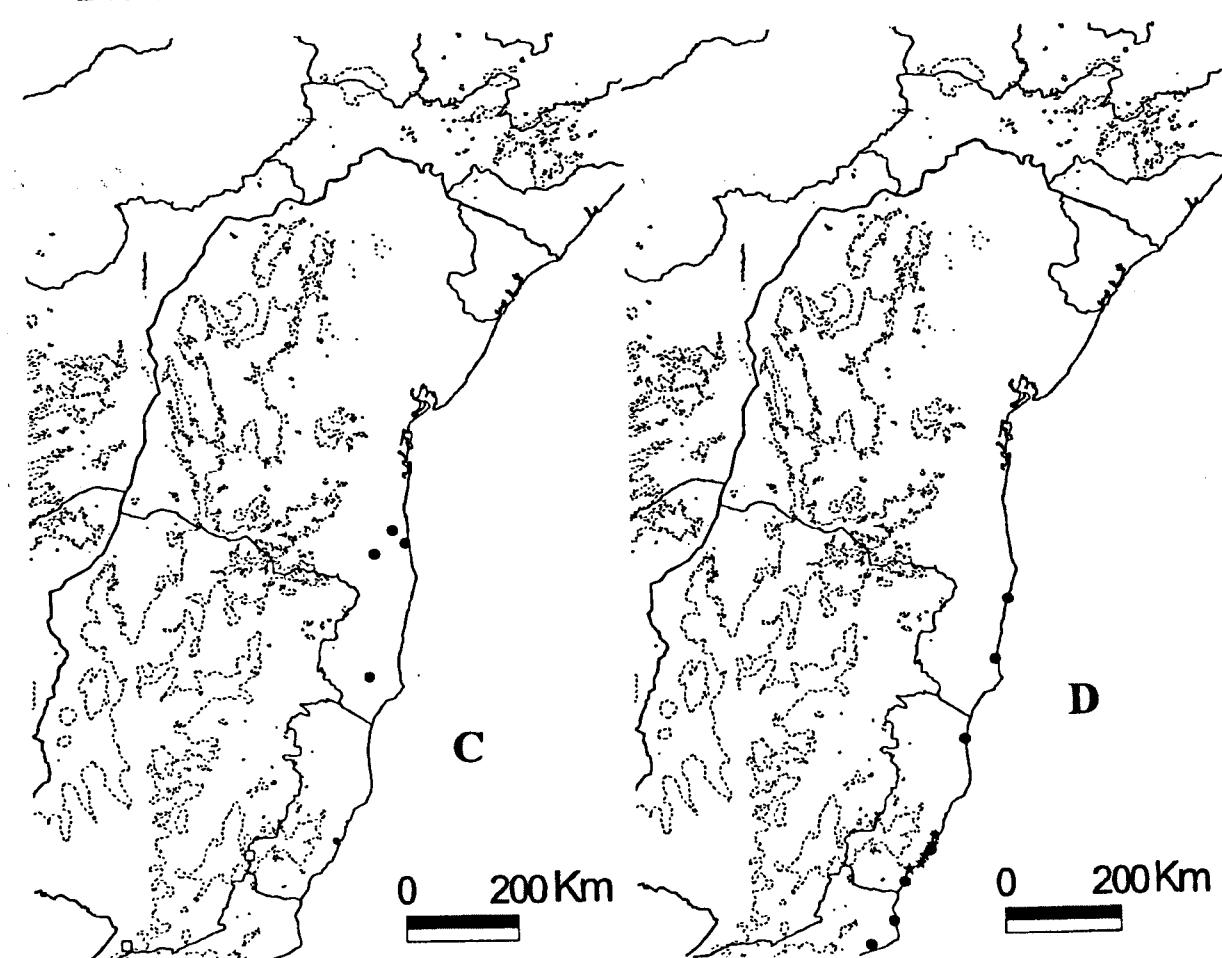


A

B

0 200 Km

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C

D

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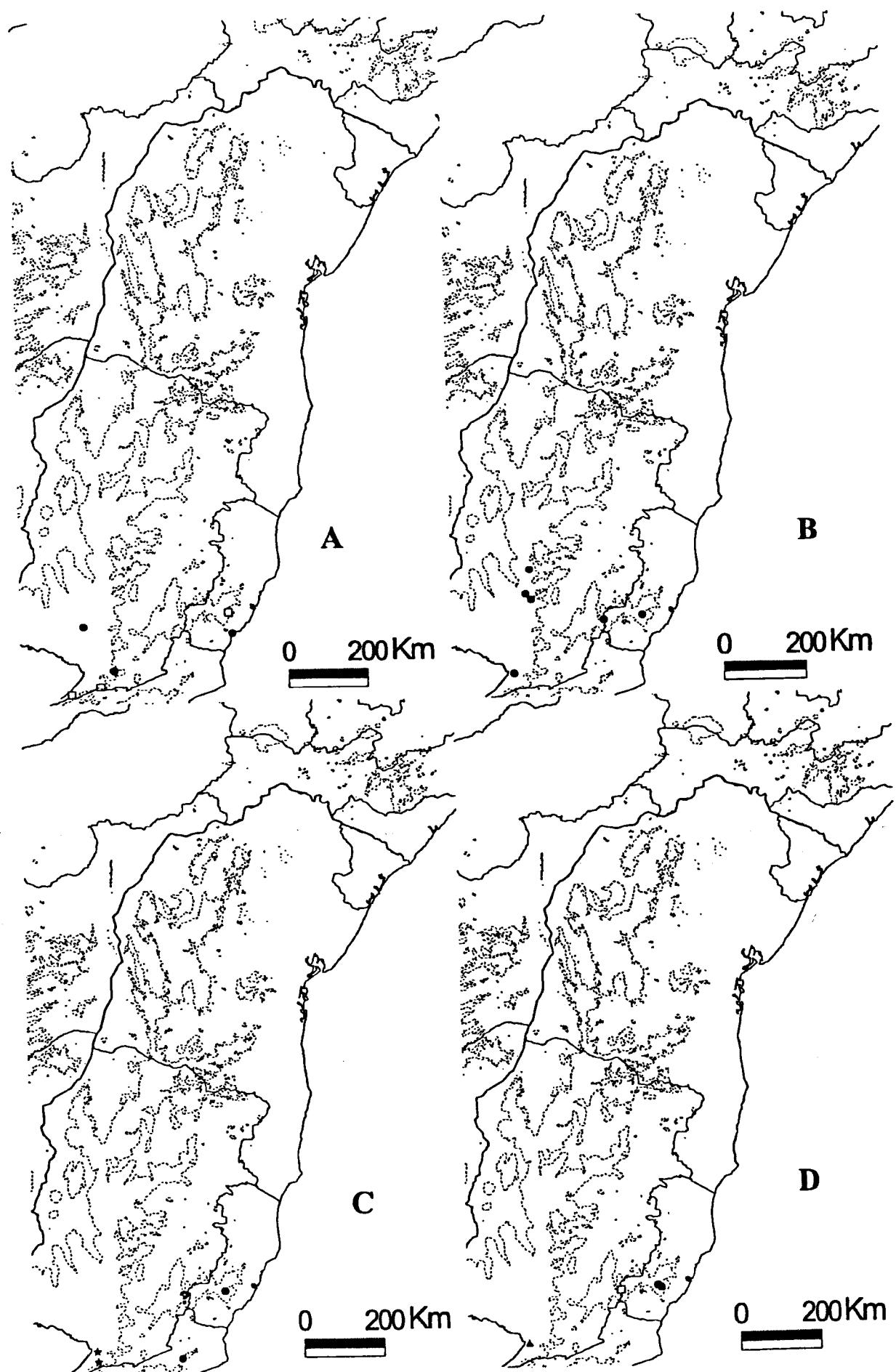
connexions with the humid forests of the Eastern Andes and in one case with the Caribbean and North-eastern South America (*Pereskia aculeata*). According to recent molecular phylogenies (Wallace 1995: 9; Butterworth, ined.), *Pereskia grandifolia* s.l. is indeed basal to the *caatinga* species-pair, *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.

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

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* [□], (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 rupeste* 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), *Epostoopsis* (1) and *Leocereus* (1), with *Arrojadoa* (4 spp.) almost endemic. Then there are infrageneric taxa in *Pilosocereus*, *Micranthocereus*, *Coleocephalocereus* and *Melocactus*. *Facheiroa* and *Epostoopsis* 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 Espinhaço, 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).

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

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).

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):

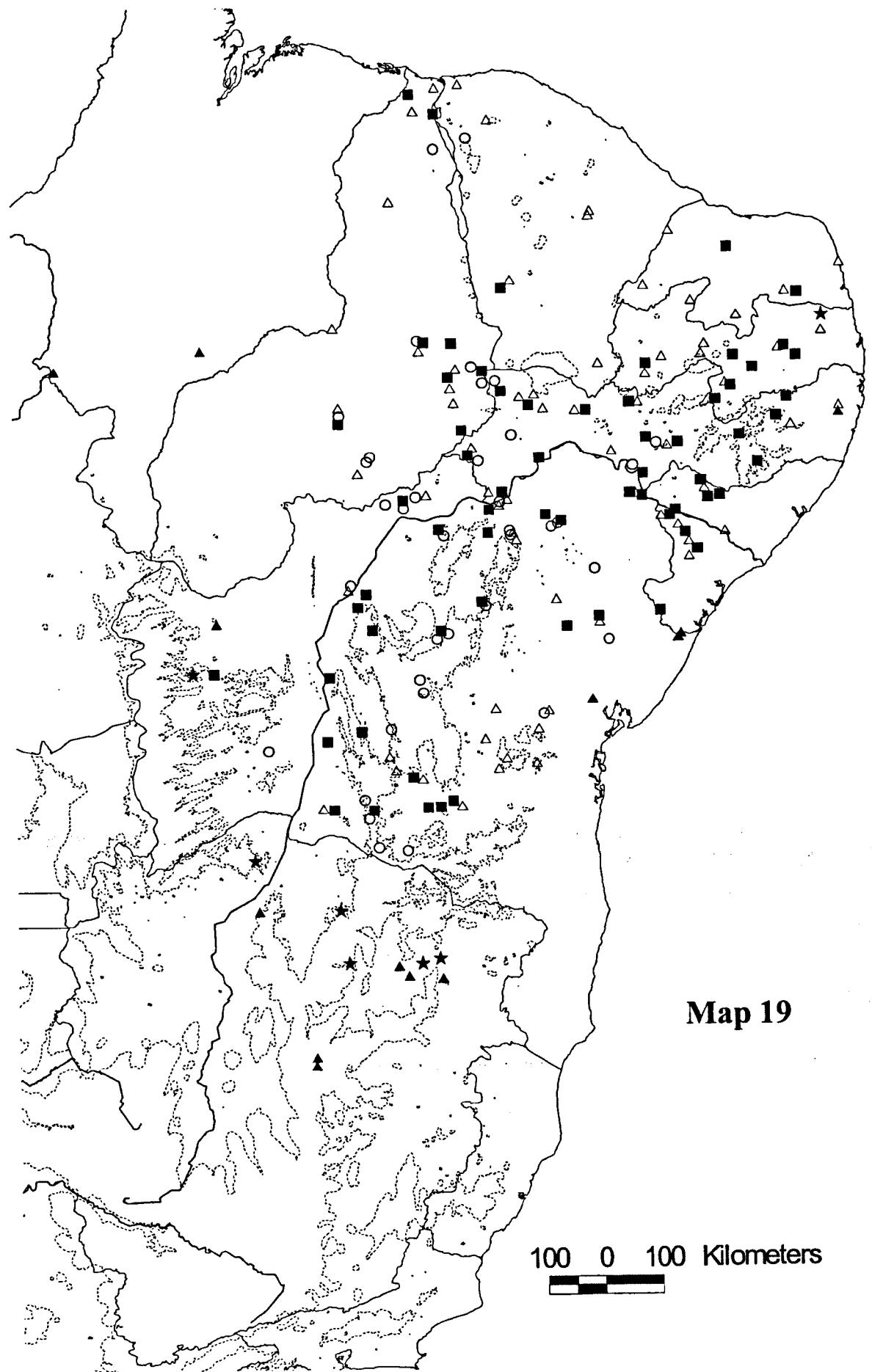
All the taxa listed here are primarily *caatinga* elements. They represent less than 28% of the taxa included in Area 3, the remainder falling into three parallel geographical and/or ecological categories (see Nos. 3b/c/d).

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

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

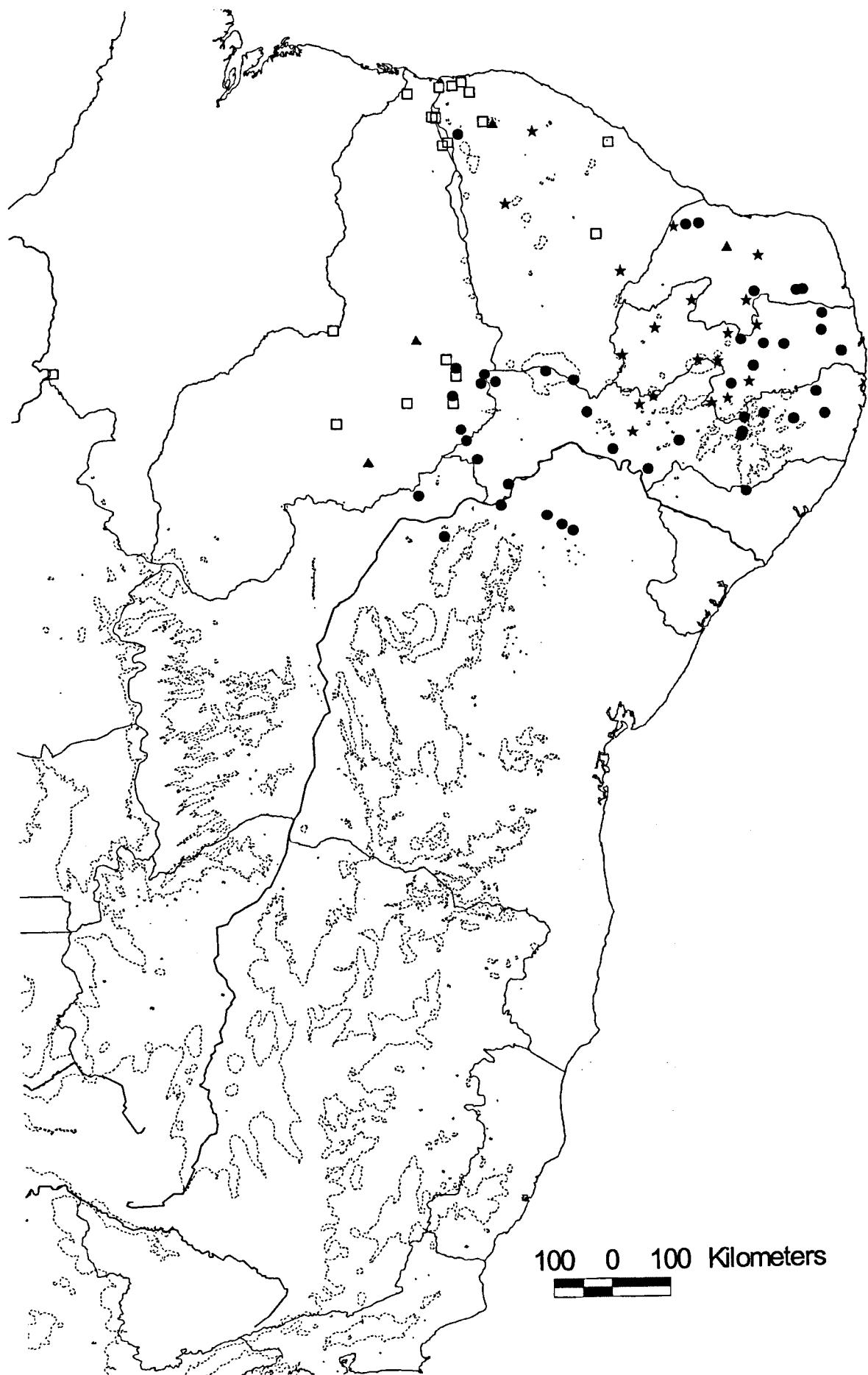
The taxa included here are amongst the cacti that are most characteristic of the *caatinga* and *agreste* of North-eastern Brazil, *T. inamoena* also ascending into the *campos rupestres*. *Cereus jamacaru* ranges further than any of the others included here, reaching W Maranhão, entering the Atlantic 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 19

100 0 100 Kilometers



Map 20. Distribution pattern 3a(ii): *Pilosocereus flavipulvinatus* [□], *P. pachycladus* subsp. *pernambucensis* [●], *P. piauhensis* [▲] and *P. chrysostele* [★].

3a(ii). *Northern caatingas* (S Piauí, N Bahia, Alagoas & Pernambuco northwards) (5 taxa, Maps 20 & 21A)

Pilosocereus flavigracilis, **P. pachycladus** subsp. **pernambucensis**, **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. flavigracilis*, 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).

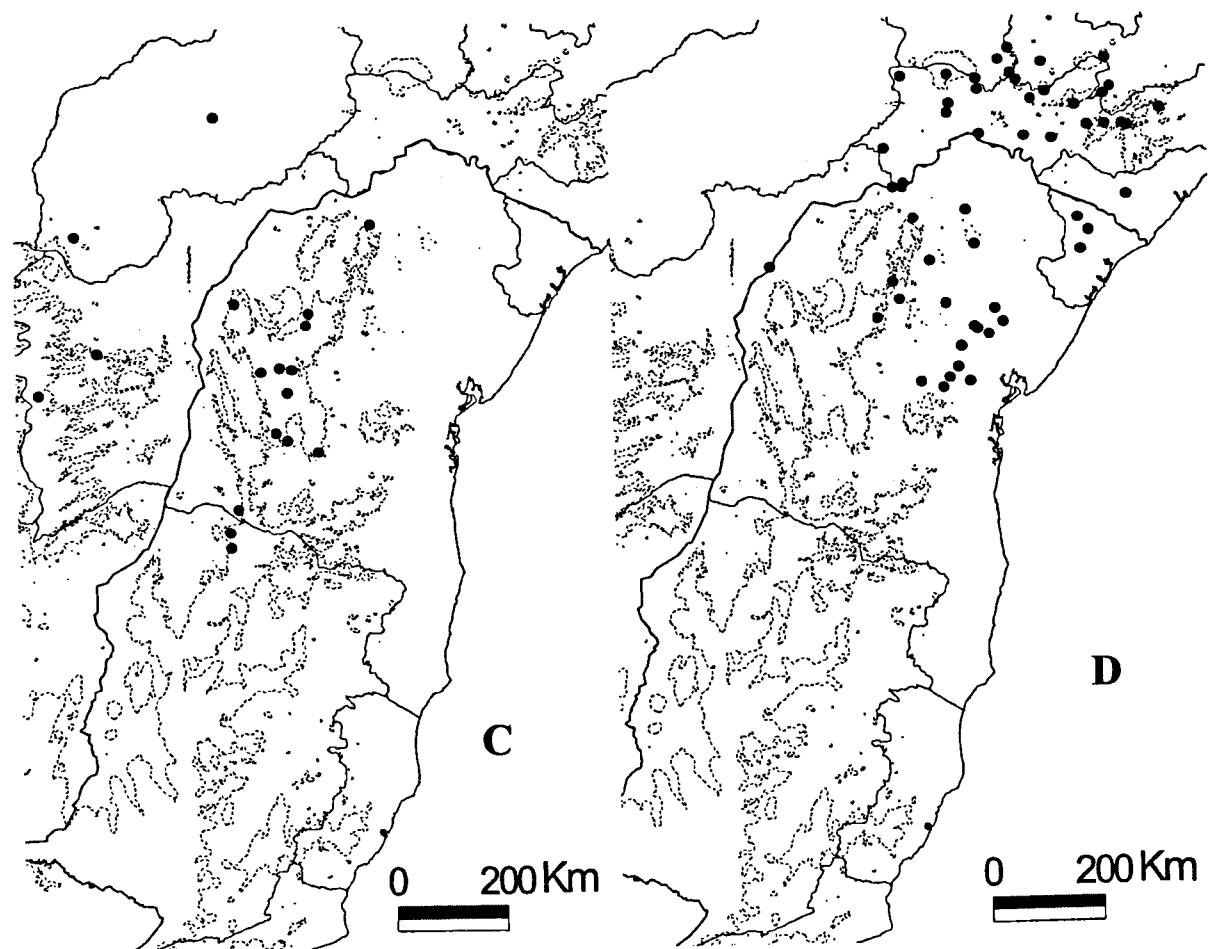
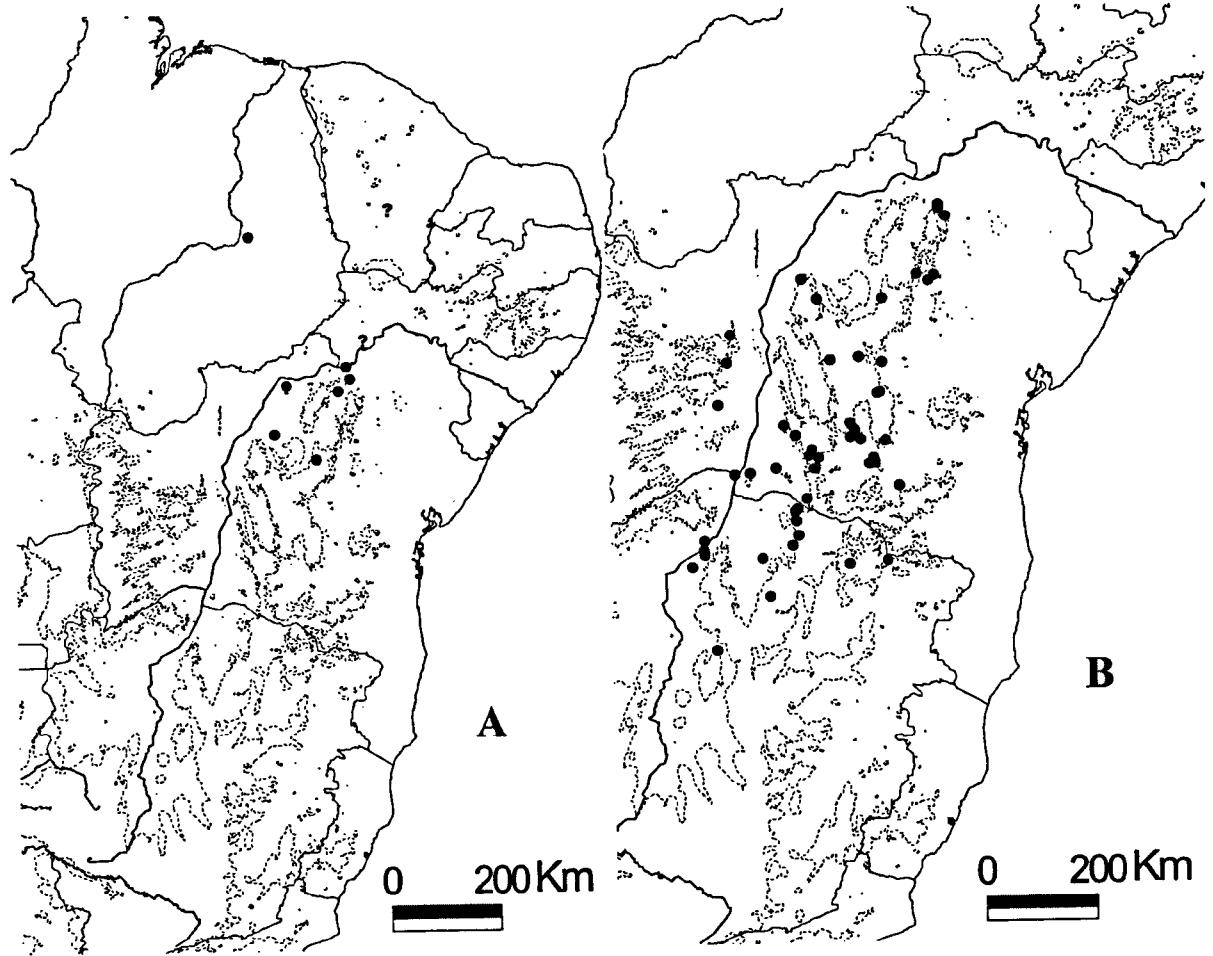
3a(iii). *Central-Southern caatingas*, from S Piauí, S Ceará, S Paraíba southwards (13 taxa):

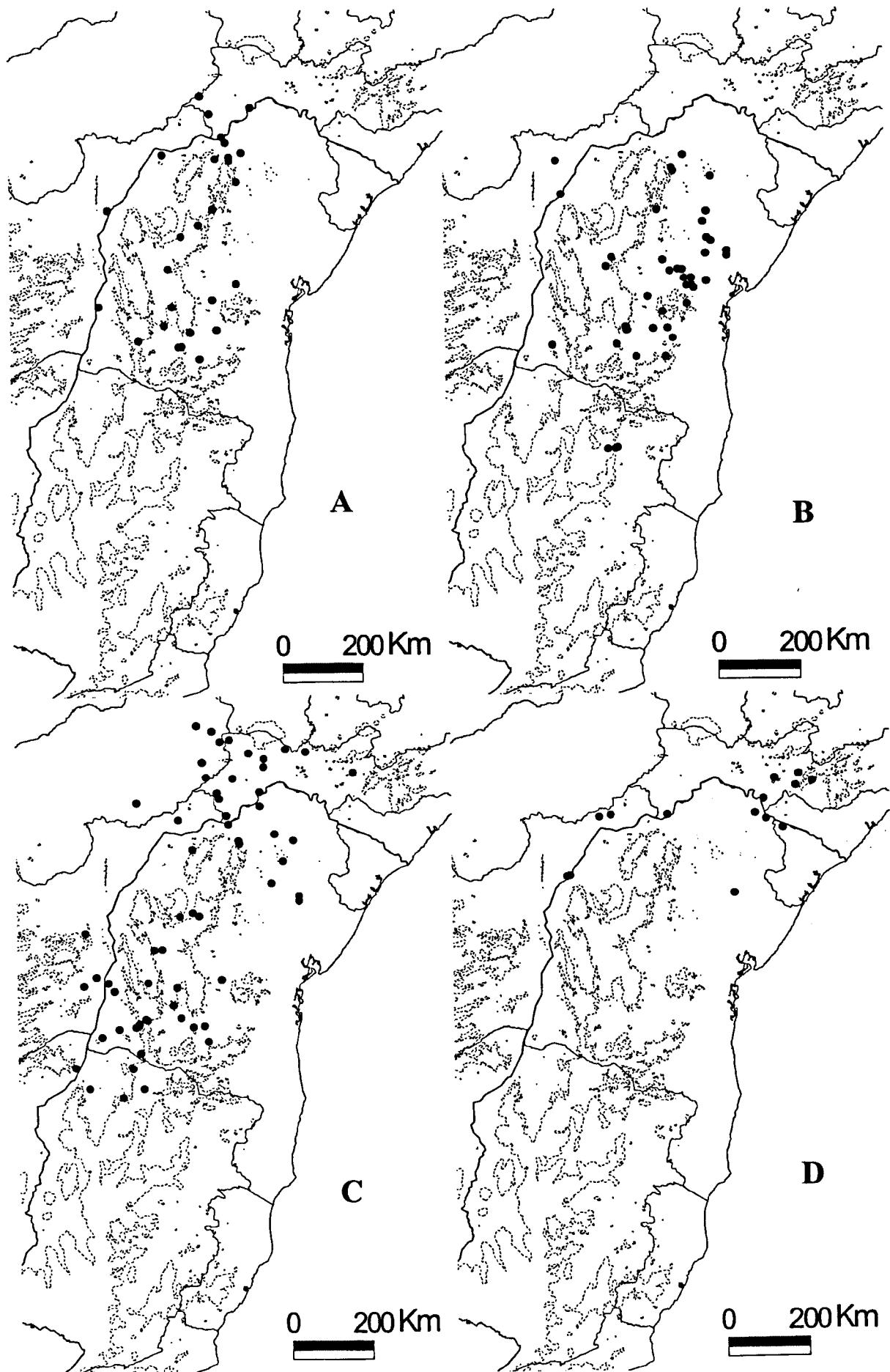
3a(iii). *Wide-ranging in the central-southern caatingas* (7 taxa, Maps 21B–22D):

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(iii), 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), 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 adscendens* 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(iiib). *Bahian caatingas*, surrounding the Chapada Diamantina (2 taxa, Map 23)

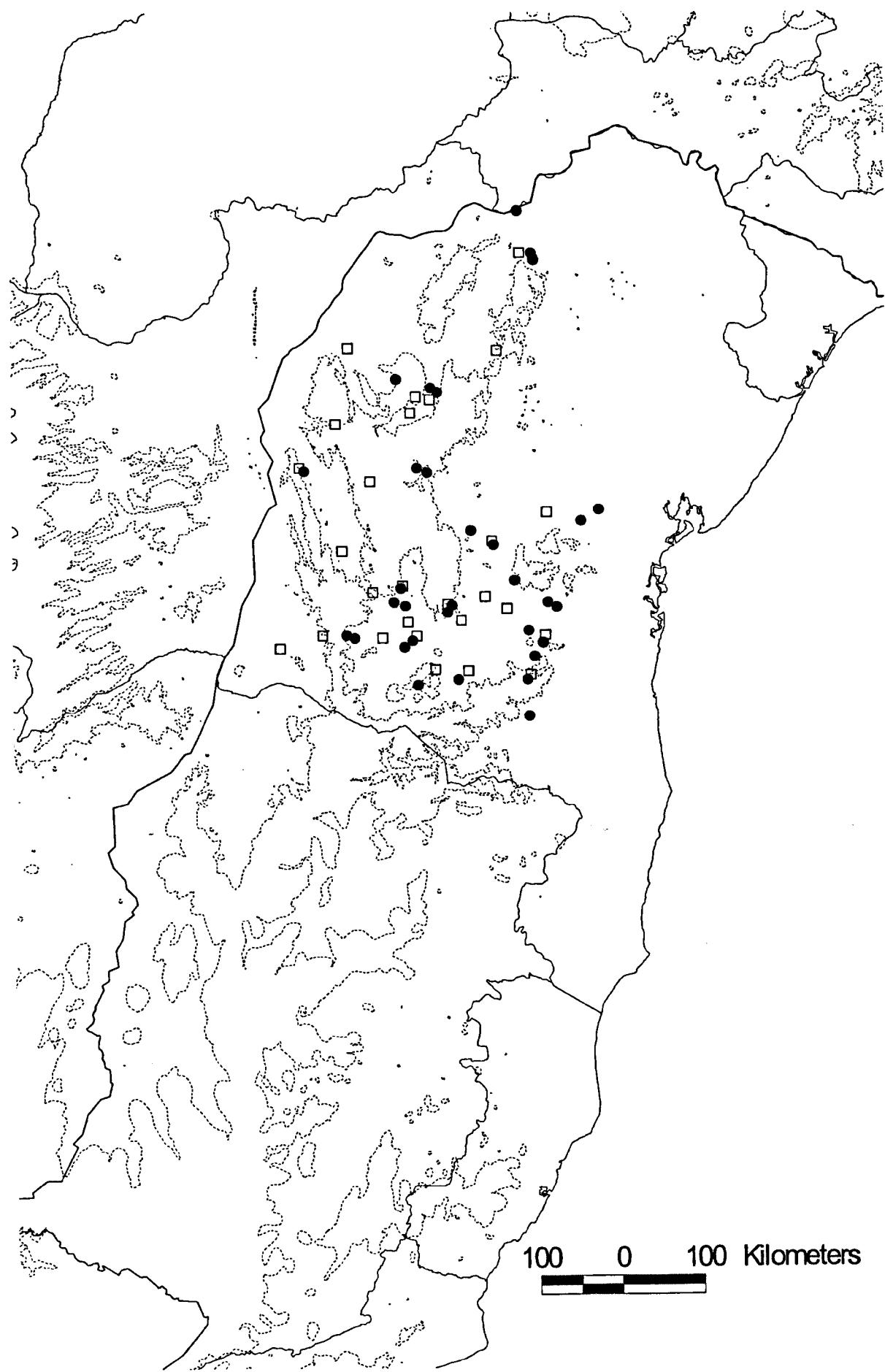
Pereskia bahiensis†, Stephanocereus (subg. Stephanocereus†) leucostele†.

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(iiic). *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(iia).

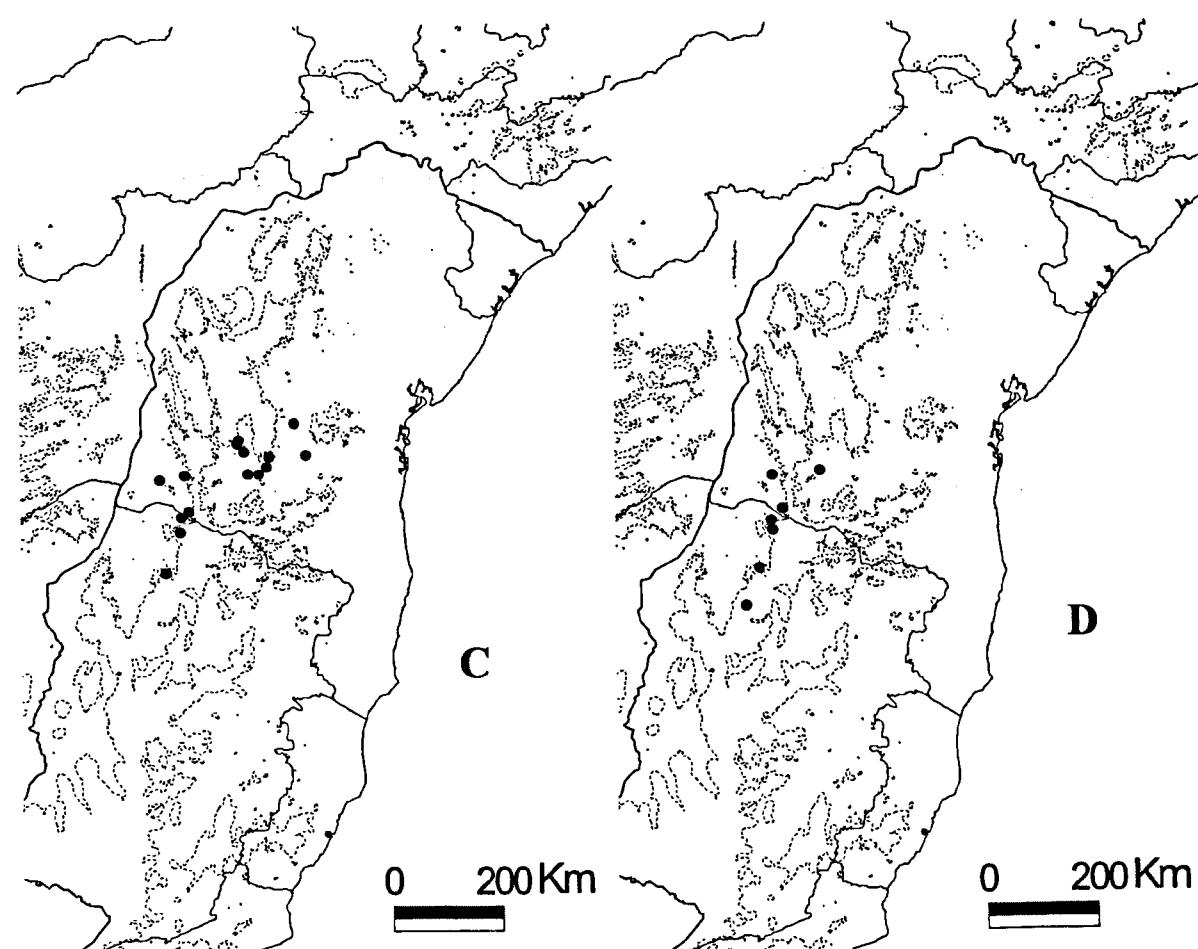
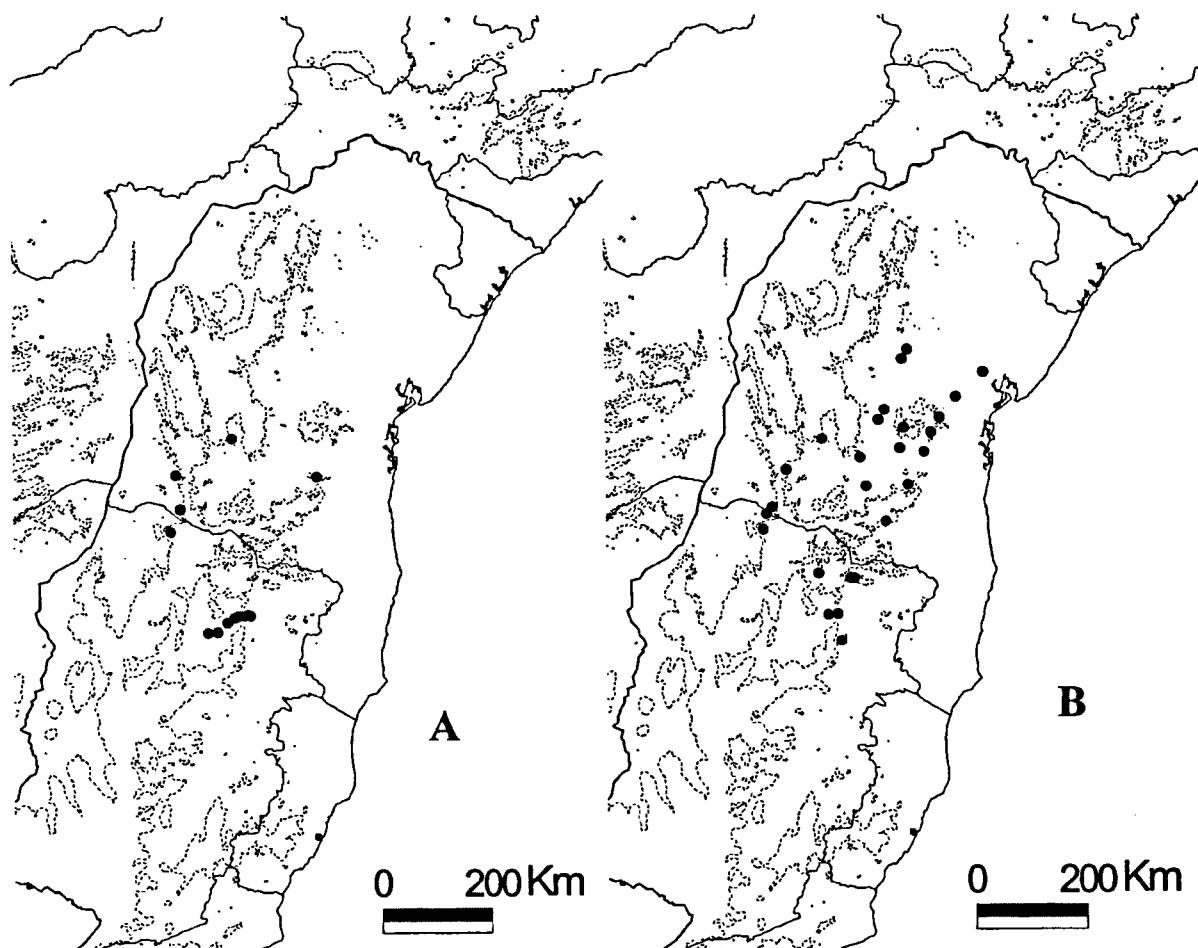


Map 23. Distribution pattern 3a(iiib), represented by *Pereskia bahiensis* [●] and *Stephanocereus leucostele* [□]. Eastern Brazil (core area).

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, e.g. *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(i/ii/iii) are lacking, the chief exceptions being *Cereus jamacaru*, *Pilosocereus pachycladus* and *Arrojadoa rhodantha*.

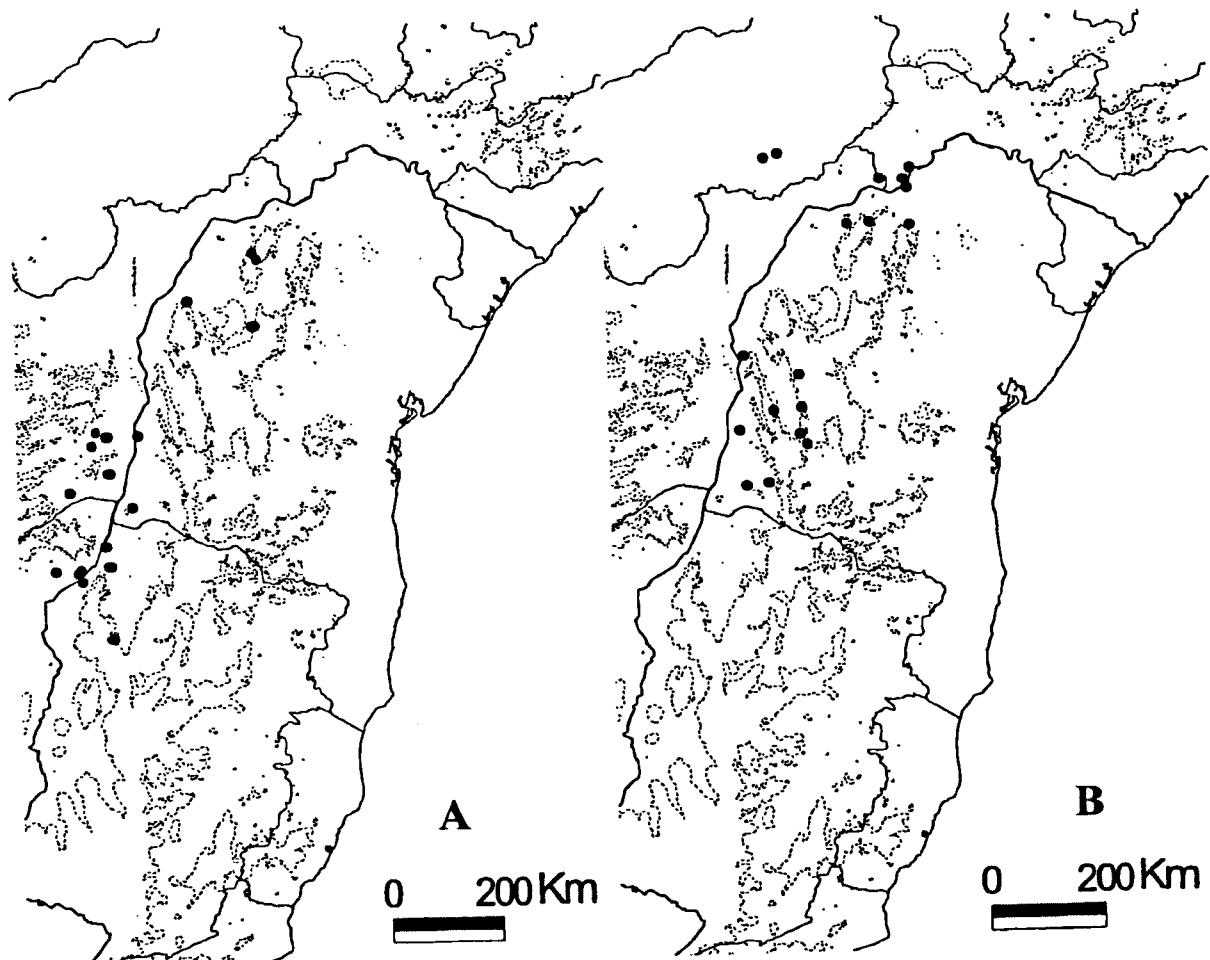
The following subdivisions are recognized, noting that Nos. 3b(ii)/(iii) conform to the limits between Köppen's semi-arid and hot/humid climates (Cavalcanti Bernardes 1951):

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 *cerrado* and marshy sand-dunes (Tricart 1985: 209–211).

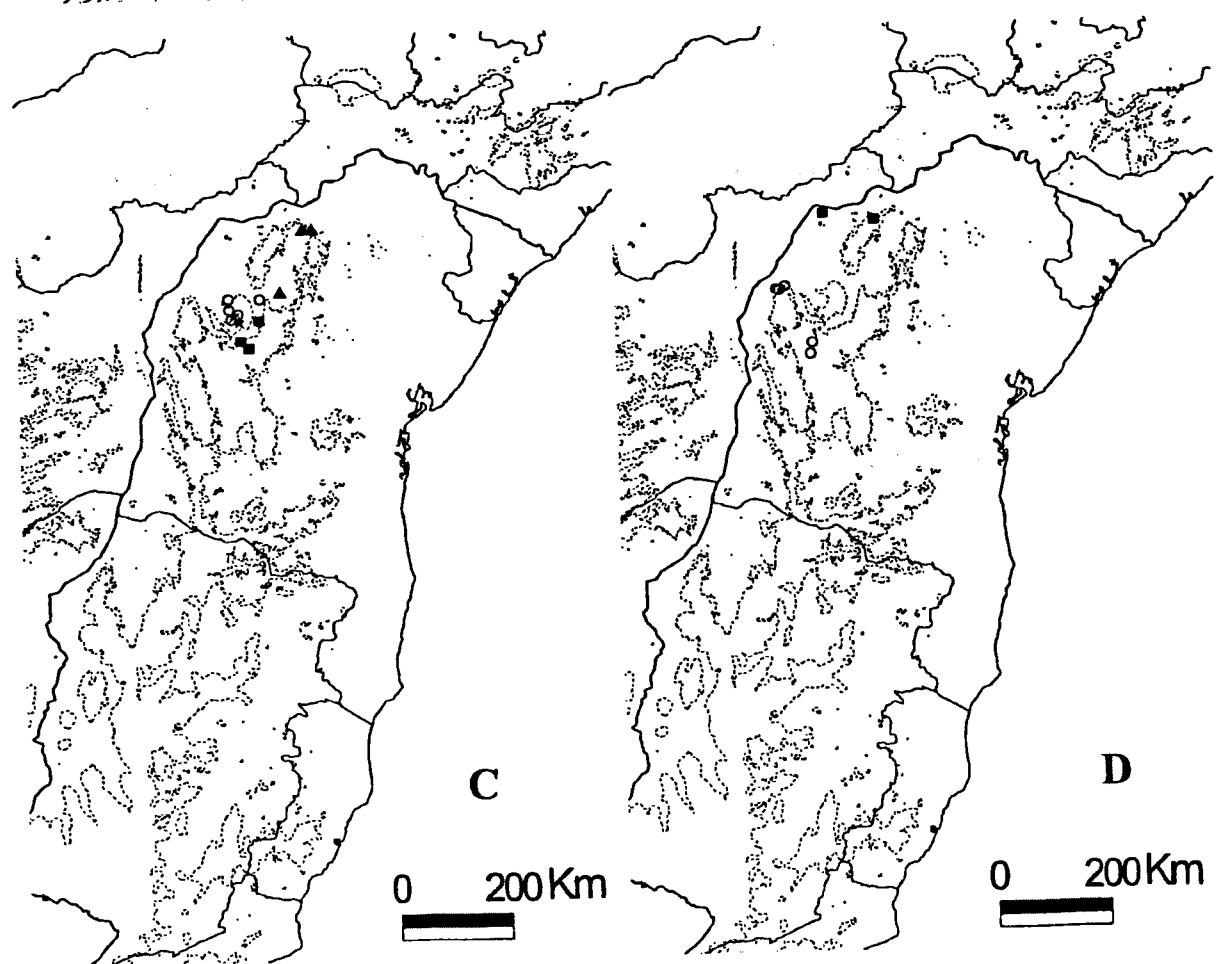
Maps 25A–25D (next page). Distribution pattern 3b(i), represented by (A) *Pilosocereus gounellei* subsp. *zehntneri* and (B) *Facheiroa squamosa*; and pattern 3b(ii), represented by (C) *Melocactus azureus* subsp. *azureus* [○] & subsp. *ferreophilus* [■] and *M. pachycanthus* subsp. *pachycanthus* [▲] & subsp. *viridis* [*] and (D) *Facheiroa ulei* [○] and *Discocactus zehntneri* subsp. *zehntneri* [■]. Eastern Brazil (core area).



A

B

0 200 Km



C

D

0 200 Km

3b(ii). *Caatingas of central-northern Bahia* (6 taxa, Maps 25C & 25D)

Melocactus azureus (2 subspp.)‡, **M. pachyacanthus** (2 subspp.)‡, **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*.

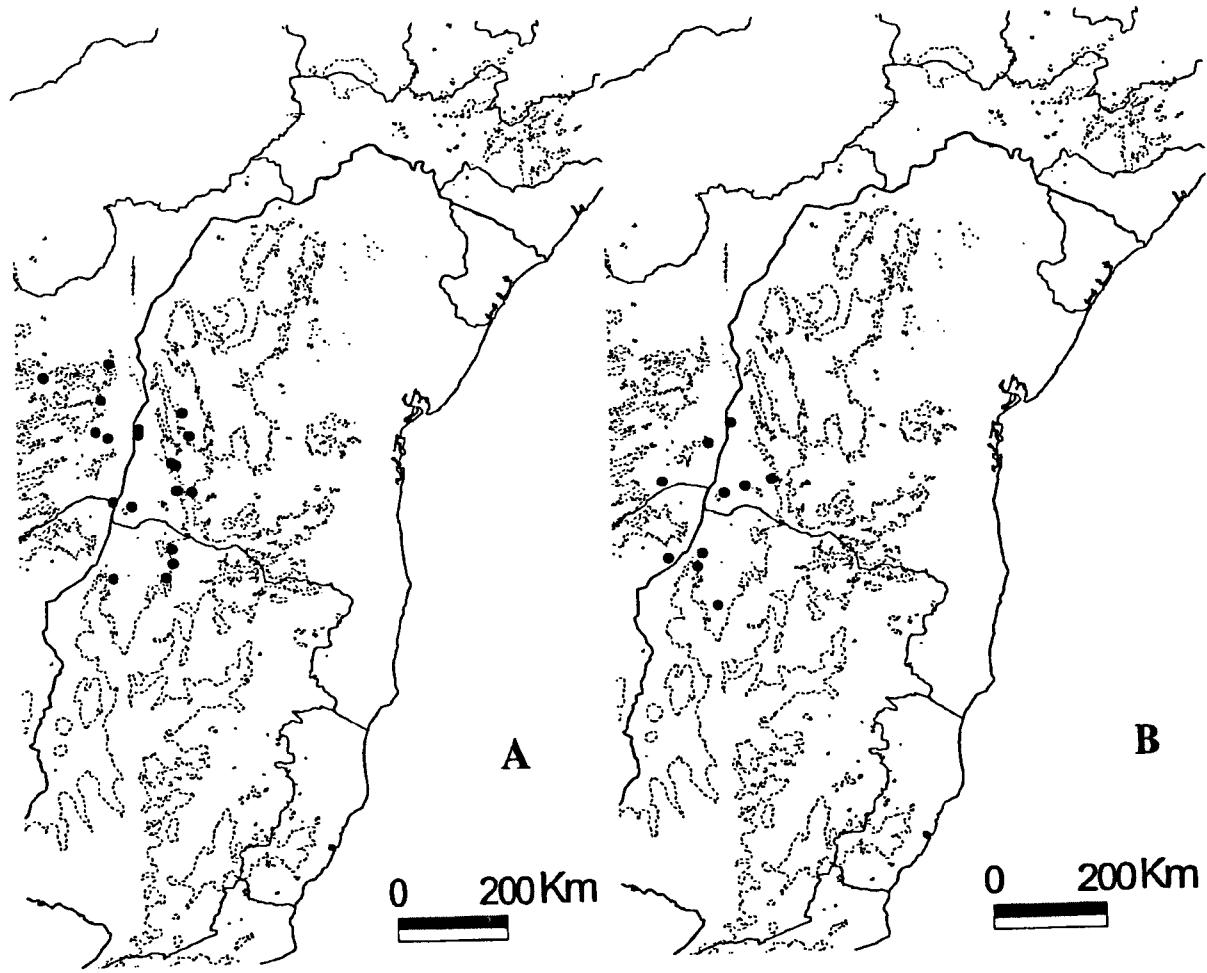
Most of the taxa included here are threatened with extinction due to extensive modification of their habitat by agriculture and the great Represa de Sobradinho dam-lake.

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):

Pereskia stenantha‡, **Quiabentia zehntneri**‡, **Tacinga saxatilis** (2 subspp.: subsp. **Pereskia stenantha**‡, **Quiabentia zehntneri**‡, **Tacinga saxatilis** (2 subspp.: subsp. **estevensis**‡§), **Cereus jamacaru** subsp. **calcirupicola**, **Pilosocereus floccosus** subsp. **floccosus**‡, **P. densiareolatus**‡, **Micranthocereus dolichospermaticus**‡, **Melocactus deinacanthus**‡§, **M. levitestatus**‡, **Facheiroa cephaliomelana** (2 subspp.: subsp. **estevensis**‡§).

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* [○] & subsp. *estevensis* [■] and (D) *Pilosocereus densiareolatus*. Eastern Brazil (core area).

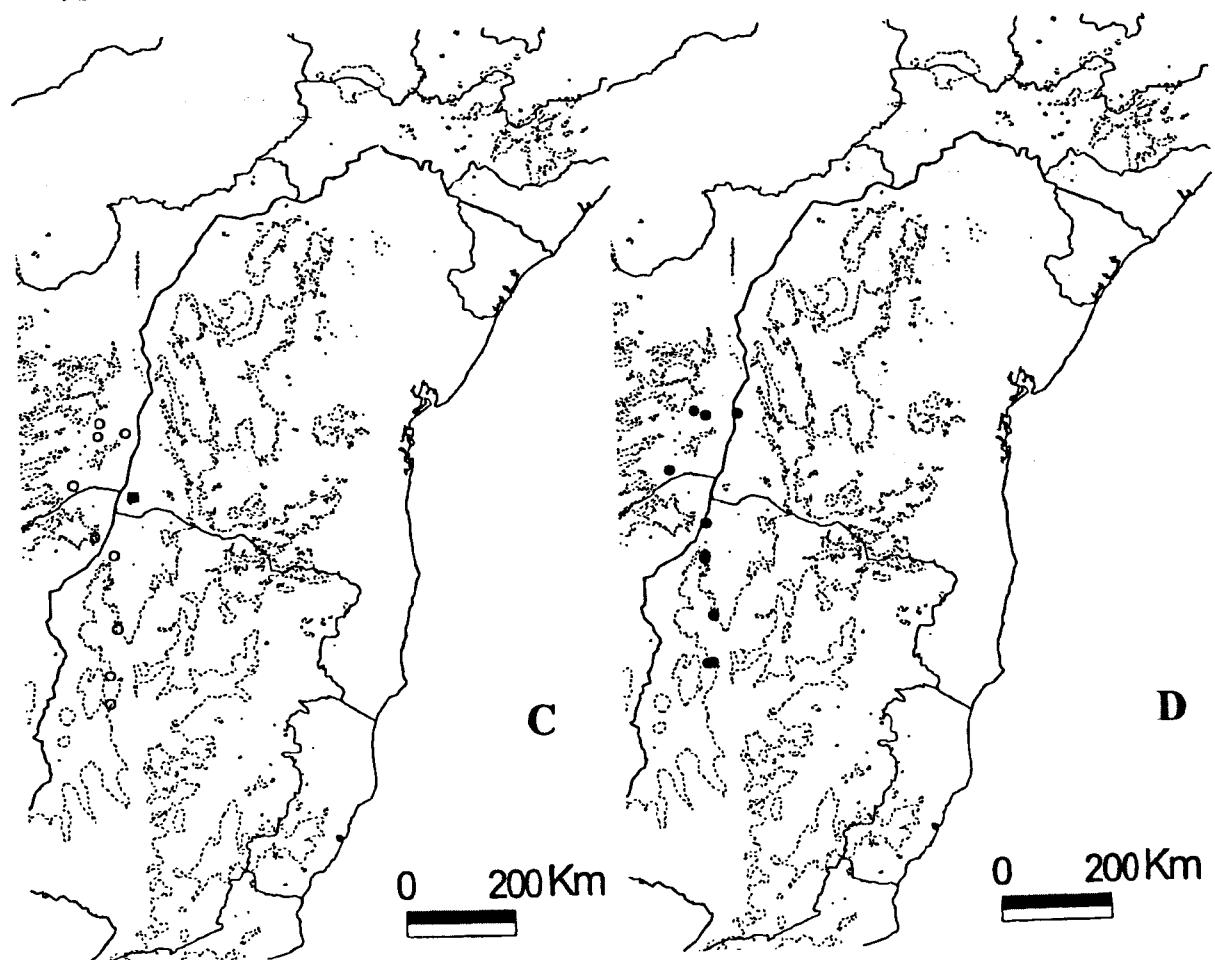


A

B

0 200 Km

0 200 Km



C

D

0 200 Km

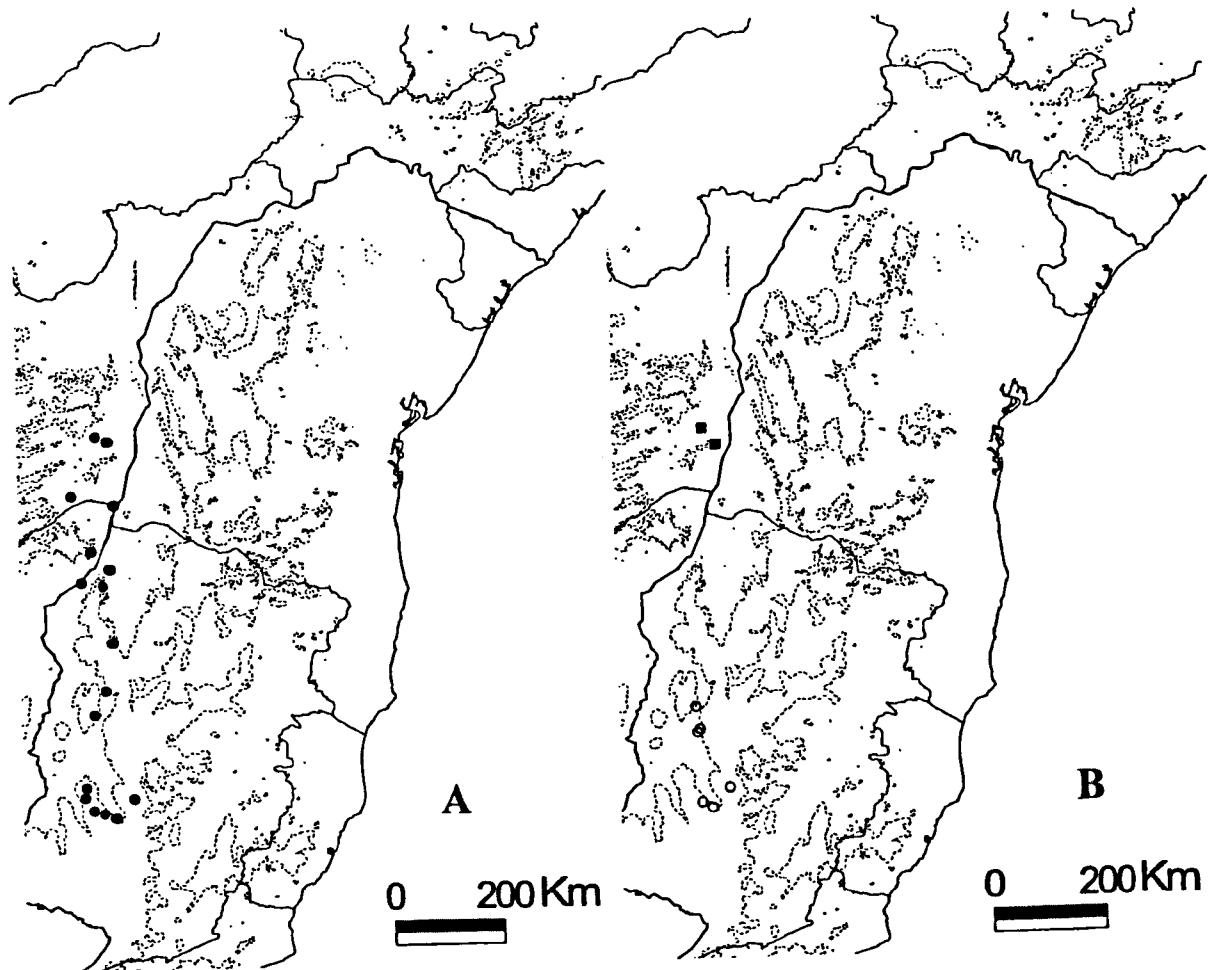
0 200 Km

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

Maps 27A–27D (next page). Distribution pattern 3b(iii), represented by (A) *Cereus jamacaru* subsp. *calcirupicola*, (B) *Pilosocereus floccosus* subsp. *floccosus* [○] and *Micranthocereus dolichospermaticus* [■], (C) *Melocactus deinacanthus* [■] and *M. levitestatus* [○] and (D) *Facheiroa cephaliomelana* subsp. *cephaliomelana* [○] & subsp. *estevensis* [■]. E Brazil (core area).

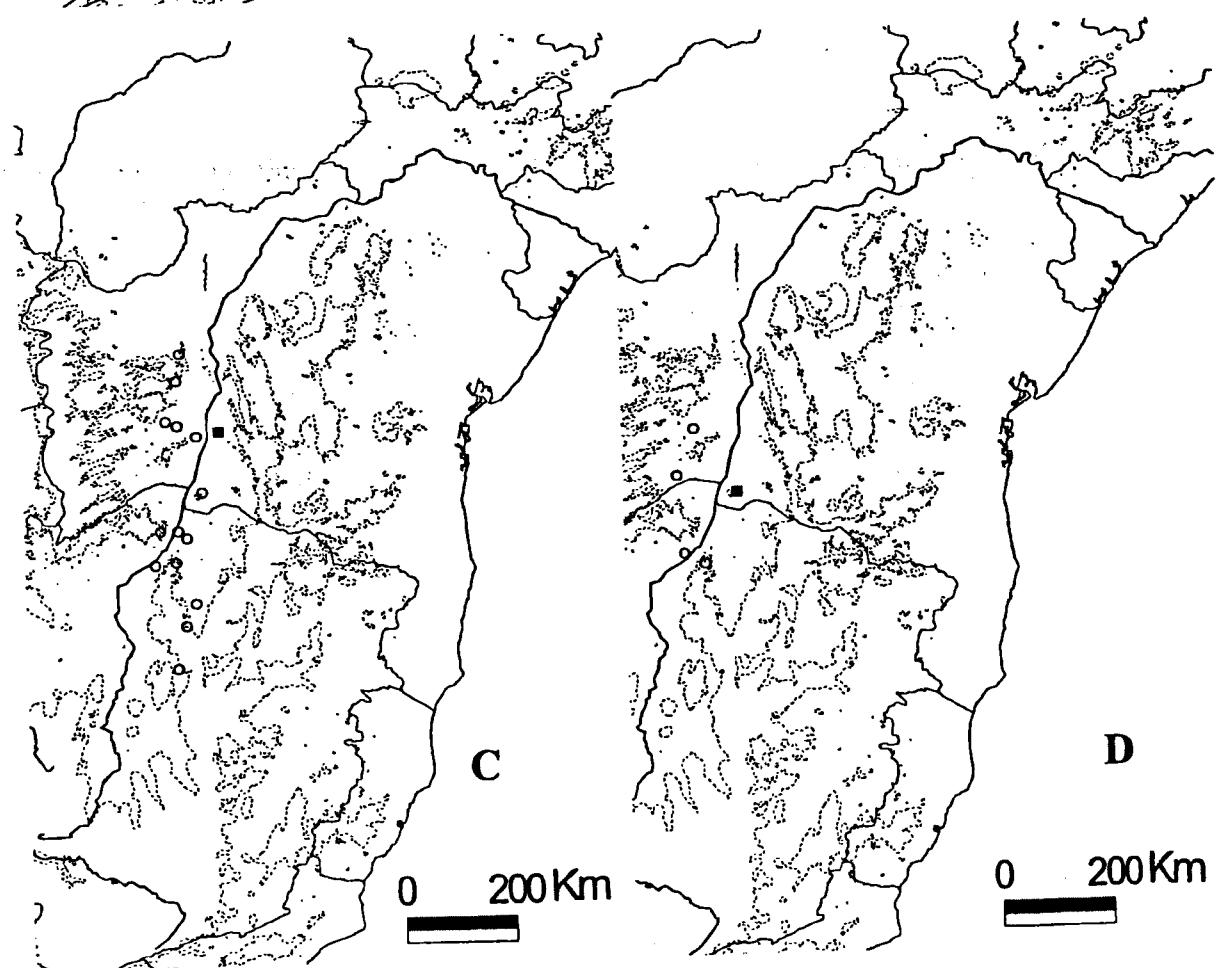


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habitats, it is curious that the genus *Discocactus* is absent from all but the northernmost part of this area (where the *caatinga* has its strongest influence), which is in stark contrast to the ecologically similar Area No. 4c (below), where the genus is well-represented.

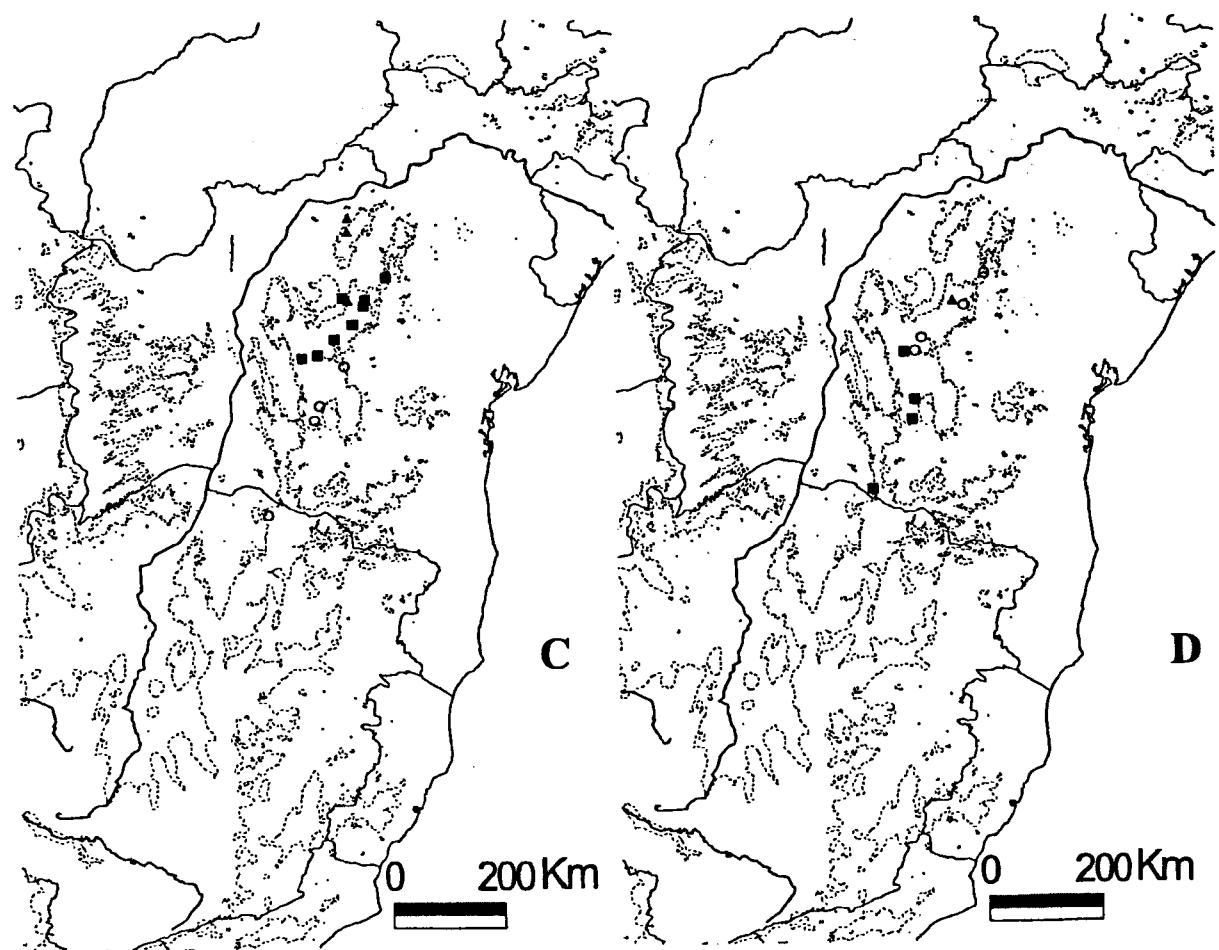
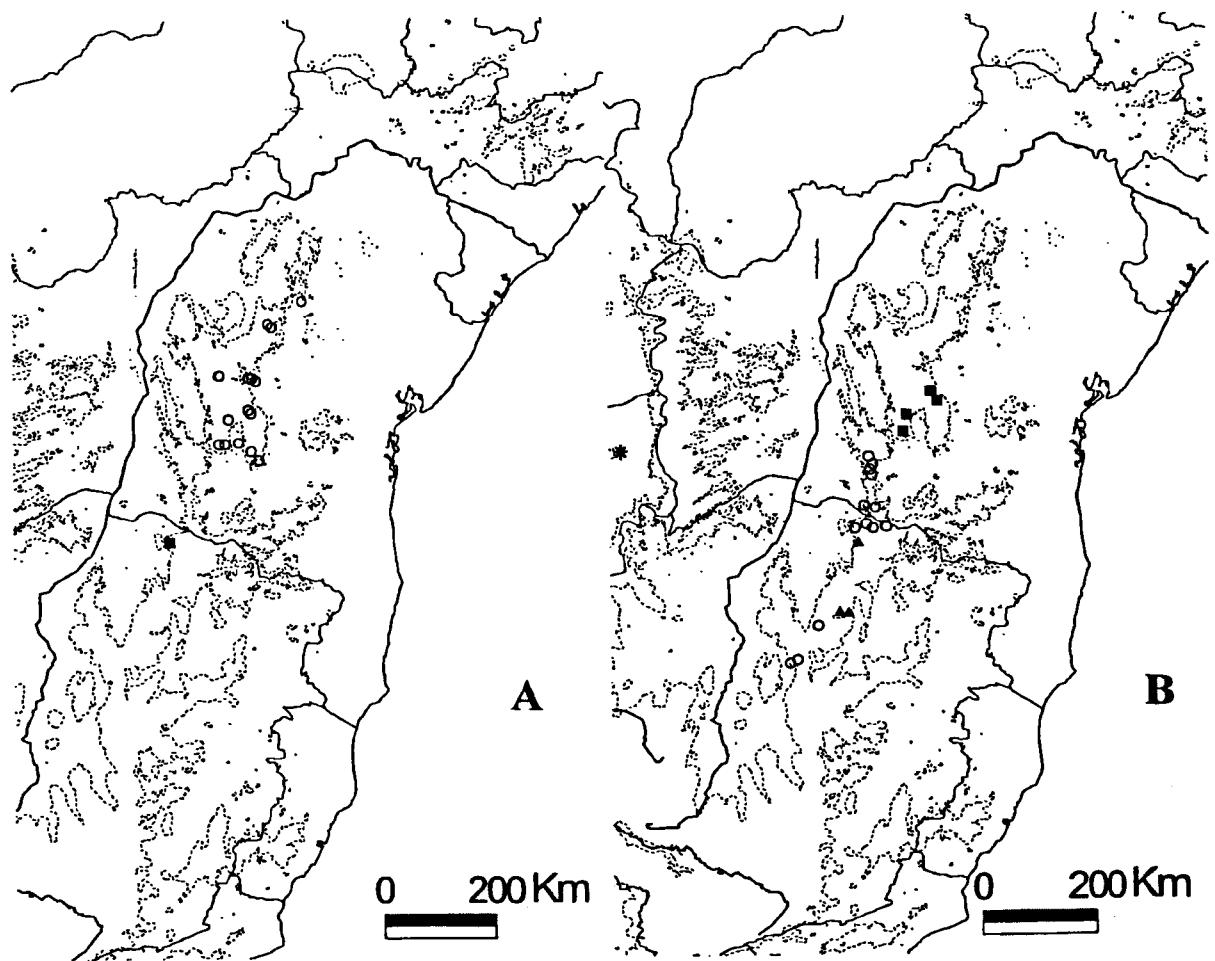
In terms of distribution area, the taxa included here display the full spectrum from widespread within either one of the two subdivisions recognized (eg. *Micranthocereus purpureus*, *Arrojadoa dinae* subsp. *dinae*), to those known from single localities (eg. *Micranthocereus streckeri*, *Cipocereus 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. *cremnophilus* [○], *M. paucispinus* [■] and *M. glaucescens* [▲]. Eastern Brazil (core area).



3c(ii). *Chapada Diamantina* (BA) (9 taxa)

Stephanocereus (subg. *Lagenopsis*†) *luetzelburgii*†, *Arrojadoa bahiensis*‡, *Pilosocereus glaucochrous*‡, *Micranthocereus purpureus*‡, *M. flaviflorus*‡, *M. streckeri*‡§, *Melocactus oreas* subsp. *cremnophilus*‡, *M. glaucescens*‡§, *Discocactus zehntneri* subsp. *boomianus*‡.

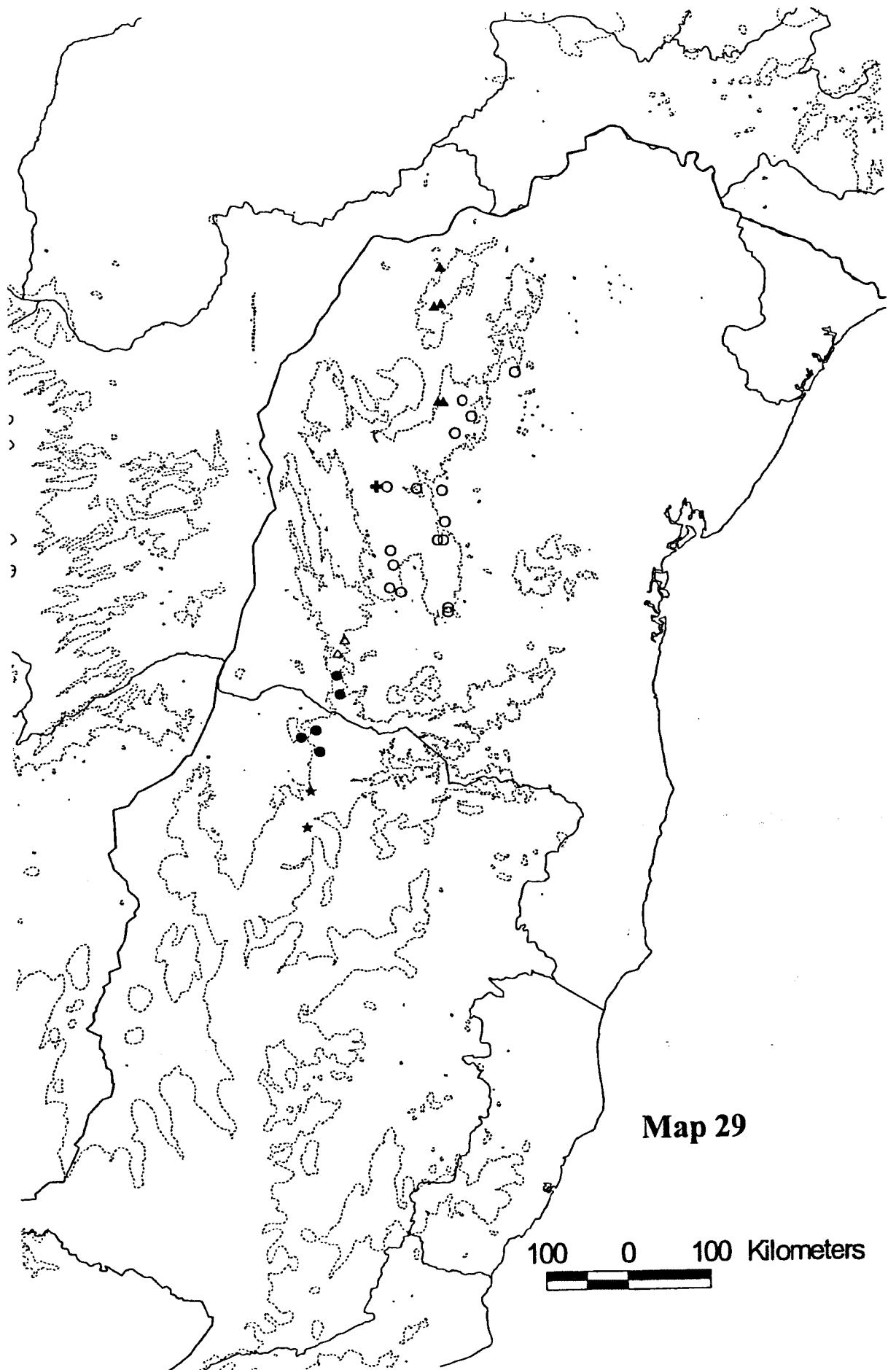
As can be seen from the above list the Chapada Diamantina has a significant number of endemic Cactaceae, although it should be noted that all of these are restricted to its eastern segment, generally east of 42°W. They are mostly allopatric or ecological-vicariant sister taxa of species from the adjacent *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. luetzelburgii* 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 violaciflorus*‡, *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* [Δ], *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.

3d. *Eastern caatingas-agrestes / campos rupestres* (Minas Gerais & Bahia, from the Serra do Espinhaço & Chapada Diamantina, eastwards & north-eastwards to Pernambuco and sometimes beyond) (23 taxa):

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 *Epostoopsis*, while the genera *Facheiroa* and *Discocactus*, characteristic of the Rio São Francisco valley, are lacking.

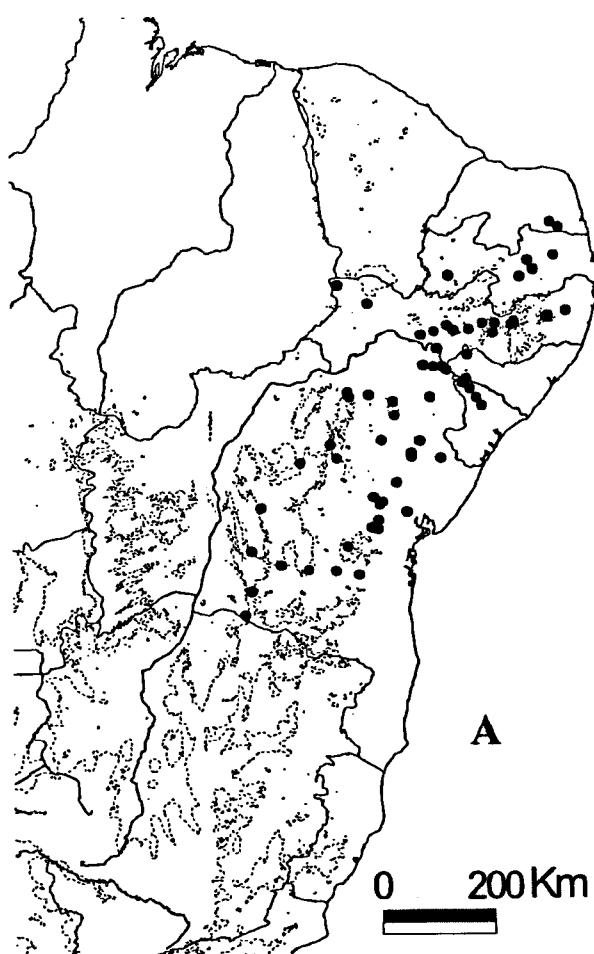
Some of the species listed below are elements of the now much depleted part of the *caatinga* biome that grades into the *agreste*, especially *Pseudoacanthocereus brasiliensis*, *Pilosocereus pentaedrophorus* and *P. catingicola*, while others also found partly associated with this transitional vegetation 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**†, **Epostoopsis dybowskii**†.

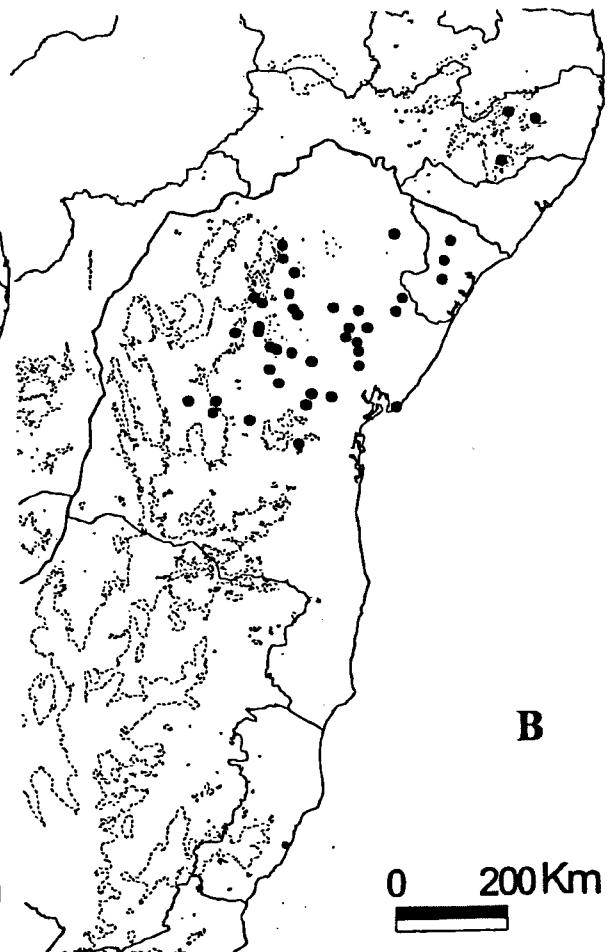
Four of the taxa included here — *Tacinga palmadora*, *Pilosocereus pentaedrophorus* subsp. *pentaedrophorus*, *Melocactus ernestii* and *M. bahiensis* subsp. *bahiensis* — are more widespread, extending northwards into Pernambuco or beyond. In contrast *Melocactus violaceus* subsp. *ritteri* is found 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, *Epostoopsis*, 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).



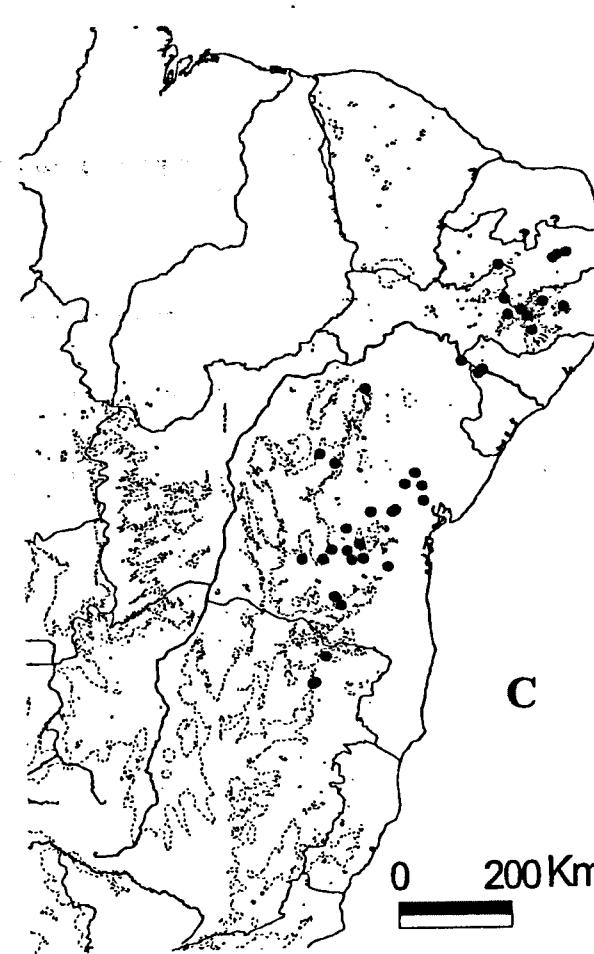
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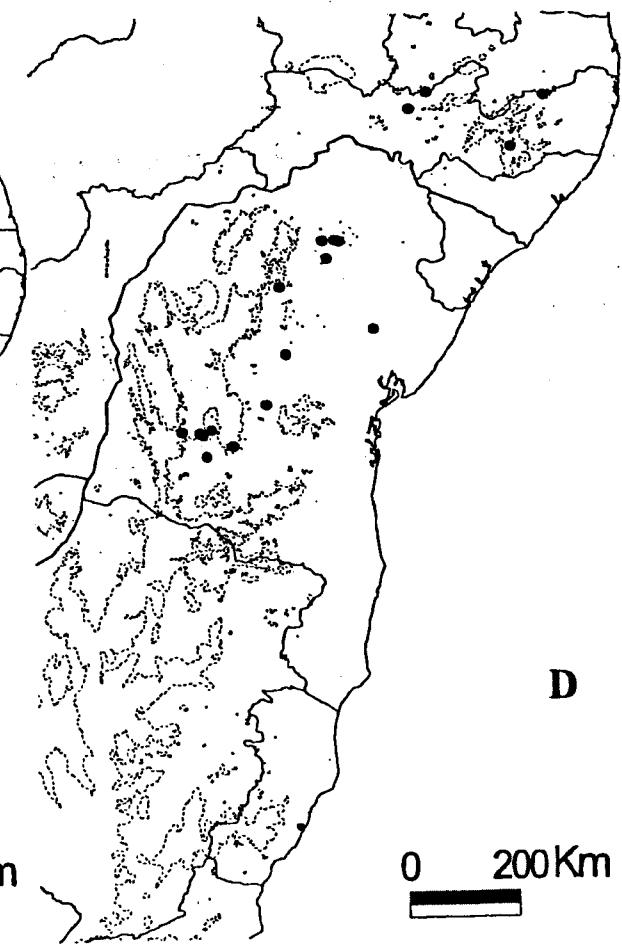
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3d(ib). Restricted to the E & SE caatingas-agrestes / and associated campos rupestres from the Rio Paraguaçu drainage (BA) southwards (6 taxa, Maps 32A–32D)

Tacinga wernerit†, Pilosocereus pentaedrophorus subsp. **robustus†**, **Melocactus oreas** subsp. **oreast†**, **M. bahiensis** subsp. **amethystinus†**, **M. conoideus†§**, **M. salvadorensis†**.

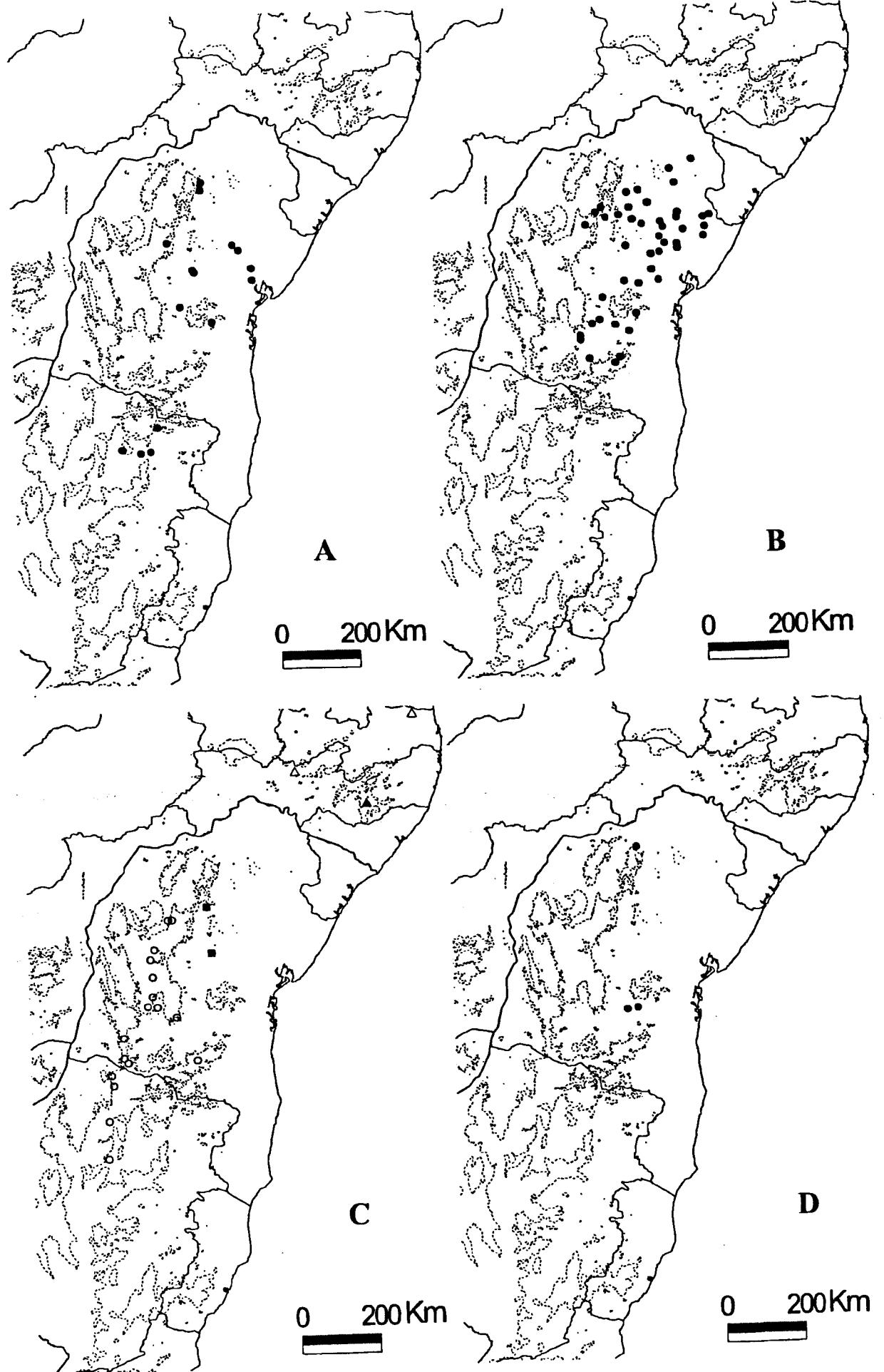
Tacinga wernerii, *Pilosocereus pentaedrophorus* subsp. *robustus* and *Melocactus bahiensis* subsp. *amethystinus* are southern relatives of taxa in category No. 3d(ia). *M. salvadorensis* replaces the more widespread *M. zehntneri* (see No. 3a(i), above) in southern and eastern Bahia (Map 32D), except 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*

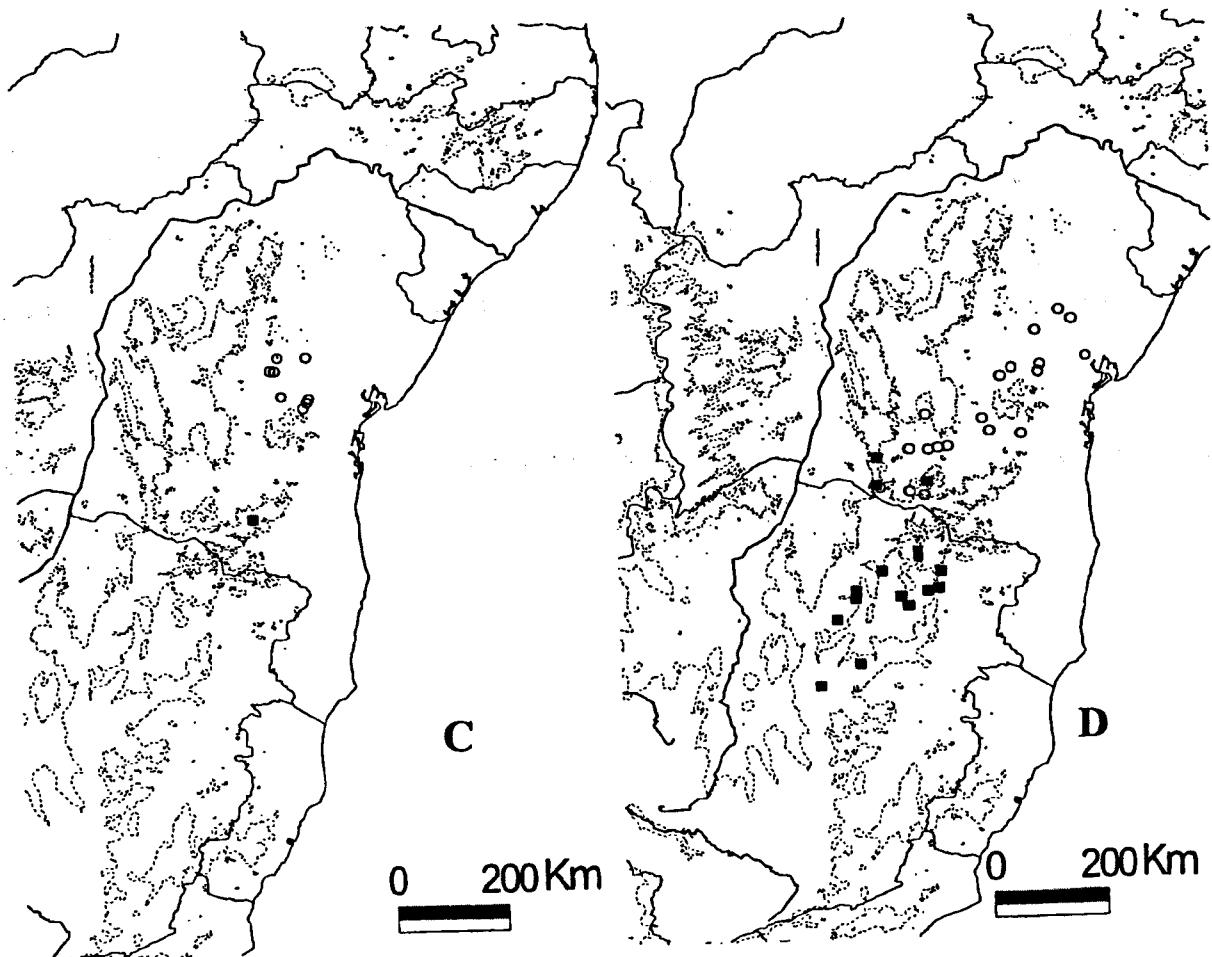
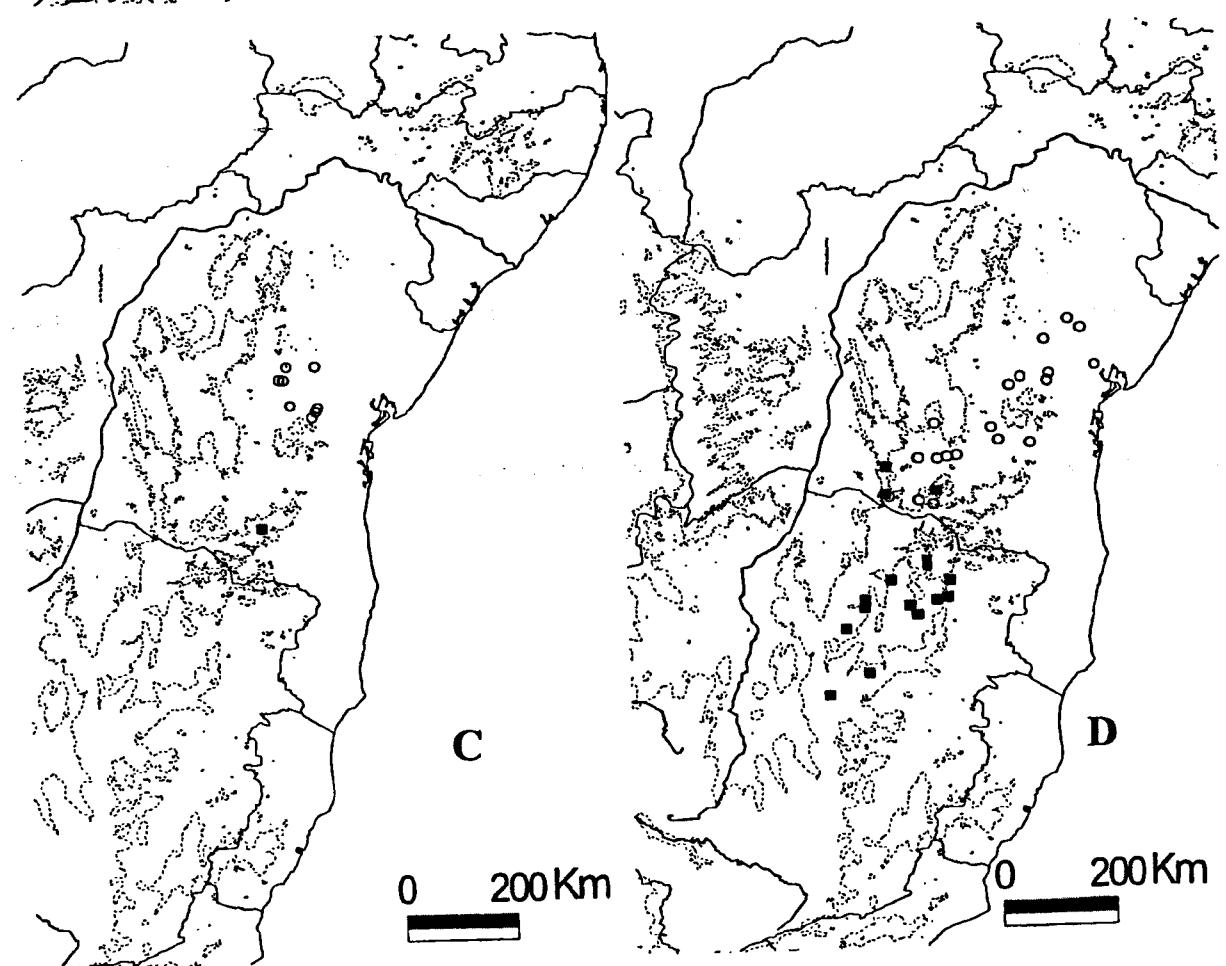
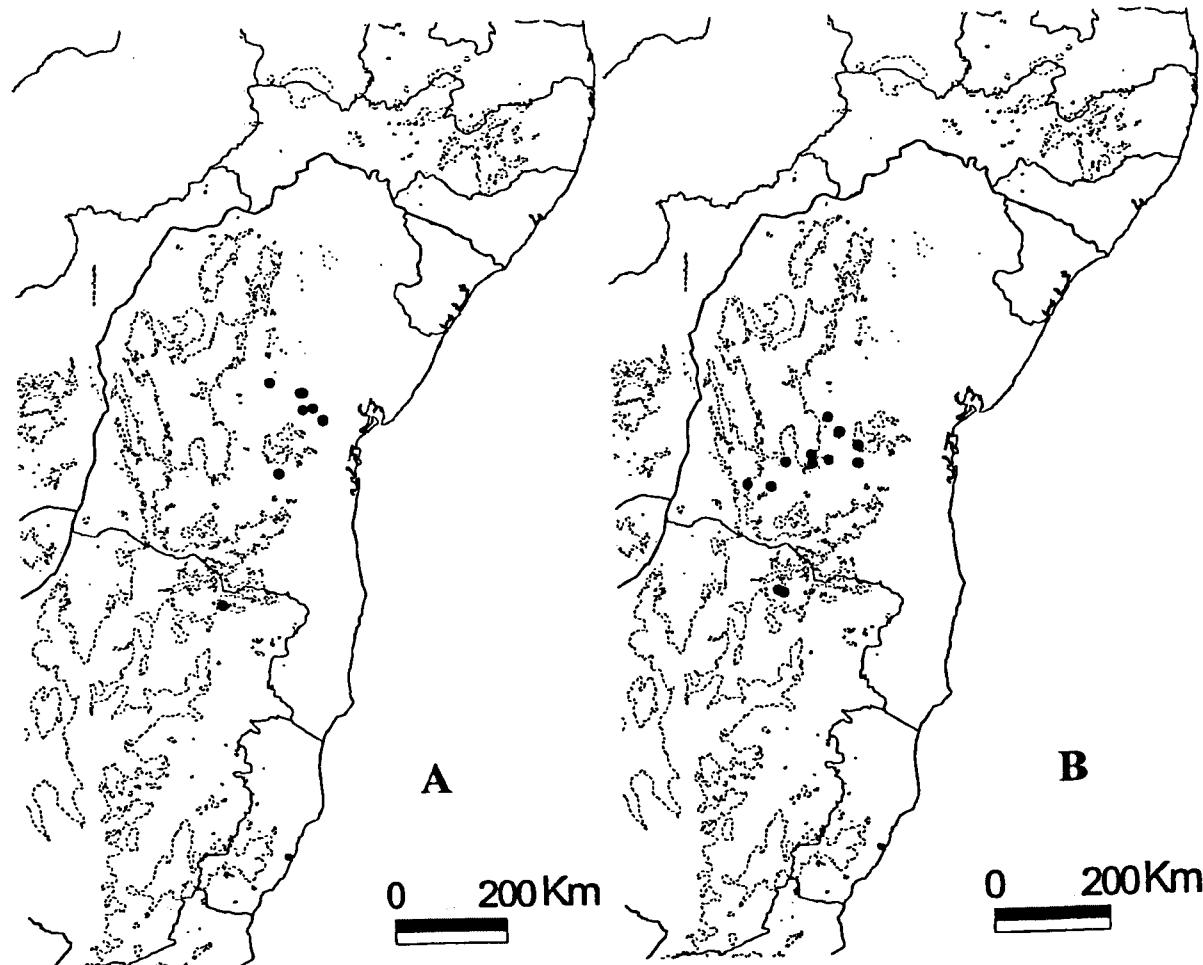
Maps 31A–31D (next page). Distribution pattern 3d(ia), represented by taxa with a more restricted range than those in Maps 30A–30D: (A) *Pseudoacanthocereus brasiliensis*, (B) *Pilosocereus catingicola* subsp. *catingicola*, (C) *M. lanssensianus* [▲, Δ = records of questionable identity], *M. concinnus* [○] and *M. violaceus* subsp. *ritteri* [■] and (D) *Epsattoopsis 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 wernerii*, (B) *Pilosocereus pentaedrophorus* subsp. *robustus*, (C) *Melocactus oreas* subsp. *oreas* [○] and *M. conoideus* [■] and (D) *M. bahiensis* subsp. *amethystinus* [■] and *M. salvadorensis* [○]. Eastern Brazil (core area).

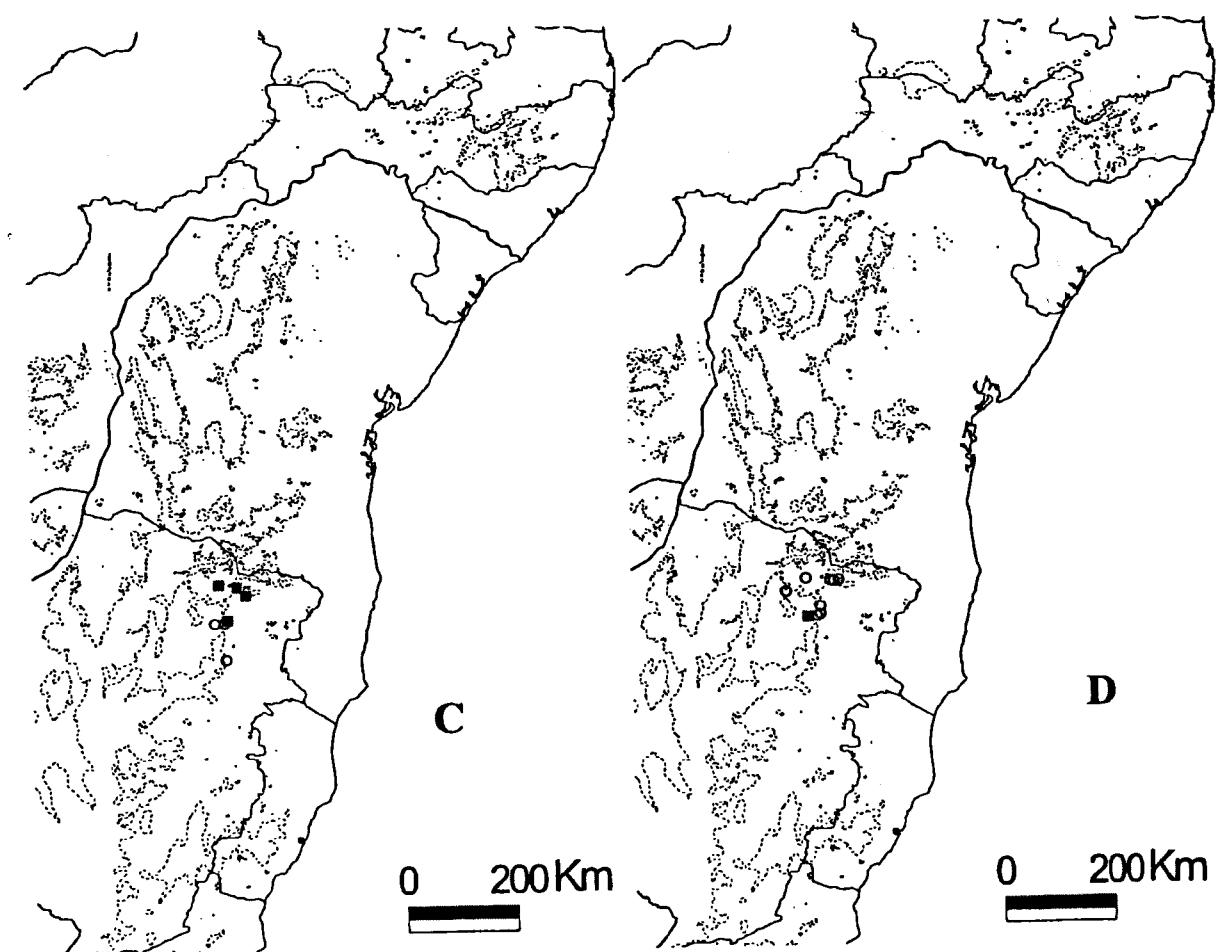
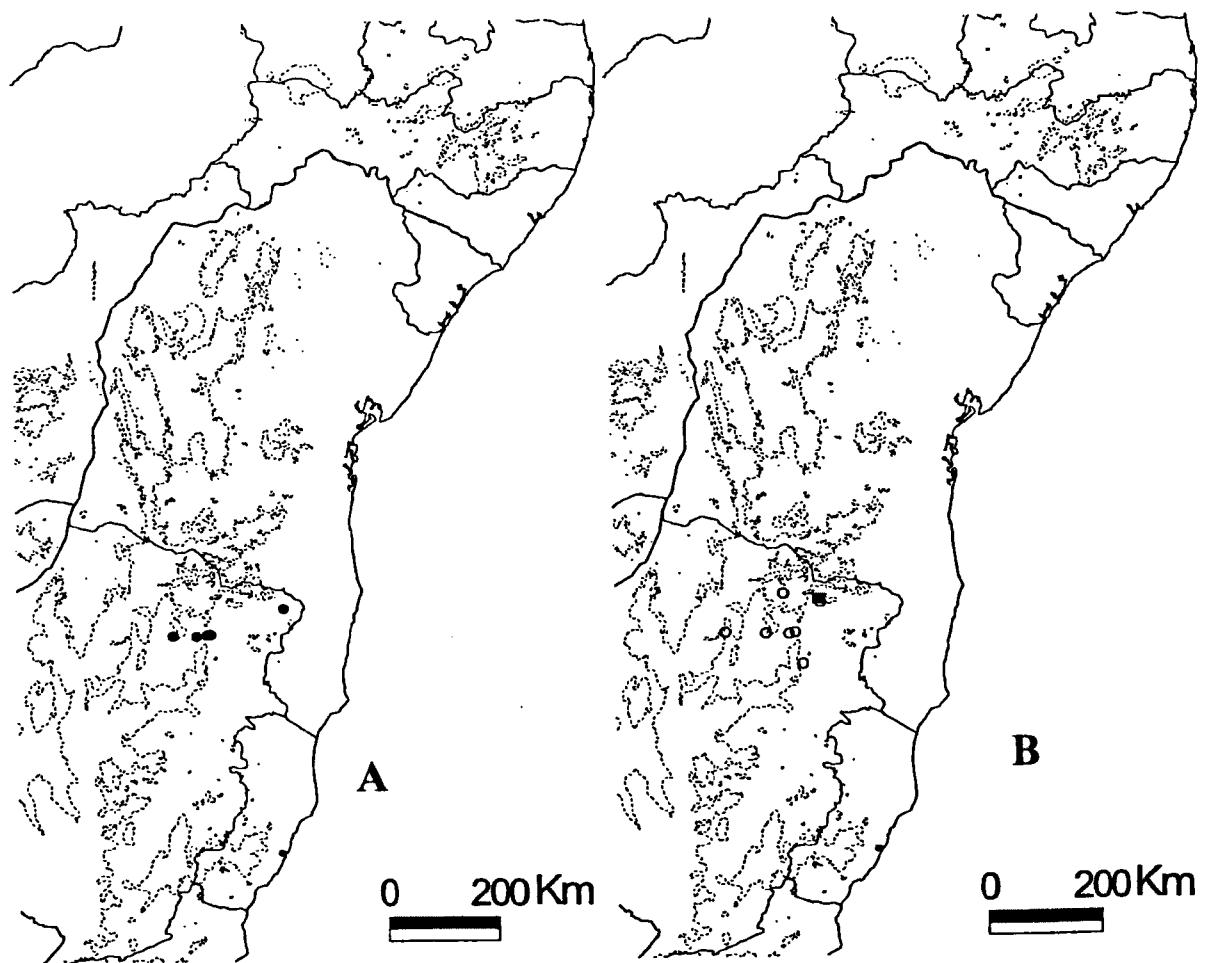


campos rupestres etc. eastwards and north-eastwards from within or to the east of the latter mountain system, with 23 taxa.

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. estevesii*, *Pilosocereus densiareolatus* / *P. diersianus* and *P. floccosus* / *P. albisummus* — or further afield, eg. *Facheiroa* has possible relatives in the east Bolivian *Yungasocereus* Ritter and *Vatricania* Backeberg (~ *Epostoa* 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 Paraíba, 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. multicostatus* [■] and (D) *Coleocephalocereus aureus* [○] & *C. purpureus* [■]. E. Brazil (core area).



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.

<i>Caatinga</i> area	Endemic/characteristic Cactaceae
3a(ii). Northern <i>caatingas</i> : MA, PI, CE, RN, PB, PE, AL, northern BA	<i>Pilosocereus flavipulvinatus</i> , <i>P. pachycladus</i> subsp. <i>pernambucensis</i> , <i>P. piauhensis</i> , <i>P. chrysostele</i> , <i>Discocactus bahiensis</i>
3a(iii). Central-southern <i>caatingas</i> : PI [part], PB [part], PE, AL, BA, SE, MG	<i>Pereskia aureiflora</i> , <i>P. bahiensis</i> , <i>Tacinga funalis</i> , <i>Brasilicereus phaeacanthus</i> , <i>Stephanocereus leucostele</i> , <i>Arrojadoa penicillata</i> , <i>A. rhodantha</i> , <i>Pilosocereus tuberculatus</i> , <i>Coleocephalocereus goebelianus</i> , <i>Melocactus ernestii</i> subsp. <i>longicarpus</i> , <i>Harrisia adscendens</i>
3b. <i>Caatingas</i> of the Rio São Francisco drainage (MG, BA, PE) and adjacent south-eastern PI	<i>Pereskia stenantha</i> , <i>Quiabentia zehntneri</i> , <i>Tacinga saxatilis</i> , <i>Pilosocereus gounellei</i> subsp. <i>zehntneri</i> , <i>P. densiareolatus</i> , <i>Micranthocereus dolichospermaticus</i> , <i>Melocactus deinacanthus</i> , <i>M. levitestatus</i> , <i>M. azureus</i> , <i>M. pachyacanthus</i> , <i>Discocactus zehntneri</i> subsp. <i>zehntneri</i> , <i>Facheiroa</i> (3 spp.)
3d(i). Eastern <i>caatingas-agrestes</i> : CE [part] & RN southwards to central BA & north-eastern MG (from the E Brazilian Highlands eastwards)	<i>Tacinga wernerii</i> , <i>T. palmadora</i> , <i>Pseudoacanthocereus brasiliensis</i> , <i>Pilosocereus pentaedrophorus</i> , <i>P. catingicola</i> subsp. <i>catingicola</i> , <i>Melocactus oreas</i> subsp. <i>oreas</i> , <i>M. ernestii</i> subsp. <i>ernestii</i> , <i>M. salvadorensis</i> , <i>M. concinnus</i> , <i>Epspostoopsis dybowskii</i>
3d(ii). South-eastern <i>caatingas-agrestes</i> : endemics of north-eastern MG	<i>Tacinga braunii</i> , <i>Pilosocereus azulensis</i> , <i>P. floccosus</i> subsp. <i>quadricostatus</i> , <i>P. magnificus</i> , <i>P. multicostatus</i> , <i>Coleocephalocereus</i> subg. <i>Buiningia</i> (2 spp.)

Table 4.4. Geographical subdivision of the *caatingas* dominion based on the distribution of Cactaceae

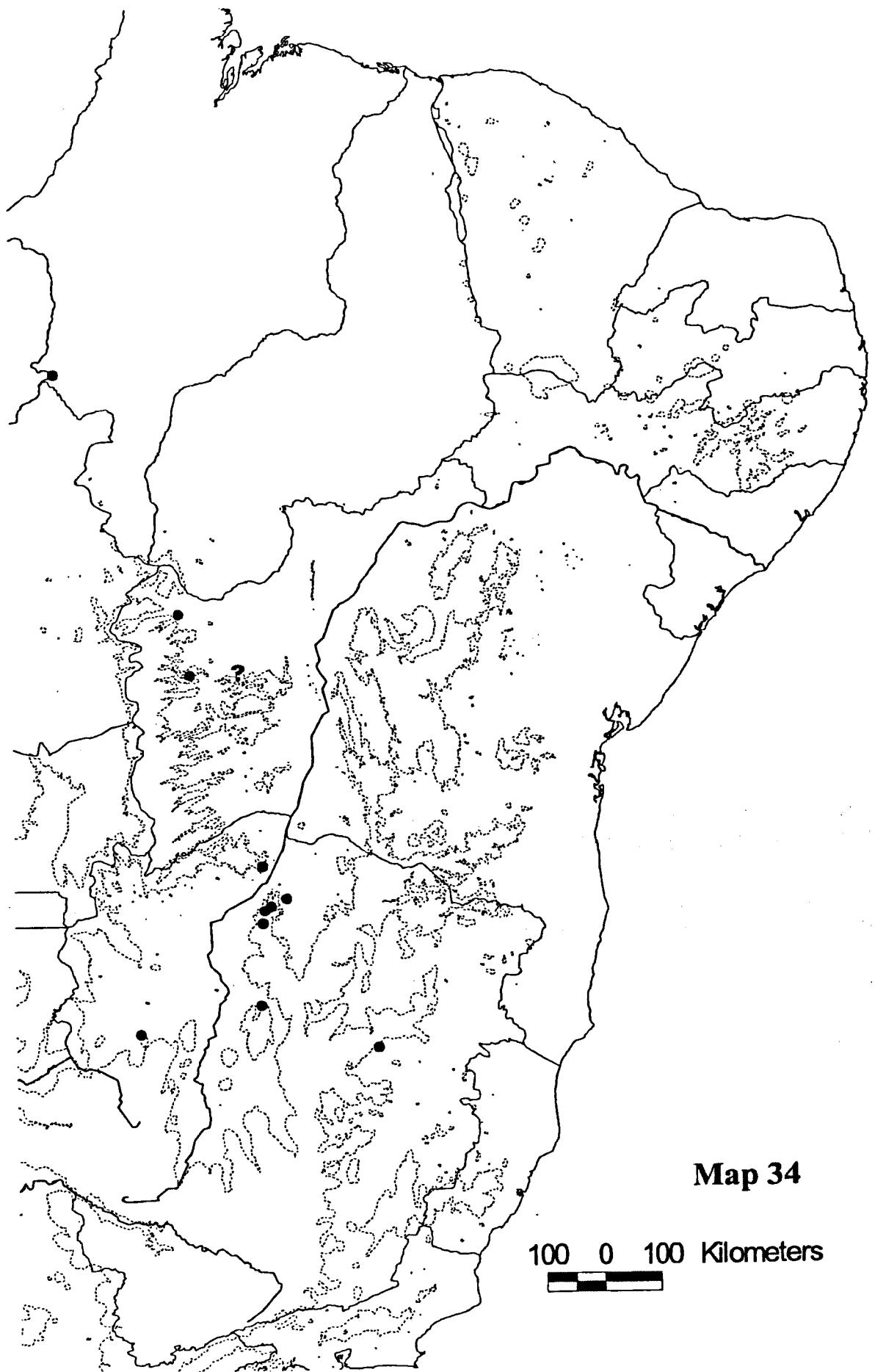
4. *Cerrados* and South-eastern *campos rupestres* (Minas Gerais) [Map 10, west of line A-B & south of line B-C] (28 taxa; 17% of the total)

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 Cereeae, 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 *Arthrocereus* (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(iiic)] & *B. markgrafii* [4c(ia)] and *Cereus albicaulis* [3a(iia)] 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).

<i>Campo rupeste</i> areas within E Brazil	Characteristic taxa of Cactaceae
Area 3. Northern <i>campos rupestres</i> (and included <i>cerrados</i>): Bahia & northern Minas Gerais	<i>Stephanocereus</i> subg. <i>Lagenopsis</i> , <i>Arrojadoa</i> p.p. (2 spp.), <i>Pilosocereus pachycladus</i> ¹ , <i>Melocactus concinnus</i> ¹ , <i>M. paucispinus</i> , <i>M. oreas</i> subsp. <i>cremnophilus</i> , <i>M. violaceus</i> subsp. <i>ritteri</i> , <i>Micranthocereus</i> subg. <i>Austrocephalocereus</i> (3 spp.), <i>M. polyanthus</i> , <i>M. flaviflorus</i> , <i>Leocereus</i> ¹ , <i>Discocactus zehntneri</i> subsp. <i>boomianus</i>
Area 4. South-eastern <i>campos rupestres</i> (and included <i>cerrados</i>): Minas Gerais	<i>Uebelmannia</i> , <i>Cipocereus</i> p.p. (4 spp.), <i>Arthrocereus</i> p.p. (3 spp.), <i>Brasilicereus markgrafii</i> , <i>Pilosocereus aurisetus</i> , <i>P. fulvilanatus</i> , <i>Micranthocereus auriazureus</i> , <i>Discocactus placentiformis</i> , <i>D. pseudoinsignis</i>

Table 4.5. Cactaceae defining the Northern and South-eastern *campo rupeste* 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].



Map 34

100 0 100 Kilometers

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. AURISSETUS 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. aurisetus* [category No. 4c(i)]. In

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)*

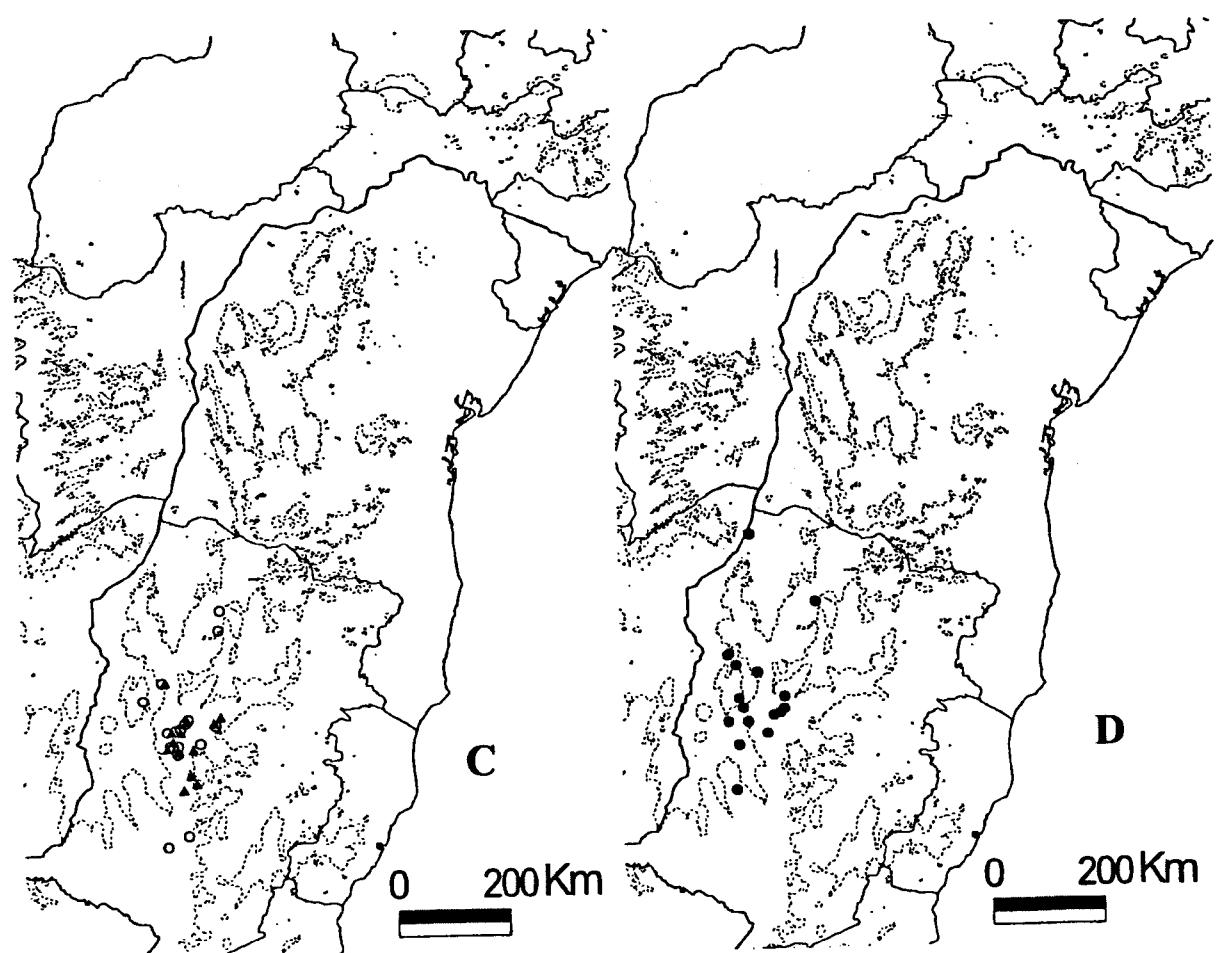
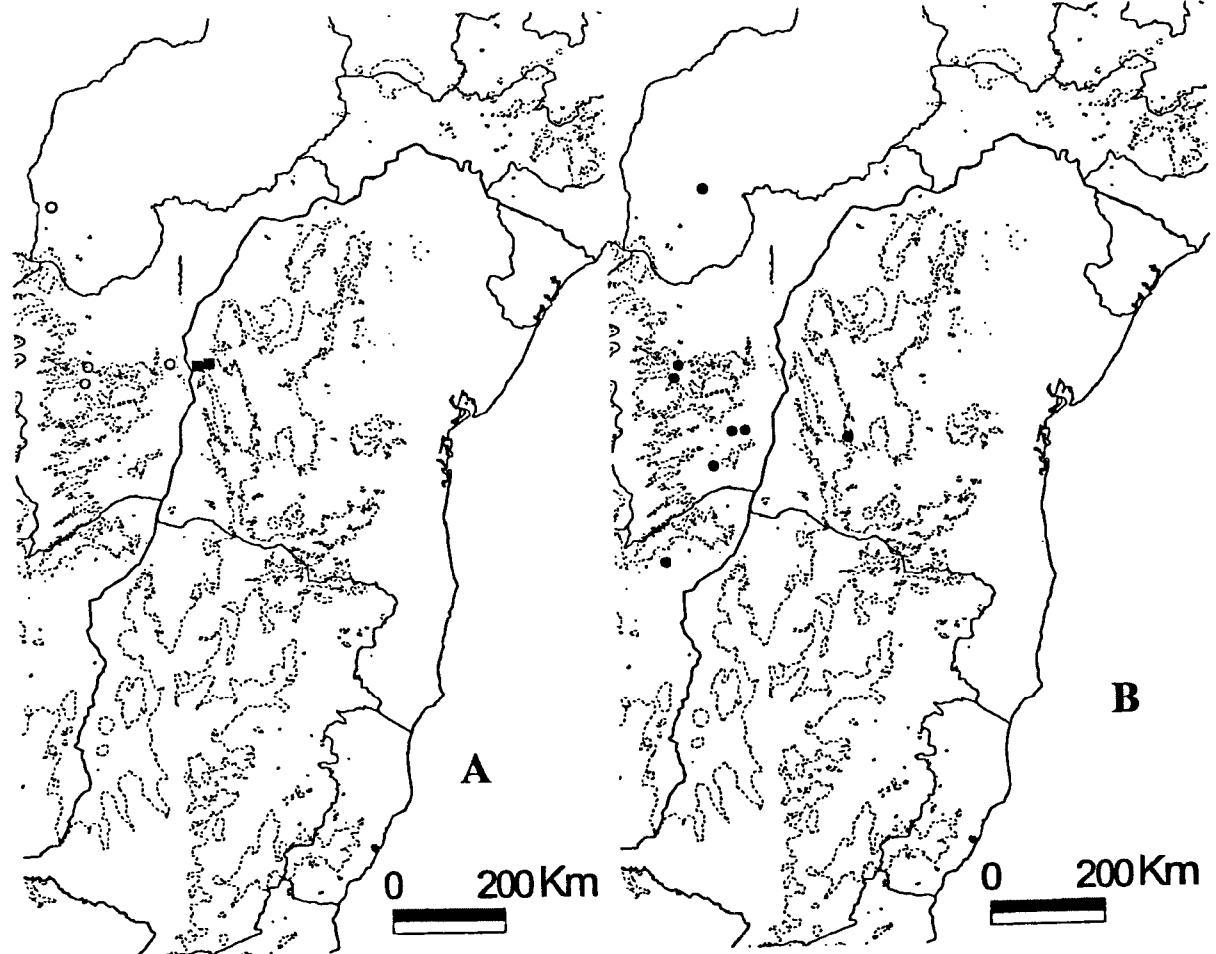
Nearly all the taxa listed here are endemic to the core area of Eastern Brazil and none of the species restricted to this type of habitat is common to that of comparable No. 3c (Chapada Diamantina and N Serra do Espinhaço), where there are only 17 taxa, although some genera are shared. The absence of 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.

Maps 35A–35D (next page). Distribution pattern 4b, represented by (A) *Pilosocereus machrisii* [○] and *P. aureispinus* [■], (B) *Discocactus heptacanthus* subsp. *catingicola*; and pattern 4c(i), represented by (C) *Cipocereus minensis* subsp. *minensis* [○] and *Pilosocereus aurisetus* subsp. *aurisetus* [▲] and (D) *Discocactus placentiformis*. Eastern Brazil (core area).



4c(ii). Northern part of area (16 taxa):

4c(iia). *Municípios 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'Sáber 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)

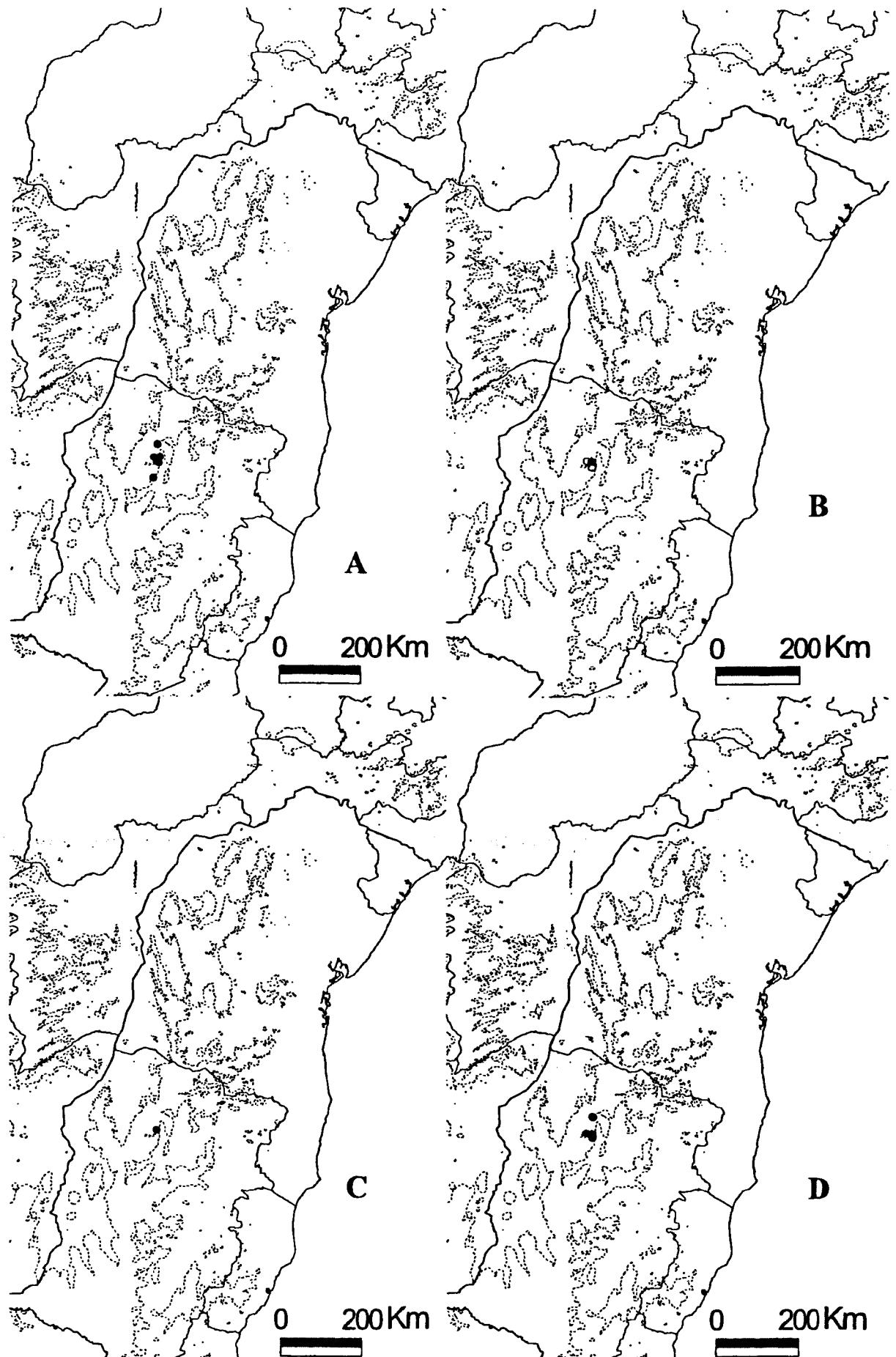
Cipocereus bradei†, **Pilosocereus fulvilanatus** subsp. **rosae**†§, **P. aurisetus** subsp. **aurilanatus**†, **Arthrocereus rondonianus**†, **Uebelmannia pectinifera** subsp. **horrida**†§.

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 crassispalus†, **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(iia), 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)

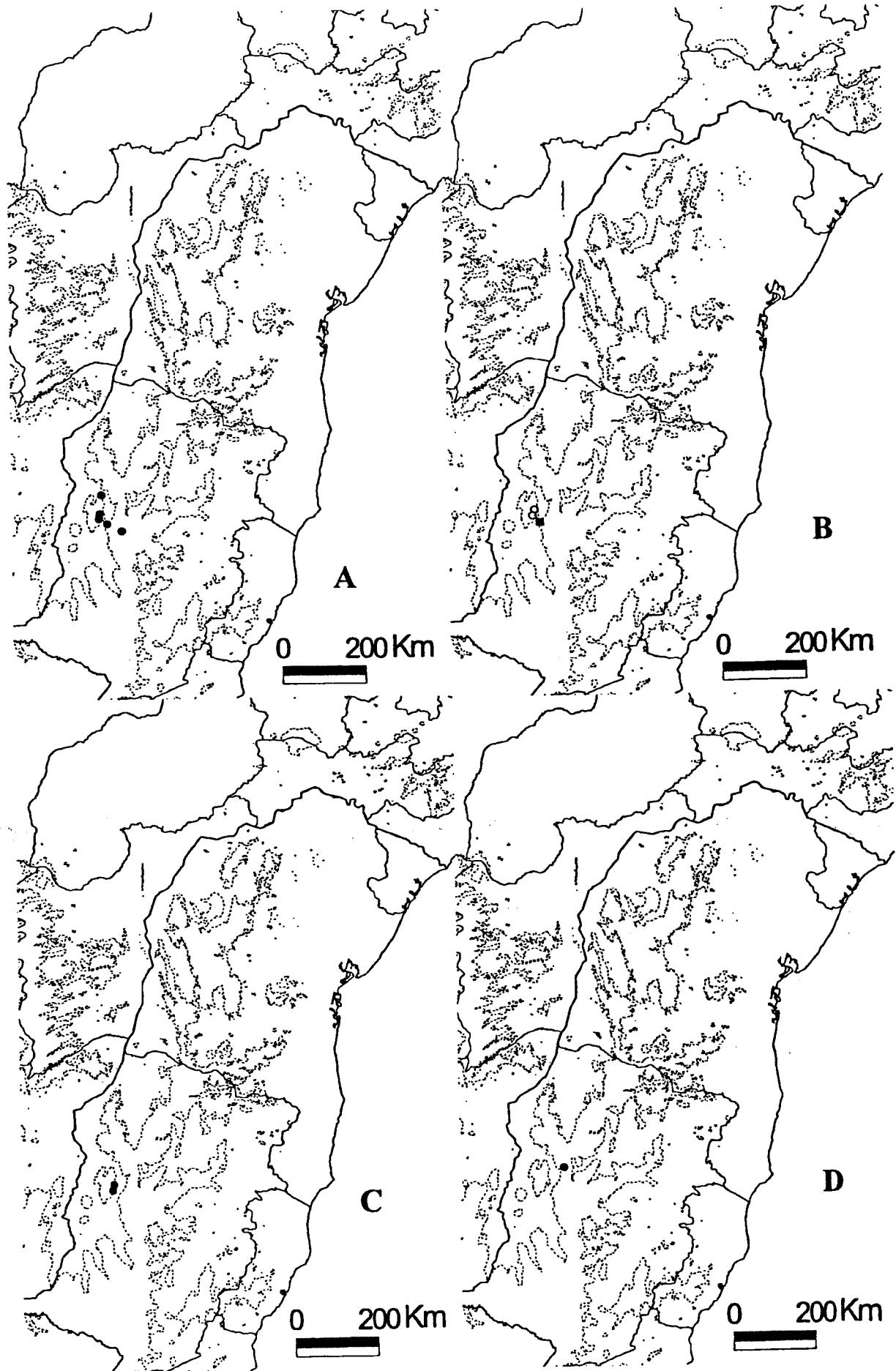
Cipocereus laniflorus†§, *C. minensis* subsp. *pleurocarpus*†, *Arthrocereus glaziovii*†, *A. melanurus* (3 subspp. [2 subspp.†§]).

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. *Astrocephalocereus* (3 spp.) and

Maps 37A–37D (next page). Distribution pattern 4c(iiB), 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).

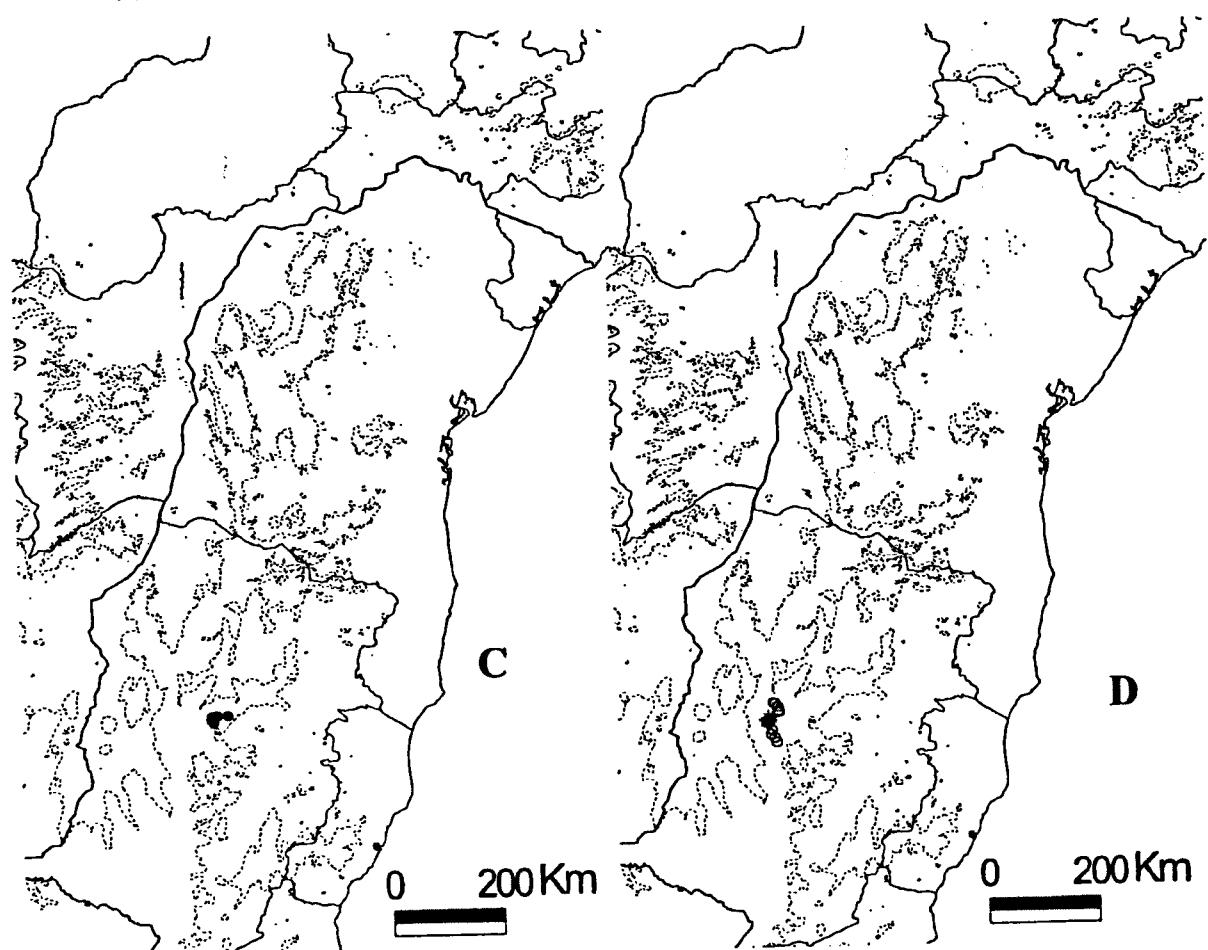
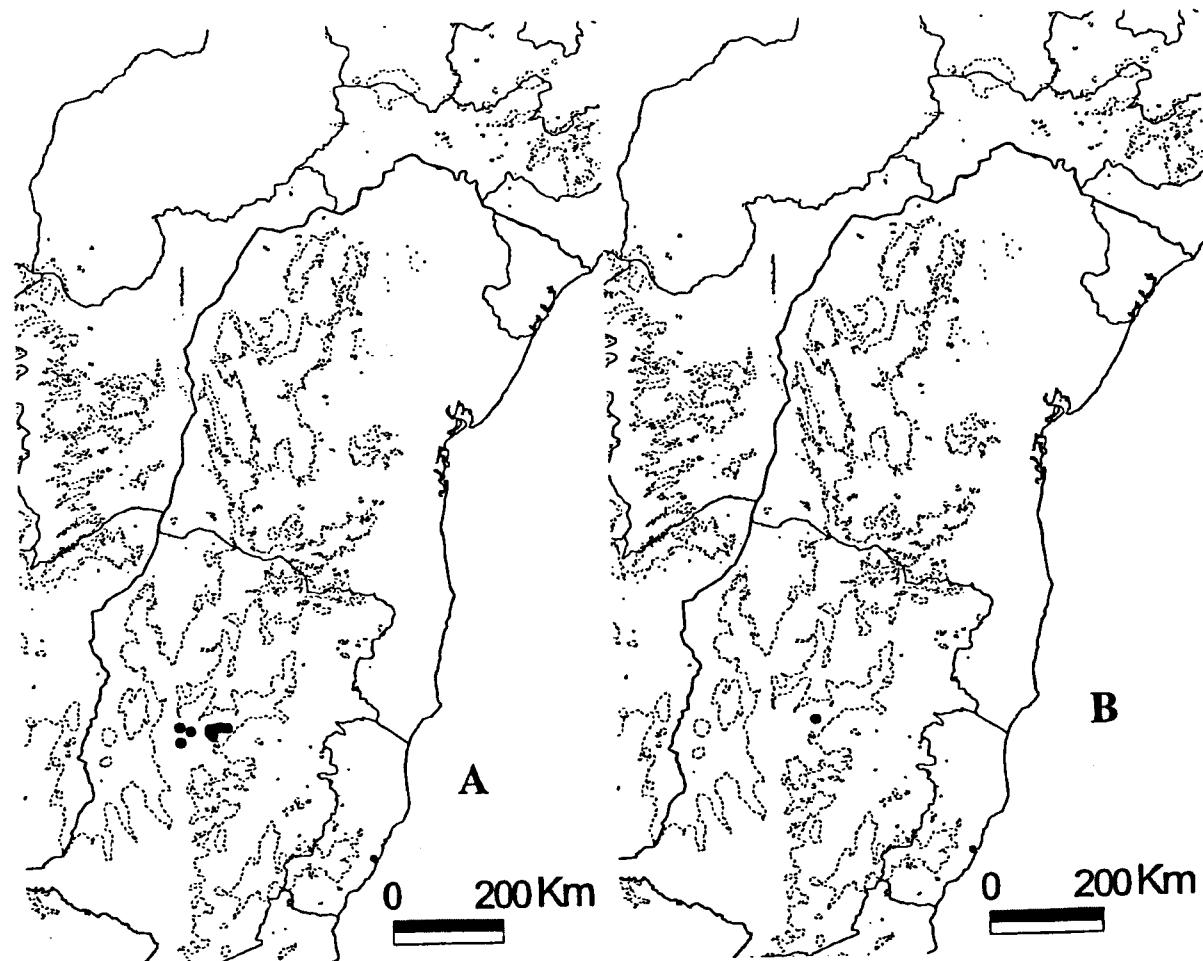


Stephanocereus subg. *Lagenopsis* (1 sp.). Making the same analysis for species found only in the *caatinga-agreste*, we have a total of 58 taxa or 36%, of which 49 (c. 31%) are endemics

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

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

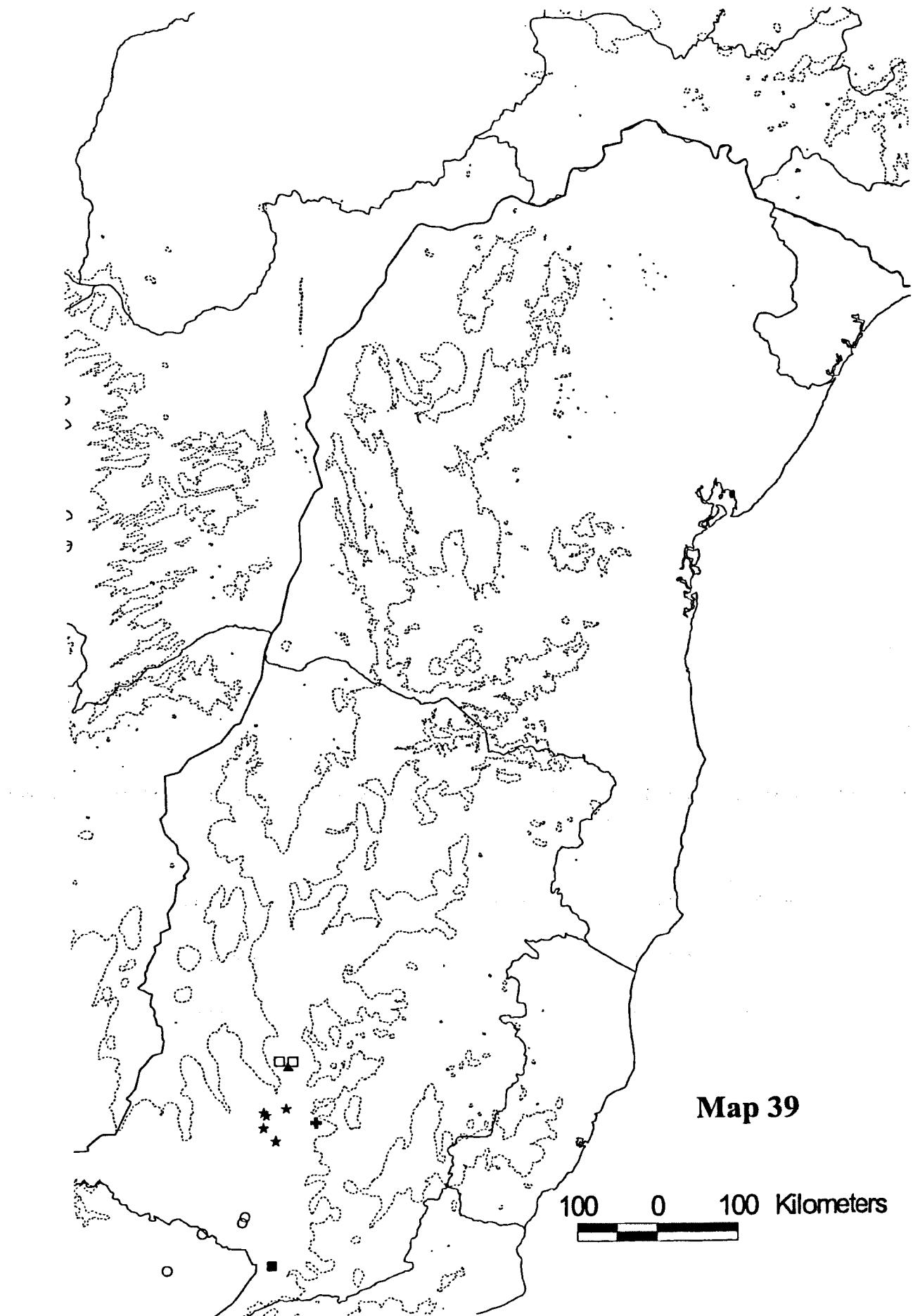
Maps 38A–38D (next page). Distribution pattern 4c(iic), represented by (A) *Cipocereus crassisepalus*, (B) *Uebelmannia buiningii*, (C) *U. gummifera* and (D) *U. pectinifera* subsp. *pectinifera* [○] & subsp. *flavispinus* [★]. Eastern Brazil (core area).



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. *Astrocephalocereus* (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 glaziovii* [★] and *A. melanurus* subsp. *melanurus* [○], subsp. *magnus* [■] & subsp. *odoros* [▲]. Eastern Brazil (core area).

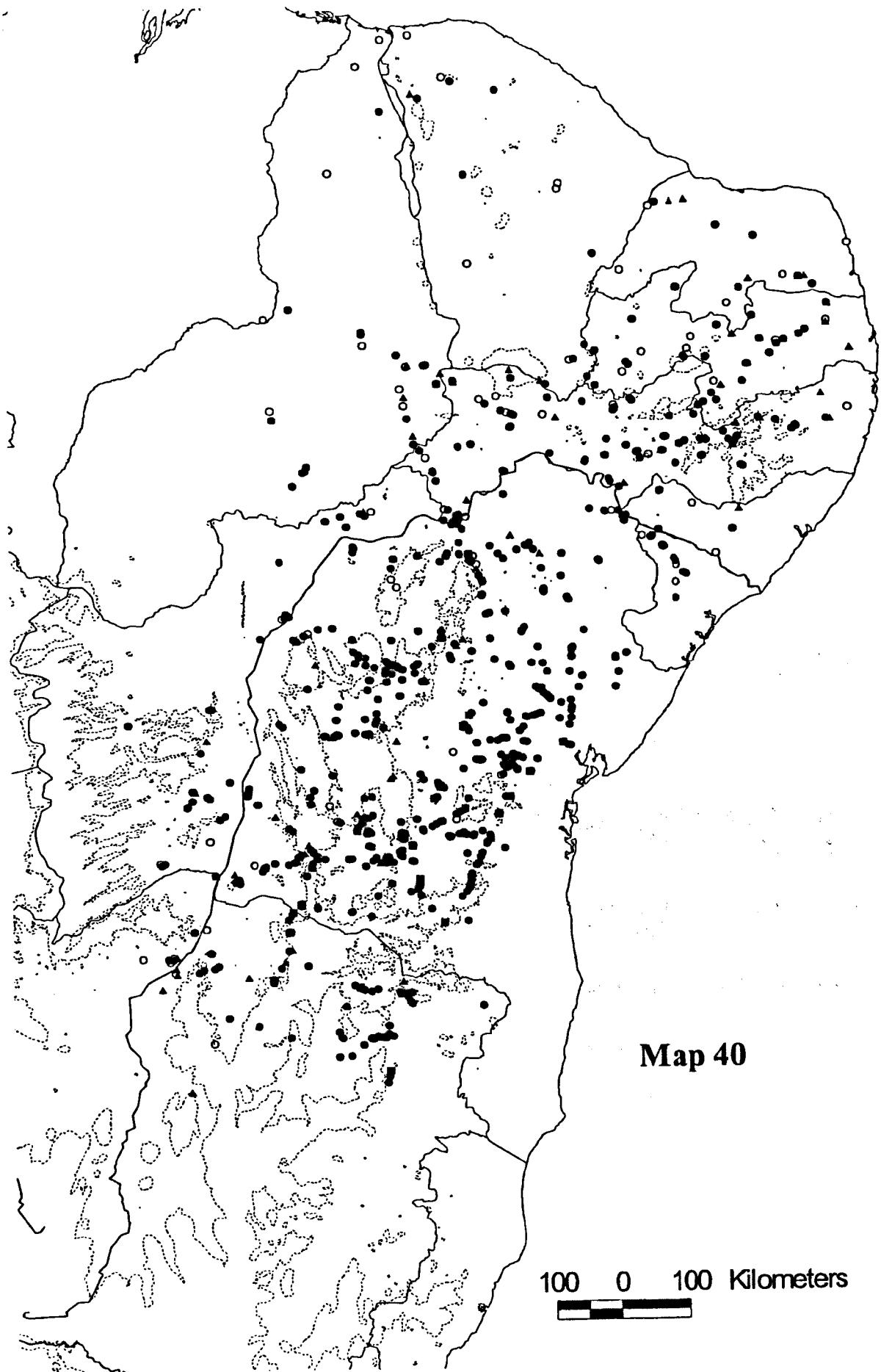


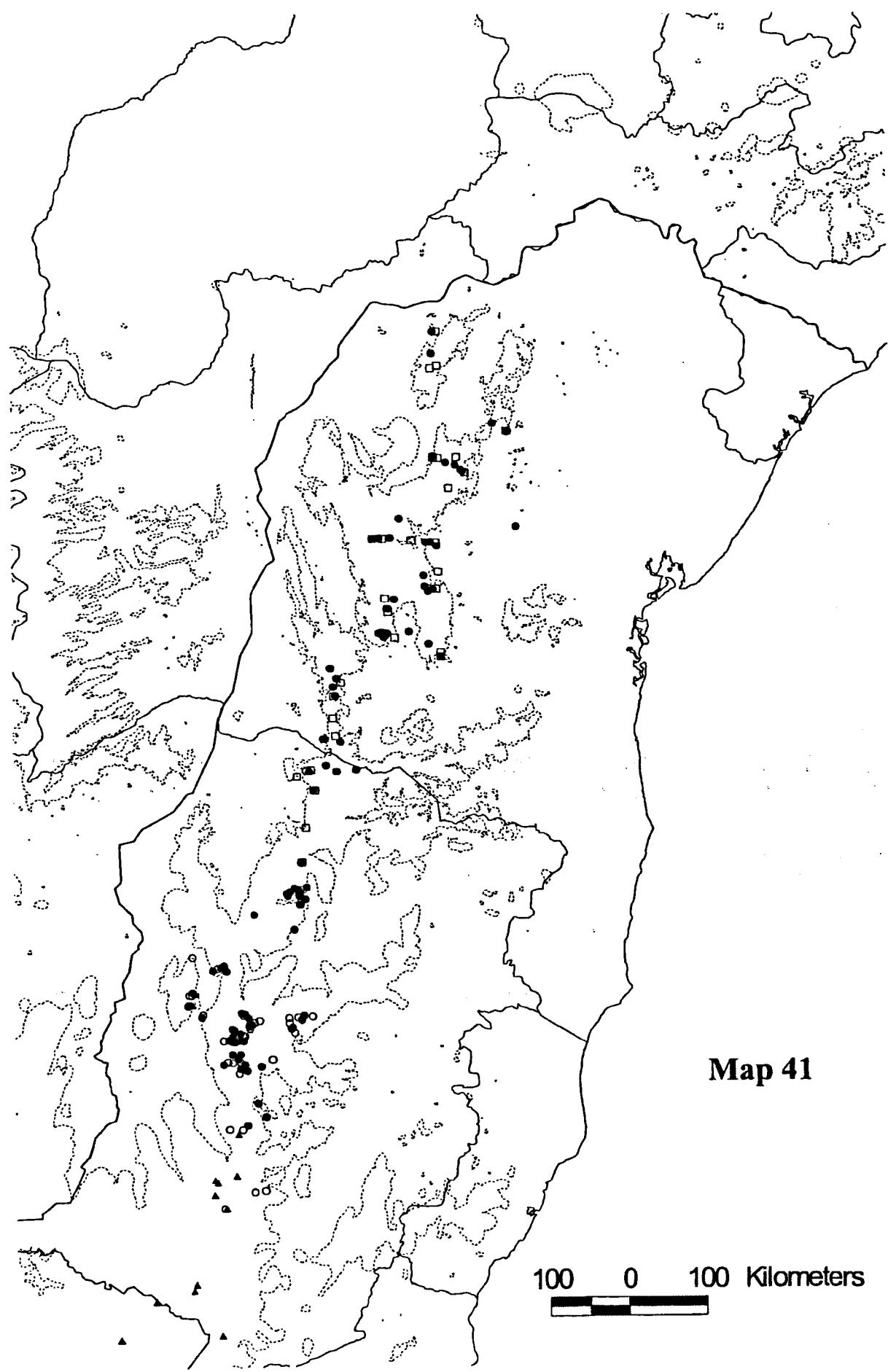
4.6. Reproductive and dispersal strategies

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 *Brasilicereus 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. *Astrocephalocereus*) [□], *Cipocereus* [○] and *Arthrocereus* [▲]. Eastern Brazil (core area).





TAXON	DISPERSAL VECTOR	HABITAT	RANGE
<i>Pereskia aculeata</i>	mammal	Mata atlântica, s.l.	widespread
<i>P. grandifolia</i> ssp. <i>grandifolia</i>	ground-feeding mammal (wild boar?)	"	"
<i>P. grandifolia</i> ssp. <i>violacea</i> †	"	"	restricted
<i>P. bahiensis</i> †	"	caatinga	"
<i>P. stenantha</i> †	"	"	"
<i>P. aureiflora</i> †	mammal	"	"
<i>Quiabentia zehntneri</i> †	?	"	"
<i>Tacinga fusca</i> †	?	"	"
<i>T. braunii</i> †	?	"	"
<i>T. (Opuntia) wernerii</i> †	mammal	"	widespread
<i>T. (Opuntia) palmadora</i> †	mammal	"	restricted
<i>T. (Opuntia) saxatilis</i> ssp. <i>saxatilis</i>	mammal	"	single site
<i>T. (Opuntia) saxatilis</i> ssp. <i>estevensis</i> †	mammal	"	widespread
<i>T. (Opuntia) inamoena</i> †	mammal	"	"
<i>Brasiliopuntia (Opuntia) brasiliensis</i>	ground-feeding mammal (wild boar?)	diverse forest	"
<i>Opuntia monacantha</i>	mammal &/or bird	Mata atlântica: dunes	restricted
<i>Hylocereus setaceus</i>	mammal (bat/primate?) & bird	diverse forest	widespread
<i>Epiphyllum phyllanthus</i>	mammal: primate (•) & bat (?); bird?	"	widespread
<i>Pseudoacanthocereus brasiliensis</i> †	ground-feeding mammal (wild boar?)	caatinga	restricted
<i>Lepismium houltianum</i>	bird & small monkeys	Mata atlântica	restricted
<i>L. warmingianum</i>	"	"	"
<i>L. cruciforme</i>	"	"	widespread
<i>Rhipsalis russellii</i>	"	Mata atlântica & campo rupestre	"
<i>R. elliptica</i>	"	Mata atlântica	restricted
<i>R. oblonga</i>	"	"	"
<i>R. crispata</i>	"	"	single site
<i>R. floccosa</i> ssp. <i>floccosa</i>	"	"	widespread
<i>R. floccosa</i> ssp. <i>oreophila</i> †	"	"	restricted
<i>R. floccosa</i> ssp. <i>pulvinigera</i>	"	"	widespread
<i>R. paradoxa</i> ssp. <i>septentrionalis</i> †	"	"	single site
<i>R. pacheco-leonis</i> ssp. <i>catenulata</i>	"	"	"
<i>R. cereoides</i>	"	"	"
<i>R. sulcata</i> †	"	"	widespread
<i>R. lindbergiana</i>	"	"	restricted
<i>R. teres</i>	"	"	restricted
<i>R. baccifera</i> ssp. <i>baccifera</i>	"	Mata atlântica / de neblina	"
<i>R. baccifera</i> ssp. <i>hileiabaiana</i> †	"	"	"
<i>R. pulchra</i>	"	Mata atlântica	"
<i>R. burchellii</i>	"	"	"
<i>R. juengeri</i>	"	"	"
<i>R. clavata</i>	"	"	widespread
<i>R. cereuscula</i>	"	"	restricted
<i>R. pilocarpa</i>	"	"	single site
<i>R. hoelleri</i> †	"	"	widespread
<i>Hatiora salicornioides</i>	"	Mata atlântica & campo rupestre	"
<i>Schlumbergera kautskyi</i> †	"	Mata atlântica	restricted
<i>S. microsphaerica</i>	"	mata de neblina	"
<i>S. opuntioides</i>	"	"	"
<i>Brasilicereus phaeacanthus</i> †	bat?	caatinga-agreste	restricted
<i>B. markgrafii</i> †	"	campo rupestre	"
<i>Cereus mirabella</i>	mammal	cerrado	widespread
<i>C. albicaulis</i> †	"	caatinga	"
<i>C. fernambucensis</i> ssp. <i>fernambuc.</i>	bat, other mammal & bird	restinga	"
<i>C. fernambucensis</i> ssp. <i>sericifer</i>	"	Mata atlântica	restricted
<i>C. insularis</i> †	?	restinga	"
<i>C. jamacaru</i> ssp. <i>jamacaru</i> †?	bird (•)	caatinga-agreste	widespread
<i>C. jamacaru</i> ssp. <i>calcirupicola</i>	"	"	restricted
<i>C. hildmannianus</i>	bat & bird	Mata atlântica	"
<i>Cipocereus laniflorus</i> †	"	campo rupestre	"
<i>C. crassipeplus</i> †	"	campo rupestre/cerrado	"
<i>C. bradei</i> †	"	campo rupestre	"
<i>C. minensis</i> ssp. <i>minensis</i> †	"	"	"
<i>C. minensis</i> ssp. <i>pleurocarpus</i> †	"	"	single site
<i>C. pusilliflorus</i> †	"	"	restricted
<i>Stephanocereus leucostele</i> †	bat	caatinga	"
<i>S. luetzelburgii</i> †	"	campo rupestre	"
<i>Arrojadoa bahiensis</i> †	bird?	"	"

<i>A. dinae</i> ssp. <i>dinae</i> ♀	bird & mammal?	campo rupestre/cerrado	"
<i>A. dinae</i> ssp. <i>eriocaulis</i> ♀	"	"	"
<i>A. penicillata</i> ♀	"	caatinga	"
<i>A. rhodantha</i> ♀	"	"	widespread
<i>Pilosocereus tuberculatus</i> ♀	bat	"	restricted
<i>P. gounellei</i> ssp. <i>gounellei</i> ♀	bat, insect (wasp ●) & water	"	widespread
<i>P. gounellei</i> ssp. <i>zehntneri</i> ♀	"	"	restricted
<i>P. catingicola</i> ssp. <i>catingicola</i> ♀	bird (●) & bat	"	restricted
<i>P. catingicola</i> ssp. <i>salvadorensis</i> ♀	bat (Locatelli et al. 1997)	caatinga-agreste & restinga	restricted
<i>P. azulensis</i> ♀	bat	caatinga-agreste	single site?
<i>P. arrabidae</i>	lizard (●), bat & bird?	restinga	restricted
<i>P. brasiliensis</i> ssp. <i>brasiliensis</i>	bat & bird?	"	"
<i>P. brasiliensis</i> ssp. <i>ruschianus</i> ♀	"	Mata atlântica	"
<i>P. flavigulvinatus</i> ♀	"	caatinga	restricted
<i>P. pentaedrophorus</i> ssp. <i>pentaedr.</i> ♀	"	caatinga-agreste	widespread
<i>P. pentaedrophorus</i> ssp. <i>robustus</i> ♀	"	"	restricted
<i>P. glaucochrous</i> ♀	"	caatinga de altitude	widespread
<i>P. floccosus</i> ssp. <i>floccosus</i> ♀	"	mata seca	restricted
<i>P. floccosus</i> ssp. <i>quadricostatus</i> ♀	"	caatinga-agreste	"
<i>P. fulvilanatus</i> ssp. <i>fulvilanatus</i> ♀	"	campo rupestre	"
<i>P. fulvilanatus</i> ssp. <i>rosae</i> ♀	"	"	single site
<i>P. pachycladus</i> ssp. <i>pachycladus</i> ♀	"	caatinga & campo rupestre	widespread
<i>P. pachycl. ssp. pernambucoensis</i> ♀	"	caatinga-agreste	"
<i>P. magnificus</i> ♀	"	"	restricted
<i>P. machrisii</i>	"	rocks in cerrado	"
<i>P. aurisetus</i> ssp. <i>aurisetus</i> ♀	"	campo rupestre	"
<i>P. aurisetus</i> ssp. <i>aurilanatus</i> ♀	"	"	"
<i>P. aureispinus</i> ♀	bat, bird (?) & ant	rocks in cerrado	"
<i>P. multicostatus</i> ♀	bat & bird?	caatinga-agreste	"
<i>P. piauhensis</i> ♀	"	caatinga	"
<i>P. chrysostele</i> ♀	"	"	"
<i>P. densiareolatus</i> ♀	"	"	"
<i>Micranthocereus violaciflorus</i> ♀	ant?	campo rupestre	"
<i>M. albicephalus</i> ♀	"	"	"
<i>M. purpureus</i> ♀	bat & bird (●)	"	"
<i>M. auriazureus</i> ♀	bird	"	single site
<i>M. streckeri</i> ♀	"	"	"
<i>M. polyanthus</i> ♀	"	"	restricted
<i>M. flaviflorus</i> ♀	"	"	"
<i>M. dolichospermaticus</i> ♀	wind	caatinga	"
<i>Coleocephaloc. buxbaumianus</i> , s.l. ♀	ant (●) (also bird/bat?)	Mata atlântica	"
<i>C. fluminensis</i> ssp. <i>fluminensis</i>	" (ant ●)	"	"
<i>C. fluminensis</i> ssp. <i>decumbens</i> ♀	"	"	"
<i>C. pluricostatus</i> ♀	"	"	"
<i>C. goebelianus</i> ♀	" (ant ●)	caatinga	"
<i>C. aureus</i> ♀	" (ant ●)	"	"
<i>C. purpureus</i> ♀	"	"	single site
<i>Melocactus oreas</i> ssp. <i>oreas</i> ♀	lizard (●) & bird	"	restricted
<i>M. oreas</i> ssp. <i>cremnophilus</i> ♀	"	campo rupestre	"
<i>M. ernestii</i> ssp. <i>ernestii</i> ♀	" (lizard ●)	caatinga	widespread
<i>M. ernestii</i> ssp. <i>longicarpus</i> ♀	"	"	restricted
<i>M. bahiensis</i> ssp. <i>bahiensis</i> ♀	"	caatinga & campo rupestre	restricted
<i>M. bahiensis</i> ssp. <i>amethystinus</i> ♀	"	"	"
<i>M. conoideus</i> ♀	"	cerrado de altitude	single site
<i>M. deinacanthus</i> ♀	"	caatinga	"
<i>M. levitestatus</i> ♀	"	"	restricted
<i>M. azureus</i> , s.l. ♀	"	"	"
<i>M. pachyacanthus</i> , s.l. ♀	"	"	"
<i>M. salvadorensis</i> ♀	"	"	"
<i>M. zehntneri</i> ♀	" (lizard ●)	"	widespread
<i>M. lanssensianus</i> , s.l. ♀	"	"	restricted
<i>M. glaucescens</i> ♀	"	campo rupestre	single site
<i>M. concinnus</i> ♀	"	caatinga & campo rupestre	restricted
<i>M. paucispinus</i> ♀	"	cerrado de altitude	"
<i>M. violaceus</i> ssp. <i>violaceus</i>	" (lizard ●)	restinga	widespread
<i>M. violaceus</i> ssp. <i>ritteri</i> ♀	"	campo rupestre	restricted
<i>M. violaceus</i> ssp. <i>margaritaceus</i> ♀	"	restinga	"
<i>Harrisia adscendens</i> ♀	bat, other mammal & bird	caatinga	widespread
<i>Leocereus bahiensis</i> ♀	"	campo rupestre & caatinga	"
<i>Facheiroa ulei</i> ♀	bat	caatinga	restricted
<i>F. cephaeliomelana</i> ssp. <i>cephaeliomelana</i> ♀	"	"	single site
<i>F. cephaeliomelana</i> ssp. <i>estevessii</i> ♀	"	"	restricted
<i>F. squamosa</i> ♀	"	"	"

<i>Epostoopsis dybowskii</i> †	bat & bird	"	"
<i>Arthrocereus melanurus</i> ssp. <i>melanurus</i>	bat, other mammal & bird	campo rupestre	"
<i>A. melanurus</i> ssp. <i>magnus</i> †	"	"	single site
<i>A. melanurus</i> ssp. <i>odoros</i> †	"	"	
<i>A. rondonianus</i> †	"	"	restricted
<i>A. glaziovii</i> †	"	"	"
<i>Discocactus zehntneri</i> ssp. <i>zehntneri</i> †	ant	caatinga	restricted
<i>D. zehntneri</i> ssp. <i>boomianus</i> †	"	campo rupestre	"
<i>D. bahiensis</i> †	ant (●) & water	caatinga	"
<i>D. heptacanthus</i> ssp. <i>catingicola</i> †	ant	cerrado	"
<i>D. placentiformis</i> †	" (●)	campo rupestre/cerrado	"
<i>D. pseudoinsignis</i> †	"	cerrado	"
<i>D. horstii</i> †	"	campo rupestre/cerrado	single site
<i>Uebelmannia buiningii</i> †	ant?	"	restricted
<i>U. gummifera</i> †	"	"	"
<i>U. pectinifera</i> ssp. <i>pectinifera</i> †	ant?	campo rupestre	"
<i>U. pectinifera</i> ssp. <i>flavispina</i> †	"	"	"
<i>U. pectinifera</i> ssp. <i>horrida</i> †	"	"	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 zochory 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 Hylocereeae (*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 ('sagüis') 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 Trichocereeae, 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 are equally threatened taxa in the genera *Cipocereus*, *Arthrocereus* and *Epostoopsis* 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, e.g. *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. zehntneri*, *Pereskia aureiflora*, *Pseudoacanthocereus brasiliensis*, *Pilosocereus catingicola*, *sens. lat.*, *P. floccosus* subsp. *quadricostatus*, *P. flavigelinatus*, *P. glaucochrous*, *P. pentaedrophorus*, *sens. lat.*, *Stephanocereus leucostele*, *Tacinga palmadora*, *T. braunii* and *T. finalis*. 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. levitestatus*, *Micranthocereus dolicho-spermaticus*, *Pilosocereus densiareolatus*, *P. floccosus*, *P. gounellei* subsp. *zehntneri*, *Tacinga saxatilis* subspp. *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*, *Epspostoopsis 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 *caatingas-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 Aiuba’ (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(iiic) & 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. *estevensis* and *Tacinga saxatilis* subsp. *estevensis*). 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. *eriocaulis*), *Arthrocereus rondonianus*, *Brasilicereus markgraffii*, *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 *Arthrocereus 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 *Arthrocereus 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.*

salicornioides, *Lepismium cruciforme*, *L. houletteianum*, *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. *cylindrica*, *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.*

fernambucensis), 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.

Brejo locality (state)	Cactaceae (date of most recent record), notes
Serra de Baturité (Ceará)	<i>Rhipsalis baccifera</i> subsp. <i>baccifera</i> (1979)
N slope of Chapada do Araripe (Ceará)	<i>Pereskia grandifolia</i> subsp. <i>grandifolia</i> (1971)
Areia (Paraíba)	<i>Rhipsalis baccifera</i> subsp. <i>baccifera</i> (1998)
Taquaritinga do Norte (Pernambuco)	<i>Lepismium cruciforme</i> (1983), <i>Rhipsalis cereuscula</i> (1972)
Poção (Pernambuco)	<i>Pereskia aculeata</i> (1991)
Brejo da Madre de Deus (Pernambuco)	<i>Rhipsalis floccosa</i> (1980), <i>R. cereuscula</i> (1995), <i>Melocactus ernestii</i> (1993)
Caruaru (Pernambuco)	<i>Rhipsalis crispata</i> (1970), <i>R. floccosa</i> (1971) — these species records urgently need re-confirmation in habitat
Serra Negra, Inajá (Pernambuco)	<i>Brasiliopuntia brasiliensis</i> & <i>Rhipsalis lindbergiana</i> (1995)
Serra do Cumanati (Pernambuco)	<i>Rhipsalis floccosa</i> (1969) — this brejo may have been destroyed, since it does not figure in Rodal <i>et al.</i> (1998)
Mata Grande (Alagoas)	<i>Brasiliopuntia brasiliensis</i> (1974)
Rui Barbosa (Bahia)	<i>Pereskia aculeata</i> (1973), <i>Brasiliopuntia brasiliensis</i> (1978)
Monte Verde, Itaberaba (Bahia)	<i>Pereskia aculeata</i> (1973)
Três Braços, Ubaíra (Bahia)	<i>Lepismium cruciforme</i> (1994), <i>Rhipsalis floccosa</i> (1994)
Jaguaquara (Bahia)	<i>Pereskia aculeata</i> , <i>Brasiliopuntia brasiliensis</i> , <i>Rhipsalis russellii</i> (all 1915) — brejo assumed to have been destroyed
Venceslau Guimarães (Bahia)	<i>Hatiora salicornioides</i> f. <i>cylindrica</i> (1993) — in protected area
Almadina / Floresta Azul (Bahia)	<i>Rhipsalis russellii</i> (before 1966), <i>R. baccifera</i> subsp. <i>hileiabaiana</i> (before 1966), <i>R. cereuscula</i> (1972)
Juçari/Jussari (Bahia)	<i>Rhipsalis paradoxa</i> subsp. <i>septentrionalis</i> (before 1966)
Camacã/Camacan (Bahia)	<i>Lepismium cruciforme</i> (1971), <i>Rhipsalis russellii</i> (1971), <i>R. oblonga</i> (1971), <i>R. paradoxa</i> subsp. <i>septentrionalis</i> (before 1979)

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 km² for CR, 5000/500 km² for EN, 20000/2000 km² 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 km²) 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, e.g. some Mexican Pachycereeae.)

* 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).

Conservation short-list score (see Formal Taxonomic Treatment, Supplement 1) / shared priority order / taxon / (state codes)	IUCN Category (criteria)/ CITES App.†	Area (Table 5.3 qv)	References to protected area proposals and other recommendations
24 1. <i>Espostoopsis dybowskii</i> (BA)	EN (B1/2bce) / App. II	3d(ia)	Taylor in Oldfield (1997): 143, prop. 105(b). Other sites are recommended for protection here (see below).
1. <i>Melocactus deinacanthus</i> (BA)	CR (B1/2c) / App. I	3b(iii)	The only known site is recommended for protection here (see below).
20 2. <i>Cipocereus laniflorus</i> (MG)	CR (D) / App. II	4c(iii)	Costa <i>et al.</i> (1998): 63, prop. C10; Taylor in Oldfield (1997): 144, prop. 105(m).
2. <i>C. pusilliflorus</i> (MG)	CR (D) / App. II	3c(iii)	Taylor in Oldfield (1997): 144, prop. 105(e).
2. <i>Uebelmannia buiningii</i> (MG)	CR (C2) / App. I	4c(iiC)	Costa <i>et al.</i> (1998): 62, prop. C7; Taylor in Oldfield (1997): 144, prop. 105(l).
2. <i>U. pectinifera</i> subsp. <i>horrida</i> (MG)	CR (B1/2ce) / App. I	4c(iiB)	Costa <i>et al.</i> (1998): 62, prop. C7.

18			
3. <i>Arrojadoa dinae</i> subsp. <i>eriocaulis</i> (MG)	EN (B1/2c) / App. II	3c(iii)	Costa <i>et al.</i> (1998): 64, prop. N22; Taylor in Oldfield (1997): 144, props 105(f/h).
3. <i>Arthrocereus glaziovii</i> (MG)	EN (B1/2-bcd) / App. II	4c(iii)	Costa <i>et al.</i> (1998): 63, prop. C10.
3. <i>Uebelmannia gummifera</i> (MG)	EN (B2ce/3d) / App. I	4c(iic)	Costa <i>et al.</i> (1998): 62, prop. C7; Taylor in Oldfield (1997): 144, prop. 105(l).
3. <i>U. pectinifera</i> subsp. <i>pectinifera</i> (MG)	EN (B1/2e) / App. I	4c(iic)	Costa <i>et al.</i> (1998): 62, prop. C7; Taylor in Oldfield (1997): 144, prop. 105(k).
3. <i>U. pectinifera</i> subsp. <i>flavispina</i> (MG)	EN (B1/2e) / App. I	4c(iic)	Costa <i>et al.</i> (1998): 62, prop. C7; Taylor in Oldfield (1997): 144, prop. 105(k).
16			
4. <i>Pilosocereus azulensis</i> (MG)	CR (C2) / App. II	3d(ii)	Taylor in Oldfield (1997): 143, prop. 105(a).
4. <i>Micranthocereus violaciflorus</i> (MG)	CR (B1/2c) / App. II	3c(iii)	Costa <i>et al.</i> (1998): 62, prop. N22?; Taylor in Oldfield (1997): 144, prop. 105(g).
4. <i>M. streckeri</i> (BA)	CR (B1/2c) / App. II	3c(ii)	Taylor in Oldfield (1997): 144, prop. 105(c).
4. <i>Melocactus conoideus</i> (BA)	CR (B1/2c) / App. I	3d(ib)	Adequate protection for a recently designated site is needed (see below).
4. <i>M. pachyacanthus</i> subsp. <i>pachyacanthus</i> (BA)	CR (A2c) / App. II	3b(ii)	Conservation <i>ex situ</i> may be the only option available.
4. <i>M. glaucescens</i> (BA)	CR (B1/2c) / App. I	3c(ii)	Taylor in Oldfield (1997): 144, prop. 105(b).
4. <i>Discocactus horstii</i> (MG)	CR (B1/2c) / App. I	4c(iia)	Costa <i>et al.</i> (1998): 64, prop. N22*; Taylor in Oldfield (1997): 144, prop. 105(h).
15			
5. <i>Cipocereus minensis</i> subsp. <i>pleurocarpus</i> (MG)	EN (B1/2c) / App. II	4c(iii)	Eastern part of range included in 'Parque Nacional Serra do Cipó'.
5. <i>Facheiroa cephaliomelana</i> subsp. <i>estevensis</i> (BA)	EN (C2b) / App. II	3b(iii)	Taylor in Oldfield (1997): 143, prop. 105(c): (i).
5. <i>Arthrocereus melanurus</i> subsp. <i>magnus</i> (MG)	EN (C2b) / App. II	4c(iii)	Included within the 'Parque Estadual do Ibitipoca'.
5. <i>A. melanurus</i> subsp. <i>odoros</i> (MG)	EN (B1/2c) / App. II	4c(iii)	Part of range incl. in 'Parque Nacional Serra do Cipó'.
5. <i>A. rondonianus</i> (MG)	EN (B1/2c) / App. II	4c(iib)	Costa <i>et al.</i> (1998): 63, prop. C6; Taylor in Oldfield (1997): 144, prop. 105(i).
5. <i>Discocactus bahiensis</i> (BA/PI/CE)	EN (A1ac) / App. I	3a(ii)	A site is recommended for protection here (see below).

14			
6. <i>Facheiroa cephaliomelana</i> subsp. <i>cephaliomelana</i> (BA/MG)	VU (B1/2b-d) / App. II	3b(iii)	Taylor in Oldfield (1997): 143–144, prop. 105(c)(ii).
12			
7. <i>Pseudoacanthocereus brasiliensis</i> (BA/MG)	VU (C1/2a) / App. II	3d(ia)	Taylor in Oldfield (1997): 143, prop. 105(a).
7. <i>Schlumbergera kautskyi</i> (ES)	EN (B1/2c) / App. II	2d(ii)	Sites are recommended for protection here (see below).
7. <i>Arrojadoa bahiensis</i> (BA)	VU (D2) / App. II	3c(ii)	Probably not a high priority for further protection, but see discussion below relating to <i>Melocactus paucispinus</i> .
7. <i>A. dinae</i> subsp. <i>dinae</i> (BA/MG)	VU (B1/2c) / App. II	3c(iii)	Taylor in Oldfield (1997): 144, prop. 105(e).
7. <i>Pilosocereus aurisetus</i> subsp. <i>aurilanatus</i> (MG)	EN (B1/2c) / App. II	4c(iib)	Costa <i>et al.</i> (1998): 63, prop. C6; Taylor in Oldfield (1997): 144, prop. 105(i).
7. <i>Coleocephalocereus purpureus</i> (MG)	EN (C2b) / App. II	3d(ii)	Taylor in Oldfield (1997): 143, prop. 105(a).
7. <i>C. fluminensis</i> subsp. <i>decumbens</i> (MG)	EN (B1/2c) / App. II	2d(i)	Costa <i>et al.</i> (1998): 67, prop. E7?
7. <i>Melocactus azureus</i> subsp. <i>azureus</i> (BA)	EN (B1/2bcd) / App. II	3b(ii)	Conservation within the ‘Área de Proteção Ambiental’ (APA): ‘Gruta dos Brejões / Vereda do Romão Gramacho’ is best option for this taxon.
7. <i>M. pachyacanthus</i> subsp. <i>viridis</i> (BA)	CR (B1/2a–e/C2a/D) / App. II	3b(ii)	Conservation <i>ex situ</i> may be the only option available.
7. <i>M. paucispinus</i> (BA)	EN (B1/2ce) / App. I	3c(i)	Taylor in Oldfield (1997): 144, prop. 105(c). A second site is recommended for protection here (see below).
7. <i>M. violaceus</i> subsp. <i>ritteri</i> (BA)	CR (B1/2c) / App. II	3d(ia)	Sites are recommended for protection here (see below).
7. <i>Discocactus zehntneri</i> subsp. <i>zehntneri</i> (BA)	EN (B1/2b–d) / App. I	3b(ii)	Requires further field studies to determine conservation options.
7. <i>D. pseudoinsignis</i> (MG)	EN (B1/2c) / App. I	4c(iia)	Costa <i>et al.</i> (1998): 64, prop. N22*; Taylor in Oldfield (1997): 144, prop. 105(h).
10			
8. <i>Tacinga wernerii</i> (BA/MG)	VU (B1/2b–e) / App. II	3d(ib)	Taylor in Oldfield (1997): 143, prop. 105(a/b).
8. <i>Rhipsalis russellii</i> (BA/MG/ES?)	VU (B1/2b–e) / App. II	1b	Part of range incl. within ‘Parque Nacional Chapada Diamantina’ (nr Mucugê, BA) and, possibly, ‘Parque Nac. de Monte Pascoal’ (SE Bahia).

10 (cont.)			
8. <i>R. pilocarpa</i> (MG/ES)	VU (B1/2a–d) / App. II	2d(ii)	See site recommended for <i>Schlumbergera kautskyi</i> here.
8. <i>Brasilicereus markgraffii</i> (MG)	VU (C2a) / App. II	4c(iia)	Costa <i>et al.</i> (1998): 64, prop. N22*; Taylor in Oldfield (1997): 144, prop. 105(g/h).
8. <i>Cipocereus crassisepalus</i> (MG)	VU (B1/2c) / App. II	4c(iic)	Costa <i>et al.</i> (1998): 62, prop. C7; Taylor in Oldfield (1997): 144, prop. 105(k/l).
8. <i>C. bradei</i> (MG)	VU (C2a) / App. II	4c(iib)	Costa <i>et al.</i> (1998): 63, prop. C6; Taylor in Oldfield (1997): 144, prop. 105(i).
8. <i>Micranthocereus flaviflorus</i> (BA)	VU (B1/2c) / App. II	3c(ii)	Taylor in Oldfield (1997): 144, prop. 105(b).
8. <i>Arthrocereus melanurus</i> subsp. <i>melanurus</i> (MG)	VU (B1/2c) / App. II	4c(iii)	Costa <i>et al.</i> (1998): 64, prop. S9.
8. <i>Discocactus placentiformis</i> (MG)	VU (B2b–e / 3d) / App. I	4c(i)	Costa <i>et al.</i> (1998): 62, prop. C7; Taylor in Oldfield (1997): 144, prop. 105(h–k).
9			
9. <i>Tacinga saxatilis</i> subsp. <i>estevessii</i> (BA)	EN (C2b) / App. II	3b(iii)	Taylor in Oldfield (1997): 143, prop. 105(c): (i).
9. <i>Rhipsalis paradoxa</i> subsp. <i>septentrionalis</i> (PE/BA/MG/ES)	EN (A2b / B 1/2) / App. II	2a	Costa <i>et al.</i> (1998): 67, prop. C12?
9. <i>Pilosocereus fulvilanatus</i> subsp. <i>rosae</i> (MG)	EN (C2b) / App. II	4c(iib)	Taylor in Oldfield (1997): 144, prop. 105(j).
9. <i>Melocactus azureus</i> subsp. <i>ferreophilus</i> (BA)	EN (B1/2c–e) / App. II	3b(ii)	Conservation <i>ex situ</i> 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. I taxa 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

* 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

Priority hot-spots (sum of taxon scores from Table 5.2)	Endemics (no. × score)
A). Second order Area subdivisions	
1 (93). South-eastern <i>campos rupestres</i> (MG): Southern part [4c(iii)]	1×20, 1×18, 3×15, 1×10
2 (84). SE <i>campos rupestres</i> (MG): Diamantina eastwards [4c(iiC)]	1×20, 3×18, 1×10
3 (66). SE <i>campos rupestres</i> (MG): Serra do Cabral etc. [4c(iiB)]	1×20, 1×15, 1×12, 1×10, 1×9
3bis (66). Northern <i>campos rupestres</i> : N Serra do Espinhaço [3c(iii)]	1×20, 1×18, 1×16, 1×12
4 (62). Rio São Francisco <i>caatingas</i> : southern <i>caatingas</i> etc. [3b(iii)]	1×24, 1×15, 1×14, 1×9
5 (61). Rio São Francisco <i>caatingas</i> : cent.-northern Bahia [3b(ii)]	1×16, 3×12, 1×9
6 (54). Northern <i>campos rupestres</i> : Chapada Diamantina (BA) [3c(ii)]	2×16, 1×12, 1×10
7 (48). Eastern <i>caatingas-agrestes</i> / <i>campos rupestres</i> [3d(ia)]	1×24, 2×12
8 (38). SE <i>campos rupestres</i> (MG): Grão Mogol etc. [4c(ia)]	1×16, 1×12, 1×10
B). First order Area subdivisions	
1 (291). South-eastern <i>campos rupestres</i> (Minas Gerais) [4c]	3×20, 4×18, 1×16, 4×15, 2×12, 5×10, 1×9
2 (132). Northern <i>campos rupestres</i> (BA/MG) [3c]	1×20, 1×18, 3×16, 3×12, 1×10
3 (123). Rio São Francisco <i>caatingas</i> (BA/MG) [3b]	1×24, 1×16, 1×15, 1×14, 3×12, 2×9
4 (102). Eastern <i>caatingas-agrestes</i> / <i>campos rupestres</i> [3d]	1×24, 2×16, 3×12, 1×10
5 (34). Southern subhumid/humid forest and inselbergs (MG/ES) [2d]	2×12, 1×10

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: 2nd the Northern *campos rupestres* (3c), 3rd the *Caatingas* of the Rio São Francisco (3b) and 4th 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 Dárdano 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

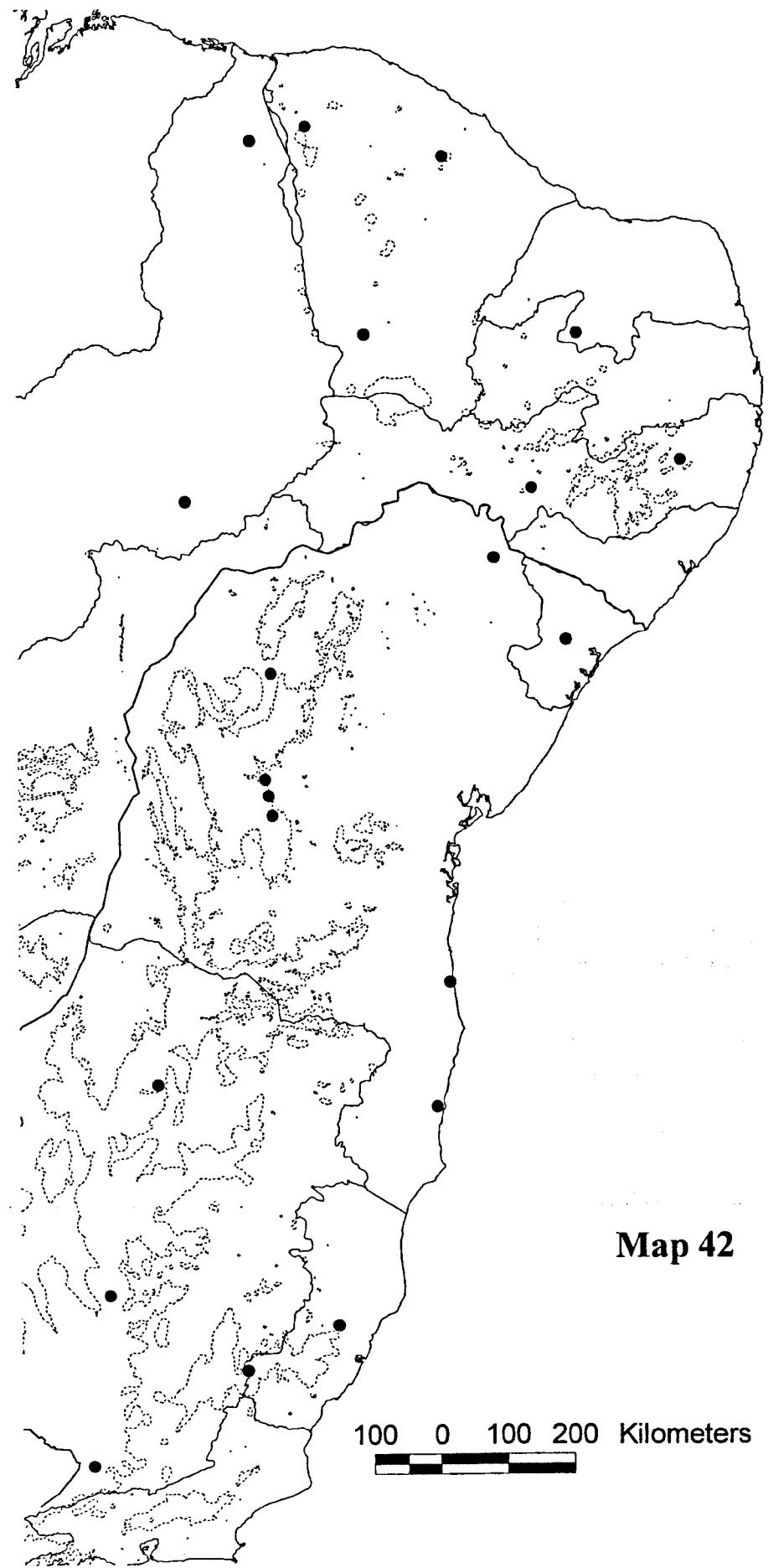
Brazilian states from the area covered in this study need to emulate. It is only to be hoped that the recommendations in this ground breaking report will be actioned by the authorities empowered to do so, and especially, since the present study identifies by far the greatest concentration of conservation 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, *Epostoopsis 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 pachecoleonis* 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. *ritteri*, 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*

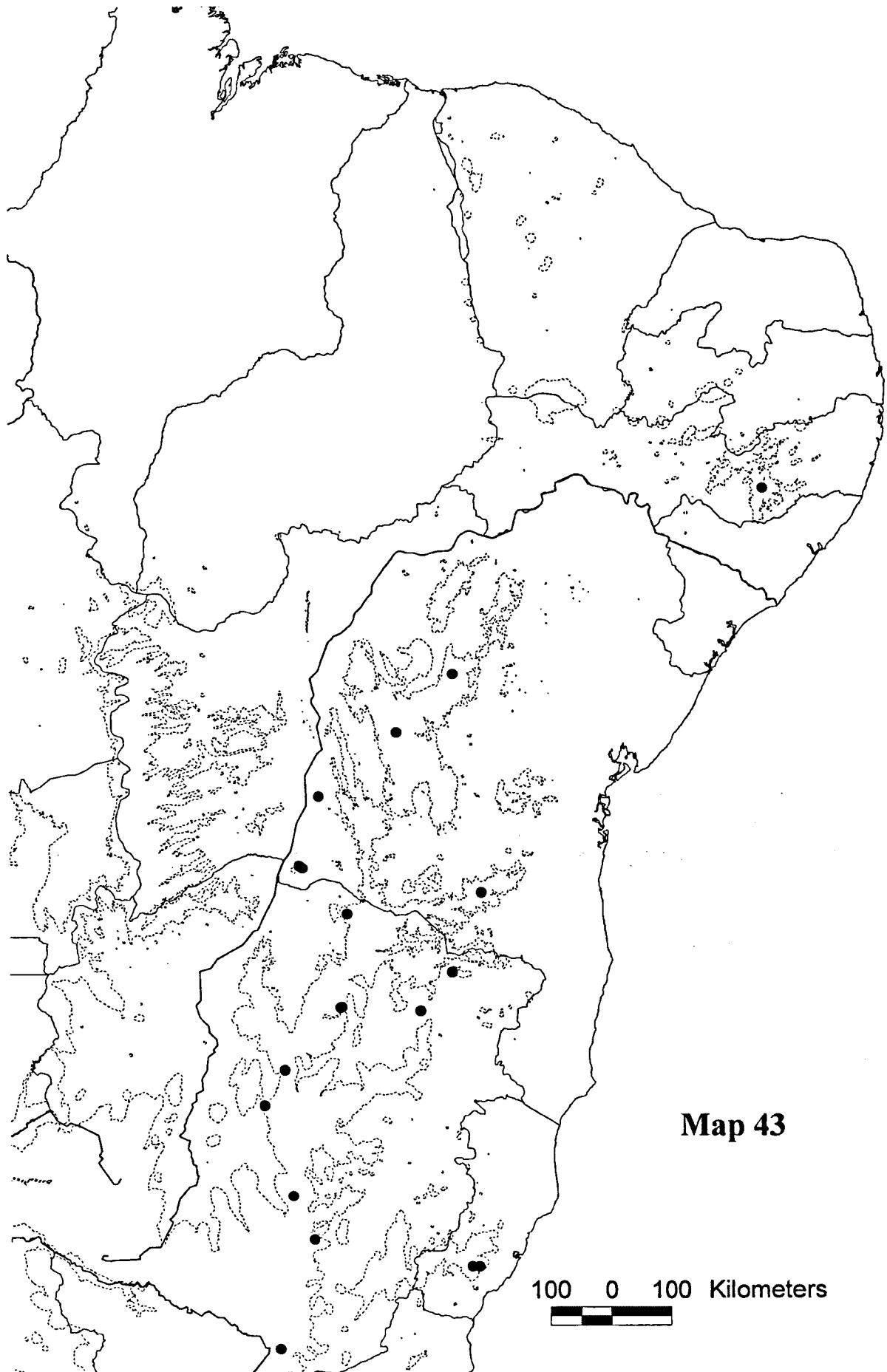
Regular monitoring of the status in the wild of many of the taxa documented in the ‘Formal Taxonomic Treatment’ (Supplement 1) is essential, whether or not these are currently rated as threatened (eg. those listed in Table 5.1, above). Many taxa presently assessed as ‘Lower Risk’ are likely to become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

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).



Map 42

100 0 100 200 Kilometers



Map 43

100 0 100 Kilometers

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.

Region / migration route (Map refs)	Vicariant taxa / ranges (country codes [+ Brazilian state codes]: E Brazilian vegetation types)	Notes
(i) Caribbean & 'Guajira province', via Amazonia (see Maps 5 & 6)	(1) <i>Pereskia guamacho</i> (CO, VE) & allies (Caribbean): <i>P. aureiflora</i> (S caatingas-agrestes) (2) <i>Pseudoacanthocereus sicariguensis</i> (CO, VE): <i>P. brasiliensis</i> (E caatingas-agrestes) (3) <i>Cereus hexagonus</i> (CO, VE, GY, GF, SR, BR[RR, PA]): <i>C. jamacaru</i> (caatingas-agrestes) (4) <i>Harrisia</i> subg. <i>Harrisia</i> (Caribbean): <i>H. adscendens</i> (caatingas)	(1) & (3) were examples in Prado, l.c.; (1) & (4) are now confirmed by molecular evidence. NB. <i>Pseudoacanthocereus</i> has only 2 species
(ii) Ibid., via dry cent. Andean valleys and the 'Pleistocene Arc' (see Map 2)	(1) <i>Praecereus</i> (CO, VE, EC, PE, BO, PY, AR, BR[MS, SP, PR]): <i>Brasilicereus</i> (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) <i>Hylocereus setaceus</i> complex (MX, BE, CO, EC, PE, BO, PY, AR, GY, SR, BR[RR, PA, MS, RJ, SP, PR]) / caatingas & Mata atlântica	See Chap. 3.2 & Supplement 1 for notes on this complex

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

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

Brazil (see Map 19). Equally significant is *Pilosocereus flavigulvinatus*, 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. flavigulvinatus* 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 finalis*, *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* & South-eastern *campos rupestres* 17%. Significantly, the *campos rupestres* are divisible 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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Appendix 1

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

TAXA (IN SYSTEMATIC ORDER) Key: † = endemic to total area; ‡ = endemic to core area	Earliest illustration or herbarium record as native in Eastern Brazil; state; author reference / collector(s)	Date of earliest correctly applied valid Latin name; origin of type; author(s)
<i>Pereskia aculeata</i>	1896; MG; Silveira	1753; ex cult.; Linnaeus
<i>P. grandifolia</i> ssp. <i>grandifolia</i>	1815/1816; ES/RJ; Wied-Neuwied	1819; Rio de Janeiro; Haworth
<i>P. grandifolia</i> ssp. <i>violacea</i> †	1922; MG; Santos	1986; Minas Gerais; Leuenberger
<i>P. bahiensis</i> †	1906; BA; Ule	1908; Bahia; Gürke
<i>P. stenantha</i> †	1912; BA; Zehntner	1979; Bahia; Ritter
<i>P. aureiflora</i> †	1950; BA; Pinto	1979; Minas Gerais; Ritter
<i>Quiabentia zehntneri</i> †	1912; BA; Zehntner	1919; Bahia; Britton & Rose
<i>Tacinga funalis</i> †	Before 1915; BA; Zehntner	1919; Bahia; Britton & Rose
<i>T. braunii</i> †	Before 1890; MG; <i>anon.</i> in Glaziou	1989; Minas Gerais; Esteves Pereira
<i>T. (Opuntia) wernerii</i> †	1915; BA; Rose & Russell	1992; Bahia; Eggli
<i>T. (Opuntia) palmadora</i> †	Before 1645; NE Brazil; see Whitehead & Boeseman (1989: tt. 89b, 99b)	1919; Bahia; Britton & Rose
<i>T. (Opuntia) saxatilis</i> ssp. <i>saxatilis</i>	1959; MG; Ritter	1979; Minas Gerais; Ritter
<i>T. (Opuntia) saxatilis</i> ssp. <i>estevesii</i> †	1984; BA; Esteves Pereira	1990; Bahia; Braun
<i>T. (Opuntia) inamoena</i> †	Before 1890; MG; <i>anon.</i> in Glaziou	1890; Minas Gerais; Schumann
<i>Brasiliopuntia (Opuntia) brasiliensis</i>	Before 1645; NE Brazil; see Whitehead & Boeseman (1989: tt. 3a, 7a, 51b)	1814; NE Brazil; Willdenow
<i>Opuntia monacantha</i>	1959; MG; Ritter	1819; 'Barbados'; Haworth
<i>Hylocereus setaceus</i>	Before 1867; MG; Warming (1908)	1828; Brazil; Salm-Dyck
<i>Epiphyllum phyllanthus</i>	[data not available]	1753; ex cult.; Linnaeus
<i>Pseudoacanthocereus brasiliensis</i> †	1912; BA; Zehntner	1920; Bahia; Britton & Rose
<i>Lepismium houletteianum</i>	1978; MG; Martinelli	1858; Brazil; Lemaire
<i>L. warmingianum</i>	Before 1867; MG; Warming (1908)	1890; Minas Gerais; Schumann
<i>L. cruciforme</i>	1944; MG; Heringer	1827; ex cult.; Haworth
<i>Rhipsalis russellii</i>	1915; BA; Rose & Russell	1923; Bahia; Britton & Rose
<i>R. elliptica</i>	1959; MG; Castellanos	1890; São Paulo; Schumann
<i>R. oblonga</i>	1971; BA; dos Santos	1918; Rio de Janeiro; Löfgren
<i>R. crispatula</i>	1970; PE; Andrade-Lima	1830; Brazil; Haworth
<i>R. floccosa</i> ssp. <i>floccosa</i>	1915; BA; Rose & Russell	1837; Brazil; Pfeiffer
<i>R. floccosa</i> ssp. <i>oreophila</i> †	1964; MG; Ritter	1979; Minas Gerais; Ritter
<i>R. floccosa</i> ssp. <i>pulvinigera</i>	1915; MG; Hoehne	1889; Brazil; Lindberg
<i>R. paradoxa</i> ssp. <i>septentrionalis</i> †	Before 1966; BA; Martins	1995; Bahia; Taylor & Barthlott
<i>R. pacheco-leonis</i> ssp. <i>catenulata</i>	1986; ES; Rauh & Kautsky	1992; Rio de Janeiro; Kimnach
<i>R. cereoides</i>	1986; ES; Rauh & Kautsky	1936; Rio de Janeiro; Backeberg & Voll
<i>R. sulcata</i> †	1986; ES; Rauh & Kautsky	1898; ex cult.; Weber
<i>R. lindbergiana</i>	Before 1823; MG; Saint-Hilaire	1890; Rio de Janeiro; Schumann
<i>R. teres</i>	1898; MG; Jaguaribe	1829; Rio de Janeiro; Vellozo
<i>R. baccifera</i> ssp. <i>baccifera</i>	1945; CE; Cutler	1770–1777; ex cult.; Mueller
<i>R. baccifera</i> ssp. <i>hileiabaiana</i> †	Before 1857; BA; Blanchet	1995; Bahia; Taylor & Barthlott
<i>R. pulchra</i>	1970; MG; Krieger	1915; Rio de Janeiro; Löfgren
<i>R. burchellii</i>	1986; ES; Rauh	1923; São Paulo; Britton & Rose
<i>R. juengeri</i>	1991; MG; Zappi	1995; ex cult.; Barthlott & Taylor
<i>R. clavata</i>	1986; ES; Rauh & Kautsky	1892; Rio de Janeiro; Weber
<i>R. cereuscula</i>	1893; MG; Silveira	1830; Brazil; Haworth
<i>R. pilocarpa</i>	1986; ES; Rauh & Kautsky	1903; São Paulo; Löfgren
<i>R. hoelleri</i> †	1987; ES; Orssich	1995; Espírito Santo; Barthlott & Taylor
<i>Hatiora salicornioides</i>	1892; MG; Ule	1819; Rio de Janeiro; Haworth
<i>Schlumbergera kautskyi</i> †	1986; ES; Kautsky	1991; Esp. Santo; Horobin & McMillan
<i>S. microsphaerica</i>	1941; MG; Brade	1890; Rio de Janeiro; Schumann
<i>S. opuntioides</i>	1991; MG; Zappi	1905; Rio de Janeiro; Löfgren & Dusén

<i>Brasilicereus phaeacanthus</i> †	1906; BA; Ule	1908; Bahia; Gürke
<i>B. markgrafii</i> †	1938; MG; Markgraf et al.	1950; Minas Gerais; Backeberg & Voll
<i>Cereus mirabella</i>	1964; MG; Ritter	1979; Minas Gerais; Ritter
<i>C. albicaulis</i> †	1915; BA; Rose & Russell	1920; Bahia; Britton & Rose
<i>C. fernambucensis</i> ssp. <i>fernambucensis</i>	Before 1645; NE Brazil; see Whitehead & Boeseman (1989: tt. 45, 93, 97)	1839; Pernambuco; Lemaire
<i>C. fernambucensis</i> ssp. <i>sericifer</i>	1917; ES; Lützelburg	1979; Rio de Janeiro; Ritter
<i>C. insularis</i> †	Before 1877; F. de Noronha; Moseley	1884; F. de Noronha; Hemsley
<i>C. jamacaru</i> (nom. cons.) ssp. <i>jamacaru</i> †?	Before 1645; NE Brazil; see Whitehead & Boeseman (1989: tt. 70, 78b, 89b, 99b)	1828; NE Brazil; De Candolle
<i>C. jamacaru</i> ssp. <i>calcirupicola</i>	Before 1867; MG; Warming (1908)	1979; Minas Gerais; Ritter
<i>C. hildmannianus</i>	Before 1890; MG; Glaziou (1909)	1890; SE Brazil; Schumann
<i>Cipocereus laniflorus</i> †	1987; MG; Zappi & Scatena	1997; Minas Gerais; Taylor & Zappi
<i>C. crassisepalus</i> †	1959; MG; Ritter	1973; Minas Gerais; Buin. & Brederoo
<i>C. bradei</i> †	Before 1935; MG; Brade?	1942; Minas Gerais; Backeberg & Voll
<i>C. minensis</i> ssp. <i>minensis</i> †	1932; MG; Werdermann	1933; Minas Gerais; Werdermann
<i>C. minensis</i> ssp. <i>pleurocarpus</i> †	1949; MG; Duarte	1979; Minas Gerais; Ritter
<i>C. pusilliflorus</i> †	1964; MG; Ritter	1979; Minas Gerais; Ritter
<i>Stephanocereus leucostele</i> †	1906; BA; Ule	1908; Bahia; Gürke
<i>S. luetzelburgii</i> †	1913; BA; Lützelburg	1923; Bahia; Vaupel
<i>Arrojadoa bahiensis</i> †	1981; BA; Furian et al.	1993; Bahia; Braun & Esteves Pereira
<i>A. dinae</i> ssp. <i>dinae</i> †	1964; BA; Ritter	1973; Bahia; Buin. & Brederoo
<i>A. dinae</i> ssp. <i>eriocalyx</i> †	1972; MG; Horst	1973; Minas Gerais; Buin. & Brederoo
<i>A. penicillata</i> †	1906; BA; Ule	1908; Bahia; Gürke
<i>A. rhodantha</i> †	1907; PI; Ule	1908; Bahia; Gürke
<i>Pilosocereus tuberculatus</i> †	1932; PE; Werdermann	1933; Pernambuco; Werdermann
<i>P. gounellei</i> ssp. <i>gounellei</i> †	Before 1645; NE Brazil; see Whitehead & Boeseman (1989: t. 80)	1897; Pernambuco; Weber
<i>P. gounellei</i> ssp. <i>zehntneri</i> †	1917; BA; Zehntner	1920; Bahia; Britton & Rose
<i>P. catingicola</i> ssp. <i>catingicola</i> †	c. 1907; BA; Ule	1908; Bahia; Gürke
<i>P. catingicola</i> ssp. <i>salvadorensis</i> †	1915; BA; Rose & Russell	1933; Bahia; Werdermann
<i>P. azulensis</i> †	1968; BA/MG; Castellanos	1997; Minas Gerais; Taylor & Zappi
<i>P. arrabidae</i>	1973; ES; Horst & Uebelmann	1862; Rio de Janeiro; Lemaire
<i>P. brasiliensis</i> ssp. <i>brasiliensis</i>	1990; ES; O.J. Pereira	1920; Rio de Janeiro; Britton & Rose
<i>P. brasiliensis</i> ssp. <i>ruschianus</i> †	1917; ES; Lützelburg	1980; Espírito Santo; Buin. & Brederoo
<i>P. flavipulvinatus</i> †	1935; CE; Drouet	1979; Piauí; Buin. & Brederoo
<i>P. pentaedrophorus</i> ssp. <i>pentaedrophorus</i> †	Before 1853; BA; Morel	1858; Bahia; Cels
<i>P. pentaedrophorus</i> ssp. <i>robustus</i> †	1972; BA; Horst & Uebelmann	1994; Bahia; Zappi
<i>P. glaucochrous</i> †	1932; BA; Werdermann	1933; Bahia; Werdermann
<i>P. floccosus</i> ssp. <i>floccosus</i> †	Before 1867; MG; Warming (1908)	1949; Minas Gerais; Backeberg & Voll
<i>P. floccosus</i> ssp. <i>quadricostatus</i> †	1965; MG; Ritter	1979; Minas Gerais; Ritter
<i>P. fulvilanatus</i> ssp. <i>fulvilanatus</i> †	1968; MG; Horst	1973; Minas Gerais; Buin. & Brederoo
<i>P. fulvilanatus</i> ssp. <i>rosae</i> †	1982; MG; Horst & Uebelmann	1984; Minas Gerais; Braun
<i>P. pachycladus</i> ssp. <i>pachycladus</i> †	1907; BA; Ule (1908)	1975; Bahia; Buin. & Brederoo
<i>P. pachycladus</i> ssp. <i>pernambucensis</i> †	1915; BA; Rose & Russell	1979; Pernambuco; Ritter
<i>P. magnificus</i> †	1968; MG; Horst & Uebelmann	1972; Minas Gerais; Buin. & Brederoo
<i>P. machrisii</i>	Before 1975; BA; Horst & Uebelmann	1957; Goiás; Dawson
<i>P. aurisetus</i> ssp. <i>aurisetus</i> †	Before 1862; MG; anon.	1933; Minas Gerais; Werdermann
<i>P. aurisetus</i> ssp. <i>aurilanatus</i> †	1964; MG; Ritter	1979; Minas Gerais; Ritter
<i>P. aureispinus</i> †	c. 1972; BA; Horst & Uebelmann	1974; Bahia; Buin. & Brederoo
<i>P. multicostatus</i> †	1965; MG; Ritter	1979; Minas Gerais; Ritter
<i>P. piauhyensis</i> †	1907; PI; Ule	1908; Piauí; Gürke
<i>P. chrysostele</i> †	1920; PB/PE; Lützelburg	1923; Paraíba/Pernambuco; Vaupel
<i>P. densiareolatus</i> †	1936; MG; Duarte	1979; Minas Gerais; Ritter
<i>Micranthocereus violaciflorus</i> †	1968; MG; Buining	1969; Minas Gerais; Buining
<i>M. albicephalus</i> †	1964; MG; Ritter	1979; Minas Gerais; Buin. & Brederoo
<i>M. purpureus</i> †	c. 1906; BA; Ule	1908; Bahia; Gürke
<i>M. auriazureus</i> †	1971; MG; Buining	1973; Minas Gerais; Buin. & Brederoo
<i>M. streckeri</i> †	1985; BA; van Heek & van Crikinge	1986; Bahia; van Heek & van Crikinge
<i>M. polyanthus</i> †	1932; BA; Werdermann	1932; Bahia; Werdermann
<i>M. flavidiflorus</i> †	1912; BA; Zehntner	1974; Bahia; Buin. & Brederoo
<i>M. dolichospermaticus</i> †	1972; BA; Horst & Uebelmann	1974; Bahia; Buin. & Brederoo
<i>Coleocephaloc. buxbaum</i> ssp. <i>buxbaum</i> †	1972; MG; Buining & Horst	1974; Minas Gerais; Buining
<i>C. buxbauianus</i> ssp. <i>flavisetus</i> †	1965; MG; Ritter	1979; Minas Gerais; Ritter
<i>C. fluminensis</i> ssp. <i>fluminensis</i>	1980; ES; Braamhaar	1838; Rio de Janeiro; Miquel
<i>C. fluminensis</i> ssp. <i>decumbens</i> †	1965; MG; Ritter	1968; Minas Gerais; Ritter
<i>C. pluricostatus</i> †	1917; MG/ES; Lützelburg	1971; Minas Gerais; Buin. & Brederoo
<i>C. goebelianus</i> †	Before 1920; BA; Zehntner	1923; Bahia; Vaupel
<i>C. aureus</i> †	1964; MG; Ritter	1968; Minas Gerais; Ritter
<i>C. purpureus</i> †	1971; MG; Horst & Uebelmann	1973; Minas Gerais; Buin. & Brederoo

<i>Melocactus oreas</i> ssp. <i>oreas</i> †	Before 1840; BA; <i>anon.</i>	1840; Bahia; Miquel
<i>M. oreas</i> ssp. <i>cremophilus</i> †	1971; BA; <i>Harley</i>	1972; Bahia; Buin. & Brederoo
<i>M. ernestii</i> ssp. <i>ernestii</i> †	c. 1906; BA; <i>Ule</i>	1920; Bahia; Vaupel
<i>M. ernestii</i> ssp. <i>longicarpus</i> †	1964; BA; <i>Ritter</i>	1974; Minas Gerais; Buin. & Brederoo
<i>M. bahiensis</i> ssp. <i>bahiensis</i> †	1915; BA; <i>Rose & Russell</i>	1922; Bahia; Britton & Rose
<i>M. bahiensis</i> ssp. <i>amethystinus</i> †	1959; MG; <i>Ritter</i>	1972; Bahia; Buin. & Brederoo
<i>M. conoideus</i> †	1972; BA; <i>Horst</i>	1973; Bahia; Buin. & Brederoo
<i>M. deinacanthus</i> †	1971; BA; <i>Horst</i>	1973; Bahia; Buin. & Brederoo
<i>M. levitestatus</i> †	1964; MG; <i>Ritter</i>	1973; Bahia; Buin. & Brederoo
<i>M. azureus</i> ssp. <i>azureus</i> †	1968; BA; <i>Horst</i>	1971; Bahia; Buin. & Brederoo
<i>M. azureus</i> ssp. <i>ferreophilus</i> †	1967; BA; <i>Horst</i>	1973; Bahia; Buin. & Brederoo
<i>M. pachyacanthus</i> ssp. <i>pachyac.</i> †	1972; BA; <i>Horst</i>	1975; Bahia; Buin. & Brederoo
<i>M. pachyacanthus</i> ssp. <i>viridis</i> †	1988; BA; <i>Taylor & Zappi</i>	1991; Bahia; Taylor
<i>M. salvadorensis</i> †	1932; BA; <i>Werdermann</i>	1934; Bahia; Werdermann
<i>M. zehntneri</i> †	1915; BA; <i>Rose & Russell</i>	1922; Bahia; Britton & Rose
<i>M. lanssensianus</i> †	1977; PE; <i>Horst</i>	1986; Pernambuco; Braun
<i>M. glaucescens</i> †	1967; BA; <i>Horst</i>	1972; Bahia; Buin. & Brederoo
<i>M. concinnus</i> †	1964; BA; <i>Ritter</i>	1972; Bahia; Buin. & Brederoo
<i>M. paucispinus</i> †	1981; BA; <i>Heimen et al.</i>	1983; Bahia; Heimen & Paul
<i>M. violaceus</i> s.l.	Before 1645; NE Brazil; see Whitehead & Boeseman (1989: t. 48c)	1835; Brazil; Pfeiffer
<i>M. violaceus</i> ssp. <i>violaceus</i>	1837; PE; <i>Gardner</i>	as above
<i>M. violaceus</i> ssp. <i>ritteri</i> †	1964; BA; <i>Ritter</i>	1979; Bahia; Ritter
<i>M. violaceus</i> ssp. <i>margaritaceus</i> †	Before 1858; BA; <i>anon.</i>	1857/58; Bahia; Miquel
<i>Harrisia adscendens</i> †	Before 1645?; NE Brazil; see Whitehead & Boeseman (1989: tt. 89b, 99b)?	1908; Bahia; Gürke
<i>Leocereus bahiensis</i> †	1912; BA; <i>Zehntner</i>	1920; Bahia; Britton & Rose
<i>Facheiroa ulei</i> †	1907; BA; <i>Ule</i>	1908; Bahia; Gürke
<i>F. cephaliomelana</i> ssp. <i>cephaliom.</i> †	1959; MG; <i>Ritter</i>	1975; Bahia; Buin. & Brederoo
<i>F. cephaliomelana</i> ssp. <i>estevessii</i> †	1984; BA; <i>E. Esteves Pereira</i>	1986; Bahia; Braun
<i>F. squamosa</i> †	1907; PI; <i>Ule</i>	1908; Piaui; Gürke
<i>Espositoopsis dybowskii</i> †	Before 1908; BA; <i>Dybowski</i>	1908; Bahia; Roland-Gosselin
<i>Arthrocereus melanurus</i> ssp. <i>melan.</i>	Before 1890; MG; <i>Glaziou</i>	1890; Minas Gerais; Schumann
<i>A. melanurus</i> ssp. <i>magnus</i> †	1969; MG; <i>Krieger</i>	1997; Minas Gerais; Taylor & Zappi
<i>A. melanurus</i> ssp. <i>odoros</i> †	1964; MG; <i>Ritter</i>	1979; Minas Gerais; Ritter
<i>A. rondonianus</i> †	Before 1935; MG; <i>Brade</i> ?	1951; Minas Gerais; Backeberg & Voll
<i>A. glaziovii</i> †	Before 1832; MG; <i>Sello</i>	1890; Minas Gerais; Schumann
<i>Discocactus zehntneri</i> ssp. <i>zehntn.</i> †	c. 1915; BA; <i>Zehntner</i>	1922; Bahia; Britton & Rose
<i>D. zehntneri</i> ssp. <i>boomianus</i> †	1967; BA; <i>Horst</i>	1971; Bahia; Buin. & Brederoo
<i>D. bahiensis</i> †	c. 1915; BA; <i>Zehntner</i>	1922; Bahia; Britton & Rose
<i>D. heptacanthus</i> ssp. <i>catingicola</i> †	1972; BA; <i>Horst</i>	1974; Bahia; Buin. & Brederoo
<i>D. placentiformis</i> †	Before 1826; MG; <i>Riedel</i> ?	1826; Brazil; Lehmann
<i>D. pseudoinsignis</i> †	1972; MG; <i>Horst</i>	1991; Minas Gerais; Taylor & Zappi
<i>D. horstii</i> †	1972; MG; <i>Horst</i>	1973; Minas Gerais; Buin. & Brederoo
<i>Uebelmannia buningii</i> †	1966; MG; <i>Horst</i>	1968; Minas Gerais; Donald
<i>U. gummifera</i> †	1938; MG; <i>Mello-Barreto</i>	1949; Minas Gerais; Backeberg & Voll
<i>U. pectinifera</i> ssp. <i>pectinifera</i> †	1966; MG; <i>Horst</i>	1967; Minas Gerais; Buining
<i>U. pectinifera</i> ssp. <i>flavispina</i> †	c. 1972; MG; <i>Horst & Uebelmann</i>	1973; Minas Gerais; Buin. & Brederoo
<i>U. pectinifera</i> ssp. <i>horrida</i> †	1982; MG; <i>Horst & Uebelmann</i>	1984; Minas Gerais; Braun

Appendix 2

INDEX TO SPECIFIC AND INFRASPECIFIC EPITHETS

Accepted names (or their epithets) are indicated in **bold** type, synonyms, inadequately known taxa, orthographic variants and invalid names by *italics*. Synonyms based on types collected outside the Eastern Brazil area, in adjacent regions of Brazil, are also included. Other names of taxa from outside the region or those that are only doubtfully represented, which are mentioned in discussion or cited as the types of generic names, are not usually included, unless given in plain Roman type. Autonyms representing accepted names of included taxa are also listed. The accepted names of introduced or widely cultivated taxa are followed by an asterisk (*). Authority citations are omitted except for misapplied names and homonyms (the citation in the former case, if given in abbreviated form, being of the author who misapplied the name or published the homonym in question). Entries are referenced by the number of the accepted generic name, followed, after a colon, by the species number and, if applicable, the letter(s) indicating the accepted infraspecific classification. Binomials referenced with 'see' to the generic number only are discussed under the given genus heading in Chapter 3; similarly, those followed by a genus:species number. Hybrid taxa are indicated by means of a multiplication sign (×) connecting the species numbers, eg. **Tacinga × quipa** (**T. palmadora** × **T. inamoena**) is indicated as 3:5×3:6.

<i>Acanthocereus albicaulis</i>	16:2	<i>lehmannianus</i>	21:3
<i>brasiliensis</i>	10:1	<i>purpureus</i>	21:3
ARROJADOA	19	<i>purpureus</i> Backeb.	22:4
<i>albiflora</i>	19:2×19:4	<i>salvadorensis</i>	20:3b
<i>aureispina</i>	19:4	BRASILICEREUS	15
var. <i>anguinea</i>	19:4	<i>breviflorus</i>	15:1
var. <i>guanambensis</i>	19:4	<i>markgrafii</i>	15:2
<i>bahiensis</i>	19:1	<i>phaeacanthus</i>	15:1
<i>beataeae</i>	19:2a	subsp. <i>breviflorus</i>	15:1
<i>canudosensis</i>	19:4	BRASILIOPUNTIA	4
<i>cremnophila</i>	19:1	<i>bahiensis</i>	4:1
<i>dinae</i>	19:2	<i>brasiliensis</i>	4:1
subsp. <i>dinae</i>	19:2a	<i>subacarpa</i>	4:1
subsp. <i>eriocaulis</i>	19:2b	<i>Buiningia aurea</i>	22:5
subsp. <i>nana</i>	19:2a	<i>brevicyndrica</i>	22:5
var. <i>nana</i>	19:2a	var. <i>elongata</i>	22:5
<i>eriocaulis</i>	19:2b	var. <i>longispina</i>	22:5
subsp. <i>albicoronata</i>	19:2b	<i>purpurea</i>	22:6
var. <i>albicoronata</i>	19:2b	<i>Cactus alteolens</i>	29:4?
var. <i>rosenbergeriana</i>	19:2b	<i>arboreus</i>	4:1
<i>heimenii</i>	19:2a	<i>bahiensis</i>	23:3
<i>horstiana</i>	19:4	<i>brasiliensis</i>	4:1
<i>multiflora</i>	19:2a	<i>cochenillifera</i>	5:1
<i>penicillata</i>	19:3	<i>cruciformis</i>	11:3
var. <i>decumbens</i>	19:3	<i>dillenii</i>	6:2
var. <i>spinosior</i>	19:3	<i>ficus-indica</i>	6:3
<i>polyantha</i>	21:6	<i>grandifolius</i>	1:2
rhodantha	19:4	<i>heptagonus</i> Vell. non L.	20:5
subsp. <i>aureispina</i>	19:4	<i>heterocladius</i>	4:1
subsp. <i>canudosensis</i>	19:4	<i>hexagonus</i> Vell. non L.	20:5
subsp. <i>reflexa</i>	19:4	<i>melocactoides</i>	23:15?
var. <i>anguinea</i>	19:4	<i>melocactus</i> Vell. non L.	22:2
var. <i>guanambensis</i>	19:4	<i>opuntia</i>	6:3
var. <i>occibahiensis</i>	19:4	<i>oreas</i>	23:1
var. <i>theunisseniana</i>	19:4	<i>pereskia</i>	1:1
<i>theunisseniana</i>	28	<i>phyllanthus</i>	9:1
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<i>campos-portoi</i>	28:3	<i>teres</i>	12:11
<i>damazioi</i> P.V. Heath	28:3	<i>triangularis</i> Vellozo	7:1
<i>glaziovii</i>	28:3	<i>urumbeba</i>	6:1
<i>itabiriticola</i>	28:3	<i>zehntneri</i>	23:10
<i>melanurus</i>	28:1	<i>Cassytha baccifera</i>	12:12
subsp. <i>estevensis</i>	28:1a	<i>Cephalocereus arrabidae</i>	20:5
subsp. <i>magnus</i>	28:1b	<i>bradei</i>	17:3
subsp. <i>melanurus</i>	28:1a	<i>brasiliensis</i>	20:6
subsp. <i>mello-barretoi</i>	28:1a	<i>catingicola</i>	20:3
subsp. <i>odorus</i>	28:1c	<i>chrysostele</i>	20:19
var. <i>estevensis</i>	28:1a	<i>cuyabensis</i>	20:14
<i>mello-barretoi</i>	28:1a	<i>dybowskii</i>	27:1
<i>microsphaericus</i>	14:2	<i>exerens</i> sensu (K. Schum.) Rose	20:5
<i>microsphaericus</i> sensu Berger	28:3	<i>fluminensis</i>	22:2
<i>odoros</i>	28:1c	<i>glaucescens</i>	see sub 20:20
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<i>spinossissimus</i>	see 28	<i>gounellei</i>	20:2
<i>Austrocephalocereus albicephalus</i>	21:2	<i>hapalacanthus</i>	20:3b
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<i>dybowskii</i>	27:1	<i>leucostele</i>	18:1
<i>fluminensis</i>	22:2	<i>luetzelburgii</i>	18:2

<i>machrisii</i>	20:14	<i>macrogonus</i> Warming (1892)	20:10
<i>melocactus</i>	22:2	<i>markgrafii</i>	15:2
<i>minensis</i>	17:4	<i>melanurus</i>	28:1
<i>penicillatus</i>	19:3	<i>melocactus</i>	22:2
<i>pentaedrophorus</i>	20:8	<i>microsphaericus</i>	14:2
<i>phaeacanthus</i>	15:1	<i>milesimus</i>	16:6a
<i>piauhyensis</i>	20:18	<i>minensis</i>	17:4
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<i>rhodanthus</i>	19:4	<i>obtusangulus</i>	14:2
<i>rupicola</i>	20:3b	<i>obtusus</i>	16:3?
<i>salvadorensis</i>	20:3b	<i>parvisetus</i>	28:1c?
<i>sergipensis</i>	20:3b	<i>parvulus</i>	14:2?
<i>ulei</i> Gürke	26:1	<i>penicillatus</i>	19:3
<i>zehntneri</i>	20:2b	<i>pentaedrophorus</i>	20:8
<i>Cereastreae pentaedrophorus</i>	20:8	<i>pernambucensis</i>	16:3
CEREUS	16	<i>peruvianus</i> auctt. p.p.	16:6a
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<i>albicaulis</i>	16:2	<i>piauhyensis</i>	20:18
<i>bahiensis</i>	25:1	<i>pitajaya</i> Hook. non (Jacq.) DC	16:3a
<i>brasiliensis</i>	10:1	<i>rhodanthus</i>	19:4
<i>calcirupicola</i>	16:5b	<i>ridleii</i>	16:4?
subsp. <i>cabralensis</i>	16:5b	<i>sericifer</i>	16:3b
subsp. <i>cipoensis</i>	16:5b	<i>setaceus</i>	7:1
var. <i>albicans</i>	16:5b	<i>setosus</i>	11:3
var. <i>cabralensis</i>	16:5b	<i>setosus</i> Gürke non Loddiges	20:2a
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var. <i>pluricostatus</i>	16:5b	<i>squamulosus</i>	11:3
<i>catingicola</i>	20:3	<i>sublanatus</i>	20:6?
<i>chrysostele</i>	20:19	<i>tenuis</i>	11:3
<i>coerulescens</i> sensu Warming	16:5b	<i>tenuispinus</i>	11:3
<i>crassisepalus</i>	17:2	<i>triangularis</i> K. Schum. p.p.	7:1
<i>cruciformis</i>	11:3	<i>ulei</i> sensu Lützelb.	20:12a
<i>damazioi</i>	14:2	<i>undatus</i>	7:2
<i>damazioi</i> auctt. non Weingart	28:3	<i>undatus</i> sensu Lützelb.	7:1
<i>dybowskii</i>	27:1	<i>variabilis</i> auctt. non Pfeiffer	16:3
<i>fernambucensis</i>	16:3	<i>vellozoi</i>	22:2
subsp. <i>fernambucensis</i>	16:3a	<i>warmingii</i>	20:5
subsp. <i>sericifer</i>	16:3b	CIPOCEREUS	17
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<i>goebelianus</i>	22:4	<i>laniflorus</i>	17:1
<i>goiasensis</i>	16:5a	<i>minensis</i>	17:4
<i>hildmannianus</i>	16:6	subsp. <i>minensis</i>	17:4a
subsp. <i>hildmannianus</i>	16:6a	subsp. <i>pleurocarpus</i>	17:4b
subsp. <i>uruguayanus</i>	see 16:6a	<i>pleurocarpus</i>	17:4b
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<i>jamacaru</i>	16:5	COLEOCEPHALOCEREUS	22
subsp. <i>calcirupicola</i>	16:5b	<i>albicephalus</i>	21:2
subsp. <i>goiasensis</i>	16:5a	<i>aureispinus</i>	20:16
subsp. <i>jamacaru</i>	16:5a	<i>aureus</i>	22:5
<i>jamacaru</i> sensu Scheinvar (1985)	16:6a	<i>braunii</i>	22:1a
<i>leucostele</i>	18:1	<i>brevicylindricus</i>	22:5
<i>luetzelburgii</i>	18:2	var. <i>elongatus</i>	22:5
<i>macrogonus</i> K. Schum. (1890)	20:5	var. <i>longispinus</i>	22:5

<i>buxbaumianus</i>	22:1	<i>subsp. pulvinicapitatus</i>	29:4
subsp. <i>buxbaumianus</i>	22:1a	<i>lehmannii</i>	29:4
subsp. <i>flavisetus</i>	22:1b	<i>lindaianus</i>	29:3
<i>decumbens</i>	22:2b	<i>lindanus</i>	29:3
<i>diersianus</i>	22:2a	<i>linkii</i>	29:4
<i>dybowskii</i>	27:1	<i>multicolorispinus</i>	29:4
<i>estevessii</i>	22:1b	<i>nigrisaetosus</i>	29:3a
<i>flavisetus</i>	22:1b	<i>piauiensis</i>	29:3a
<i>fluminensis</i>	22:2	<i>placentiformis</i>	29:4
subsp. <i>braamhaarpii</i>	22:2a	subsp. <i>alteolens</i>	29:4?
subsp. <i>decumbens</i>	22:2b	subsp. <i>multicolorispinus</i>	29:4
subsp. <i>fluminensis</i>	22:2a	subsp. <i>pugionacanthus</i>	29:4
subsp. <i>paulensis</i>	22:2a	var. <i>alteolens</i>	29:4?
var. <i>braamhaarpii</i>	22:2a	var. <i>pugionacanthus</i>	29:4
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<i>minensis</i>	17:4	<i>pseudolatispinus</i>	29:4
<i>pachystele</i>	22:4	<i>pugionacanthus</i>	29:4
<i>paulensis</i>	22:2a	<i>pulvinicapitatus</i>	29:4
<i>pluricostatus</i>	22:3	<i>rapirhizus</i>	29:3
subsp. <i>uebelmanniorum</i>	22:3	<i>spinosior</i>	29:3a
<i>pleurocarpus</i>	17:4b	<i>squamibaccatus</i>	29:3
<i>purpureus</i>	22:6	<i>subnudus</i>	see 29:6
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<i>alteolens</i>	29:4?	<i>tricornis</i>	29:4
<i>araneispinus</i>	29:1b	<i>woutersianus</i>	see 29:6
<i>bahiensis</i>	29:2	<i>zehntneri</i>	29:1
subsp. <i>subviridigriseus</i>	29:2	f. <i>albispinus</i>	29:1a
<i>besleri</i>	29:4	subsp. <i>albispinus</i>	29:1a
<i>boomianus</i>	29:1b	subsp. <i>araneispinus</i>	29:1b
<i>bueneckeri</i>	29:1b?	subsp. <i>boomianus</i>	29:1b
<i>cangaensis</i>	29:3	subsp. <i>bueneckeri</i>	29:1b?
<i>catingicola</i>	29:3a	subsp. <i>horstiorum</i>	29:1b
subsp. <i>griseus</i>	29:3	subsp. <i>zehntneri</i>	29:1a
subsp. <i>rapirhizus</i>	29:3	var. <i>albispinus</i>	29:1a
var. <i>griseus</i>	29:3	var. <i>araneispinus</i>	29:1b
var. <i>nigrisaetosus</i>	29:3a	var. <i>boomianus</i>	29:1b
<i>cephalioaciculosus</i>	29:3	var. <i>horstiorum</i>	29:1b
subsp. <i>nudicephalus</i>	29:3	<i>Echinocactus alteolens</i>	29:4?
<i>crassispinus</i>	29:3	<i>bahiensis</i>	29:2
subsp. <i>araguaiensis</i>	29:3	<i>centeterius</i>	see sub 30:3c
<i>crystallophilus</i>	29:4	<i>placentiformis</i>	29:4
<i>diuersianus</i>	29:3	<i>subnudus</i>	see 29:6
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var. <i>goianus</i>	29:3	<i>Epiphyllanthus candidus</i>	14:2
<i>estevessii</i>	29:3	<i>microsphaericus</i>	14:2
<i>goianus</i>	29:3	<i>obovatus</i>	14:3
<i>griseus</i>	29:3	<i>obtusangulus</i>	14:2
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<i>pentaedrophorus</i>	20:8	subsp. <i>oreophila</i>	12:5b
<i>pernambucensis</i>	20:12b	subsp. <i>pulvinigera</i>	12:5c
<i>pernambucoensis</i>	20:12b	<i>gonocarpa</i>	11:2
var. <i>caesioides</i>	20:12b	<i>gracilis</i>	12:11
var. <i>montealtoi</i>	20:12a	<i>heteroclada</i>	12:11
<i>piauhyensis</i>	20:17	<i>hoelleri</i>	12:19
<i>polyedrophorus</i>	20:8	<i>houletteana</i>	11:1
<i>pusillibaccatus</i>	20:14	var. <i>regnellii</i>	11:1
<i>quadricostatus</i>	20:10b	<i>houlettei</i>	11:1
<i>robustus</i>	20:3a	<i>juengeri</i>	12:15
<i>rupicola</i>	20:3b	<i>knightii</i>	11:3
<i>ruschianus</i>	20:6b	<i>lindbergiana</i>	12:10
<i>salvadorensis</i>	20:3b	<i>linearis</i>	11:2
<i>sergipensis</i>	20:3b	<i>macahensis</i>	12:13
<i>splendidus</i>	20:12a	<i>macropogon</i>	11:3
<i>superbus</i>	20:12a	<i>maricaensis</i>	12:11
var. <i>gacapaensis</i>	20:12a	<i>mittleri</i>	11:3
var. <i>lanosior</i>	20:12a	<i>monteazulensis</i>	12:5b
var. <i>regius</i>	20:12a	<i>myosurus</i>	11:3
<i>superfloccosus</i>	20:2b	<i>oblonga</i>	12:3
<i>tuberculatus</i>	20:1	<i>pacheco-leoni</i>	12:7
<i>werdermannianus</i>	20:15a	<i>pacheco-leonis</i>	12:7
var. <i>densilanatus</i>	20:15a	subsp. <i>catenulata</i>	12:7a
var. <i>diamantinensis</i>	20:15a	<i>paradoxa</i>	12:6
<i>zehntneri</i>	2	subsp. <i>septentrionalis</i>	12:6a
QUIABENTIA	2:1	var. <i>catenulata</i>	12:7a
<i>zehntneri</i>	12	<i>penduliflora</i>	12:17
RHIPSALIS	12:11	<i>penduliflora</i> sensu K. Schum.	12:11
<i>alboareolata</i>	12:6	<i>pilocarpa</i>	12:18
<i>alternata</i>	11:3	<i>platycarpa</i> Lützelb.	see 12
<i>anceps</i>	12:12	<i>prismatica</i>	12:11
<i>baccifera</i>	12:12a	<i>pulchra</i>	12:13
subsp. <i>baccifera</i>	12:12b	<i>pulvinigera</i>	12:5c
subsp. <i>hileiabaiana</i>	11:3	<i>radicans</i>	11:3
<i>brevibarbis</i>	12:14	<i>ramosissima</i>	11:3?
<i>burchellii</i>	12:11a	<i>regnellii</i>	11:1
<i>capilliformis</i>	see 12:14	<i>rhombaea</i> sensu Löfgren	12:4
<i>campos-portoana</i>	11:3	<i>robusta</i> Lützelb.	see 12
<i>cavernosa</i>	12:12a	<i>russellii</i>	12:1
<i>cassutha</i>	12:12a	<i>saglionis</i>	12:17
<i>cassuthopsis</i>	12:12a	<i>salicornioides</i>	13:1
<i>cassythoides</i>	12:12a	var. <i>cylindrica</i>	13:1b
<i>cassythoides</i>	12:12a	var. <i>villigera</i>	13:1a
<i>cereoides</i>	12:8	<i>salicornoides</i>	13:1
<i>cereuscula</i>	12:17	<i>squamulosa</i>	11:3
<i>chloroptera</i>	12:2	<i>sulcata</i>	12:9
<i>clavata</i>	12:16	<i>teres</i>	12:11
<i>clavata</i> Lützelb.	see 12	f. <i>capilliformis</i>	12:11a

<i>f. heteroclada</i>	12:11	<i>var. rubra</i>	30:2
<i>f. prismatica</i>	12:11	<i>horrida (nom. nud.)</i>	30:3c
<i>tetragona</i>	12:11	<i>meninensis</i>	30:2
<i>virgata</i>	12:11	<i>var. antenaensis (nom. nud.)</i>	30:2
<i>vollii</i>	11:3	<i>var. rubra</i>	30:2
<i>warmingiana</i>	11:2	pectinifera	30:3
<i>Rhodocactus grandifolius</i>	1:2	<i>subsp. crebrispina (nom. nud.)</i>	30:3b
SCHLUMBERGERA	14	<i>subsp. flavispina</i>	30:3b
<i>kautskyi</i>	14:1	<i>subsp. horrida</i>	30:3c
<i>microsphaerica</i>	14:2	<i>subsp. pectinifera</i>	30:3a
<i>f. obtusangula</i>	14:2	<i>var. crebrispina (nom. nud.)</i>	30:3b
<i>f. parvula</i>	14:2?	<i>var. elegans (nom. nud.)</i>	30:3
<i>subsp. candida</i>	14:2	<i>var. heteracantha (nom. nud.)</i>	30:3
<i>obtusangula</i>	14:2	<i>var. horrida</i>	30:3c
<i>opuntioides</i>	14:3	<i>var. multicostata</i>	30:3a
<i>truncata</i> subsp. <i>kautskyi</i>	14:1	<i>var. pseudopectinifera</i>	30:3a
var. <i>kautskyi</i>	14:1	<i>pseudopectinifera (nom. nud.)</i>	30:3a
SELENICEREUS	8	<i>warasii</i>	30:3b
<i>anthonyanus*</i>	see 8	<i>Zehntnerella chaetacantha</i>	26:3
<i>rizzinii</i>	7:1	<i>var. montealtoi</i>	26:3
<i>setaceus</i>	7:1	<i>polygona</i>	26:3
<i>Siccobaccatus dolichospermaticus</i>	21:8	<i>squamulosa</i>	26:3
STEPHANOCEREUS	18	<i>Zygocactus candidus</i>	14:2
<i>leucostele</i>	18:1	<i>obtusangulus</i>	14:2
<i>luetzelburgii</i>	18:2	<i>opuntioides</i>	14:3
TACINGA	3		
<i>atropurpurea</i>	3:1		
var. <i>zehntnerioides</i>	3:1		
<i>braunii</i>	3:2		
<i>funalis</i>	3:1		
<i>subsp. atropurpurea</i>	3:1		
var. <i>atropurpurea</i>	3:1		
<i>inamoena</i>	3:6		
<i>luetzelburgii</i>	3:1		
<i>palmadora</i>	3:4		
<i>xquipa</i>	3:5x3:6		
<i>saxatilis</i>	3:5		
<i>subsp. estevesii</i>	3:5b		
<i>subsp. saxatilis</i>	3:5a		
<i>werneri</i>	3:3		
<i>zehntneri</i>	3:1		
<i>Trichocereus campos-portoi</i>	28:3		
<i>damazioi</i>	14:2		
<i>damazioi</i> sensu Werderm.	28:3		
<i>glaziovii</i>	28:3		
	30		
UEBELMANNIA			
<i>ammotrophus (nom. nud.)</i>	30:3a		
<i>antonensis (nom. nud.)</i>	30:2		
<i>buiningii</i>	30:1		
<i>buiningiana (orth. var.)</i>	30:1		
<i>centeteria</i>	see sub 30:3c		
<i>cinerea (nom. nud.)</i>	30:2		
<i>crebrispina (nom. nud.)</i>	30:3b		
<i>flavispina</i>	30:3b		
var. <i>longispina (nom. nud.)</i>	30:2		
<i>gummifera</i>	30:2		
<i>subsp. meninensis</i>	30:2		
var. <i>gigantea (nom. nud.)</i>	30:2		

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 estevesii† (RR)
 - M. neryi (AM,RR,RO?)
 - M. smithii (syn. M. roraimensis, Echinocactus amazonicus?) (RR)
 - Micranthocereus (subg. Siccobaccatus) estevesii (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 hammerschmidii (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) estevesii (GO)
 - Opuntia cf. quimilo (MS)
 - O. sp. indet. (O. elata?) (MS)
 - Pereskia aculeata (GO)
 - P. sacharosa (MS, MT) ©
 - Praecereus euchlorus subsp. euchlorus (syn. Monvillea alticostata, 'M. cavendishii') (MS) ©
 - Pilosocereus diersianus† (GO)
 - P. machrisii (many synonyms)

- P. vilaboensis (syn. P. rizzoanus) † (GO)
Rhipsalis russellii (GO, MT)
- [© = cited as Chaco element in Prado (1991)]
- 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 albicolumnaris† (RS)
 - F. castanea (RS)
 - F. cataphracta (RS)
 - F. curvispina† (RS)
 - F. gracillima (RS)
 - F. horstii† (RS)
 - F. lepida† (RS)
 - F. mammifera (RS)
 - F. perumbilicata† (RS)
 - F. phaeodisca (RS)
 - F. pumila (RS)
 - F. pygmaea (RS)
 - Gymnocalycium buenekeri† (RS)
 - G. denudatum (RS)
 - G. horstii† (RS)
 - G. uruguayense (RS)
 - Hatiora epiphyloides† (SP, RJ)
 - H. gaertneri† (PR, SC, RS)
 - H. herminiae† (SP)
 - H. rosea† (PR, SC, RS)
 - H. salicornoides (PR, SP, RJ, MG)
 - Hylocereus setaceus (PR, SP, RJ, MG)
 - Lepismium cruciforme
 - L. houltianum
 - L. lumbricoides
 - L. warmingianum
 - Micranthocereus (subg. Siccobaccatus) estevesii (MG)
 - Opuntia monacantha (syn. O. arechavaletae)
 - Parodia alacriportana† (RS, SC)
 - P. buiningii (RS)
 - P. caespitosa (RS)
 - P. concinna (RS)
 - P. crassigibba† (RS)
 - P. erinacea (RS)
 - P. graessneri† (RS, SC)
 - P. haselbergii† (RS, SC)
 - P. herteri (RS)
 - P. horstii† (RS)
 - P. leninghausii s.l. (syn. P. schumanniana, P. warasii, P. claviceps etc) (RS)

* Seen in the nursery of the Jardim Botânico de Brasília, 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.

<i>P. magnifica</i> † (RS)	<i>R. floccosa</i> (sspp. <i>floccosa</i> & <i>pulvinigera</i>)
<i>P. mammulosa</i> (RS)	<i>R. grandiflora</i> † (RJ,SP,PR)
<i>P. neohorstii</i> † (RS)	<i>R. lindbergiana</i> (RJ,SP)
<i>P. ottonis</i>	<i>R. mesembryanthemoides</i> † (RJ)
<i>P. scopa</i> (RS)	<i>R. neves-armondii</i> †
<i>P. sucinea</i> † (RS)	<i>R. olivifera</i> † (SP,RJ)
<i>Pereskia aculeata</i>	<i>R. ormindo</i> † (RJ)
<i>P. grandifolia</i> (SP)	<i>R. pacheco-leonis</i> (subsp. <i>pacheco-leonis</i> †) (RJ)
<i>P. nemorosa</i> (RS)	<i>R. pachyptera</i> †
<i>Pilosocereus albisummus</i> † (cf. <i>P. floccosus</i>) (MG)	<i>P. paradoxa</i> (subsp. <i>paradoxa</i> †)
<i>P. brasiliensis</i> (RJ)	<i>R. pentaptera</i> † (RJ)
<i>P. machrisii</i> (MG, SP)	<i>R. pilocarpa</i>
<i>Praecereus euchlorus</i> subsp. <i>euchlorus</i> (SP,PR)	<i>R. pulchra</i> (MG,SP,RJ)
<i>Rhipsalis baccifera</i> subsp. <i>shaferi</i> (SP)	<i>R. puniceodiscus</i> †
<i>R. burchellii</i> † (SP,PR)	<i>R. teres</i>
<i>R. campos-portoana</i>	<i>R. trigona</i> † (SP,PR,SC)
<i>R. cereoides</i> (RJ)	<i>Schlumbergera microsphaerica</i> (RJ)
<i>R. cereuscula</i>	<i>S. opuntioides</i> (SP,RJ)
<i>R. clavata</i> (SP,RJ)	<i>S. orssichiana</i> † (SP,RJ)
<i>R. dissimilis</i> † (SP,PR)	<i>S. russelliana</i> † (RJ)
<i>R. elliptica</i>	<i>S. truncata</i> † (RJ)
<i>R. ewaldiana</i> † (RJ)	<i>Tacinga saxatilis</i> (subsp. <i>saxatilis</i>) (MG)