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LEPTOCEREUS (A. BERGER) BRITTON AND ROSE: A MONOGRAPHIC STUDY OF A WEST INDIAN GENUS OF CACTACEAE (CACTOIDEAE)

Inferences from Morphological and Molecular Data

by

ALBERTO E. ARECES-MALLEA

A Dissertation Submitted to the Graduate Faculty in Biology in partial fulfillment of the requierements for the degree of Doctor of Philosophy, the City University of New York.

2003

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This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

LEPTOCEREUS (A. BERGER) BRITTON AND ROSE : A MONOGRAPHIC STUDY OF A WEST INDIAN GENUS OF CACTACEAE (CACTOIDEAE)

Inferences from Morphological and Molecular Data

by

Alberto E. Areces-Mallea

Adviser: Dr. Noel H. Holmgren

The genus *Leptocereus* (Berger) Britton and Rose is revised to include 17 species and 3 subspecies arranged in 2 subgenera and 6 sections. Subgenus *Leptocereus* is exclusively Cuban and comprises 13 species, 5 of which are new, and one new subspecies. Species of subgenus *Leptocereus* are arranged in 4 sections: sect. *Leptocereus* with *L. assurgens* (Wright) Britton and Rose, *L. chrysotyrius* Areces, *L. ekmanii* (Werderman) Knuth, *L. prostratus* Britton and Rose, and *L. albellus* Areces; sect. *Roseiflori* (*sect. nov*) with *L. wrightii* León ssp. *wrightii* and ssp. *gracilis* Areces, *L. scopulophilus* Areces, and *L. leonii* Britton and Rose; sect. *Costanthus* (*sect. nov*) with *L. arboreus* Britton and Rose and *L. carinatus* Areces; and sect. *Spinosissimus* (*sect. nov*) with *L. sylvestris* Britton and Rose, *L. maxonii* Britton and Rose, and *L. santamarinae* Areces. Subgenus *Weingartianea* Areces (*subgen. nov.*) is distinguished on the basis of stem and epidermis anatomy, seed morphology, geographical distribution, and molecular data (*trn*L intron sequences of chloroplast DNA). It includes 4 species and 2 new subspecies of Hispaniola and/or Puerto Rico. Within subgen.

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Weingartianea, 2 sections are recognized: sect. *Tenuicaulis* (*sect. nov*), including *L. weingartianus* (Hart.) Britton and Rose ssp. *weingartianus* and ssp. *demissus* Areces, and sect. *Cephaliphora* (*sect. nov*), represented by *L. paniculatus* (Lamarck) Hunt, *L. quadricostatus* (Bello) Britton and Rose ssp. *quadricostatus* and ssp. *parvispinus* Areces, and *L. grantianus* Britton and Rose. A puzzling "leptocereoid" taxon from Haiti is described under *Cereus* subgenus *Hamannia* Areces (*subgen. nov*) as a new species: *Cereus* (*Hamannia*) *fabiolae* Areces. This monograph comprises a complete taxonomic revision of the genus based on the study of herbarium and liquid-preserved material as well as extensive field observations. The introductory chapters present a survey of taxonomic history, general morphology, anatomy, seed morphology, palynology, molecular systematics, cladistic analysis, general ecology, reproductive biology, phytogeography, and conservation biology. The systematic treatment includes keys to the species and subspecies, typification of all names, descriptions of all taxonomic categories, and geographic distributions. This monograph includes 43 tables, 12 black and white figures, and 63 color plates.

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To Migdalia,
who would have liked to have seen this thesis.
To Faby and Albertico, for inspiration.
To Gabriela, my wife, with love and gratitude.

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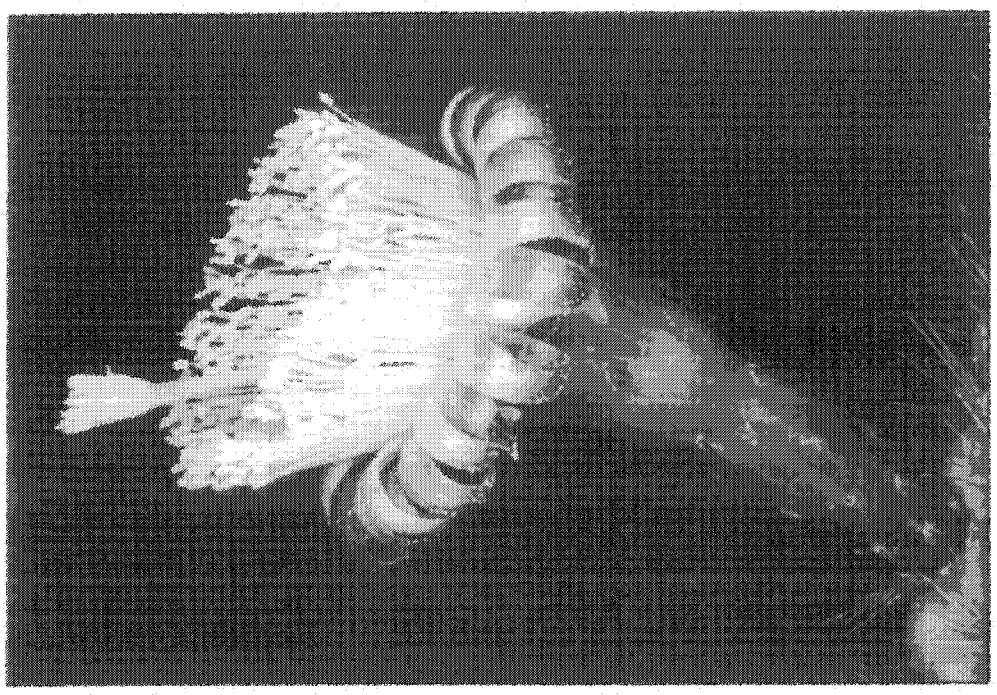

This night-blooming flower of an apparently new cereoid cactus was photographed for the first time in 1998 in a remote area of northwestern Haiti. Although the plant was never named and described according to modern rules, it was actually one of the earliest known cacti, having been depicted in the late seventeenth century by the French missionary Charles Plumier during one of his visits to the West Indies. Plumier referred to the species as *"Melocactus arborescens folio striato spinosissimo fructu luteo suboblongo"* in his still unpublished *Botanicon americanum seu historia plantarum in Americanis insulis nascentium.* Half a century after Plumier's death in 1704, Johannes Burman published the drawing of this puzzling cactus (as plate 195) in his *Plantarum americanarum fasciculus.* Although the identification of "Plumier's plates" has engaged numerous renowned botanists, including Linnaeus, Lamarck, De Candolle, Haworth, Britton and Rose, Urban, and D. Hunt, plate 195 remained a mystery until 1998 when the enigmatic plant was finally traced on a Haitian coastal terrace. The species that inspired Plumier's original polynomial and drawing became *Cereus (Hamannia) fabiolae* Areces, more than 300 years after its first collection.

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1. INTRODUCTION

For the Cactaceae the task of recognizing, delimiting and naming species and other taxonomic categories above this rank has had a long and complicated history. In Linnaeus' *Species Plantarum* (1753), the starting point for the nomenclature of vascular plants, only 22 species of cacti were named and placed into a single genus: *Cactus* L. In 1768 Philip Miller wrote in the eighth edition of his *Gardener's Dictionary*, referring directly to cacti: "by increasing the number of genera, the specific differences may be better ascertained." As Elizabeth A. Shaw (1976) pointed out wittily, this suggestion was taken much to heart by later writers on the family. In fact, from those humble beginnings we now have over 11,000 published Latin binomials for cacti (Gibson and Nobel, 1986), most of which are illegitimate, invalid, or superfluous. The West Indian barrel cactus *Melocactus macracanthos*, for example, possess one of the largest synonymies amongst the flowering plants. This notoriously variable species, which was originally named by Salm-Dyck in 1820 as *Cactus macracanthos*, has been described under at least 108 binomials (most binomials can be found in Britton and Rose 1919-1923, 3: 222-224). The polymorphism exhibited by this and many other cactus species is in great part responsible for this situation.

Another major problem with cactus taxonomy is that in the evolution of the group a great amount of morphological convergence has occurred, so that the same growth form, floral designs (depending upon pollination ecology), and even fruit and seed characteristics have appeared in completely unrelated evolutionary lineages.

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In undertaking a revision of the cactus genus *Leptocereus*, all the "faults" of cactus taxonomy became apparent and had to be resolved. Consideration of the important features of Cactaceae and an evaluation of problems in cactus taxonomy was necessary in developing a strategy to be followed. This was necessary in order to establish the generic limits of *Leptocereus*.

1.1. The Cactaceae

The cactus family is composed of perennial, usually succulent plants. The leaves are absent, except in the primitive genus *Pereskia*, where they are large, flat and fleshy, and in *Maihuenia*, *Opuntia,* and close relatives of *Opuntia*, where they are much reduced, terete or subulate and caducous. The Cactaceae are characterized morphologically by the presence of stems bearing specialized, felted short-shoots termed areoles, which usually develop the spines (modified leaves) that represent the familiar hallmark of the family. The flowers are usually perfect, actinomorphic (rarely zygomorphic), and solitary, but occasionally clustered in corymbs or panicles. The receptacle tube consists of axial tissue that completely envelopes the ovary and extends beyond. Within the Cactaceae there is an evolutionary trend for the receptacle tube to progressively lose the axial leaves, spines, and hairs. The unilocular ovary is almost always inferior, with three to many placentas in a secondary position. The fruit may be juicy or dry and may or may not bear leafy scales, axillary spines, bristles or hairs. The seeds are often numerous.

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Except for one species of *Rhipsalis* (*R. baccifera* —Neotropics and African tropics eastwards to Sri Lanka), the family is endemic to the New World. In the Americas they range from southern Canada to Patagonia, being most frequent in the dry climatic areas between 35° north and south latitude. The Cactaceae comprise 21 to 233 genera depending upon the authority, and 1500-2000 species distributed within three subfamilies, namely the primitively leaf-bearing *Pereskioideae*, the highly derived *Opuntioideae* with barbed spines and glochids, and the leafless, morphologically complex *Cactoideae*. The last of these, containing the bulk of the family, is divisible into seven or eight tribes, each of which has a characteristic geographical range. Within the tribe *Leptocereeae* there are species of columnar cacti that are considered to be fairly primitive, such as species of *Leptocereus,* with branching patterns not unlike typical dicotyledons (Gibson and Nobel, 1986).

There are six well-recognized centers of diversity and endemism for cacti, the fourth of which in order of importance is that of the Caribbean region, comprising the West Indies, northern South America (coastal Venezuela, northern and western Colombia), and Panama. The Caribbean islands are notable for peculiar, poorly known endemics, such as *Leptocereus* (including the giant *Neoabbottia*), *Consolea*, the massive *Dendrocereus*, and a unique group of dioecious *Pereskia* species, most of which are very rare and of particular conservation concern (Areces-Mallea, 1992, 1997).

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Taken as a whole the cactus family has a surprisingly wide climatic and ecological spectrum, encompassing almost rainless desert (*e.g.*, parts of the western Atacama in northern Chile) at one extreme and tropical rainforest receiving more than 2000 mm of rain per year at the other. In the West Indies the occurrence of cacti is most common in coastal areas with seasonally high temperatures and rainfall under 700 mm, often falling in one short annual period. The Cactaceae range from sea level to about 2000 m in the Caribbean islands (Areces-Mallea, 1997), to a reported 5000 m altitude in the Andes. They vary considerably in their resistance to frost. Their habit is also variable; epiphytes, lithophytes, 'cactus geophytes', mound-forming caespitose, decumbent, scandent and erect, freestanding tree and shrub species are frequent. Some genera, such as *Leptocereus,* exhibit a remarkable number of different habit-forms, from tree-like (*L. arboreus*) to decumbent (*L. quadricostatus*), scandent (*L. weingartianus*), prostrate (*L. prostratus*), or shrubby (*L. ekmanii*). There are no parasitic species among the Cactaceae.

Apart from the fire-resistant 'cactus geophytes' (*e.g.*, the rare *Escobaria cubensis*), among the most remarkable are small species restricted to vertical cliffs, such as the recently discovered *Mammillaria jamaicensis* in Jamaica (Areces-Mallea, 2001), and the well-known *Blossfeldia* from northern Argentina and southern Bolivia. Three Cuban species are restricted to ultrabasic serpentine rocks (Areces-Mallea 1976a, 1976b); at least four Mexican species occur only on gypsum, and isolated outcrops of other particular rock types account for a significant portion of the narrow endemism

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seen in the family. Some species are able to grow on, or are restricted to, extreme oligotrophic substrates (*Uebelmannia*).

Seed dispersal is effected by various means including mammals, birds, lizards, fish, insects (especially ants) hermit crabs (*Leptocereus*), wind (*Pterocactus*), and water (*Frailea*). Bats are a particularly important group of associated organisms on whose conservation the survival of some West Indian Cactoideae may well depend (*Pilosocereus, Dendrocereus, Harrisia, Acanthocereus*).

The family Cactaceae gets its name from A. L. De Jussieu (1789). The type genus was *Cactus* L. but since this name had become a source of confusion and there was no agreement on which part of the Linnean taxon should be used, it was rejected against *Mammillaria* at the 1905 botanical congress, which met at Vienna. *Mammillaria*, a genus described by A. Haworth in 1812 was conserved against *Cactus* L. in the first list of *nomina conservanda* ever proposed in a congress. Although mentioned only in later codes, *Mammillaria* of Haworth (op. cit.) is also conserved against the name *Mammillaria* Stackhouse, used earlier (1809) for a genus of algae. The taxonomy of Cactaceae has been directed primarily by large descriptive catalogs and has comparatively few monographs on individual genera. Still, there are a number of delimitation problems at the generic and suprageneric levels. Many genera are considered assemblages rather than units of the taxonomic hierarchy, and the tribal boundaries within the subfamily Cactoideae seem to be, in most cases, very arbitrarily delimitated. Britton and Rose (1919-1923) recognized 123 genera and since then

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taxonomists have gradually redefined these genera, sometimes lumping some together, sometimes splitting some apart, and sometimes completely reshuffling the species included in each genus. The continual re-evaluation of the same characters leading to different classifications, without support from characters other than morphology, may not represent progress. New techniques and complementary analyses are to be incorporated in future approaches. In fact, there is still a great need to resolve the natural circumscription of many genera of subfamily Cactoideae, particularly those of columnar taxa in the tribes Pachycereeae, Cereeae, Trichocereeae, Browningiae, and Leptocereeae, and this seems to be the only reasonable way to undertake the task.

1.2. The genus *Leptocereus*

The West Indian genus *Leptocereus* (A. Berger) Britton and Rose comprises a relatively small number of allopatric and rather distinct species, whose combined distribution extends in an arc from Cuba through Hispaniola to Puerto Rico and its eastern island, Culebra. Before this monographic study was initiated, only 12 species were referred to this poorly known genus, eight of them Cuban, two Hispaniolan, and two Puerto Rican.

Originally, *Leptocereus* included a small number of cacti confined to the Greater Antilles, with rather variable habit, thin, high, crenate ribs, and relatively small flowers. The generic name is from the Greek *leptos* —for thin— and from the Latin *cereus* — for wax, candle— signifying thin-cereus, referring to the ribs. As new species were

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described, it became apparent that the generic limits of this taxon were insufficient to hold the morphological variability exhibited by these plants. The prevailing current idea seems to be that any West Indian columnar Cactoideae with small flowers should fit in the genus. Redefined in its broader sense, *Leptocereus* would include tree-like to divaricate, procumbent or prostate, semi-scandent to shrubby plants with three to 16 ribs. The ribs can be thin to rather thick, high to very low, markedly crenate or undulate to perfectly straight. Its flowers will be long-tubular to short funnel-shaped, smooth or ribbed, spiny to completely unarmed. Perianth segments are pure white in strictly nyctigamous flowers, or brightly colored in flowers that are both nocturnal and diurnal. The stamens and style may be inserted, or long-exserted. The fruits are rounded to cylindrical or strongly angled, greenish, purple or yellow, hard and glutinous, to juicy and edible, totally covered with stout spines, to smooth and spineless. The genus being so small and so broadly defined within the Cactaceae it can easily be perceived as a polyphyletic assemblage.

Numerous cases of parallel evolution have contributed to disagreements about generic and tribal circumscriptions in the Cactaceae. Although Britton and Rose (1909, 1919-1923) provided a preliminary framework for understanding the identity and relationships of the species of *Leptocereus,* their taxonomies mostly reflected the distinctions of individual taxa rather than their intra- and intergeneric relationships. Buxbaum (1958) used many supposedly derived character states to determine intergeneric relationships, and rearranged the genera of the Cactaceae so as to match the distribution of the apomorphic features. Buxbaum's tribe Leptocereeae seems to

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reflect some degree of phylogenetic order, but still there are many unresolved links. It is easy to find fault with Buxbaum's generic phylogenies because they were done with very incomplete sets of data. The tribe typified by *Leptocereus,* the Leptocereeae (Table 1), is presumed to show the plesiomorphic features of the subfamily Cactoideae, which contains 80% of all cactus species. More than half of the species circumscribed to the tribe belong to *Leptocereus* and occur only in the Greater Antilles, but the Leptocereeae is also represented in Bolivia and Peru. Two genera, *Neoraimondia,* a distinctive genus with very long-lived flowering shoots, and *Armatocereus,* the species of which are distributed as far north as Costa Rica, have evolved on the western slopes of the Andes. Gibson and Nobel (1986) believe that *Pachycereus hollianus* (E. A. C. Weber) Buxbaum, from southern Mexico, and *Jasminocereus* and *Brachycereus*, from the Galápagos Archipelago, may also belong to this tribe, but it does not seem likely. Actually, the only genus that shows fairly close relationships with *Leptocereus* is the Bolivian *Samaipaticereus*. Aside from the habit and relatively small size of the flowers exhibited by the genera often included in the tribe *Leptocereeae* (excl. *Armatocereus),* which could be convergent features, most of other floral and fruit characters of *Armatocereus, Neoraimondia* (incl. *Neocardenasia*) and *Calymanthium* seem far apart from *Leptocereus*. Looking with a positive viewpoint at Buxbaum's work, and at that of his followers, a thorough revision of all the genera included in the Leptocereeae should be done, and an attempt to construct a totally revised phylogeny of the species as well. Before that, however, *Leptocereus*, the largest and presumably most primitive genus of the tribe, and also the least studied, must be well understood.

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GENERA	Nº OF SPECIES	DISTRIBUTION
Leptocereus	11	West Indies
Armatocereus	11	Peru
Samaipaticereus	2	Bolivia
Calymmanthium	1	Peru
*Neoabbottia**	1	Hispaniola
Neoraimondia	1	Peru

* *Neoabbottia* is now included in *Leptocereus* (Hunt, 1991).

Table 1. The genera of Cactaceae (Subfamily Cactoideae) in tribe Leptocereeae, according to Buxbaum, 1974.

Until now, very little was known about the genus *Leptocereus,* other than the original descriptions of its species, the last of which —without considering the novelties recently uncovered (Areces-Mallea, 1992, 1993a, 1993b)— was published more than 60 years ago (Britton, 1933). When I began this study the taxonomy of the genus was in a confused state due to several factors. The lack of extensive field research to document and voucher variability, the relatively high levels of morphological homoplasy, and the use of primarily vegetative morphological characters, made the establishment of species boundaries difficult in certain cases (*e.g.*, in *Leptocereus weingartianus).* This is surprising for a genus that is considered one of the most —if not the most— primitive group of Cactoideae (Gibson and Nobel, 1986). In fact, Buxbaum made a case for using the West Indies as the center of origin for the cactus family because, he reasoned, *Leptocereus* and other genera with putatively

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primitive features occur there. Even though the taxonomy of the Cactaceae has caused much controversy and debate, most contemporary cactus systematists have consistently recognized that many features considered to be primitive for the subfamily Cactoideae, such as typical dicotyledon branching designs, are to be found in some species of West Indian *Leptocereus*.

The reasons why *Leptocereus* remained unstudied for so many years may be explained, in part, by the fact that many professional taxonomists have purposely avoided investigating Cactaceae. First, these plants are poorly represented in herbaria, which typically provide much of the data for generic monographs. Second, when available, herbarium specimens of cacti, are often inadequate because they are fragmentary and because dried specimens do not show many of the important taxonomic features. For *Leptocereus,* as for other succulent cacti, there is a special need to study both fresh and liquid-preserved materials (Areces-Mallea, 1996). Third, the family tends to exhibit a great deal of polymorphism, so that one cannot be certain about the morphological limits of each species without detailed study of natural populations. Fourth, in the evolution of this family an incredible amount of morphological convergence has occurred, so that the same growth form, floral designs, and fruit and seed features have appeared in completely unrelated evolutionary lineages. Because of its resemblance with the Opuntioideae, for example, the genus *Maihuenia* was originally referred to as an *Opuntia*; decades later it was transferred to subfamily Pereskioideae, and now placed in its own subfamily, Maihuenioideae (Anderson, 2001). Finally, cactus taxonomy has been much complicated by the

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publication of a plethora of binomials, many of which were used for minor variants of plants grown under artificial conditions. Fortunately, the latter is not a big problem in *Leptocereus*. The relative inaccessibility of some subcoastal populations occurring in remote areas (*e.g.*, in northwestern Haiti) and especially of many inland populations located on top of very steep karstic mountains of the haystack-type (*e.g.*, in western Cuba) is, however, a major problem in this genus. Another reason that may have discouraged botanists and amateur collectors to collect and study *Leptocereus* is the fact that 72% of its species are restricted to Cuba, which for the last 40 years has been significatively isolated from the western scientific community.

1.3. Taxonomic history of *Leptocereus*

Among the earliest cacti described were those obtained by Plumier between 1689 and 1695, mostly from the island of Hispaniola, The first true *Leptocereus* was collected at that time, but was known only from manuscript descriptions. This plant was characterized by Plumier (1703) with the phrase "*Melocactus arborescens, tetragonus, flore ex albido*", a description that was repeated by Tournefort (1719) with the addition of only but one word (Plate 1, A, B). Plumier's drawing of this cactus plant was published long after his death by Burmann (1755) as Plate 192. It is noteworthy that after being referred to several genera, Plumier's plant was finally combined to *Leptocereus* (Hunt, 1991).

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Plate 1. Cactaceae plates of Plumier's *Botanicum Americanum* (inedit.) referable to *Leptocereus paniculatus* (Lam.) D. R. Hunt, and *Cereus (Hamannia) fabiolae* Areces.

A. Habit of *Leptocereus paniculatus* (Plumier's *Melocactus [seu Opuntia] arborescens tetragonus flore exalbido,* drawing no. 3: 20). **B**. Stem segment, flowers and fruit of the same (drawing 3: 21). **C**. Stem segment, flowers and sectioned fruit of *Cereus (Hamannia) fabiolae* (Plumier's *Melocactus arborescens folio striato spinosissimo fructu luteo suboblongo,* drawing no. 3:26). Hunt (1984) erroneously took this drawing, and Plumier's polynomial, for *Harrisia nashii* Britton. **D**. *Harrisia nashii* (Plumier's *Melocactus [cereiformis] ramosissimus spinosissimus fructu aureo tuberoso,* drawing no. 3: 23). The habit of the plant and tuberculate, globose or depressed-globose fruits are consistent with identification as *Harrisia*. However, the relatively small flowers with their long-exserted stigma are those of *Cereus fabiolae*. Because of the resemblance of the stems of *H. nashii* and *C. fabiolae*, Plumier may have mistaken the flowers of this latter species for those of *Harrisia nashii.*

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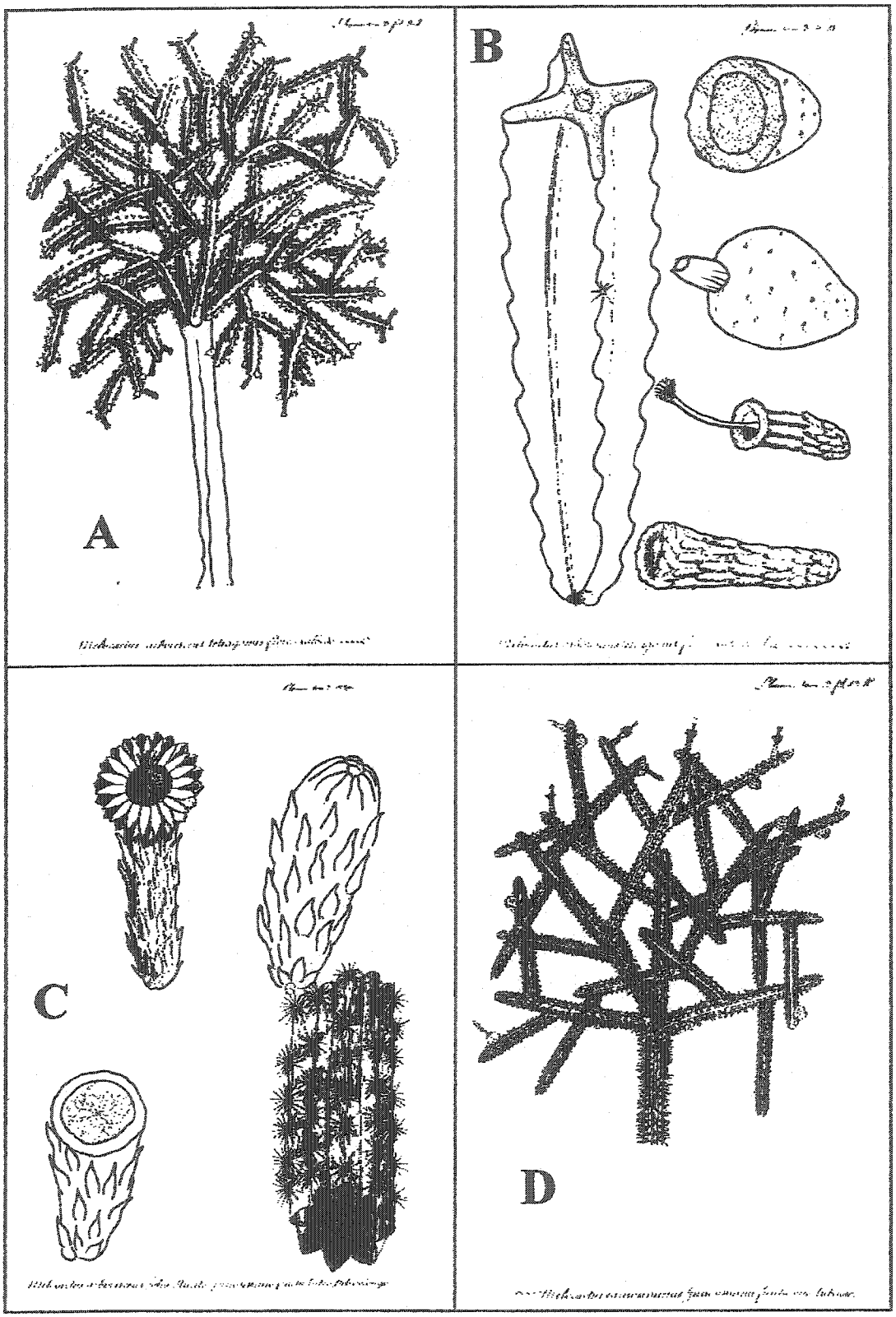

Plate 1.

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In *Species Plantarum*, the starting point for plant binomial nomenclature, Linnaeus (1753) gave scientific names to 22 species of cacti which he assigned to a single genus: *Cactus*. The specific epithets of these cacti are mostly still in use, but *Cactus* as a generic name has been discarded (Shaw, 1976; Howard and Touw, 1981), and the Linnean species have been reassigned to genera in the three cactus subfamilies: Pereskioideae (2 spp.); Opuntioideae (6 spp.), and Cactoideae (14 spp.). Among the original Linnean species were a number of columnar cacti that came from the West Indies and northeastern South America, but none of them proved to be in the *Leptocereus* lineage. The 18th century English horticulturist Philip Miller (1754) promptly removed the rib-bearing columnar cacti from *Cactus* and reclassified them in a new genus, *Cereus*, which was based on a pre-Linnean common name for this plant form. Subsequently, over 80% of the columnar cacti described since Miller's time have at some time been classified as species of *Cereus* (Gibson, 1988). As Plumier's pre-Linnean cacti polynomials were not considered in *Species Plantarum*, Lamarck (1783) gave most of them binary names under the genus *Cactus*. The first *Leptocereus* to be collected was then referred to as *Cactus paniculatus*, solely known from Plumier's short description and Burmann's plate n. 192. Since De Candolle (1828) transferred all the cereoid forms described by Plumier (*op. cit.*) to the genus *Cereus*, this plant became *Cereus paniculatus* Lam. Because this name could not be assigned to any collection prior to 1920, Plumier's tree-like cactus remained in doubt for nearly a century.

Whereas the ribbed columnar cacti were classified in the 18th century as species of either *Cactus* or *Cereus*, they were generally classified in the 19th century as species of

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Cereus. This broadly defined genus remained relatively intact throughout the 19th century, even though several authors made proposals to segregate very distinctive, unusual species from *Cereus*, such as the very hairy Cephalocerei (*Cephalocereus* Pfeiffer, in 1838 and *Pilocereus* Lemaire, in 1839).

The second species of *Leptocereus* was collected by C. Wright between 1860 and 1864 in western Cuba, and was published as *Cereus assurgens* (Grisebach, 1866). There was confusion with the application of this name because the type specimen consisted of material belonging to two different species collected at two different sites, which was not clearly mentioned in the original publication. The problem was elucidated by León (1940), who circumscribed the taxon (as *Leptocereus assurgens*) to the population occurring in the karstic haystack mountain ranges of Viñales (province of Pinar del Rio). León (*op. cit.*) described a new species (*Leptocereus wrightii*) to include the other taxon represented by a stem fragment in Wright's original collection, which proved to match the plants pertaining to a coastal population at Cojímar, north of Havana province.

Bello (1881) published the third and last species of *Leptocereus* to be described in the 19th century (as *Cereus quadricostatus* Bello), from the dry limestone shrubwoods of southwestern Puerto Rico. Both, *Leptocereus assurgens* and *L. quadricostatus* were recognized by Schumann in 1903 (as *Cereus assurgens* and *C. quadricostatus*), but placed in different sections of the genus *Cereus*, the former in his series *Tortuosi*, and

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the latter in his series *Oligogoni*. In Schumann's treatment (*op. cit.*) *Cereus paniculatus* was referred to only as a doubtful name.

Near the turn of the century Schumann (1897-98) published the first detailed classification of the Cactaceae. He recognized 16 genera in the subfamily Cactoideae (as Cereoideae) and grouped them into three tribes, one of which (Echinocacteae) included *Cereus*. His tribes were not phylogenetically sound, but he was rather progressive in recognizing many of the generic names proposed in the 19th century that are still in use.

Shortly after the turn of the century another related taxon from Hispaniola was uncovered, *Cereus weingartianus*, dedicated by Hartmann (1904) to Wilhelm Weingart, from Nauendorf, Germany. Surprisingly, Weingart himself (1905) placed this name in synonymy under the Cuban *C. assurgens*. Although very distinctive, Urban (1920-1921) also considered *Cereus weingartianus* as identical to *C. assurgens*. At the same time he recognized the puzzling *Cereus paniculatus* as a good species, after apparently being "rediscovered" by W. Buch in Haiti (Urban, *op. cit.*).

In the 19th century most investigators were occupied full time with discovering new plants in the wild and describing them in publications. In the 20th century the growth phase of finding new taxa decreased. Eventually scientists would have adequate materials to compare all of the known species, and the diversification of each group would have to be accounted for. So when the number of taxonomists in universities and

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botanical institutions increased, and coupled with a desire to unravel the evolutionary history of each plant and animal group, revisions of the 19th century genera were undertaken.

Cactaceae with columnar growth forms were often assigned to *Cereus* in the 19th century. However, in the 20th century many botanists realized that the diversity within this genus was equaling the diversity of vegetative and reproductive parts found in entire families of other flowering plants. By lumping all species into one genus, the phylogenetic units and evolutionary histories of the various taxa is obscured. Therefore, from an evolutionary perspective, it is desirable to have the evolutionary branches of the columnar cacti clearly identified. Only by doing so will scientists be able to trace the multiple origins of the epiphytic lineages and the many different and often unrelated groups of small, terrestrial cacti from columnar ancestors. In fact, scientists have learned so much about the ribbed columnar cacti that nearly all workers now interpret Miller's *Cereus* to include only a small group of South American columnar cacti. This narrow definition of the genus has been widely accepted in the U.S. for nearly half a century by all except Benson (1982).

The first major overhaul of *Cereus* was made by Britton and Rose (1919-1923) who subdivided it into many smaller and more homogeneous units. Actually, *Leptocereus* had already been segregated within *Cereus* (as a subgenus) by Berger (1905) to distinguish a group of "tropical *Cerei* with short flowers and climbing, elongated stems." Berger (*op. cit.*) included three species in his new subgenus: *Cereus*

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assurgens (type), and the unrelated *C. gonzalezii* Weber and *C. tonduzii* Weber. In 1909, Britton and Rose raised Berger's subgenus *Leptocereus* to generic rank to include *Cereus assurgens*, giving to the segregated taxon a different, more natural circumscription (*Cereus gonzalezii* and *C. tonduzii* were transferred to other genera). In Britton and Rose's system (1919-1923), *Leptocereus* was placed in the tribe Cereeae, subtribe Cereanae. Although *Leptocereus* and a great majority of the other 78 generic names authored by Britton and Rose —some of them greatly redefined— are still widely regarded as phylogenetically sound taxa, these authors very much confused the overall phylogenetic picture of the family by classifying convergent North and South American genera in the same subtribe. Notwithstanding, it is a great credit to Britton and Rose that in cactus systematics, the modern generic concept, although never strictly defined by them, often corresponds fairly closely to that presented by these knowledgeable scholars.

Prior to the publication of their monograph (1919-1923), Britton and Rose (1912) had published two new species of *Leptocereus* from western and central Cuba, *L. leonii* and *L. arboreus,* respectively. Shortly after, Vaupel (1912), not accepting *Leptocereus* as a genus, transferred these two species to *Cereus*. In their monograph, Britton and Rose described three more Cuban species: *Leptocereus prostratus, L. maxonii,* and *L. sylvestris.* They also included the old *L. quadricostatus* and *L. weingartianus*, approaching the generic limits of the genus as upheld today. However, *Cereus paniculatus*, which has long been in doubt, was not accepted by Britton and Rose in

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their treatment (1919-1923) as a distinct species. Instead, it was listed in a doubtful category under "published species, perhaps of *Leptocereus*."

After the collecting expedition of W. L. Abbott and E. C. Leonard in Haiti (April, 1920), which brought material similar to Buch's specimen described in a note under *Cereus paniculatus* by Urban (1920-1921), Britton and Rose accepted the existence of this taxon. Mainly because of the presence of a "kind of cephalium" in terminal branches, these authors proposed a monotypic subgenus, *Neoabbottia*, to include Plumier's puzzling species (Britton and Rose, 1921). *Neoabbottia* was recently questioned as a genus different from *Leptocereus*, and Hunt (in Hunt and Taylor, 1991) finally recombined the species to this genus.

In 1931 the very conservative Werderman described a new *Cereus ekmanii* from a collection made by E. L. Ekman in western Cuba. Four years later Knuth (*in* Backeberg and Knuth, 1935) transferred this name to *Leptocereus*. The last species of this genus to be published in the 1930's was *Leptocereus grantianus*, described by Britton (1933) from the island of Culebra, Puerto Rico.

Around 1950, Buxbaum, who deserves full credit for initiating a movement to produce a phylogenetic system of classification for the Cactaceae, began to examine the anatomical and cellular nature of cactus organs and uncovered many apomorphic character states that had not been observed by Britton and Rose and earlier workers. Using these derived character states, Buxbaum drastically rearranged the genera and

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sometimes the species within genera to match more closely the distribution of the apomorphic features, particularly using the flowers and seeds. In his first tribal classification of subfamily Cactoideae, Buxbaum (1958) proposed the tribe Leptocereeae to include *Leptocereus*, and a few other genera primarily occurring in northwestern South America and Central America. Although Buxbaum revised his system through the 1970's shifting a number of genera between tribes, the generic circumscription of the Leptocereeae, and *Leptocereus* itself, remained unaltered. In 1988, however, Barthlott drastically changed this scheme by placing *Leptocereus* in the most relictual position of tribe Echinocereeae. The International Organization of Succulent Plant Studies (IOS) Working Party (Hunt and Taylor, 1990) agreed to place *Leptocereus* within the Echinocereeae, but proposed an informal "Group 1a" basically made of former members of tribes Leptocereeae and Echinocereeae emphasizing those with hard fibrous wood (Table 2). This treatment, which I believe is artificial and thus unacceptable, is not well supported by the molecular data presented in this study.

More recently a number of undescribed taxa of *Leptocereus*, not referable to previously published concepts, have been discovered in the Greater Antilles —especially in Cuba— as a result of careful exploration of many low-altitude mountain ranges and subcoastal areas. Three novelties, *Leptocereus santamarinae, L. carinatus,* and *L. scopulophilus* have already been described (Areces-Mallea, 1992, 1993a, 1993b), whereas descriptions of two new species and three new subspecies are being prepared for publication. A supposed leptocereoid taxon recently rediscovered in western Haiti is set aside from *Leptocereus* and described here as a new species under

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ACCEPTED GENERA	INCLUDED GENERA
Acanthocereus	*Dendrocereus, Mirabella, Monvillea*
Echinocereus	*Morangaya, Wilcoxia*
Harrisia	*Eriocereus, Roseocereus*
Leptocereus	*Neoabbottia*
Pseudoacanthocereus*	

*A group frequently regarded as part of *Acanthocereus.*

Table 2. The six genera contained in IOS Group 1a (Hunt and Taylor, 1990).

Cereus subgenus *Hamannia* Areces (*subgen. nov.*). This puzzling plant was depicted and described by Plumier in the late seventeenth century, but never named and described according to modern rules of nomenclature. In this work a total number of 17 species and three heterotypic subspecies arranged in two subgenera and six sections are recognized in *Leptocereus* (Tables 3 and 4).

1.4. General study methods

At the outset of this study most species were only known from their type collections and a sparsity of other collections. Except for the better-known Puerto Rican species *Leptocereus quadricostatus*, there were practically no flowers or fruits preserved in liquid other than those of Britton *et al.* documenting three taxa. Thus, it was necessary to collect both complete herbarium specimens and liquid-preserved

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TAXA	DISTRIBUTION
Genus ***Leptocereus*** (A. Berger) Britton & Rose	Greater Antilles, excl. Jamaica
Subgenus ***Leptocereus***	Cuba
Section ***Leptocereus***	W Cuba
1. ***L. assurgens*** (C. Wright) Britton & Rose	Viñales range
2. ***L. chrysotyrius*** Areces	La Güira range
3. ***L. ekmanii*** (Werderm.) F. M. Knuth	Guane range
4. ***L. prostratus*** Britton & Rose	Sumidero mountains
5. ***L. albellus*** Areces	San Carlos range
Section ***Roseiflori*** Areces	W-Central Cuba
6. ***L. wrightii*** León	
subsp. ***wrightii***	Coasts of Havana-P. del Rio
subsp. ***gracilis*** Areces	San Diego, Pinar del Rio
7. ***L. scopulophilus*** Areces	Somorrostro range
8. ***L. leonii*** Britton & Rose	Anafe range
Section ***Costanthus*** Areces	East-Central Cuba
9. ***L. arboreus*** Britton & Rose	Cienfuegos-Trinidad coast
10. ***L. carinatus*** Areces	Najasa range
Section ***Spinosissimus*** Areces	East Cuba
11. ***L. sylvestris*** Britton & Rose	Coasts of Pilón
12. ***L. maxonii*** Britton & Rose	Coasts of Santiago-Gtmo.
13. ***L. santamarinae*** Areces	Coasts of North East Cuba

Table 3. Circumscription of genus *Leptocereus*, subgenus *Leptocereus*, as proposed in this work.

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TAXA	DISTRIBUTION
Genus ***Leptocereus*** (A. Berger) Britton & Rose	Greater Antilles, excl. Jamaica
Subgenus ***Weingartianea*** Areces	Hispaniola-Puerto Rico
Section ***Tenuicaulis*** Areces	Hispaniola
14. ***L. weingartianus*** (E. Hartmann) Britton & Rose	
subsp. ***weingartianus***	N Haiti-Dominican Rep.
subsp. ***demissus*** Areces	S Haiti-SW Dominican Rep.
Section ***Cephaliphora*** Areces	Hispaniola-Puerto Rico
15. ***L. paniculatus*** (Lam.) D. R. Hunt	Hispaniola
16. ***L. quadricostatus*** (Bello) Britton & Rose	
subsp. ***quadricostatus***	SW Puerto Rico
subsp. ***parvispinus*** Areces	Guánica, Puerto Rico
17. ***L. grantianus*** Britton & Rose	Culebra Island, Puerto Rico

Table 4. Circumscription of genus *Leptocereus*, subgenus *Weingartianea,* as proposed in this work.

material for use in morphological, anatomical, and molecular studies, and also gather ecological information while in the field. Cultivated collections of all hitherto recognized taxa were made in Cuba and Puerto Rico, and cuttings from these collections were sent to different botanical gardens in the United States and the Caribbean. All taxa were studied and photographed in the field during trips to 12 Cuban provinces, 4 Haitian departments, 21 Dominican provinces, nearly all coastal areas in Puerto Rico, and the island of Culebra. Although there were no reliable records of *Leptocereus* outside of Cuba, Hispaniola, Culebra, and the main island of Puerto Rico, a search was also conducted on Mona island (Puerto Rico), the three Cayman Islands,

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and on the most favorable areas of Jamaica including the Cockpit Country. In addition, nearly all available herbarium specimens have been examined from the following herbaria: B, BM, GH, GOET, IJ, JBSD, MAPR, MNHN, S, SJ, UPR, UPRRP, and US.

Whenever possible, field notes were made on the color of vegetative parts, flowers and fruits, and the dimensions of the plant body, giving special attention to the habit and branching pattern, position of flowers and fruits, and habitat. Often when specimens or entire populations were found to be in full bloom, many hours, even entire nights were spent capturing visitors to the flowers at the peak of anthesis. Branches with large buds were frequently taken to camps and hotels and kept for one to three days (until anthesis had taken place) so that detailed descriptions and close-up photographs could be made.

Mature branches of *Leptocereus* collected for herbarium purposes were cut transversally to record the diameter, general shape, rib number, and outline of the rib edge. Most specimens were sectioned longitudinally but because of the poor development of the cortex in *Leptocereus*, no parenchymatous tissues were removed (the removal of cortex tissues is mandatory in many succulent, globular or cylindrical Cactoideae). The sectioned branches were then dried between cardboard and corrugated aluminum in a portable field drier over an electric or gas heat source.

All measurements of vegetative characters (fresh state) were taken at least on 10 adult individuals of each taxon, with the exception of the rare and critically endangered

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Leptocereus scopulophilus, *L. wrightii* ssp. *wrightii*, and *L. wrightii* ssp. *gracilis*. Due to their infrequent occurrence, only two, three and two live individuals of these taxa, respectively, were measured. Likewise, quantitative characters of the stem of all but the above mentioned taxa refer on average to 10 mature, one- to two-year old segments taken from the same number of individuals. For all those vegetative characters lending themselves to quantitative expression, the following abbreviations have been used:

GH. —Growth habit following classification explained under epigraph 2.1.

LS. —Length of ultimate stem segment, in cm.

WS. —Width of ultimate stem segment, in mm.

NR. —Number of ribs.

RH. —Rib height, in mm.

WR. —Basal width of rib, in mm.

RR. —Rib-to-rib distance, taken from their margins, in mm.

SM. —Depth of stem grooves, taken from the midline between the margins of two adjoining ribs, in mm.

CW. —Cortex width. Distance between the bottom of the stem groove and the vascular cylinder, in mm.

CR. —Distance between the highest margin of rib and the vascular cylinder, in mm.

VC. —Diameter of vascular cylinder in mm.

DP. —Diameter of pith, in mm.

FC. —Presence of fibrous reticule in cortex (present: 1; absent: 2).

LA. —Longitudinal diameter of areole, in mm.

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WA. —Transversal diameter of areole, in mm.

IA. —Distance between areoles, in mm.

DS. —Depth of rib sinuses[1], in mm.

TS. —Total number of spines in areole.

TL. —Length of spines, in mm.

TW.—Diameter of spines at base, in mm.

CS. —Number of central spines in areole.

LC. —Length of central spines, in mm.

DC. —Diameter of central spines, in mm.

RS. —Number of radial spines in areole.

LR. —Length of radial spines, in mm.

DR. —Diameter of radial spines, in mm.

Important stem characters of the above list are schematically illustrated in Fig. 1. Other more specialized anatomical and palynological methods, as well as the molecular techniques applied in this study, will be discussed later under their corresponding headings. Unless otherwise stated, all photographs and drawings are by the author.

[1] In all but one species of *Leptocereus* (*L. prostratus*), the areoles are placed in the rib sinuses (Fig. 1, F). Because in *L. prostratus* the areoles are situated upon elevated podaria, the sinuses, strictly speaking, could only refer to the sunken interareolar spaces, and that is where (in this particular species) the DS measure was taken.

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2. GENERAL MORPHOLOGY

2.1. Habit and branching pattern

Growth form and habit, which are variable in species of *Leptocereus*, can be described in conventional vascular plant terms, although succulence often accentuates exomorphic structure. All *Leptocereus* are sympodial, the arborescent forms (*e.g.*, *L. paniculatus*) showing a diffuse ramification pattern very much like that of a typical non-succulent dicotyledon tree. As opposed to the characteristic candelabriform, verticillate, or columnar branching pattern of most tree-like Cactoideae (Plate 2, B), this diffuse ramification type, also present in the massive West Indian genus *Dendrocereus* (Plate 2, A) seems to be the ancestral condition (plesiomorphic state) in the subfamily.

In the most advanced candelabriform or verticillate Cactoideae, lateral branching is infrequent and it is completely lacking in the simple columnar forms. This is surprising since in their stems such plants may have thousands of specialized axillary buds —the areoles— potentially capable of developing branches. As opposed to *Leptocereus*, the growing shoot tip in these advanced forms seems to have a strong developmental control on the entire shoot, being able to suppress by apical dominance the outgrowth of lateral shoots. A less likely explanation for the low frequency of branching of most columnar cacti that has been advocated by some authors (*e.g.* Gibson and Nobel, 1986) is that the axillary buds are immediately converted into areoles. Because these specialized short shoots (the areoles) are already committed to a strict

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Fig. 1. Important vegetative characters lending to qualitative expression in the stem of *Leptocereus* spp. and *Cereus* subgen. *Hamannia*.

A, B. Transverse schematic sections of the normocostate stem of *Leptocereus arboreus*. **C**. Transverse section of the multicostate stem of *Cereus* (subgen. *Hamannia*) *fabiolae*. **D**. Transverse section of an 8-ribbed stem segment of *Leptocereus prostratus* showing characteristic round grooves between the ribs. **E**. A single rib of *Leptocereus quadricostatus*, transversally sectioned. **F**. A rib of *Leptocereus weingartianus* subsp. *weingartianus*, as seen in lateral view. (1. Width of stem segments —WS; 2. Distance between the crest of a rib projection (podarium) and the vascular cylinder —CR; 3. Rib-to-rib distance —RR; 4. Depth of stem grooves, taken from the midline between the margins of two adjoining ribs —SM; 5. Basal width of rib —WR; 6. Diameter of vascular cylinder —VC; 7. Diameter of pith —DP; 8. Rib height —RH; 9. Cortex width —CW; 10. Separation between areoles —IA; 11. Depth of rib sinuses —DS; 12. Longitudinal diameter of areole —LA).

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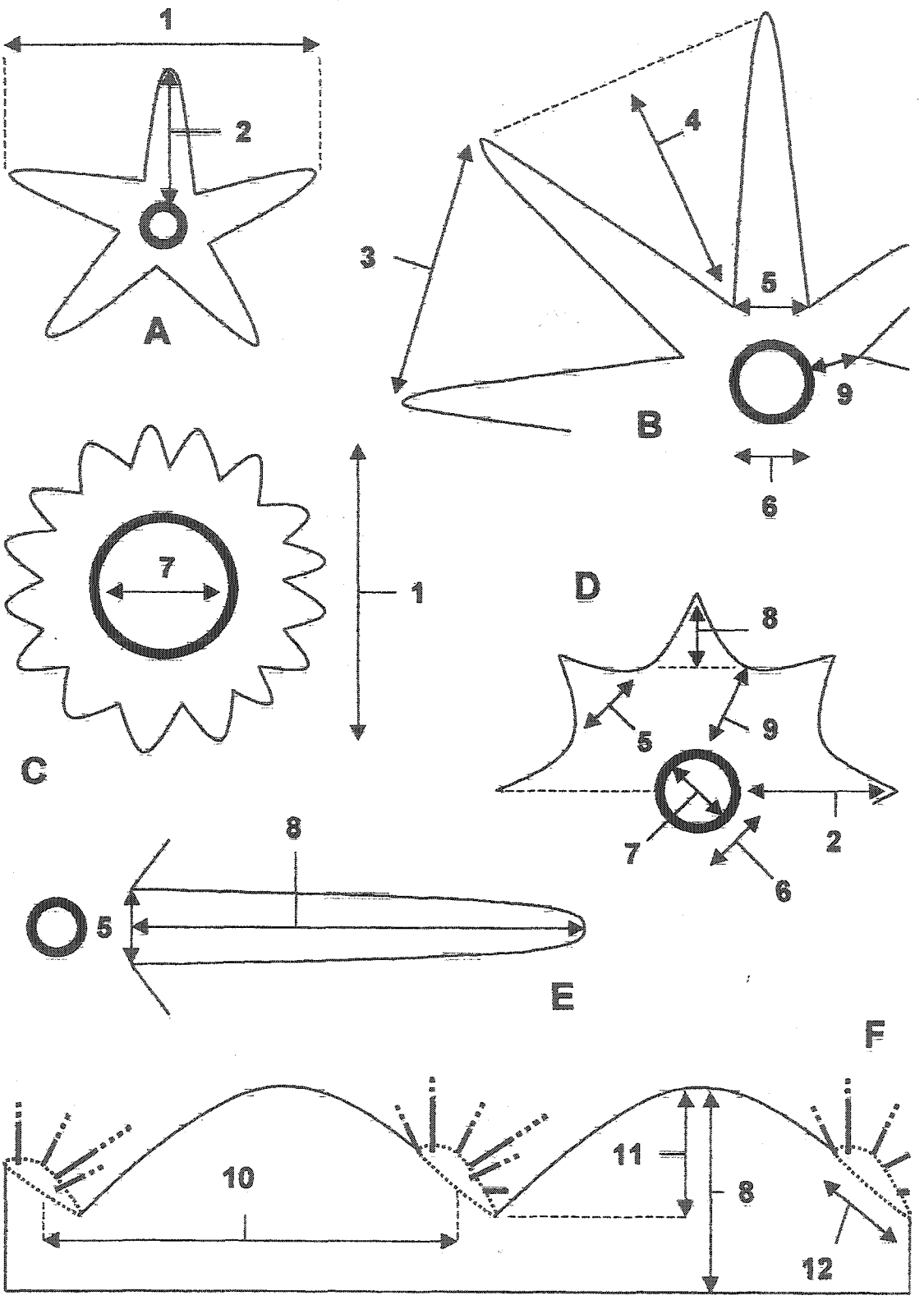

Figure 1.

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spine- and flower-producing function, and according to this theory they are not able to produce shoots. Suppression of lateral branching by specialization of areoles cannot explain frequent ramification in *Leptocereus*, and also in the primitive *Pereskia* and other leaf-bearing cacti. It just seems more probable that apical dominance was not strongly expressed in early cacti, not more than in a normal tree-like dicotyledon with its diffuse, branched crown, but over time it became a controlling influence on cactus evolution after succulence appeared. If so, the hypothetical ancestor to all members of subfamily Cactoideae must have looked very much like an arborescent *Leptocereus* species, judging from the stem architecture exhibited by these extant plants.

In the arborescent and shrubby forms of *Leptocereus* that have many lateral, discrete stem segments, the joints that are produced usually do not arise from areoles on the growing segment. Instead, they develop from one or several of the upper areoles of the shoot of the previous growing period. Although rigorous experimental studies are needed to understand this branching pattern, it seems that the areoles in the stems of *Leptocereus* are stimulated to grow while the shoot tip is inactive, that is, during the dormant period, or more likely, shortly before growth is initiated in the rainy season. Even though the arborescent and shrubby *Leptocereus* have this diffuse ramification pattern, they still display an interesting range of growth habits: tree-like to divaricate, procumbent or prostate (sometimes with dangling branches), semi-scandent to shrubby, 0.2 to 10 m tall. A clear tendency for reduction in habit, similar to that reported in tribe Cereeae as a whole (Taylor and Zappi, 1989), can be seen in *Leptocereus*. The developmental explanation for a genus that exhibits such a wide range of growth habits

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Plate 2. Growth habits of *Dendrocereus, Pilosocereus*, and *Leptocereus* spp. (I).

A. Typical tree-like growth form of *Dendrocereus undulosus* with diffuse branching pattern not unlike that of a typical dicotyledon. **B**. Candelabriform/verticillate growth form of *Pilosocereus royenii.* **C, D**. Tall arborescent growth forms of *Leptocereus paniculatus*, with diffuse branching pattern. **E, F**. Fruticose habit of *L. chrysotyrius*, with arching stems. (A, from vicinity of Jean Rabel, Haiti —19 Jan 1995; B, from Mona Island, Puerto Rico —28 Feb 1994; C, from Baie de Henne, Haiti —18 Jan 1995; D, from vicinity of El Limón, Enriquillo Valley, Dominican Republic —7 Jan 1995; E, F, from San Diego, Pinar del Rio province, Cuba —3 Nov 1976).

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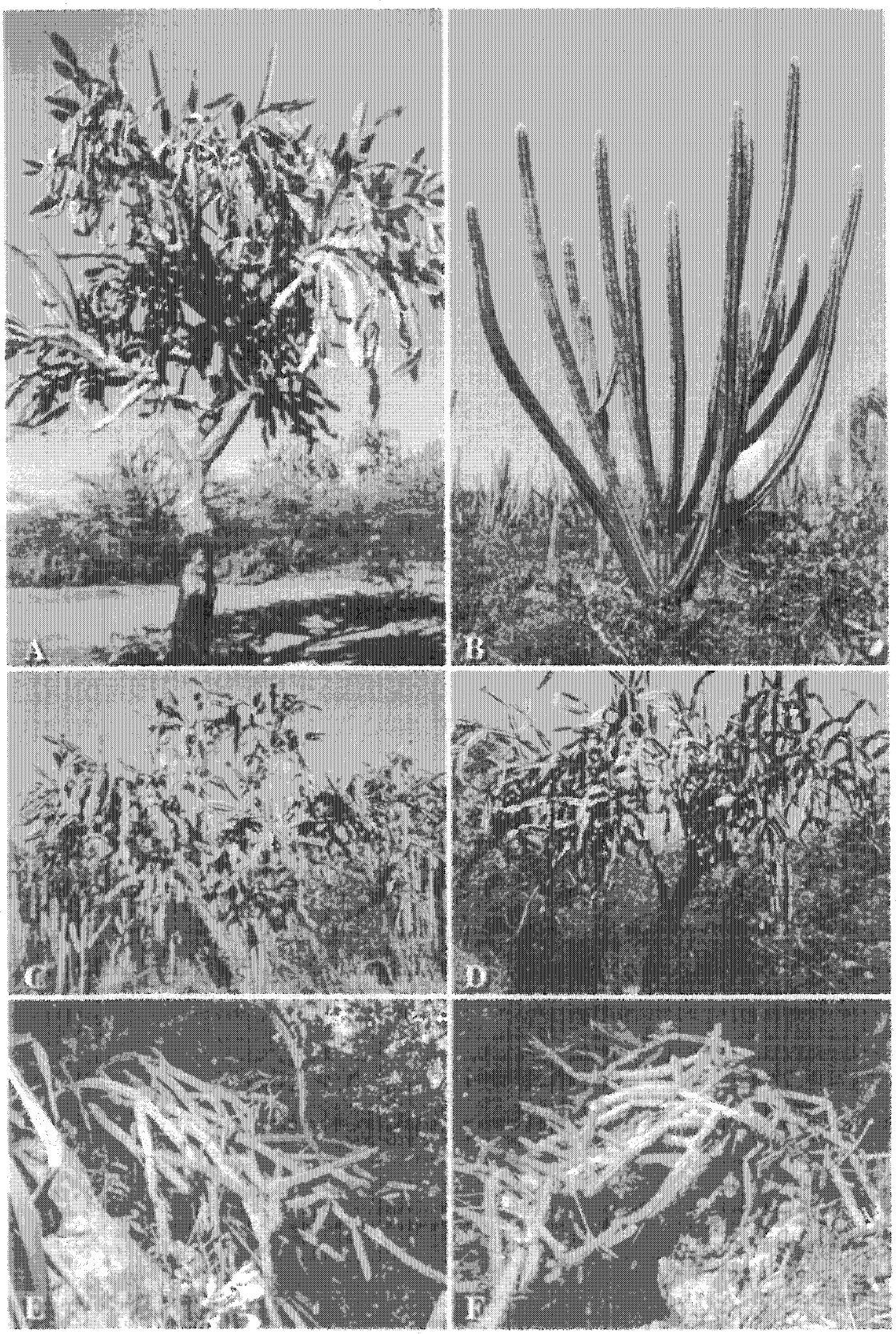

Plate 2.

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Plate 3. Growth habits of *Leptocereus* spp. (II).

A, B, C. Arborescent growth forms of *Leptocereus santamarinae*. **D.** Young exemplar of the same species, growing as a shrub. **E.** Habit of cliff-dweller *L. albellus*, with relatively few dangling branches. **F.** Tall arborescent habit of *L. arboreus*. **G.** Fruticose habit of the type specimen of *L. scopulophilus*, with erect branches. **H.** Small arborescent form of *L. sylvestris*. **I.** Young *L. wrightii* ssp. *wrightii* growing as a shrub. (A, B, C, D, from vicinity of Santa Lucía beach, Cuba —15 Apr 1990; E, from Sierra de San Carlos, Cuba —28 Mar 1992; F, from Yaguanabo, Cuba —9 Jul 1993; G, from the summit of Somorrostro Hill, Cuba, —17 Apr 1976; H, from Boca del Rio Las Puercas, Pilón, Cuba —4 May 1993; I, from Cojímar, Cuba —photograph taken by H. Liogier in 1957 or 1958).

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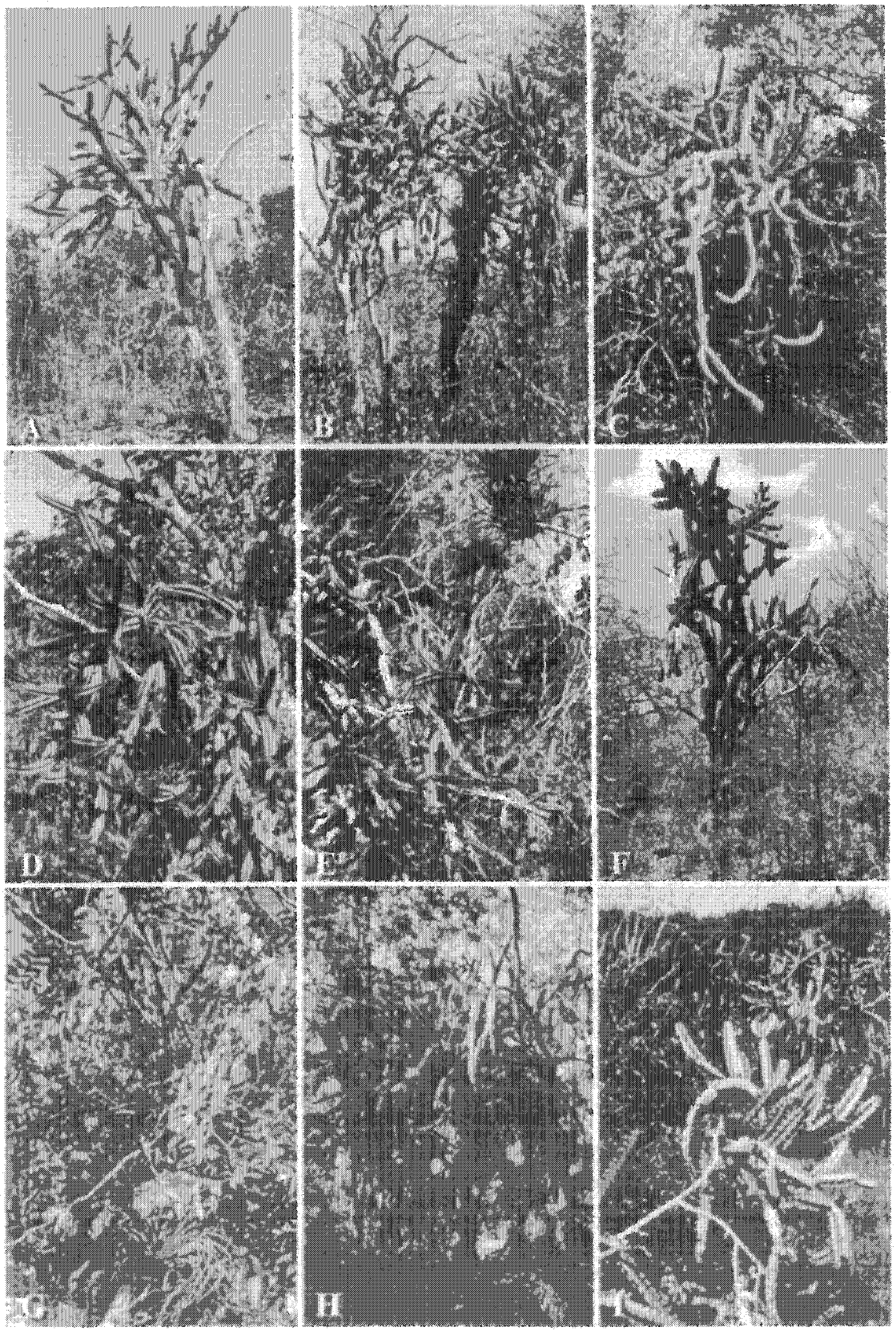

Plate 3.

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Plate 4. Growth habits of *Leptocereus* spp. (III).

A. The highly variable *Leptocereus weingartianus* ssp. *weingartianus* growing as a shrub. **B**. Large fruticose specimen of *L. weingartianus* ssp. *weingartianus* branched near ground level and above it. **C**, **D**, **E**. The slender-stemmed *L. weingartianus* spp. *demissus* with long trailing and scandent branches. **F**. Small arborescent *L. wrightii* ssp. *wrightii* with definite trunk. **G**. Close up of the stem segments of same plant. **H**. Arborescent growth form of *L. arboreus*. (A, from Cabo Samaná, Dominican Republic —8 Jun 1991; B, from vicinity of Bayahibe, Dominican Republic —22 Jan 1991; C, D, E, from Pedernales, ca. Cabo Rojo, Dominican Republic —31 May 1991; F, G, from Cojímar, Cuba —photograph taken by H. Liogier in 1957 or 1958; H, from Yaguanabo, Cuba —9 Jul 1993).

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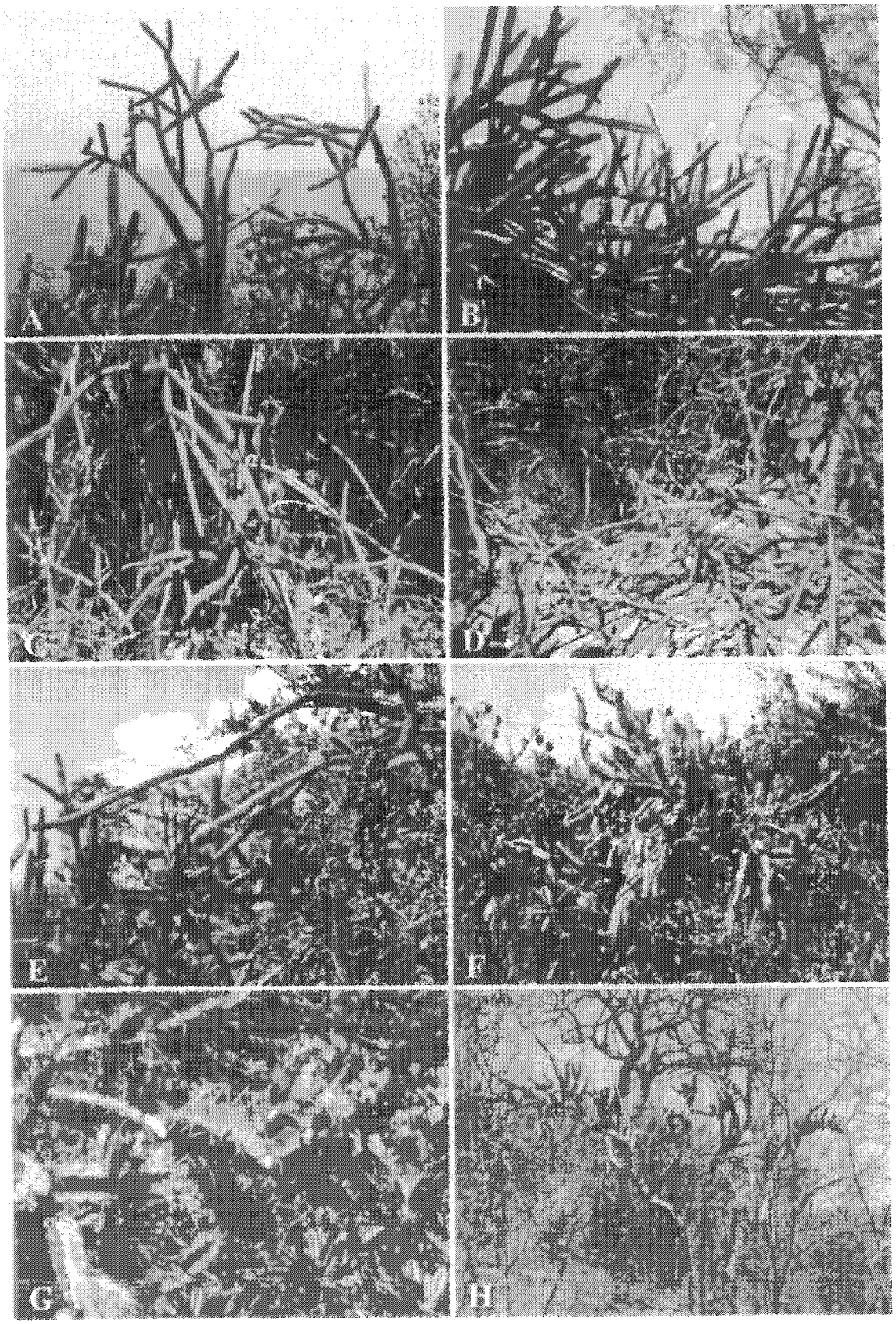

Plate 4.

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Plate 5. Growth habits of *Leptocereus* spp. (IV).

A. Ultimate stem segments of *Leptocereus assurgens*. **B**. Young fruticose individual of the same species. **C**. Mature segments of *L. ekmanii*. **D**. Shrubby habit of *L. quadricostatus* ssp. *parvispinus*. **E, F**. Large fruticose forms of *L. quadricostatus* ssp. *quadricostatus* with numerous branches. **G, H**. Tall arborescent growth forms of *L. weingartianus* spp. *weingartianus*. **I**. Miniature arborescent form of *L. weingartianus* spp. *weingartianus* 1.60 m high, with definite trunk and divaricate branching crown. (A, B, from Viñales, Cuba —21 Feb 1979; C, from Sierra de Guane, Cuba —6 June 1984; D, from Bosque Estatal de Guánica, Puerto Rico —23 Feb 1994; E, F, Cabo Rojo, Puerto Rico —10 Jan 1996; G, H, from vicinity of Bayahibe, Dominican Republic —22 Jan 1991; I, from Cabo Samaná, Dominican Republic —8 Jun 1991).

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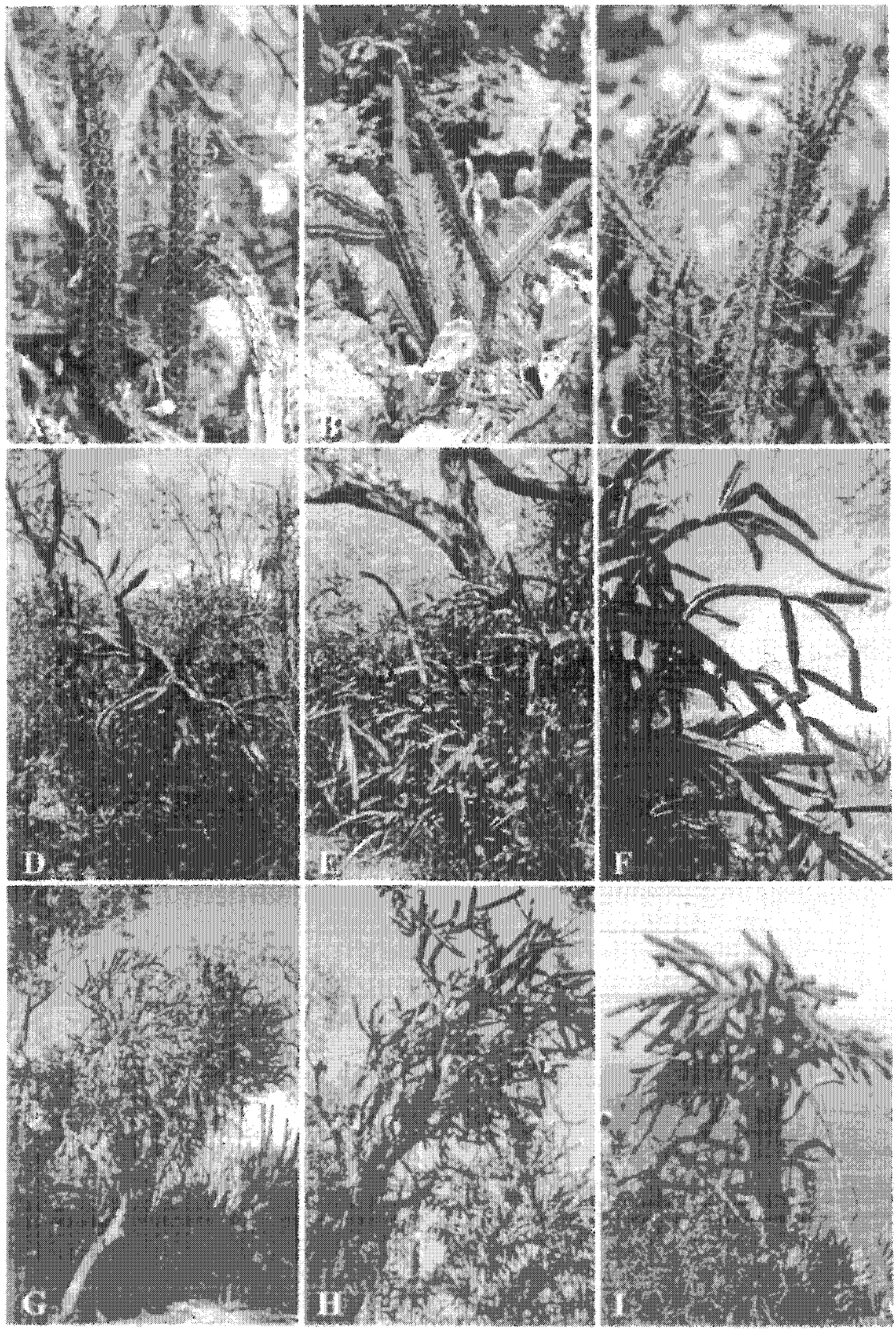

Plate 5.

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Plate 6. Growth habits of *Leptocereus* spp. and *Cereus* subgen. *Hamannia* (V).

A, B. Suffruticose growth form of *Leptocereus ekmanii*. **C.** Large fruticose form of *L. grantianus* ramified near ground level and above it. **D.** Fruticose habit of *L. maxonii* with erect branches ascending from or near the base. **E.** *L. quadricostatus* ssp. *quadricostatus*, with growth habit similar to *L. grantianus* (q.v.). **F.** Arborescent form of *Leptocereus santamarinae*. **G.** Atypical suffruticose form of *L. sylvestris* on sterile coraline limestone (such atypical forms seldom bear fruit). **H.** Branching pattern of *Cereus* (*Hamannia*) *fabiolae* showing segmented stems. (A, B, from Sierra de Guane, Cuba —6 June 1984; C, from Culebra island, Puerto Rico —8 Mar 1994; D, from valley of Rio Tacre, Guantánamo, Cuba —21 Mar 1990; E, from dry forests between Punta Melones and Laguna de Boquerón, Puerto Rico —13 Jun 1995; F, from vicinity of Santa Lucía beach, Cuba —15 Apr 1990; G, from coastal limestone terraces at Cabo Cruz, Cuba —4 May 1993; H, from Môle St. Nicolas, Haiti —19 Jan 1995).

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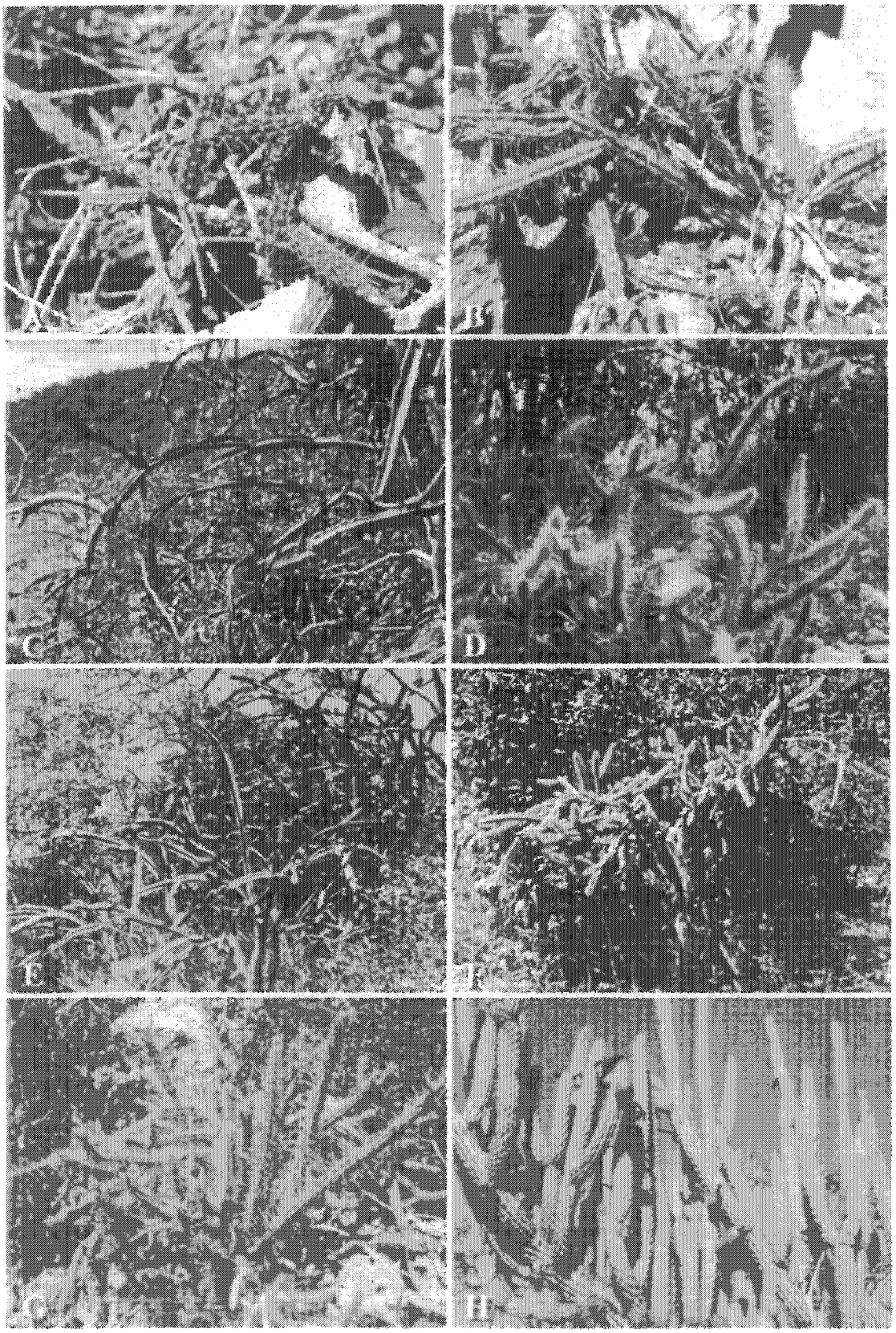

Plate 6.

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Plate 7. Growth habits of *Leptocereus* spp., *Cereus* subgen. *Hamannia*, and *Samaipaticereus corroanus* (VI).

A. Young erect stems of *Leptocereus maxonii* with their characteristic long central spines. **B.** Fruticose habit of the same species, its erect branches arching with age. **C, D.** Tall arborescent growth forms of *L. paniculatus,* with definite trunk and crown of diffuse branching design. **E, F.** Segmented stems of *Cereus* (*Hamannia*) *fabiolae*. **G.** Tall arborescent exemplar of the same species showing its compact crown of erect branches. **H, I.** Young, erect, 4-6-ribbed branches emerging on a fallen tree of *Samaipaticereus corroanus*. (A, B, from valley of Rio Tacre, Guantanamo, Cuba —21 Mar 1990; C, D, from El Limón, south to Enriquillo lake, Dominican Republic —30 Jan 1991; E, F, G, from Môle St. Nicolas, Haiti —19 Jan 1995; H, I, from vicinity of Samaipata, Bolivia —photograph taken in 1998 by Ramón Vargas).

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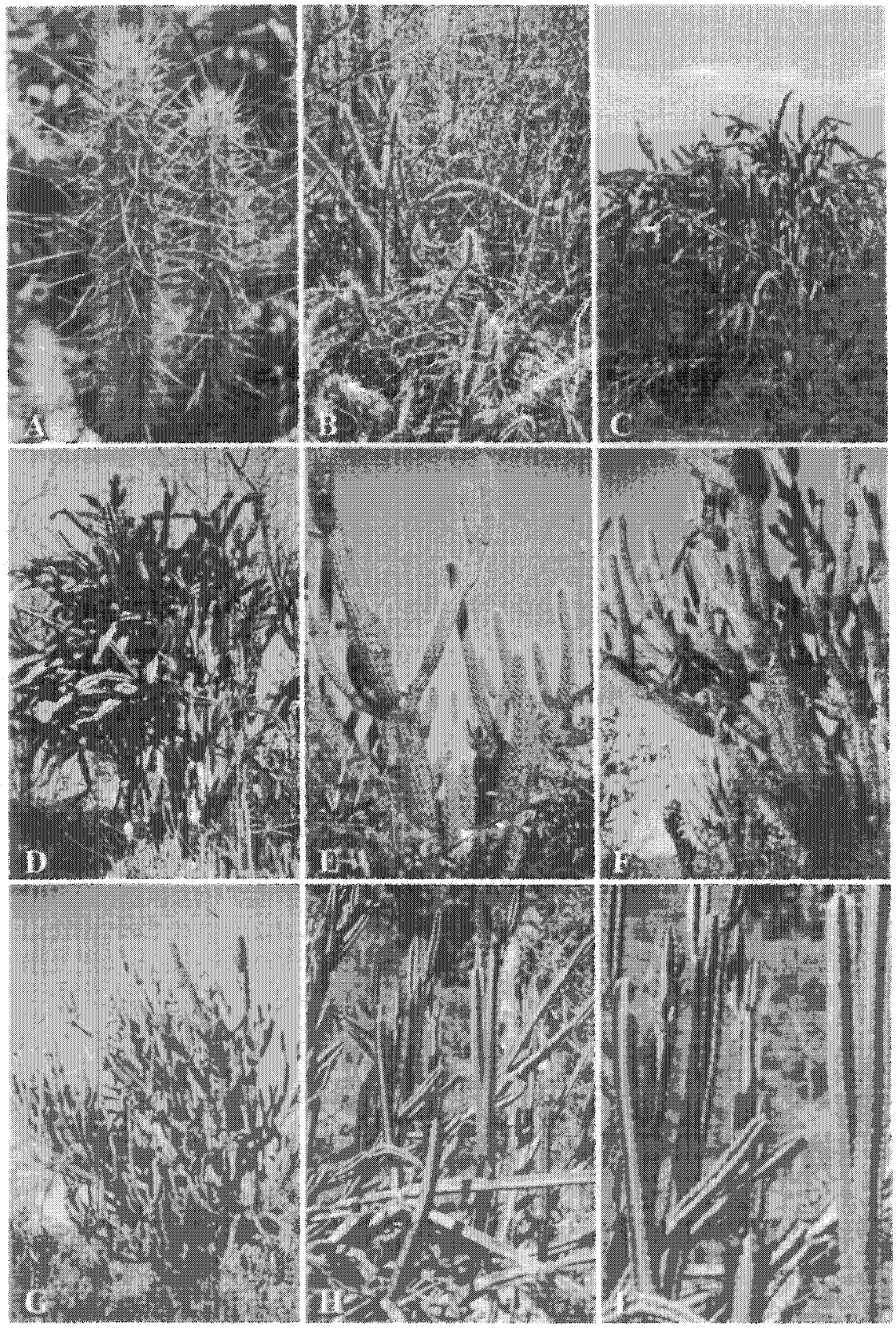

Plate 7.

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could be that apical dominance of an ancestral tall tree with diffuse branching design was altered to produce all the other procumbent, prostrate or scandent forms present in *Leptocereus*.

The variation in stem height in all the arborescent and many shrubby *Leptocereus* species correlates with variation in the height of surrounding vegetation. Being an upper canopy tree in the Étang Saumatre-Enriquillo basin in Hispaniola, for example, *Leptocereus paniculatus* grows as tall as the dry forests of this area. *Leptocereus santamarinae* —another example, may either be a small tree 3 m tall or an 8 m tall tree, depending on whether it grows in coastal shrublands or dry littoral forests. This is obviously a physiological response to photosynthetically active radiation and perhaps other abiotic factors of habitat. Because the surrounding vegetation tends to reduce the available radiation, these arborescent species apparently respond by producing the appropriate plant form, that is, the stems grow into the upper canopy positions. Despite the fact that the photosynthetically active radiation, age of the individual, availability of water, substrate, relief, and nature of neighboring vegetation may strongly influence the expression of habit in cacti, most species of *Leptocereus* have a specific growth pattern. The only remarkable exception is *L. weingartianus*, with tall arborescent forms to 8 m high, relatively compact fruticose plants with short trunk, and divaricate shrubs with numerous, long spreading stems that are moderate in thickness (subsp. *weingartianus*), to scandent and usually slender-stemmed (subsp. *demissus*). Such variability makes it impossible to apply a clear-cut categorization of growth habit to this particular species. The following is a practical classification design of all *Leptocereus* taxa, and the

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puzzling *Cereus* subgen. *Hamannia* of Haiti, each growth habit based on the largest and most typical design of a taxon (abbreviations of these growth habits are used in Tables 5 to 8):

I. TALL ARBORESCENT, MORE THAN 5 M HIGH (Plate 2, C, D; Plate 3, A, B, F; Plate 4, H; Plate 5, G, H; Plate 6, H; Plate 7, C, D, E, F, G).

A. Tall and often massive, to 10 m high, with a well-developed trunk and decurrent main branches that ramify diffusely to form an umbrella-like crown of short, articulated stems that are relatively thick [2] to moderate in thickness and oligo- to normocostate[3], having 4 to 6 ribs. These stems, which have narrow pith, may become pendent with age. —*Leptocereus arboreus* (Plate 3, F; Plate 4, H), *L. santamarinae* (Plate 3, A, B; also growth habit II.A), *L. weingartianus* ssp. *weingartianus* (Plate 5, G, H; also growth habits II.D and III.A), and *L. paniculatus* (Plate 2, C, D; Plate 7, C, D).

B. Tall, to 8 m high, with a distinct trunk and several arching main branches that give rise to numerous ascending, multicostate (10-16 ribs), cylindrical stems with wide pith. These stems, which are thick to moderate in thickness and have wide pith,

---

[2] The relative degree of stem thickness is based upon the following scale: Thick —3.6-6 cm in diameter; moderately thick —2.5-3.5 cm in diameter; slender —1-2.4 cm in diameter.

[3] The relative term "normocostate" is herein applied to rib numbers 5 and 6 in *Leptocereus* stems, which is the most common condition. Likewise, oligocostate stands for stems with 3 and 4 ribs, and multicostate for 7 or more ribs.

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may arch or curve with age but never pendent. —*Cereus* (subgen. *Hamannia*) *fabiolae* (Plate 6, H; Plate 7, E, F, G).

II. SMALL ARBORESCENT AND LARGE FRUTICOSE, 3 TO 5 M HIGH (Plate 3, C, D H; Plate 4, B, F; Plate 5, D, E, F; Plate 6, C, E, F).

A. Small trees with a definite trunk 0.7 to 1.5 m long and numerous arching stems that are longer than in group I.A, thick to moderate in thickness, and oligo- to normocostate, having 4 to 6 ribs. —*Leptocereus wrightii* subsp. *wrightii* (Plate 4, F), *L. wrightii* subsp. *gracilis*, *L. sylvestris* (Plate 3, H), and *L. santamarinae* (Plate 3, C, D; Plate 6, F; also growth habit I.A).

B. Small trees/large shrubs with definite but very short, relatively thick trunk 25 to 40 cm long and a dense crown of numerous, arching stems that are slender and normocostate, having 5 to 6 ribs. —*Leptocereus leonii.*

C. Large shrubs branched near ground level and above it, with numerous oligocostate, 3- to 4-ribbed (very rarely 5-ribbed), relatively thick stems that ascend and arch diffusely, the apex frequently touching the ground and giving rise to new ascending/arching stems that may root in contact with soil. —*Leptocereus quadricostatus* subsp. *quadricostatus* (Plate 5, E, F; Plate 6, E), *L. quadricostatus* subsp. *parvispinus* (Plate 5, D), and *L. grantianus* (Plate 6, C).

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D. Large shrubs branched near ground level and above it, with numerous, normocostate, 5 to 6-ribbed, moderately thick stems that grow long, extending and often leaning on neighboring vegetation for support. —*Leptocereus weingartianus* ssp. *weingartianus* (Plate 4, B; also growth habits I.A and III.A).

III. MINIATURE ARBORESCENT AND FRUTICOSE, 1.5 TO 2.9 M HIGH (Plate 2, E, F; Plate 4, A, B; Plate 5, B, I; Plate 7, B).

A. Miniature arborescent with a definite trunk and divaricate branching crown, the stems normocostate, 5- or 6-ribbed and moderately thick. —*Leptocereus weingartianus* subsp. *weingartianus* (Plate 4, A; Plate 5, I; also growth habits I.A and II.D).

B. Fruticose plants ramified near ground level, with relatively long, erect branches that ascend from or near the base and arch or curve with age. Ultimate stem segments erect, ascending, oligo- to multicostate, and with variable thickness. —*Leptocereus scopulophilus* (Plate 3, G), *L. carinatus,* and *L. maxonii* (Plate 7, B).

C. Fruticose plants ramified near ground level or above it, with rather multicostate (usually 7- or 8-ribbed), spreading, diffusely branched stems that are slender and

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may lean on neighboring vegetation for support. —*Leptocereus assurgens* (Plate 5, B).

D. Fruticose plants with arching stems from a common base, that repeatedly branch and slope gradually downward in one direction. The stems are moderate in thickness and normocostate/ multicostate, having 6 or 7 ribs. —*Leptocereus chrysotyrius* (Plate 2, E, F).

IV. SUFFRUTICOSE, LESS THAN 1.5 M HIGH (Plate 5, C; Plate 6, A, B).

A. Suffruticose and ramified near ground level or above it, with short, straight, normocostate/multicostate stems (6- or 7-ribbed) that are erect or spreading, and slender. —*Leptocereus ekmanii* (Plate 5, C; Plate 6, A, B).

V. SCANDENT (Plate 4, C, D, E).

A. Normocostate/multicostate yet slender-stemmed plants with relatively few long scandent or trailing branches. Because the inner tissues cannot ensure rigidity the stems curve randomly, the resulting curvatures being determined by the presence (or absence) of supporting points. The basal and distal parts of each axis are

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morphologically identical. —*Leptocereus weingartianus* subsp. *demissus* (Plate 4, C, D, E).

VI. PROCUMBENT OR DANGLING (Plate 3, E).

A. **Procumbent**-arched or lying flat on the ground, but only rooting eventually at nodes. The divaricate, moderately thick and short to moderately long stems which are multicostate arise from a common base and extend outwards, crawling. There is a slight differentiation between the dorsal and ventral sides of the stem, the vascular cylinder often being a little excentrical. —*Leptocereus prostratus.*

B. **Low** plant with few, moderate to relatively thick, normocostate/multicostate segmented long branches arising from a short base. At first the branches extend horizontally, becoming pendent with age. No dorsiventral differentiation is present. Because these plants are cliff dwellers, their dangling stems may reach 4 m long. —*Leptocereus albellus* (Plate 3, E).

2.2. Roots

All *Leptocereus* taxa have long, shallow horizontal roots that radiate from the plant in all directions. They are generally unbranched and are no more than five to 20 cm below the soil surface. These roots are fully lignified, and have a fairly thin cylinder

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Table 5. Contrasted quantitative stem characters in *Leptocereus* (I). GH, growth habit following classification explained under epigraph 2.1; LS, length of ultimate stem segment (cm); WS, width of ultimate stem segments (mm); NR, number of ribs; RH, rib height (mm); WR, basal width of rib (mm).

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TAXON	GH	LS	WS	NR	RH	WR
L. assurgens	III.C	30-200	15-25	6-10	2-6	2-4
L. chrysotyrius	III.D	15-100	25-30	6-7	8-13	4-8
L. ekmanii	IV.A	10-50	10-17	6-7	3-5	2-3
L. prostratus	VI.A	30-150	15-30	7-8	5-8	7-9
L. albellus	VI.B	38-190	30-40	6-7	9-13	7-10
L. wrightii						
subsp. *wrightii*	II.A	15-165	40-60	4-5	14-24	6-9
subsp. *gracilis*	II.A	25-190	38-55	4-5	13-22	6-10
L. scopulophilus	III.B	25-150	25-42	4-6	8-12	3-9
L. leonii	II.B	10-90	15-23	5-8	9-11	4-7
L. arboreus	I.A	15-100	42-60	4-6	15-25	5-10
L. carinatus	III.B	30-200	25-40	4-6	8-17	3-7
L. sylvestris	II.A	23-110	20-32	5-7	9-16	5-7
L. maxonii	III.B	20-95	21-35	5-7	5-15	6-9
L. santamarinae	I.A	25-110	35-55	5-6	10-21	3-9
L. weingartianus	I.A, II.D					
subsp. *weingartianus*	III.A	15-150	20-35	5-6	6-12	6-10
subsp. *demissus*	V.A	30-300	13-20	6-7	2.5-6	3-5
L. paniculatus	I.A	15-80	42-60	4-6	13-26	8-15
L. quadricostatus						
subsp. *quadricostatus*	II.C	15-120	25-62	3-4	9-23	5-9
subsp. *parvispinus*	II.C	15-130	35-63	3-4	10-25	6-9
L. grantianus	II.C	15-150	30-60	3-5	10-24	5-9
Cereus (Hamannia) fabiolae	I.B	25-180	30-50	10-16	6-9	3.5-9

Table 5.

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Table 6. Contrasted quantitative stem characters in *Leptocereus* (II). RR, rib-to-rib distance, taken from their margins (mm); SM, depth of stem grooves, taken from the midline between the margins of two adjoining ribs (mm); CW, cortex width (distance between the bottom of the stem groove and the vascular cylinder, in mm); CR, distance between the crest of a rib projection (podarium) and the vascular cylinder (mm); VC, diameter of vascular cylinder (mm); DP, diameter of pith (mm).

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TAXON	RR	SM	CW	CR	VC	DP
L. assurgens	5-10	3-5	3-4	7-8	4-5	2.5-3.5
L. chrysotyrius	12-15	5-10	4-5	11-13	5-6	3.6-4
L. ekmanii	4-6	2-3	3-6	5-6	2-3	1-1.9
L. prostratus	9-13	3-5	5-8	9-13	6-8	3.7-4.3
L. albellus	15-20	5-8	4-6	13-15	6-8	3.5-5
L. wrightii						
subsp. *wrightii*	23-42	10-16	2-4	18-26	5-7	3-5.2
subsp. *gracilis*	22-38	6-12	3-4	18-23	5-7	2.8-4.8
L. scopulophilus	14-18	4-8	2-3	11-13	5-7	3-3.8
L. leonii	10-13	3-8	3-4	10-11	3-5	1.8-2
L. arboreus	23-44	11-16	3-5	23-25	7-8	5.2-5.4
L. carinatus	17-25	6-14	3-4	13-15	5-6	3-3.5
L. sylvestris	14-21	6-12	3-5	14-16	4-8	2.6-5
L. maxonii	9-13	2-6	6-7	12-14	5-7	3.9-4.7
L. santamarinae	17-25	6-14	4-5	14-22	6-9	4.6-5.6
L. weingartianus						
subsp. *weingartianus*	10-19	3-8	3-5	8-14	4-6	2.6-5
subsp. *demissus*	7-10	1-2	3-5	5-7	3-4	2.2-2.6
L. paniculatus	20-36	7-15	5-6	21-25	9-10	6-6.2
L. quadricostatus						
subsp. *quadricostatus*	22-32	6-14	3-5	19-22	5-6	2.8-3.4
subsp. *parvispinus*	23-44	6-15	4-5	20-21	5-6	2.9-3.1
L. grantianus	21-31	6-15	3-4	20-23	5-6	2.8-3.5
Cereus (Hamarnia) fabiolae	6-10	3.5-4.5	4.5-7	10-14	11-18	10-15

Table 6.

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Table 7. Contrasted quantitative stem characters in *Leptocereus* (III). FC, presence of fibrous reticle in cortex (present: 1; absent: 2); LA, longitudinal diameter of areole (mm); WA, transversal diameter of areole (mm); IA, distance between areoles (mm); DS, depth of rib sinuses (mm);. TS, total number of spines in areole; TL, length of spines (mm).

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TAXON	FC	LA	WA	IA	DS	TS	TL
L. assurgens	1	2-3	2-2.5	9-15	1-1.5	10-16	5-20
L. chrysotyrius	1	4-5	3.5-5	15-20	1-2	9-13	9-53
L. ekmanii	1	1.5-2.5	1.5-2.5	8-15	0.5-1	9-13	3-43
L. prostratus	1	2-4	2-4	10-19	0-1.5	15-20	6-52
L. albellus	1	3-4	3-4	9-15	1-2	10-15	6-25
L. wrightii							
subsp. *wrightii*	1	4-5	3-5	10-40	2.5-5	9-20	6-45
subsp. *gracilis*	1	4-5	3-4.5	15-27	3-4.5	6-18	1-15
L. scopulophilus	1	3-4.5	2-4	15-33	0.5-2	7-19	8-65
L. leonii	1	2-4	1.5-3	10-22	1.5-3.5	6-13	8-27
L. arboreus	1	3-4	2.6-3.5	16-40	2-4	8-17	5-35
L. carinatus	1	4-6	3-4.5	14-35	3.5-5	5-11	7-61
L. sylvestris	1	3-4	2.5-3	10-23	3-6	15-20	5-34
L. maxonii	1	3.5-4.5	3-4.5	12-23	2-4	17-24	5-70
L. santamarinae	1	3-4.5	3-4	12-18	1.5-3	8-25	5-24
L. weingartianus							
subsp. *weingartianus*	2	3-4	2-3	11-16	1.5-4	13-20	7-35
subsp. *demissus*	2	2-4	2-4	8-16	0-1	15-22	5-25
L. paniculatus	2	3-4	2.5-4	15-25	1.5-3.5	12-21	4-20
L. quadricostatus							
subsp. *quadricostatus*	2	2-6	2-5	20-30	3-5.5	8-11	4-40
subsp. *parvispinus*	2	3.5-6	2.5-5	20-29	2-4.5	10-15	3-13
L. grantianus	2	2-4	2-3	20-28	2.5-5	0-4	0.5-2
Cereus (Hamannia) fabiolae	2	3-4.5	3-4.5	13-22	2-3.5	10-22	6-45

Table 7.

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Table 8. Contrasted quantitative stem characters in *Leptocereus* (IV). TW, diameter of spines at base (mm); CS, number of central spines in areole; LC, length of central spines (mm); DC, diameter of central spines (mm); RS, number of radial spines in areole; LR, length of radial spines (mm); DR, diameter of radial spines (mm).

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TAXON	TW	CS	LC	DC	RS	LR	DR
L. assurgens	0.1-0.2	3-4	9-20	0.2-0.3	7-12	5-15	0.1-0.2
L. chrysotyrius	0.2-0.7	3-5	22-53	0.4-0.7	6-9	9-24	0.2-0.5
L. ekmanii	0.1-0.3	1-4	9-43	0.2-0.3	6-10	3-30	0.1-0.2
L. prostratus	0.1-0.5	6-10	13-52	0.2-0.5	9-12	6-15	0.1-0.2
L. albellus	0.1-0.5	4	15-25	0.4-0.5	6-11	6-18	0.1-0.4
L. wrightii							
subsp. *wrightii*	0.1-0.7	3-10	12-45	0.3-0.7	6-10	6-24	0.1-0.5
subsp. *gracilis*	0.1-0.4	6-18	1-15	0.1-0.4	0	0	0
L. scopulophilus	0.2-0.7	2-6	19-65	0.3-0.7	5-13	8-25	0.2-0.3
L. leonii	0.2-0.4	1-4	15-27	0.3-0.4	5-9	8-15	0.2-0.35
L. arboreus	0.2-0.4	2-7	13-35	0.3-0.4	6-10	5-14	0.2-0.3
L. carinatus	0.2-1	1-5	26-61	0.2-1	4-6	7-30	0.2-0.5
L. sylvestris	0.1-0.5	6-8	12-35	0.3-0.5	9-12	5-14	0.1-0.25
L. maxonii	0.1-0.6	7-10	12-70	0.3-0.6	10-14	5-17	0.1-0.15
L. santamarinae	0.1-0.4	2-13	9-24	0.25-0.4	6-12	5-13	0.1-0.2
L. weingartianus							
subsp. *weingartianus*	0.1-0.5	4-7	10-35	0.2-0.5	8-14	7-15	0.1-0.3
ssp. *demissus*	0.1-0.5	4-8	7-25	0.2-0.5	10-14	5-13	0.1-0.3
L. paniculatus	0.2-0.4	4-6	9-20	0.3-0.4	8-15	4-13	0.2-0.4
L. quadricostatus							
subsp. *quadricostatus*	0.2-0.6	2-3	13-40	0.4-0.6	6-8	4-20	0.2-0.6
subsp. *parvispinus*	0.1-0.5	2-4	7-13	0.3-0.5	8-10	3-10	0.1-0.5
L. grantianus	0.08-0.1	0-1	0-1	0.08	0-3	0.5-2	0.08-0.1
Cereus (Hamannia) fabiolae	0.1-0.5	2-7	19-45	0.2-0.5	7-15	6-20	0.1-0.25

Table 8.

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of cortex 1-2 mm thick and lack a pith. They are covered at a very early stage of growth by tawnish to brownish plates of corky bark. *Leptocereus weingartianus* subsp. *weingartiamus* has slightly thickened roots for water storage. Because these roots have been transformed into storage organs and have largely lost their root characteristics, their surface (periderm) is relatively smooth. There are not adventitious root systems, even in creeping or prostate terrestrial species such as *L. prostratus*.

2.3. Stem segments

All *Leptocereus* species have a determinate growth mode in their vegetative body, producing discrete shoot units (stem segments) regardless of environmental conditions. Some species, *e.g.*, *L. arboreus*, tend to have short segments, while others have much longer ones, 3 m long or more (*e.g.*, *L. weingartianus* subsp. *demissus*). Ultimate stem segments of *Leptocereus* may be straight or arched, cylindrical or somewhat attenuate at the apex, and their width varies from 1 to 6.3 cm (Table 5). No seasonal or annual constrictions are present. Their color varies from dull green, passing into grayish-blue (*glaucus*) of *Leptocereus paniculatus*, glossy, clear, emerald green of *L. wrightii*, and the deep dark green (*atrovirens*) of *L. grantianus* (Plates 8, 9, and 10). The initial disposition of leaf bases (podaria) and areoles in the stem conforms to helically alternate phyllotaxy, producing varying numbers of orthostichies in the Fibonacci series. Outward expansion of cortex, and coalescence of the decurrent podaria in adjacent orthostichies, produces 3 to 10, winglike, rather thin vertical ribs in *Leptocereus* (Figs. 2 and 3). The presence of ribs results in a stem shape that not only

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can efficiently absorb photosynthetically active radiation without greatly increasing transpiration, but that is also capable of accordion-like expansion and contraction according to water availability. Too many ribs, however, does not seem to be convenient for those *Leptocereus* species (*e.g.*, *L. arboreus, L. santamarinae, L. paniculatus*) occurring on coastal or subcoastal areas under a dry, hot, or semi-desert (thermohemieremic) climate lacking a typical rainfall distribution. Because increasing surface area per volume by ribbing always increases potential transpiration, the highest number of ribs is more expected to occur in species that are confined to inland mountain ranges under a winter dry (mesoxerochimenic) tropical climate —subhumid type— with a mean annual rainfall over 900 or 1000 mm. Examples of such species are *L. assurgens* (Fig. 2, A), *L. chrysotyrius* (Fig. 3, F), *L. ekmanii* (Fig. 2, H), *L. prostratus* (Fig. 2, E) and *L. albellus* (Fig. 3, C). The ribs of *Leptocereus* are high (24 to 26 mm) to fairly low (2 to 3 mm), and their width at the base varies from 2 to 15 mm (Table 5). They are usually acute in transection, and in side view their margins look crenate, sinuate (sinusoidal), straight, or broadly dentate (Fig. 4). The ribs are not tuberculate along the margin, and lack the characteristic transverse folds of many columnar Cactoideae (*e.g.*, *Pilosocereus*, *Cereus*, etc.).

2.4. Areoles and spines

The areoles of *Leptocereus* are circular, broadly elliptical, or elliptic-oblong proleptic axillary buds that produce spines and trichomes (Plates 11, 12, 13, and 14). Areoles are either horizontal, as in *L. prostratus* (Fig. 4, K1, K2) and *L. weingartianus*

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subsp. *demissus* (Fig. 4, E4), or more often inclined towards the apex, and 1.5 to 6 mm in diameter, with the long axis longitudinal to the rib axis (Table 7). Areoles are separated 0.8 to 4 cm in the rib margin, and often in *L. wrightii, L. scopulophilus*, and *L. arboreus* there is a small, shallow notch midway between them (Fig 4, C2, C3, G, J). Usually in *Leptocereus* there is no difference between vegetative and flower-bearing areoles, which seems to be the plesiomorphic character state in subfamily Cactoideae. Some species, however, produce cephalia or cephalioid structures representing substantial modifications to stem morphology, with highly modified areoles. Areole symmetry varies between superficially radial, with all spines spreading and essentially similar in length, width, and color (*e.g.*, in *Leptocereus paniculatus*), and bilateral, with more or less differentiation into central —or centrals— and radial spines (*e.g.*, in *L. prostratus*). Areoles in *Leptocereus* are all indeterminate, *i.e.*, they are subjected to enlargement and growth of additional spines after their emergence from the shoot's apical meristem. In most species this condition leads to exaggerated continuous growth of spines in trunk or basal branches (Plates 15 and 16). However, areoles are usually "dormant" during the first year of life of a stem segment, and the growth of secondary spines only occurs in two- to three-year old branches. The only exception seems to be the long central spine of *Leptocereus prostratus*, which grows continuously for a relatively long period of time after being produced (Plate 15, E, F). In *Cereus* (*Hamannia*) *fabiolae*, on the contrary, there is no dormancy period, and growth of additional spines projecting upwards at 35° to 50° starts shortly after the emergence of the areole from the stem apex (Plate 14, H).

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Plate 8. Ultimate stem segments of *Leptocereus* spp. (I).

A. *Leptocereus assurgens*. **B.** Apex of ultimate stem segment of *L. wrightii* subsp. *wrightii*. **C.** Apex of ultimate stem segment of *L. paniculatus*. **D.** Young stem of a juvenile plant of *L. wrightii* subsp. *wrightii*. **E.** Ultimate stem segment of a mature plant of the same subspecies. **F.** Ultimate stem segment of the short-spined *L. wrightii* subsp. *gracilis*. (A, from Moncada, West of Viñales, Cuba —collected and photographed by F. Areces-Berazaín, 18 Jul 1997; B, D, E, from Bahia Honda, Cuba —12 Dec 1993; C, from La Descubierta, Dominican Republic —7 Jan 1995; F, from San Diego, Pinar del Rio province, Cuba —27 Nov 1985).

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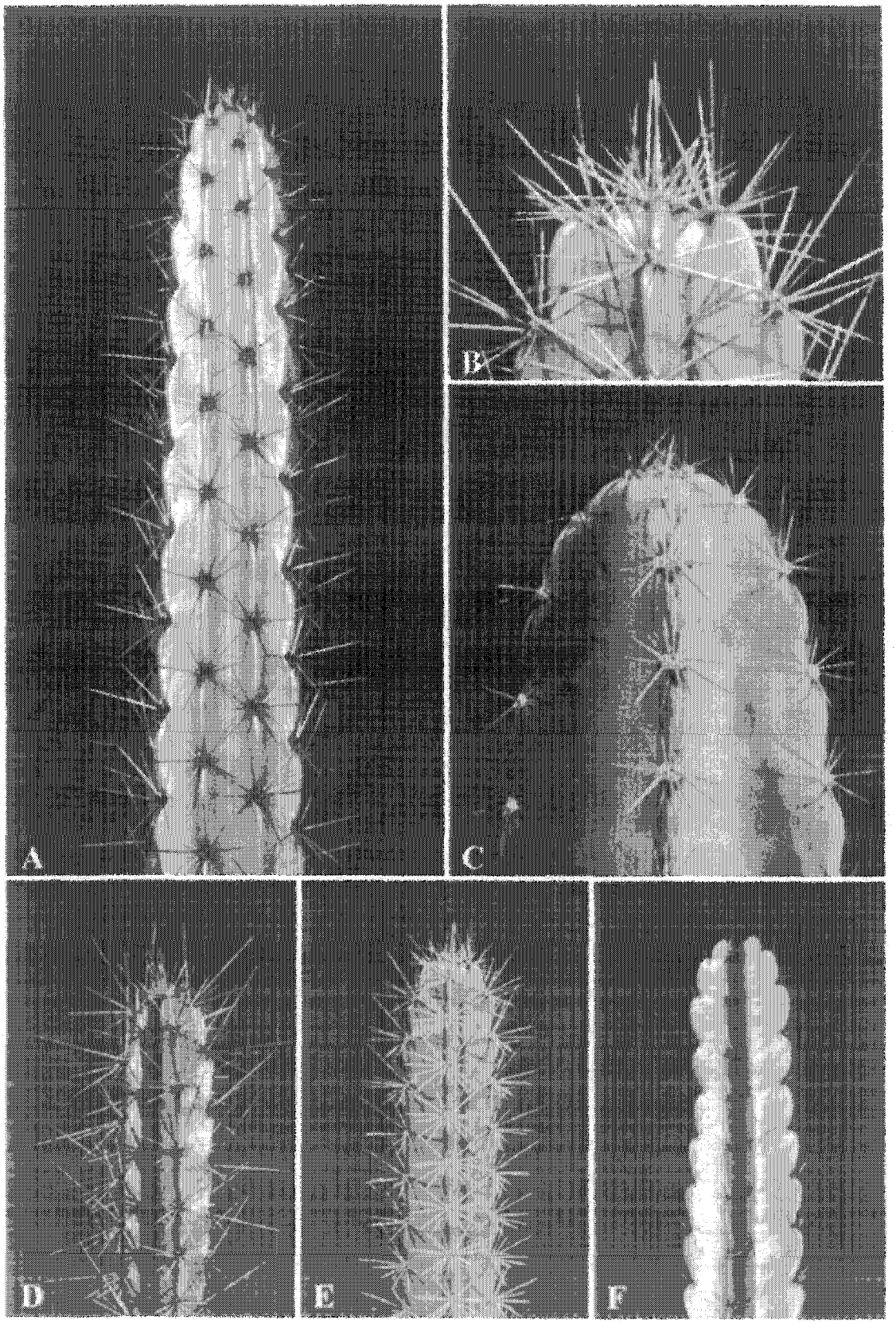

Plate 8.

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Plate 9. Ultimate stem segments of *Leptocereus* spp. (II).

A. Segment of *Leptocereus arboreus* from a plant growing in open woodland, on exposed situation. **B**. Same species, from a plant growing within a dry forest and surrounded by neighboring vegetation. **C**. *L. carinatus*. **D**. *L. chrysotyrius*. **E**. *L. ekmanii*. **F**. *L. grantianus*. **G**. *L. leonii*. **H**. *L. maxonii*. **I**. *L. paniculatus*. (A, B, from Yaguanabo, Cuba —9 Jul 1993; C, from type plant, Sierra del Chorrillo, Najasa, Cuba —12 Sep 1990; D, from San Diego, Pinar del Rio province, Cuba —3 Nov 1976; E, from Sierra de Guane, Cuba —6 Jun 1984; F, from Culebra Island, Puerto Rico —8 Mar 1994; G, from Sierra de Anafe, Cuba —29 Oct 1975; H, from valley of Rio Tacre, Guantánamo, Cuba —21 Mar 1990; I, from La Descubierta, Dominican Republic —7 Jan 1995).

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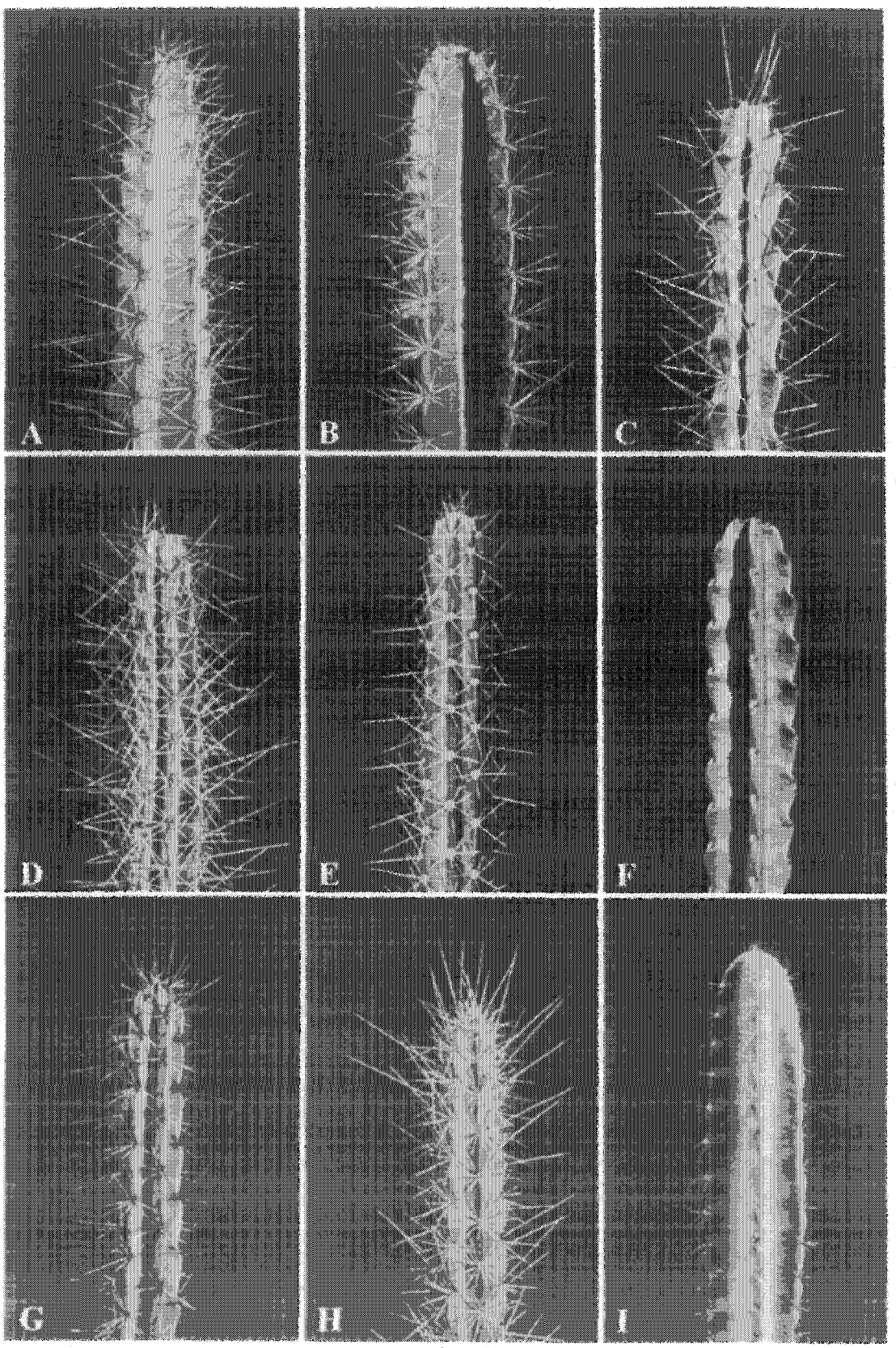

Plate 9.

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Plate 10. Ultimate stem segments of *Leptocereus* spp. and *Cereus* subgen. *Hamannia* (III).

A. *Leptocereus prostratus*. **B**. *L. quadricostatus* subsp. *quadricostatus*. **C**. *L. quadricostatus* subsp. *parvispinus*. **D**. *L. weingartianus* subsp. *weingartianus*. **E**. *L. weingartianus* subsp. *demissus*. **F**. *L. santamarinae*. **G**. *L. sylvestris*. **H**. *L. scopulophilus*. **I**. *Cereus* (*Hamannia*) *fabiolae*. (A, from type locality at Sumidero, Pinar del Rio province, Cuba —5 Mar 1992; B, from dry forests between Punta Melones and Laguna de Boquerón, Puerto Rico —13 Jun 1995; C, from Bosque Estatal de Guánica, Puerto Rico —23 Feb 1994; D, from vicinity of Bayahibe, Dominican Republic —22 Jan 1991; E, from Pedernales, ca. Cabo Rojo, Dominican Republic, —31 May 1991; F, from type plant, vicinity of Santa Lucía beach, Cuba —15 Apr 1990; G, from Boca del Rio Las Puercas, Pilón, Cuba —4 May 1993; H, from type plant, summit of Somorrostro hill, Cuba —17 Apr 1976; I, from Môle St. Nicolas, Haiti —19 Jan 1995).

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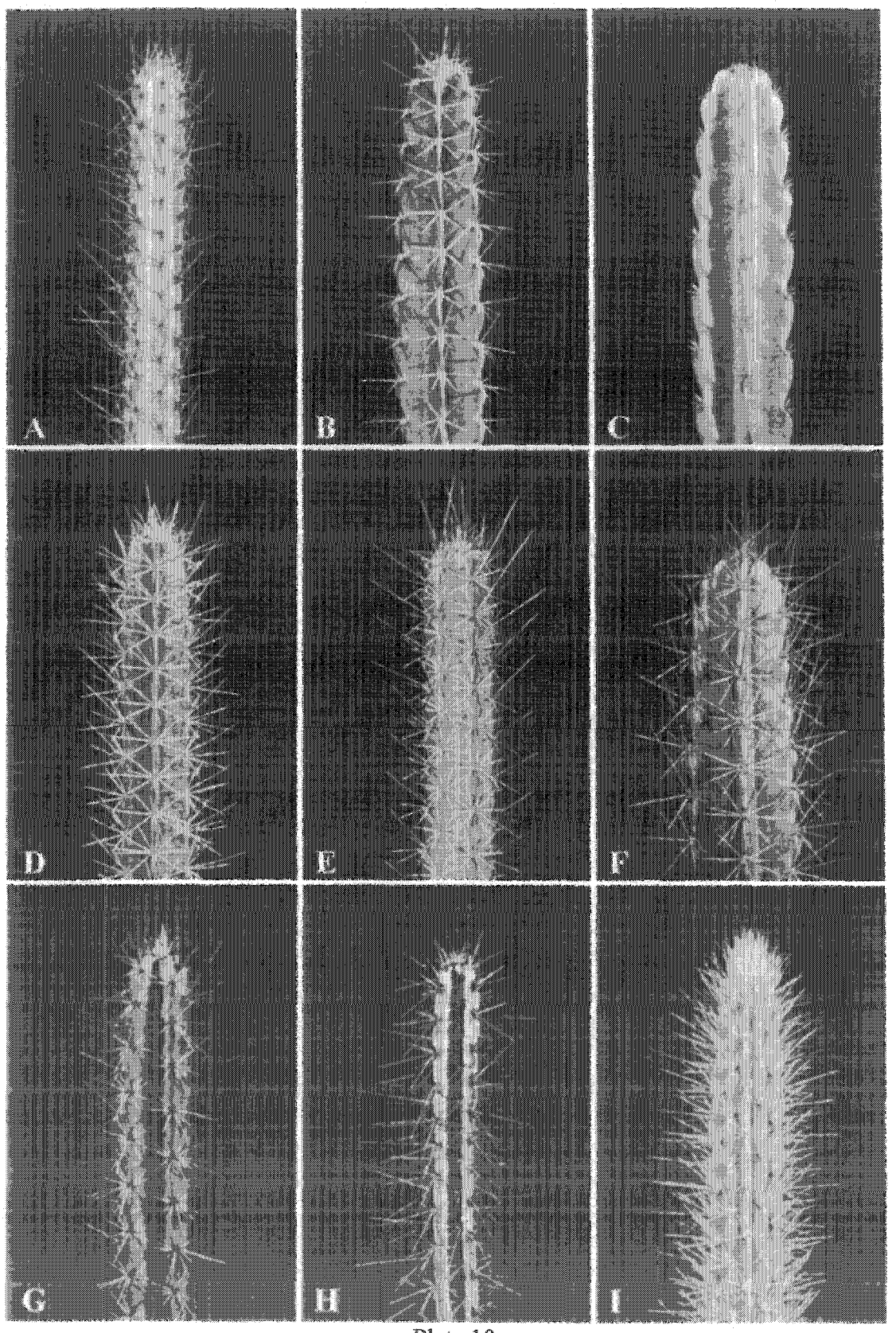

Plate 10.

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Fig. 2. Transverse sections of stems of *Leptocereus* spp. and *Cereus* subgen. *Hamannia*, and rib of this latter taxon (areoles and/or spines not depicted). All sectioned stems are one-year old, except for A2, C1, E2, J3, K1, K4, L1, and M2, which are two- to three-years old. The scale bar is 4 cm for all stem and rib drawings.

A1, **A2**. *Leptocereus assurgens*. **B1**, **B2**. *L. santamarinae*. **C1**, **C2**. *L. sylvestris*. **D**. *L. paniculatus*. **E1**, **E2**. *L. prostratus*. **F1**. Four-ribbed stem of *L. quadricostatus* subsp. *quadricostatus*; **F2**. Three-ribbed stem of same subspecies. **G1**, **G2**. Four-ribbed stems of *L. quadricostatus* subsp. *parvispinus*; **G3**. Three-ribbed stem of same subspecies. **H1**, **H2**. *L. ekmanii*. **I1**, **I2**, **I3**. *L. carinatus*. **J1**, **J2**, **J3**, **J4**. Four- and five-ribbed stems of *L. wrightii* subsp. *wrightii*. **K1**, **K2**, **K3**, **K4**. *L. weingartianus* subsp. *weingartianus*. **L1**, **L2**. *L. weingartianus* subsp. *demissus*. **M1**, **M2**. Transverse sections of *Cereus* (*Hamannia*) *fabiolae*. **M3**. Rib of same species. (A1, A2, from Moncada, West of Viñales, Cuba —collected by F. Areces-Berazaín, 18 Jul 1997; B1, B2, from type plant, vicinity of Santa Lucía beach, Cuba —15 Apr 1990; C1, C2, from Boca de Rio Las Puercas, Pilón, Cuba —4 May 1993; D, from La Descubierta, Dominican Republic —7 Jan 1995; E1, E2, from type locality at Sumidero, Pinar del Rio province, Cuba —5 Mar 1992; F1, F2, from dry forests between Punta Melones and Laguna de Boquerón, Puerto Rico —13 Jun 1995; G1, G2, G3, from Bosque Estatal de Guánica, Puerto Rico —23 Feb 1994; H1, H2, from Sierra de Guane, Cuba —6 Jun 1984; I1, I2, I3, from type plant, Sierra del Chorrillo, Najasa, Cuba —12 Sep 1990; J1, J2, from Bahia Honda, Cuba —12 Dec 1993; J3, J4, from Cojímar, Cuba —1 Jun 1976; K1, K2, from Cabo Samaná, Dominican Republic —8 Jun 1991; K3, K4, from vicinity of Bayahibe,

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Fig. 2 (cont.).

Dominican Republic —22 Jan 1991; L1, L2, from Pedernales, ca. Cabo Rojo, Dominican Republic —31 May 1991; M1, M2, M3, from Môle St. Nicolas, Haiti —19 Jan 1995).

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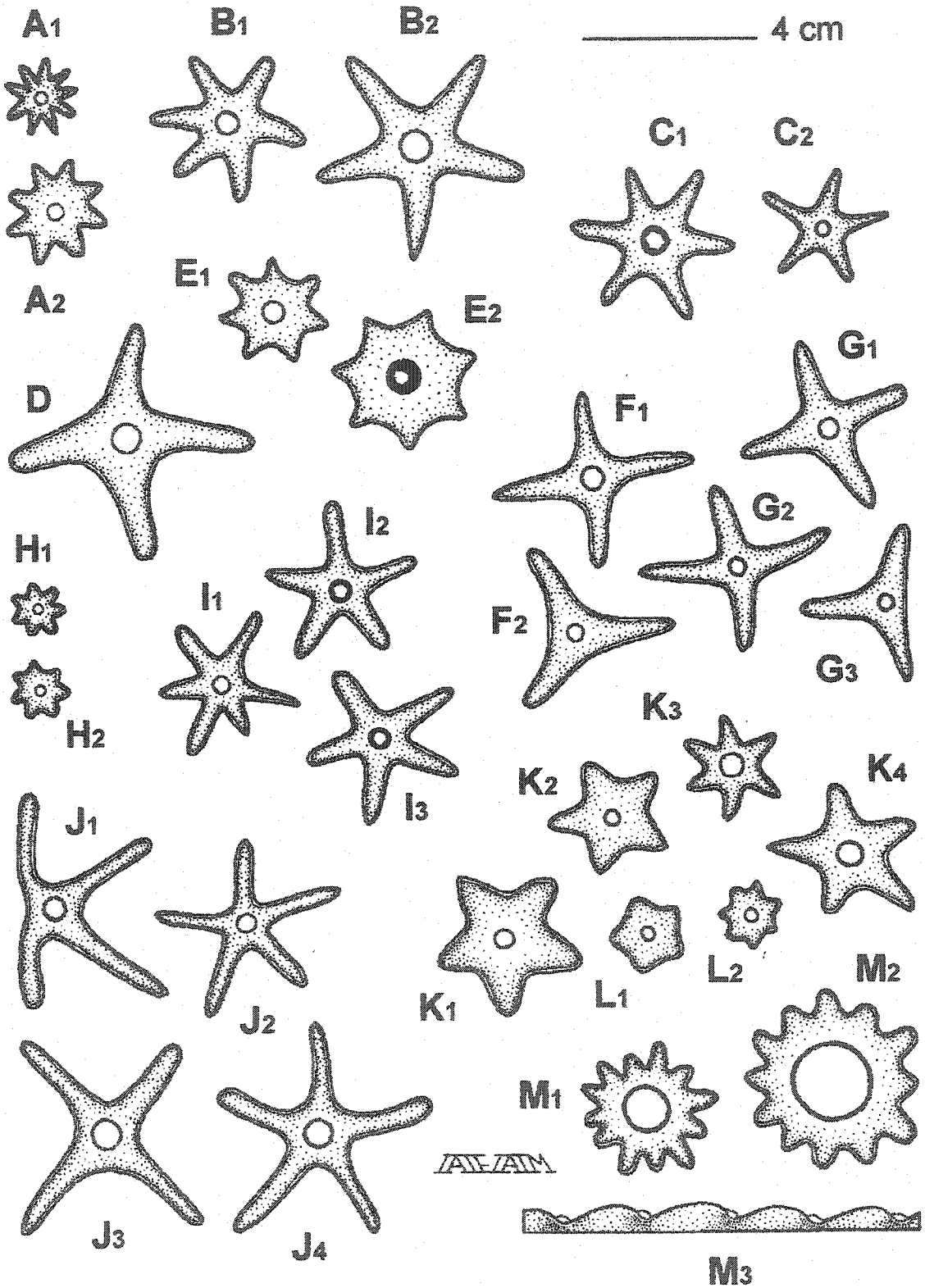

Figure 2.

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Fig. 3. Transverse sections of stems, flowers, and fruits of *Leptocereus* spp. (areoles and spines in transverse sections not depicted). All sectioned stems are one-year old, except for A, D3, and G2, which are two- to three-years old. The scale bars are 4 cm for stem sections, and 1 cm for all flower and fruit drawings.

A. *Leptocereus wrightii* subsp. *gracilis*. **B**. *L. grantianus*. **C1**, **C2**. *L. albellus*. **D1**, **D2**, **D3**. *L. scopulophilus*. **E**. *L. leonii*. **F1**, **F2**. *L. chrysotyrius*. **G1**, **G2**. *L. maxonii*. **H**. *L. arboreus*. **I1**. Flower of *L. scopulophilus*. **I2**. Flower of same species, longitudinally sectioned. **J**. Fruit of same species. **K1**. Fruit of *L. leonii*. **K2**. Fruit of same species, longitudinally sectioned. **L**. Flower of same species. (A, from San Diego, Pinar del Rio province, Cuba —27 Nov 1985; B, from Culebra Island, Puerto Rico —8 Mar 1994; C1, C2, from Sierra de San Carlos, Cuba —28 Mar 1992; D1, D2, D3, from type plant, summit of Somorrostro hill, Cuba —17 Apr 1976; E, from type locality at Sierra de Anafe, Cuba —29 Oct 1975; F1, F2, from San Diego, Pinar del Rio province, Cuba —3 Nov 1976; G1, G2, from valley of Rio Tacre, Guantánamo, Cuba —21 Mar 1990; H, from Yaguanabo, Cuba —9 Jul 1993; I1, I2, from the type collection, summit of Somorrostro hill, Cuba —17 Apr 1976; J, from an original sketch by Bro. León (*León 11446,* GH), same locality —12 Apr 1923; K1, K2, L, from cultivated specimen collected in type locality, Sierra de Anafe, Cuba —29 Oct 1975).

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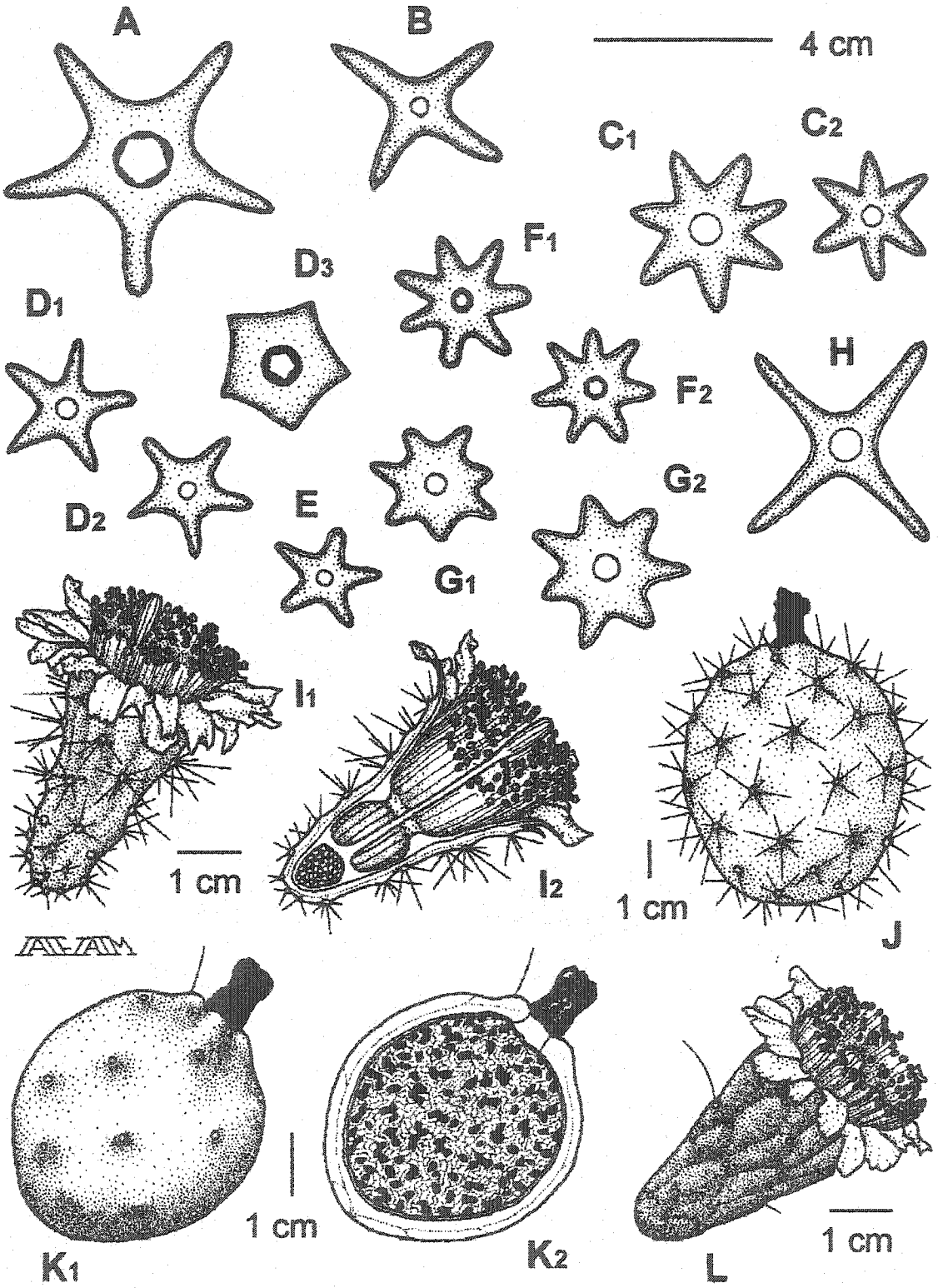

Figure 3.

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Fig. 4. Ribs of *Leptocereus* spp. (spines not depicted). The scale bar is 2 cm for all rib drawings.

A. *Leptocereus albellus*. **B1**, **B2**. *L. maxonii*. **C1**, **C2**, **C3**. *L. wrightii* subsp. *wrightii*. **C4**. *L. wrightii* subsp. gracilis. **D**. *L. ekmanii*. **E1**, **E2**, **E3**. *L. weingartianus* subsp. *weingartianus*. **E4**. *L. weingartianus* subsp. *demissus*. **F1**, **F2**. *L. santamarinae*. **G**, *L. arboreus*. **H**. *L. leonii*. **I**. *L. chrysotyrius*. **J**. *L. scopulophilus*. **K1**, **K2**. *L. prostratus*. **L**. *L. carinatus*. **M1**, **M2**. *L. sylvestris*. **N**. *L. assurgens*. **O1**. *L. quadricostatus* subsp. *quadricostatus*. **O2**. *L. quadricostatus* subsp. *parvispinus*. **P**. *L. grantianus*. **Q**. *L. paniculatus*. (A, from Sierra de San Carlos, Cuba —28 Mar 1992; B1, B2, from valley of Rio Tacre, Guantánamo, Cuba —21 Mar 1990; C1, from Bahia Honda, Cuba —12 Dec 1993; C2, C3, from Cojímar, Cuba —1 Jun 1976; C4, from San Diego, Pinar del Rio province, Cuba —27 Nov 1985; D, from Sierra de Guane, Cuba —6 Jun 1984; E1, from Cabo Samaná, Dominican Republic —8 Jun 1991; E2, E3, from vicinity of Bayahibe, Dominican Republic —22 Jan 1991; E4, from Pedernales, ca. Cabo Rojo, Dominican Republic —31 May 1991; F1, F2, from type plant, vicinity of Santa Lucía beach, Cuba —15 Apr 1990; G. from Yaguanabo, Cuba —9 Jul 1993; H, from type locality at Sierra de Anafe, Cuba —29 Oct 1975; I, from San Diego, Pinar del Rio province, Cuba —3 Nov 1976; J, from type plant, summit of Somorrostro hill, Cuba —17 Apr 1976; K1, K2, from type locality at Sumidero, Pinar del Rio province, Cuba —5 Mar 1992; L, from type plant, Sierra del Chorrillo, Najasa, Cuba —12 Sep 1990; M1, M2, from Boca de Rio Las Puercas, Pilón, Cuba —4 May 1993; N, from Moncada, West of Viñales, Cuba —collected by F. Areces-Berazaín, 18 Jul 1997; O1, from dry

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Fig. 4 (cont.).

forests between Punta Melones and Laguna de Boquerón, Puerto Rico —13 Jun 1995; O2, from Bosque Estatal de Guánica, Puerto Rico —23 Feb 1994; P, from Culebra Island, Puerto Rico —8 Mar 1994; Q, from La Descubierta, Dominican Republic —7 Jan 1995).

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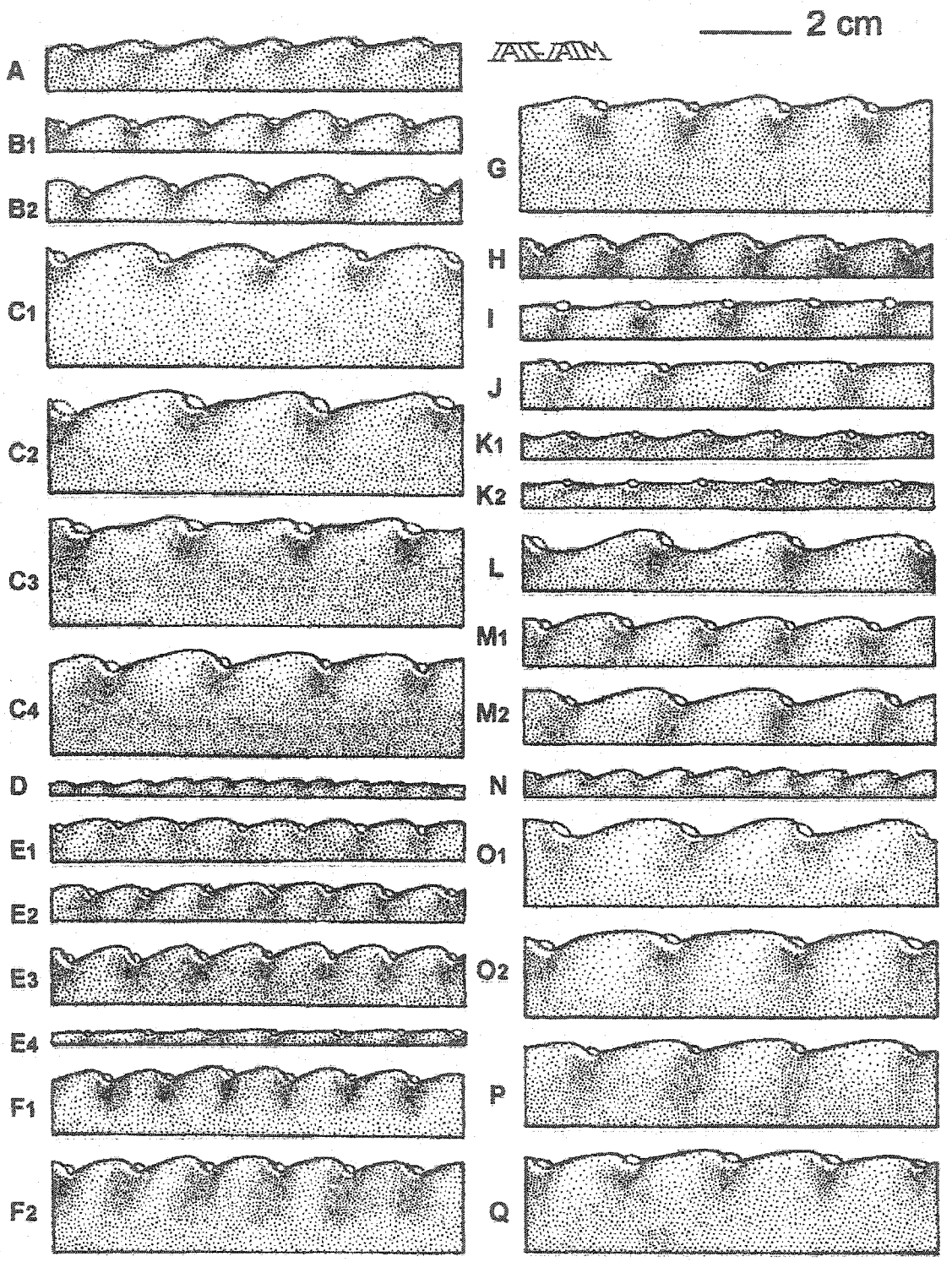

Figure 4.

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Plate 11. Areoles of *Leptocereus* spp. and *Cereus* (*Hamannia*) *fabiolae* (I. SEM observations). All areoles were removed from one-year old ultimate stem segments of mature plants.

A. Areole of *Leptocereus ekmanii*, with one central spine and eight radials. **B.** Areole of *L. weingartianus* subsp. *demissus* showing swollen bases of spines. **C.** Nearly unarmed areole of *L. grantianus*. **D.** Areole of *L wrightii* subsp. *gracilis*. **E.** Areole of *L. prostratus*. **F.** Areole of *L. paniculatus*. **G.** Areole of *L. carinatus*. **H.** Areole of *Cereus* (*Hamannia*) *fabiolae*, with long, thin trichomes that are much less curled than those of *Leptocereus*. (A, from Sierra de Guane, Cuba —6 Jun 1984; B, from Pedernales, ca. Cabo Rojo, Dominican Republic —31 May 1991; C, from Culebra Island, Puerto Rico —8 Mar 1994; D, from San Diego, Pinar del Rio province, Cuba —27 Nov 1985; E. from type locality at Sumidero, Pinar del Rio province, Cuba —5 Mar 1992; F, from La Descubierta, Dominican Republic —7 Jan 1995; G, from Sierra del Chorrillo, Najasa, Cuba —12 Sept 1990; H, from Môle St. Nicolas, Haiti —19 Jan 1995).

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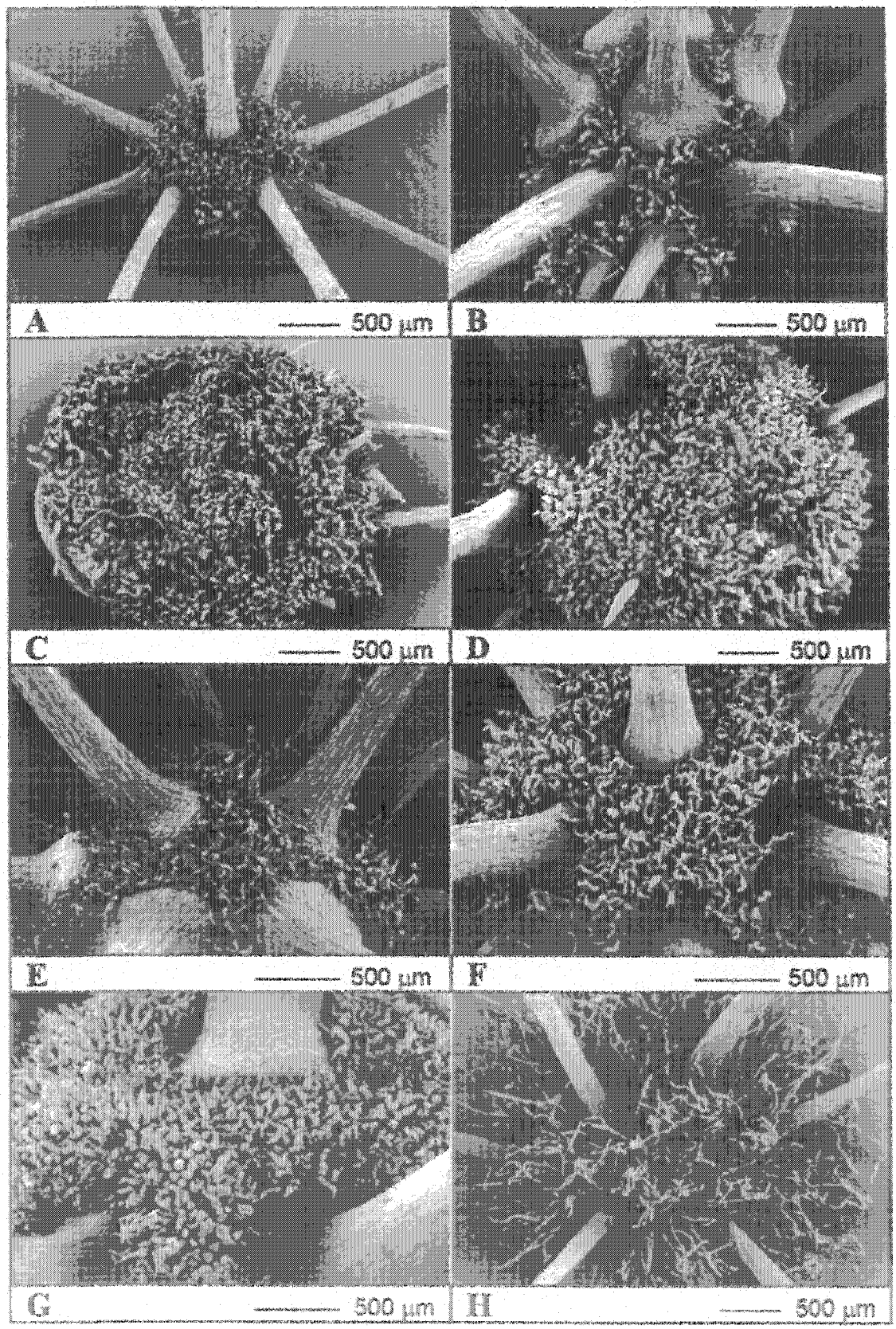

Plate 11.

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Plate 12. Areoles of *Leptocereus* spp. (II. Live plant observations). Except for D., which corresponds to the main axis of a five-years old seedling, all areoles occur in one-year old ultimate stem segments of mature plants.

A. First areoles on a nine-weeks old seedling of *Leptocereus quadricostatus* subsp. *quadricostatus*. **B.** Areoles of *L. wrightii* subsp. *gracilis*, with short spines projecting upwards. **C.** Areoles of *L. wrightii* subsp. *wrightii*. **D.** Areoles of a young shoot of the same species, showing stouter and longer spines. **E, F.** Areoles of *L. assurgens*. **G.** Nearly unarmed areoles of *L. grantianus*. (A, from dry forests between Punta Melones and Laguna de Boquerón, Puerto Rico —13 Jun 1995; B, from San Diego, Pinar del Rio province, Cuba —27 Nov 1985; C, from Bahia Honda, Cuba —12 Dec 1993; D, from Cojímar, Cuba —1 Jun 1976; E, from Moncada, West of Viñales, Cuba — collected by F. Areces-Berazaín, 18 Jul 1997; F, from Ensenada de Valle, Viñales, Cuba —21 Feb 1979; G, from Culebra Island, Puerto Rico —8 Mar 1994).

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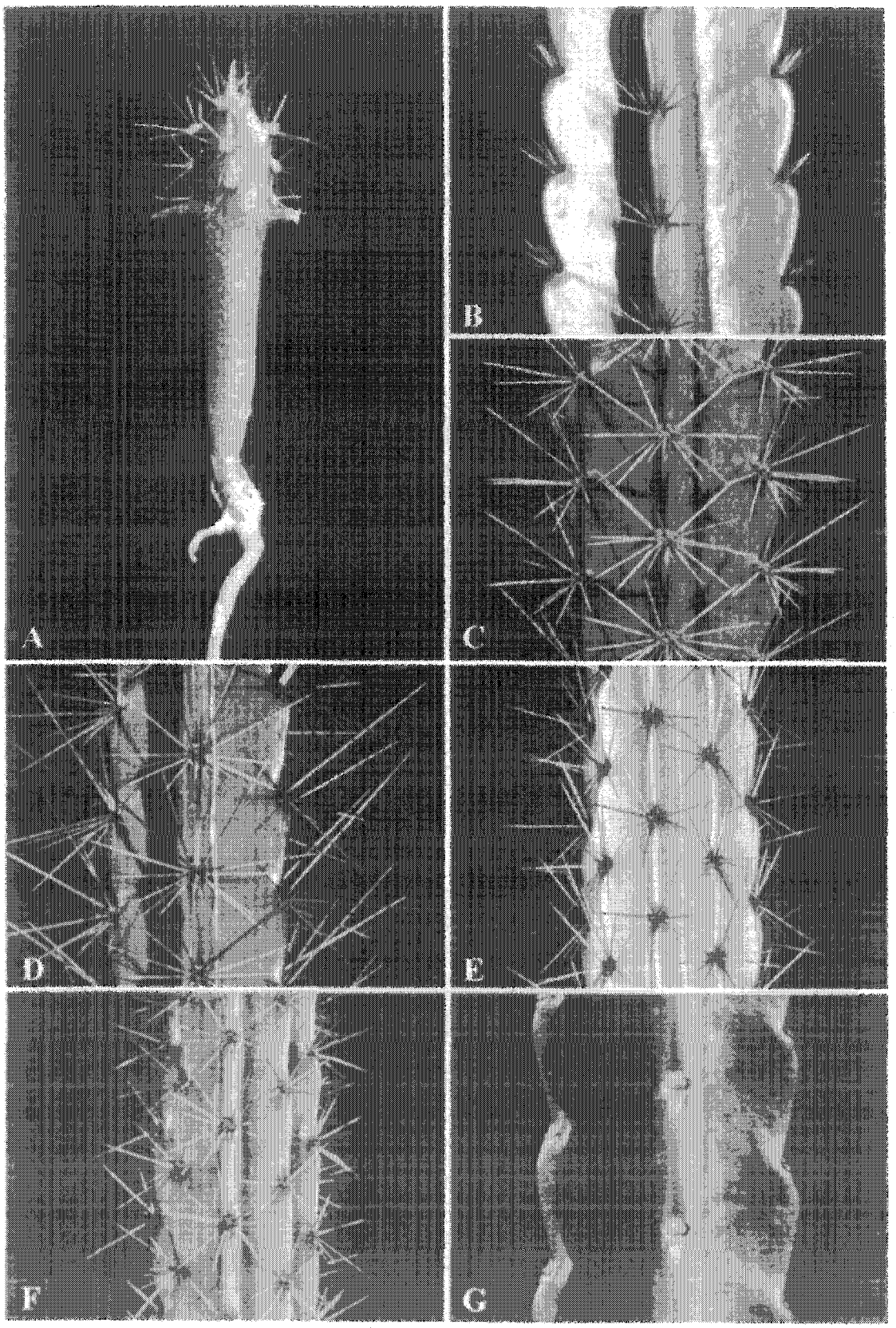

Plate 12.

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Plate 13. Areoles of *Leptocereus* spp. (III. Live plant observations). All areoles occur in one-year old ultimate stem segments of mature plants.

A. Areoles of *L. ekmanii*. **B**. Areoles of *L. paniculatus*. **C**. Areoles of *L. scopulophilus*. **D**. Areoles of *L. carinatus*. **E**. Areoles of *L. leonii*. **F**. Areoles of *L. sylvestris*. **G**. Areoles of *L. arboreus*. **H**. Areoles of *L. santamarinae*. (A, from Sierra de Guane, Cuba —6 Jun 1984; B, from La Descubierta, Dominican Republic —7 Jan 1995; C, from type plant, summit of Somorrostro hill, Cuba —17 Apr 1976; D, from type plant, Sierra del Chorrillo, Najasa, Cuba —12 Sep 1990; E, from type locality at Sierra de Anafe, Cuba —29 Oct 1975; F, from Boca de Rio Las Puercas, Pilón, Cuba —4 May 1993; G, from Yaguanabo, Cuba —9 Jul 1993; H, from type plant, vicinity of Santa Lucía beach, Cuba —15 Apr 1990).

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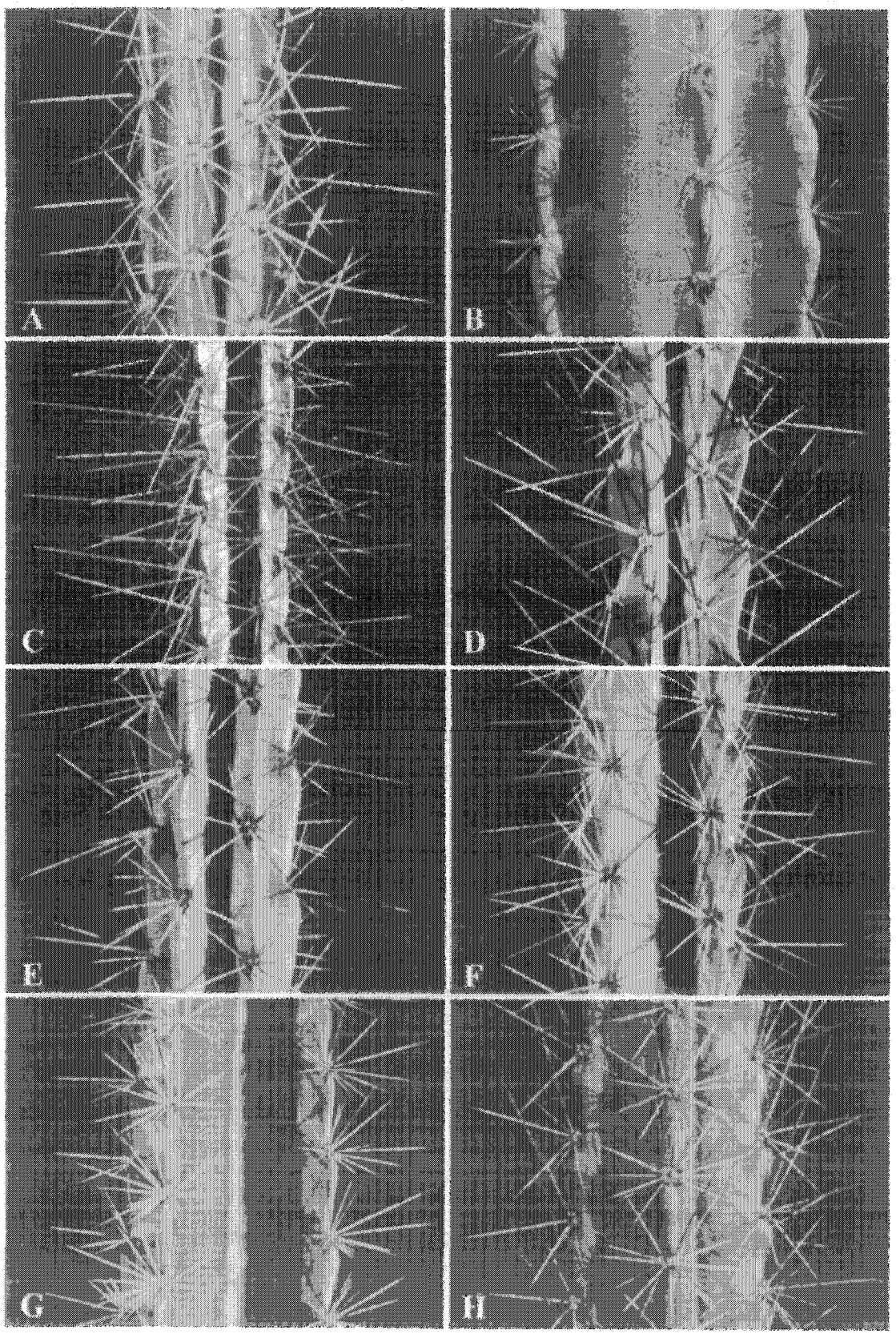

Plate 13.

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Plate 14. Areoles of *Leptocereus* spp. and *Cereus* (*Hamannia*) *fabiolae* (IV. Live plant observations). All areoles occur in one-year old ultimate stem segments of mature plants.

A. Areoles of *L. chrysotyrius*. **B**. Areoles of *L. quadricostatus* subsp. *quadricostatus*. **C**. Areoles of *L. quadricostatus* subsp. *parvispinus*. **D**. Areoles of *L. maxonii*. **E**. Areoles of *L. weingartianus* subsp. *weingartianus*. **F**. Areoles of *L. weingartianus* subsp. *demissus*. **G**. Dorsal (left) and ventral (right) areoles of *L. prostratus*, a creeping species with slight dorsiventral differentiation of stems. **H**. Areoles of *Cereus* (*Hamannia*) *fabiolae* with additional spines (mostly projecting upwards) that are being produced continuously. (A, from San Diego, Pinar del Rio province, Cuba —3 Nov 1976; B, from dry forests between Punta Melones and Laguna de Boquerón, Puerto Rico —13 Jun 1995; C, from Bosque Estatal de Guánica, Puerto Rico —23 Feb 1994; D, from valley of Rio Tacre, Guantánamo, Cuba —21 Mar 1990; E, from vicinity of Bayahibe, Dominican Republic —22 Jan 1991; F, from Pedernales, ca. Cabo Rojo, Dominican Republic —31 May 1991; G, from type locality at Sumidero, Pinar del Rio province, Cuba —5 Mar 1992; H, from Môle St. Nicolas, Haiti —19 Jan 1995).

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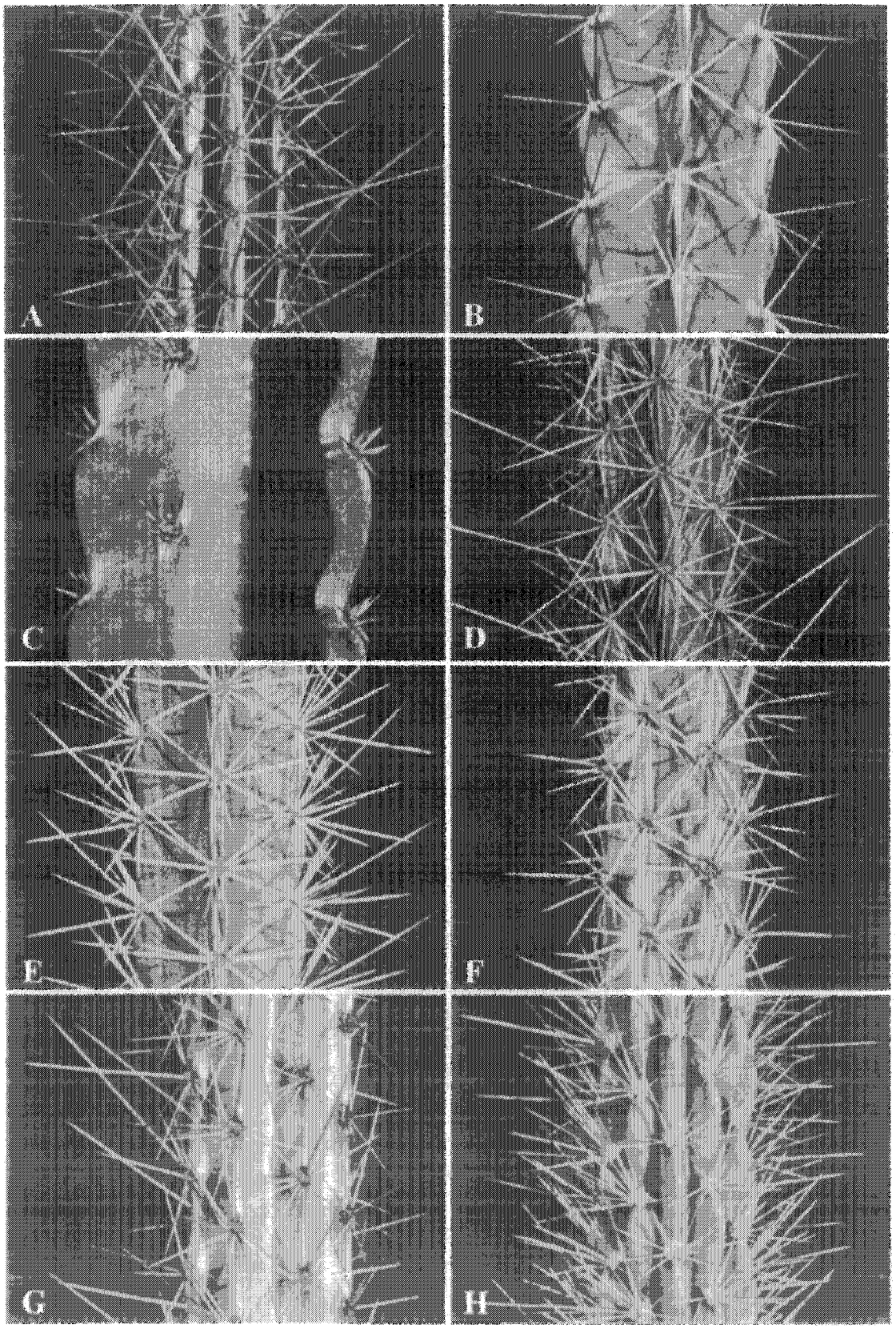

Plate 14.

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Plate 15. Indeterminate areoles of *Leptocereus* spp., and differentiation of spines (areoles not at the same scale).

A. Primary areole of *Leptocereus ekmanii* with four central spines that are darker than radials. **B**. Primary areole of *L. quadricostatus* subsp. *quadricostatus* with subradial symmetry and spreading spines. **C**. Primary areole of *L. wrightii* subsp. *wrightii*, with 15 slightly unequal spines. **D**. Four-years old areole of *L. quadricostatus* subsp. *quadricostatus* showing significant enlargement and many secondary spines. **E**. Primary areole of *L. prostratus* with its long central spine. **F**. Three-years old areole of the same species, showing great enlargement of its central spine. (A, from Sierra de Guane, Cuba —6 Jun 1984; B, D, from dry forests between Punta Melones and Laguna de Boquerón, Puerto Rico —13 Jun 1995; C, from Bahia Honda, Cuba —12 Dec 1993; E, F, from type locality at Sumidero, Pinar del Rio province, Cuba —5 Mar 1992).

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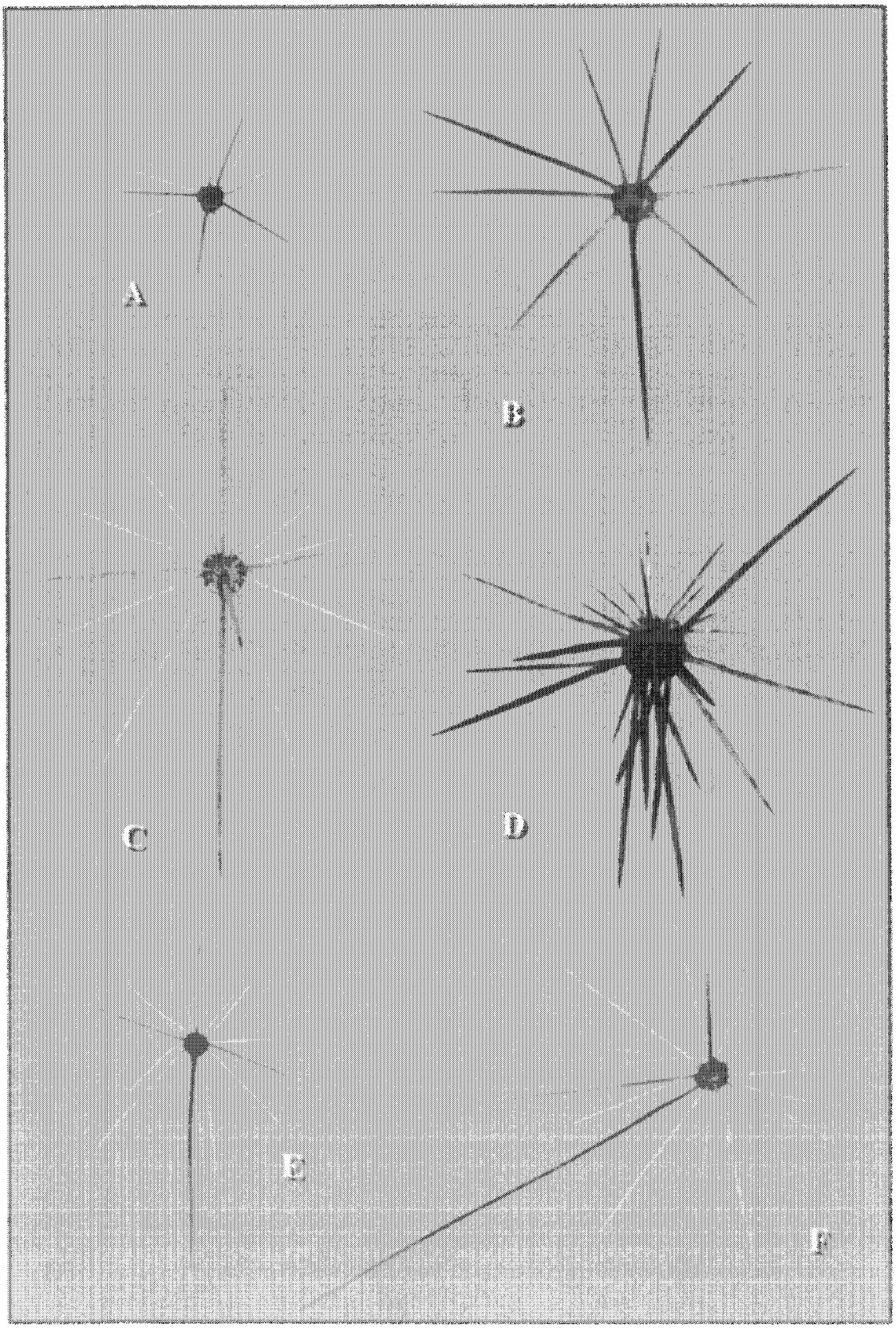

Plate 15.

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Plate 16. Enlargement of areoles in five-years old stem segments, and growth of additional spines, in cultivated species of *Leptocereus*.

A. Spines growing on enlarged areoles of *Leptocereus arboreus*, with their meristematic bases of a light green color. **B**. Additional spines on old areoles of *L. carinatus*. **C, D**. The short-spined areoles of *L. quadricostatus* subsp. *parvispinus* does not go through appreciable growth after five years in cultivation. **E**. Old, dormant areoles of *L. paniculatus*, with weathered spines. **F**. Old areoles of *L. leonii*. **G**. Remarkably enlarged areoles of *L. wrightii* subsp. *wrightii*. **H**. Areoles of *L. prostratus*, with weathered spines fading gray. **I**. Enlarged areoles of *L. quadricostatus* subsp. *quadricostatus*. (A, from Yaguanabo, Cuba —collection of 9 Jul 1993; B, from type plant, Sierra del Chorrillo, Najasa, Cuba —collection of 12 Sep 1990; **C, D**, from Bosque Estatal de Guánica, Puerto Rico —collection of 23 Feb 1994; **E**, from La Descubierta, Dominican Republic —collection of 7 Jan 1995; **F**, from type locality at Sierra de Anafe, Cuba —collection of 29 Oct 1975; **G**, from Bahia Honda, Cuba —collection of 12 Dec 1993; **H**, from type locality at Sumidero, Pinar del Rio province, Cuba —collection of 5 Mar 1992; **I**, from dry forests between Punta Melones and Laguna de Boquerón, Puerto Rico —collection of 13 Jun 1995).

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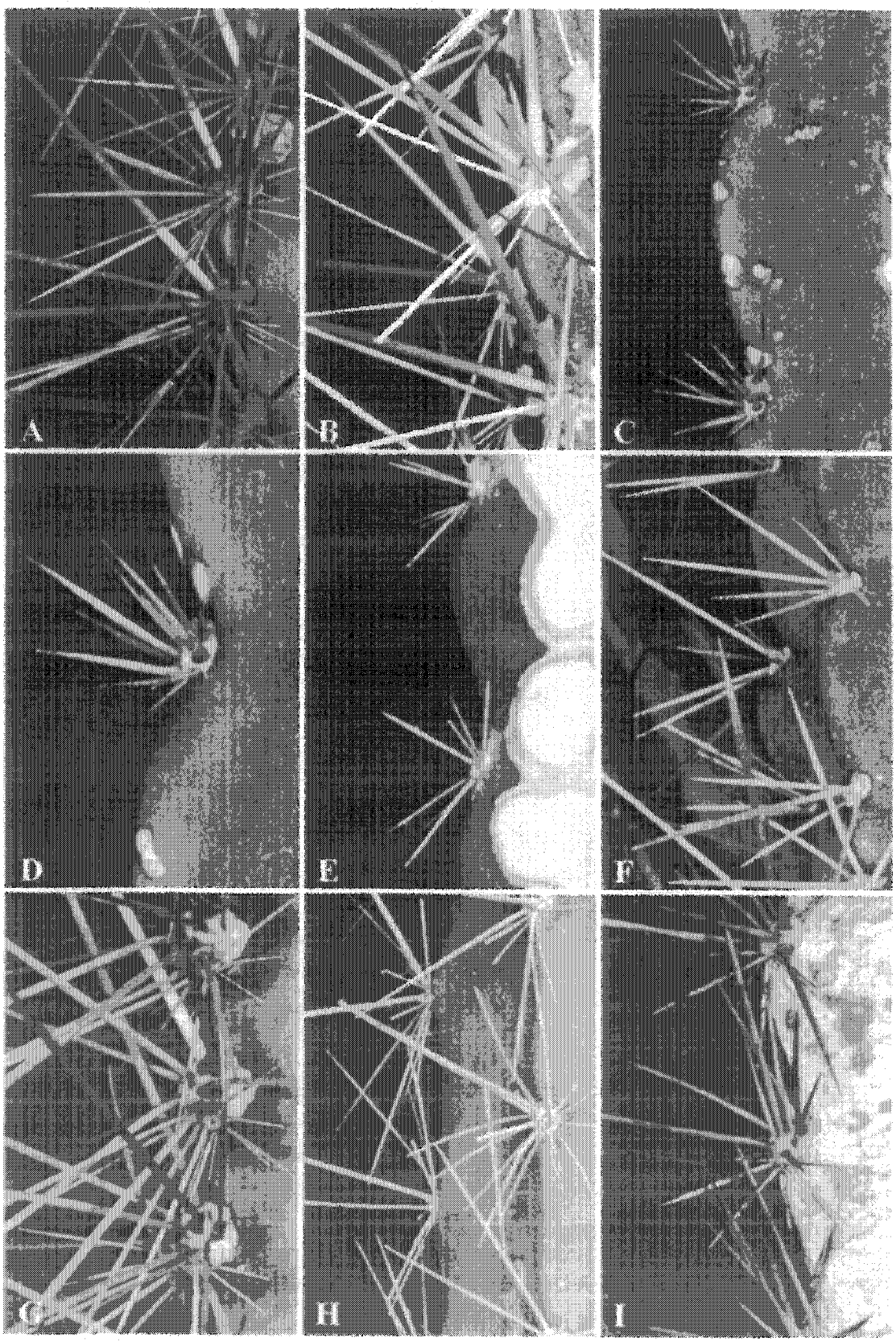

Plate 16.

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The woolly indumentum of the areoles of *Leptocereus* is formed by very curly, ribbon-like, multicellular, uniseriate trichomes that are 0.2 to 0.5 mm long and 35 to 50 μm wide. Their color varies from creamy or tawny (*e.g.*, in *Leptocereus santamarinae*), to brown or dark reddish-brown (*e.g.*, in *L. assurgens*), depending upon the degree to which the maturing cells of trichomes become stained with ergastic materials. By contrast, the trichomes of *Cereus* (*Hamannia*) *fabiolae* are longer and narrower (0.7 to 1.2 mm long, 16-20 μm wide), and less curly (Plates 11, 16 and 18). In both genera, *Leptocereus* and *Cereus*, trichomes gradually fade color over time, turning grayish. Areolar trichomes are characteristic for all the Cactaceae, and according to Boke (1954), they arise from protodermal cells at either side of the leaf primordium at the time the axillary bud is initiated. Growth of additional spines in the adaxial side of the areoles of *Leptocereus* is usually announced by flocks of new trichomes (Plate 16, G).

Spines in *Leptocereus* are produced precociously by the axillary meristem in the axil of the podaria of primary stem segments. Spine number in the young areoles of *Leptocereus* is not very constant, although it varies within certain limits (Table 7). Depending upon the species, each stem areole may have five to 24 spines that are one to 70 mm in length. An exception is the nearly unarmed *Leptocereus grantianus*, often spineless, or bearing up to four small subulate, 0.5 to 2 mm long spines in each areole. Spine arrangement varies from radially symmetrical, as in *L. paniculatus* (Plate 13, B), to bilaterally symmetrical or asymmetrical (most species), the longest spines having a central or subcentral position, or just occurring towards the adaxial (upper) side of the areole (Plate 14, A, D and G). Central spines are erect to spreading, rarely deflexed. In

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L. maxonii, L. carinatus and *L. scopulophilus* the most conspicuous central spine is remarkably long, stiff and pungent, and may attain more than 6 cm in length. This spine, which is produced by the most robust spine primordia and have the widest basal meristem, may be up to one mm thick in *L. carinatus* (Table 8). However, the long central spine found in the dorsal areoles of *L. prostratus* —not much thicker than the other accompanying spines— is longer simply because its basal meristem remains active for many weeks, long after the other ones turned inactive (Plate 15, F).

Young spines in *Leptocereus* are usually brightly colored, often light lemon-yellow, pink or pinkish, to brownish-yellow. Sometimes they have rather dark colors such as chestnut or reddish-brown (*e.g.*, in *L. leonii*), or nearly black (*e.g.*, in *L. carinatus*), and unlike most species of Cactaceae, they are usually not darker at the tip. Mature spines are variously brown or yellow, to nearly black in most species, becoming ash-gray with age. Floral spines are dark reddish-brown in species with reddish flowers or reddish floral tubes (*i.e.*, *L. chrysotyrius*, and the *Leptocereus wrightii* species group). In *L. chrysotyrius*, *L. wrightii* (both subspecies), *L. scopulophilus*, and *L. arboreus*, the basal growth zone of the spines is pale green; in the remaining species it is of a dilute yellow color. This live, basal growth zone (zone of cell elongation) is nearly twice as thick as the fully formed spine, which is a dead, dry structure. Spines actively growing are easily detached from the plant with a slight lateral pressure, because the cell walls of the basal spine meristem, and probably of the zone of cell elongation also, are thin and fragile. In contrast, mature spines of *Leptocereus* are hard to remove from the areole. In *L. sylvestris*, fruit spines become strongly fastened to the

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areole (and to other spines in the areole) by means of cork cells produced by a phellogen cambium developed at the base of the spines. Because of the production of this cork, the spines of this species are particularly easily shed as clusters when the fruits ripen.

Commonly, the spines of *Leptocereus* are straight, stiff, and sharp-pointed, even those of flowers and fruits (Plate 17, A-I). Only the floral spines of *L. ekmanii*, and of *L. leonii* —when present— are fairly thin and bristle-like, and lack rigidity. According to their form, spines can be acicular (needle-shaped), or subulate (awl-shaped). The short-spined subspecies of *L. quadricostatus* and *L. wrightii* have subulate spines, while most of the long-spined species develop acicular spines. Spine bases in *Leptocereus* are remarkably thickened and form a typical bulbose structure that firmly attaches the spine to its areole (Plates 11, B, and 17, J). When seen under the scanning electron microscope (SEM), the spines of *Leptocereus* are reminiscent of the smooth, unspecialized spine surface of *Pereskia* as illustrated by Robinson (1974). However, there are some surface cell characteristics common to all species of *Leptocereus* that, taken as a whole, may distinguish the mature spines of this genus from those of the Pereskioideae, and of other genera of columnar Cactoideae. First, in *Leptocereus* the cells of the bulbose spine base are quadrate to rectangular or rarely polygonal (their transverse boundaries are not oblique), and their anticlinal walls look thick and elevated (Plate 17, J and K). It is noteworthy that these surface cells of the spine base exhibit the same architectural pattern of the basal cells of the glochids of *Austrocylindropuntia*, a South American genus of subfamily Opuntioideae (see figure 17 of Robinson, *op. cit.*).

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Plate 17. Ultrastructure of the spines of *Leptocereus* spp. and *Cereus* (*Hamannia*) *fabiolae*.

A-I. Central spine apices: **A**. *L. paniculatus*. **B**. *L. ekmanii*. **C**. *L. maxonii*. **D**. *L. wrightii* subsp. *wrightii*. **E**. *L. wrightii* subsp. *gracilis*. **F**. *L. scopulophilus*. **G**. *L. carinatus*. **H**. *Cereus* (*Hamannia*) *fabiolae*. **I**. *L. paniculatus*. **J**. Bulbose base of a central spine of *L. weingartianus* subsp. *demissus*. **K**. Bulbose base surface of *L. prostratus*. **L**. Central spine surface of *Cereus* (*Hamannia*) *fabiolae*, midway between apex and base. **M**. *Idem*, enlarged, showing cellular arrangement (A, from from La Descubierta, Dominican Republic —7 Jan 1995; B, from Sierra de Guane, Cuba —6 Jun 1984; C, from valley of Rio Tacre, Guantánamo, Cuba —21 Mar 1990; D, from Cojímar, Cuba —1 Jun 1976; E, from San Diego, Pinar del Rio province, Cuba —27 Nov 1985; F, from from type plant, summit of Somorrostro hill, Cuba —17 Apr 1976; G, from type plant, Sierra del Chorrillo, Najasa, Cuba —12 Sep 1990; H, from Môle St. Nicolas, Haiti —19 Jan 1995; I, from from La Descubierta, Dominican Republic —7 Jan 1995; J, from Pedernales, ca. Cabo Rojo, Dominican Republic —31 May 1991; K, from type locality at Sumidero, Pinar del Rio province, Cuba —5 Mar 1992; L, M, from Môle St. Nicolas, Haiti —19 Jan 1995).

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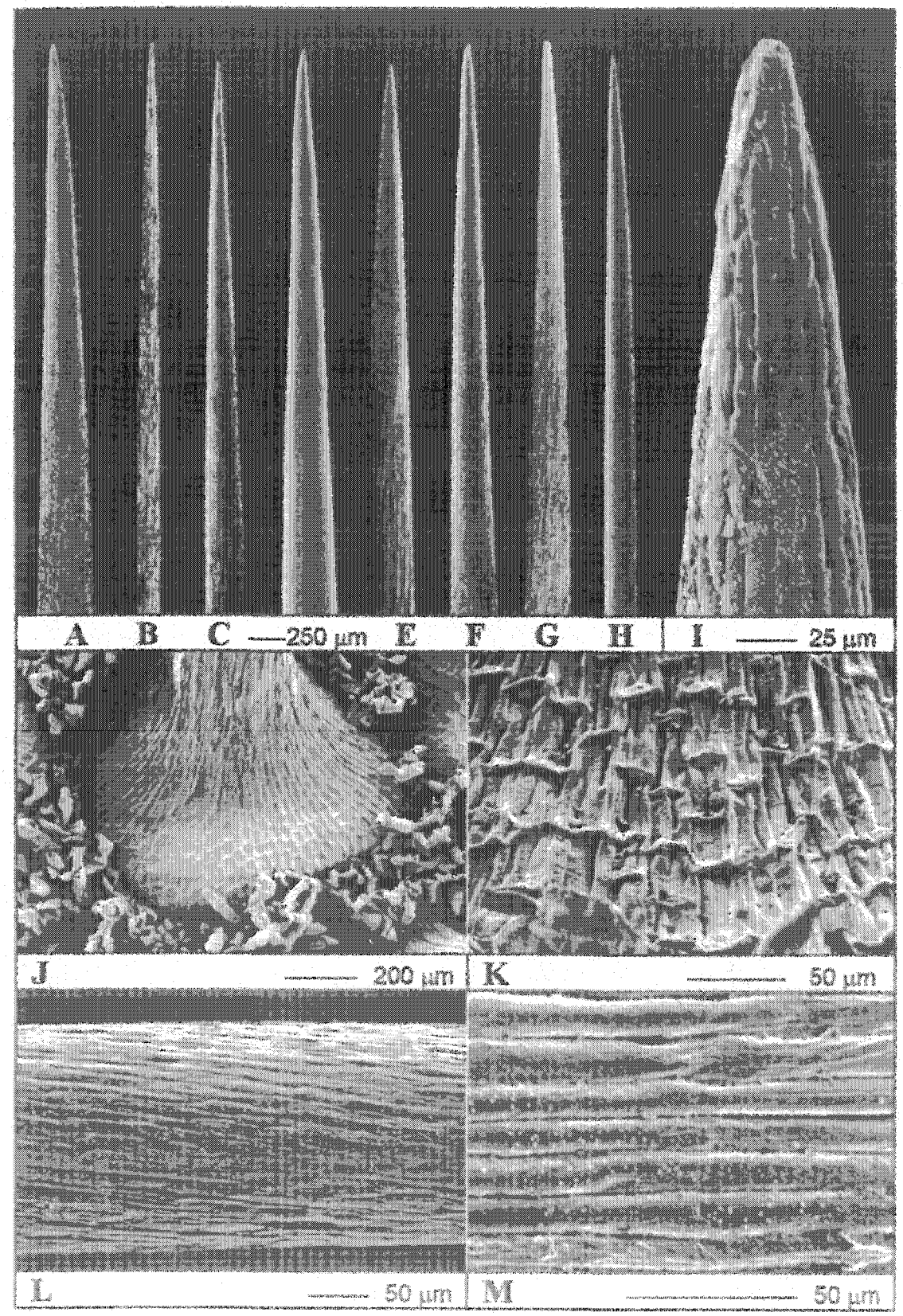

Plate 17.

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Plate 18. Ultrastructure of the spines of *Leptocereus* spp., and trichomes of *Leptocereus* spp. and *Cereus* (*Hamannia*) *fabiolae*.

A-E. Central spine surface, midway between apex and base: **A**. *L. wrightii* subsp. *wrightii*. **B, C**. *L. wrightii* subsp. *gracilis*. **D, E**. *L. maxonii*. **F-I**. Areolar trichomes: **F**. *L. wrightii* subsp. *gracilis*. **G**. *L. paniculatus*. **H, I**. *Cereus* (*Hamannia*) *fabiolae*. (A, from Cojímar, Cuba —1 Jun 1976; B, C, from San Diego, Pinar del Rio province, Cuba —27 Nov 1985; D, E, from valley of Rio Tacre, Guantánamo, Cuba —21 Mar 1990; F, from San Diego, Pinar del Rio province, Cuba —27 Nov 1985; G, from La Descubierta, Dominican Republic —7 Jan 1995; H, I, from Môle St. Nicolas, Haiti — 19 Jan 1995).

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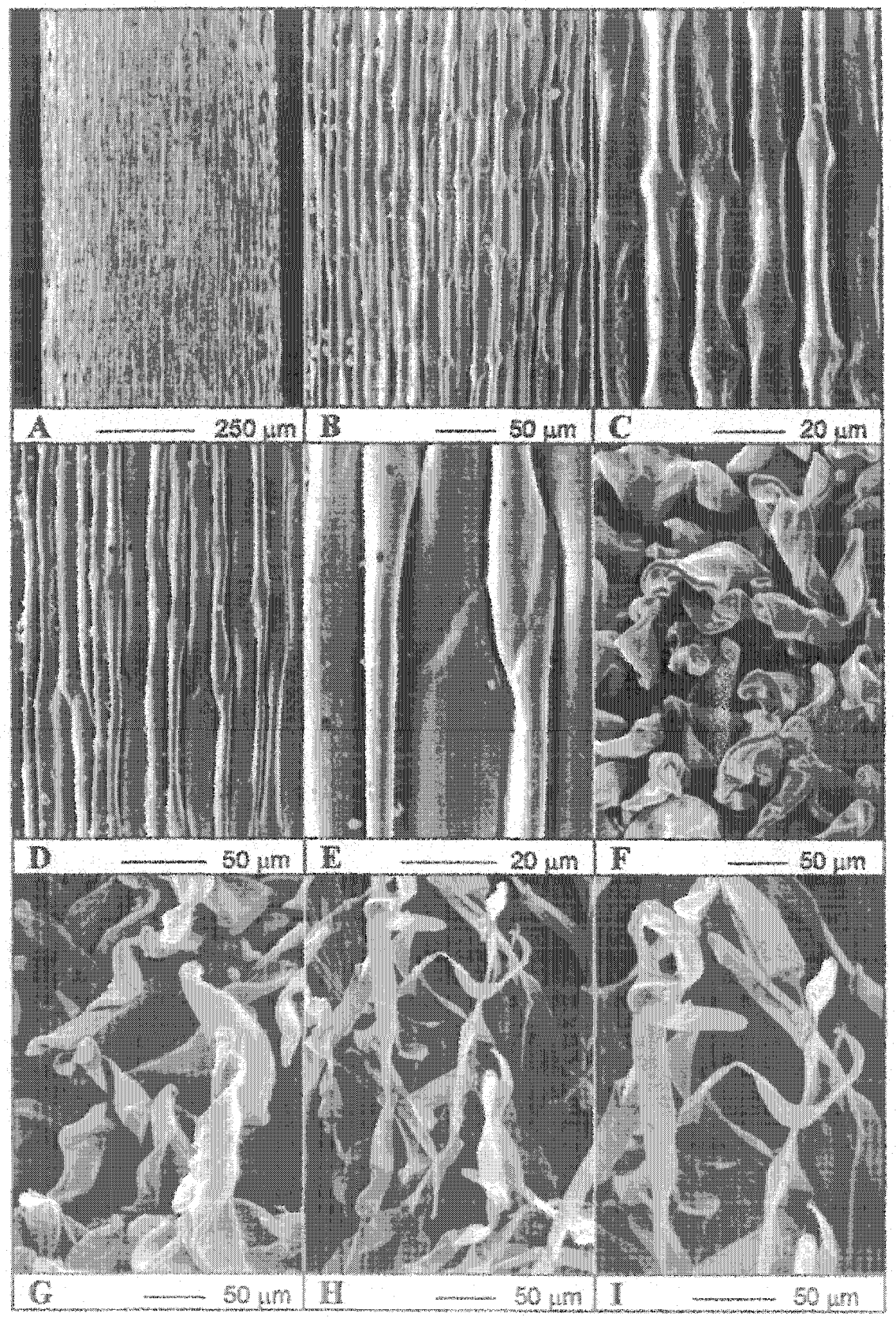

Plate 18.

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Second, in the spine bodies of *Leptocereus*, the elongated, prosenchimatic surface cells appear distinctly swollen at their ends, *i.e.*, at the upper and lower contact sites where they meet other cells of the same row. Because spine surface cells are strongly convex, these swollen ends leave relatively deep, wide spaces between the cells of a neighboring row, often giving a typical "bone" shape to each individual cell (Plate 18, B and C). Although there is essential uniformity in the spines of all *Leptocereus* with respect to this and other surface cell characters, "bone" cells are notorious in *L. wrightii*, and less conspicuous in *L. maxonii* (Plate 17, D and E). By contrast, surface prosenchimatic cells of *Cereus* (*Hamannia*) *fabiolae* have no swollen ends, and the neighboring rows of cells are in close contact, leaving very little space —if any— between them (Plate 17, M).

2.5. Cephalioid structures

In some species of *Leptocereus*, flowers are not restricted to the shoot tip and lateral areoles of a mature stem segment. In *L. paniculatus, L. quadricostatus*, and *L. grantianus*, the species that constitute section *Cephaliphora*, special floriferous areoles are formed in apical portions of the stem called a cephalium (pl. cephalia). Eventually, in these species vegetative growth of some ultimate stem segment ceases permanently and the stem-apex specializes in the production of a distinct, purely fertile and non-assimilatory flowering organ. In *Leptocereus*, this flowering stem, or cephalium, cannot revert to vegetative growth. In all three species of the genus differentiation of the fertile stem starts suddenly from the apical growing point. Fertile areoles that in contrast to

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vegetative areoles are not arranged along the ribs in orthostichies but rather run in spirostichies, densely cluster on these special stems, touching each other. Instead of spines they produce wooly hairs and short bristles that tend to wear off with age leaving a stubby, cylindrical or angular joint. The cephalium of *Leptocereus paniculatus* at first appears as a large, creamy or tawny, felted areole on the stem apex, from which several flowers are produced (Plate 19, A). This fertile stem tip slowly elongates over the years until it reaches seven or eight cm long, still producing flowers and fruits at the tip. Britton and Rose (1921) estimated that a five cm long cephalium of *L. paniculatus* had borne 20 sets of flowers and fruits and may possibly be 20 years old. However, these *Cephaliphora* species do not produce flowers exclusively in cephalia. I have seen a flower bud of *L. paniculatus* on a lateral branch, in the Enriquillo basin area (Dominican Republic), and the famous illustration by Plumier (plate 92 of Burmann's *Plantarum Americanum*, 1755) shows numerous lateral flowers, but in this species lateral flowers give rise to fruits much less frequently. As opposed to *L. paniculatus*, the Puerto Rican cephalium-bearing species, *L. quadricostatus* and *L. grantianus*, produce more flowers and fruits on lateral areoles of normal, vegetative stems, than borne on their specialized fertile stems (Plate 28, B, C). In fact, the small and slender, 1 to 3 cm long cephalia of these species do not seem to play yet any crucial role in reproduction (Plate 19, B, C, D).

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Plate 19. Cephalioid structures in *Leptocereus*.

A. Young, terminal, woolly cephalium of *L. paniculatus* with two flower buds in different stages of development. **B**. Small, simple cephalium of *L. quadricostatus* subsp. *quadricostatus*. **C**. Bifurcated cephalium of the same subspecies. **D**. Apex of the same subspecies (enlarged), showing a young cephalium bearing two very unequal flower buds. (A, from La Descubierta, Dominican Republic —7 Jan 1995; B, C, D, from dry forests between Punta Melones and Laguna de Boquerón, Puerto Rico —13 Jun 1995).

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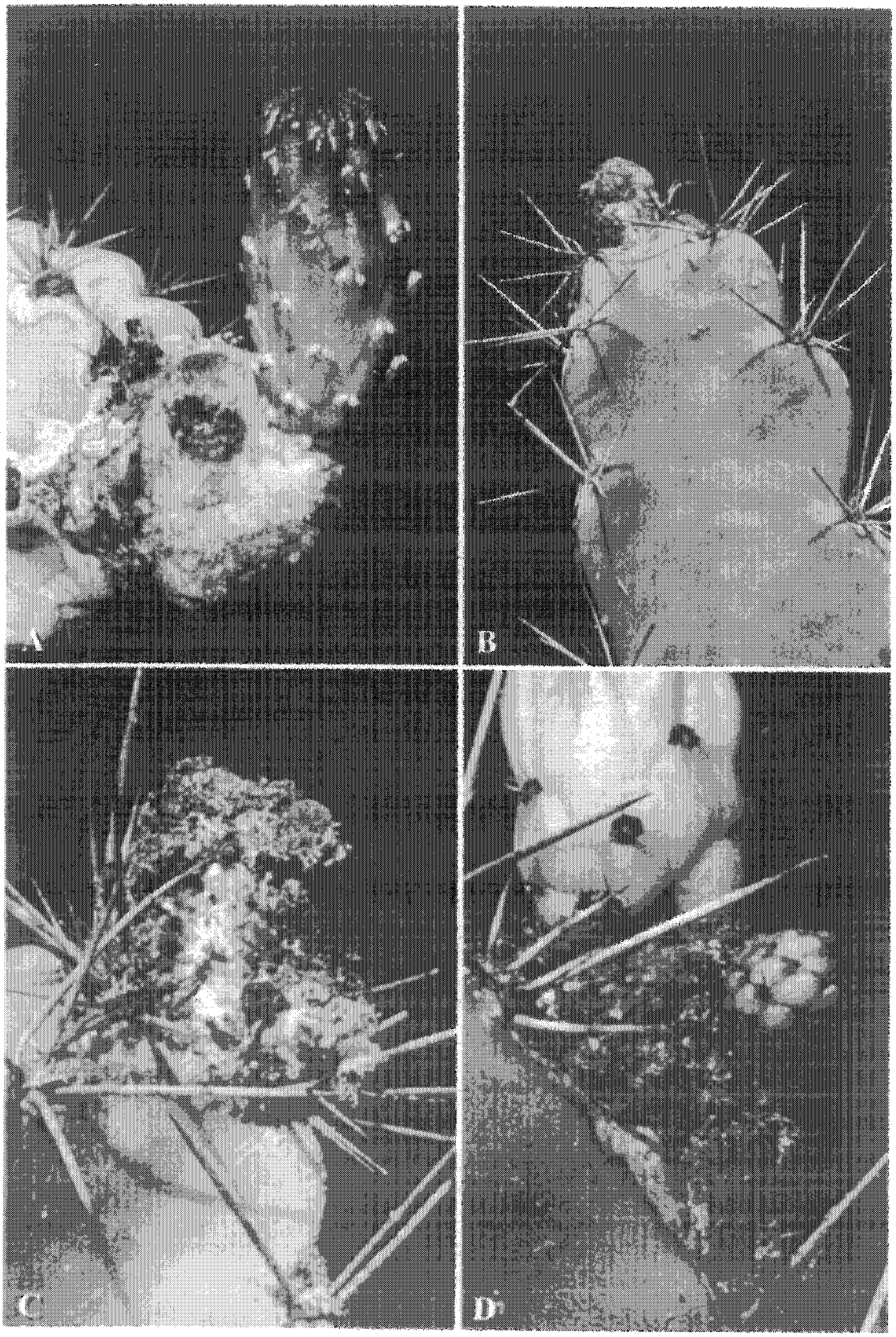

Plate 19.

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2.6. Flowers

In 14 of the 17 species of *Leptocereus* (82%) the flowers are produced exclusively in apical, subapical and lateral areoles; in their lifetime each areole can produce only one flower. The flower bud is typically cylindrical or cylindric-obconical and rounded at the apex in all stages of development, and unlike most species of subfamily Cactoideae, it never gets bulbous at the tip. *Leptocereus* has relatively small (only 2 to nearly 8 cm long at anthesis), actinomorphic, epigynous flowers that are tubular, campanulate, or funnelform, and usually scentless. As in all the Cactoideae, the ovary is inferior in position. This inferior ovary results from intercalary growth beneath the perianthium of the flower, forming a pronounced hypanthium that is commonly known as the flower- or receptacle-tube. Although the flower axis is elongated into a definite tubular structure enclosing all structures, it is possible to distinguish three regions in the flower of *Leptocereus*: (1) the free portion above the ovary, *i.e.*, the receptacle-tube; (2) the lower portion that encases the ovary, which is called the pericarpel, and (3) the usually reduced region below the pericarpel, which is known as the pedicellate zone (Fig. 3, I1, I2).

In most species of *Leptocereus* the nature of the flower as being a modified shoot is clearly demonstrable by the presence on the pericarpel and receptacle-tube of spiny areoles (Fig. 3, I1, and Plates 20 to 24), and in one species (*L. carinatus*), by the presence of distinct ribs, which is a very rare condition in subfamily Cactoideae (Plates 22, H, and 23, C). Rib-like pleats are also present on the pedicellate zone of the flower

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of *L. arboreus*, but not on the receptacle-tube. The pedicellate zone, pericarpel, and lower portion of the receptacle-tube are green and assimilatory, also making it obvious that they derive from axis tissue. As in other members of subfamily Cactoideae, the axis tissues of the receptacle-tube have been structurally integrated to the flower as a whole, but contrary to the vast majority of the Cactoideae, not just the pericarpel retains its purely vegetative character but also the receptacle-tube. In fact, in most species of *Leptocereus* this part of the flower bears larger and more spiny areoles than the pericarpel, which seems to be a plesiomorphic state in the subfamily. In *L. paniculatus*, by contrast, both the pericarpel and receptacle-tube bear conspicuous podaria, each having a depressed, felty, spineless areole in its axil, which is subtended by a minute scale.

Leptocereus has a unilocular ovary derived from five to 15 carpels, with hypanthial placentation; its numerous ovules are campylotropous, bitegmic, and crassinucellate —the most common condition in the Cactaceae— and curve towards their funicle. The style is columnar and ends in five to 15 erect, linear stigma lobes (the number depending upon the species) that barely open out. The individual stigma lobes, densely covered by minute papillae over the upper surface and along the edges, are usually included within the receptacle tube, or slightly exserted, but in *L. ekmanii* these are markedly exserted (Plate 21, E). The multistaminate androecium develops centrifugally, and the stamens bear dorsifixed anthers of the regular two-locular tetrasporangiate type, with complete longitudinal dehiscence. The stamens are evenly attached to the inner wall of the receptacle tube, and may be included —as in

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Leptocereus arboreus— to somewhat exserted —as in *L. scopulophilus*. In *L. chrysotyrius* a tight brush of stamens is exserted 4 to 6 mm from the receptacle-tube (Plates 20, H and 21, G). In *Cereus* (*Hamannia*) *fabiolae* the staminal column is exserted 10 to 17 mm from the receptacle-tube, and beyond that appears the exserted style capped with 11 to 14 long stigma lobes (Plate 26, A, C, D, E). In *Leptocereus* the first row of stamens is found on a ridge inside the receptacle-tube. This ridge limits a distinct nectar chamber filled with an abundant light honey-sweet secretion. The upper wall of the ovary forms the bottom of this nectar chamber (Fig 3, I2). Stamens and perianth-segments are produced from a meristem that encircles the proto-style in very early stages of flower formation. As a result of the tubular growth of this circular meristem, the floral axis is turned into a cupular structure where the stamens are kept inside and the short perianth segments outside, the latter originating from the leaf scales of the floral axis. In *Leptocereus* the transition from pericarpel to tube is gradual but a sharp differentiation in size and form between inner and outer perianth segments does not occur, the latter being only more "petaloid" (*i.e.*, less succulent). The perianth is usually of the spreading type (*e.g.*, in *L. quadricostatus* —Plate 25, B), but it can also be rotate (*e.g.*, in *L. paniculatus* —Plate 24, A). The most frequent color of the perianth segments is white or creamy (*L. arboreus, L. carinatus, L. maxonii, L. santamarinae, L. quadricostatus*, etc.), but depending upon the species they can also be pink or pinkish (*e.g.*, *L. scopulophilus*, and *L. leonii*), orange (*e.g.*, *L. wrightii*), or yellow (*e.g.*, *L. assurgens*, *L. chrysotyrius*, *L. ekmanii*, and *L. prostratus*). Soon after the flower opens, these perianth segments bend outward; in *L. chrysotyrius* the bending of the perianth stops when the segments are perpendicular to the axis of the receptacle-tube, and the

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inner whorl forms a daisy-like arrangement around the centrally clustered stamens (Plates 20, H, 21, G, and 25, D). In *L. paniculatus*, by contrast, perianth segments keep bending until they become strongly reflexed (Plates 20, G, and 24, A). Although seemingly uniform in many respects within the genus, the flowers of *Leptocereus* exhibit a considerable diversity of proportions and shapes. The plesiomorphic "model" for many character states seems to be represented by the large, extremely spiny and nearly straight, cylindrical flower of *L. arboreus* (Plate 20, A). A whole range of different lines involving changes in the receptacle-tube shape, spination, perianth segment arrangement, androecium, and style-stigma, can be postulated from the *L. arboreus* model. Plates 20 to 26 illustrate variation of the flowers of most recognized taxa of *Leptocereus*, and of *Cereus* (*Hamannia*) *fabiolae* and the Andean "leptocereoid" *Samaipaticereus corroanus*. Likewise, Table 9 shows some important quantitative characters taken from fresh flowers of *Leptocereus* spp. and *Cereus* (*Hamannia*) *fabiolae* (measurements were taken on at least three flowers of each taxon). For the whole set of characters listed in this table, the following abbreviations have been used:

LF. —Length of flower, from base to stigma or stamens (if exserted), in mm.

DF. —Diameter of fully expanded flower, in mm.

DR. —Diameter of stamen ring, in mm.

WF. —Width of perianth limb at anthesis, in mm.

PD. —Proximal (maximum) diameter of receptacle-tube, in mm.

WP. —Width of pericarpel, in mm.

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Plate 20. Flowers of *Leptocereus* spp. (I). All photographs are from the wild and/or cultivated material of original collections made by the author.

A. *Leptocereus arboreus*. **B, C, D, E.** *L. weingartianus* subsp. *weingartianus*. **F.** *L. sylvestris*. **G.** *L. paniculatus*. **H.** *L. chrysotyrius*. (A, from Yaguanabo, Cuba —9 Jul 1993; B, C, D, from vicinity of Bayahibe, Dominican Republic —22 Jan 1991; E, from from Cabo Samaná, Dominican Republic —8 Jun 1991; F, from from Boca de Rio Las Puercas, Pilón, Cuba —4 May 1993; G, from La Descubierta, Dominican Republic —7 Jan 1995; H, from San Diego, Pinar del Rio province, Cuba —3 Nov 1976).

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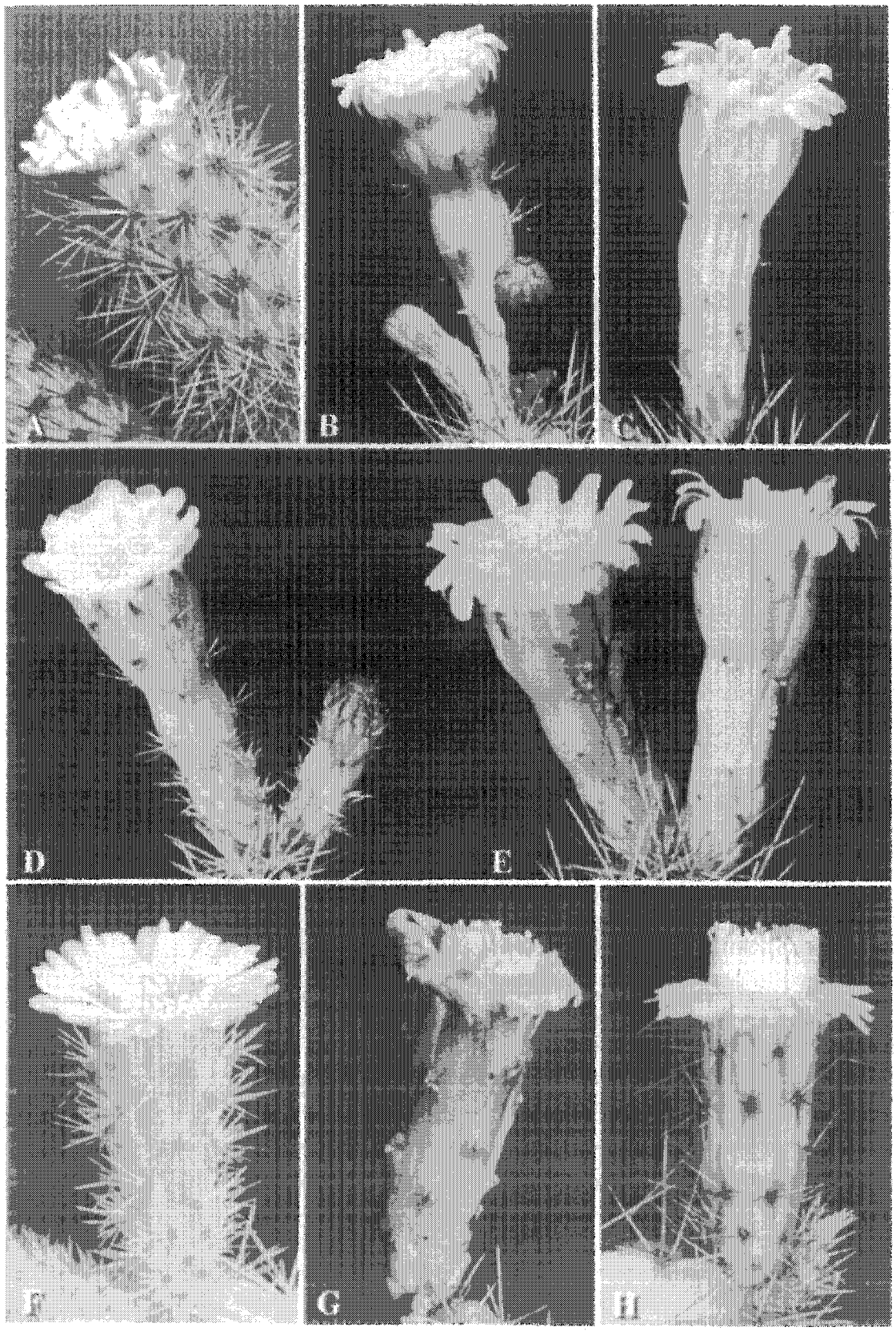

Plate 20.

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Plate 21. Flowers of *Leptocereus* spp. (II). All photographs are from the wild and/or cultivated material of original collections made by the author.

A. *Leptocereus sylvestris*. **B**. *L. weingartianus* subsp. *weingartianus*. **C**. *L. quadricostatus* subsp. *quadricostatus*. **D**. *L. santamarinae*. **E**, **F**. *L. ekmanii*. **G**. *L. chrysotyrius*. **H**. *L. maxonii*. (A, from from Boca de Rio Las Puercas, Pilón, Cuba —4 May 1993; B, from vicinity of Bayahibe, Dominican Republic —22 Jan 1991; C, from dry forests between Punta Melones and Laguna de Boquerón, Puerto Rico —13 Jun 1995; D, from type plant, vicinity of Santa Lucía beach, Cuba —15 Apr 1990; E, F, from Sierra de Guane, Cuba —6 Jun 1984; G, from San Diego, Pinar del Rio province, Cuba —3 Nov 1976; H, from valley of Rio Tacre, Guantánamo, Cuba —21 Mar 1990).

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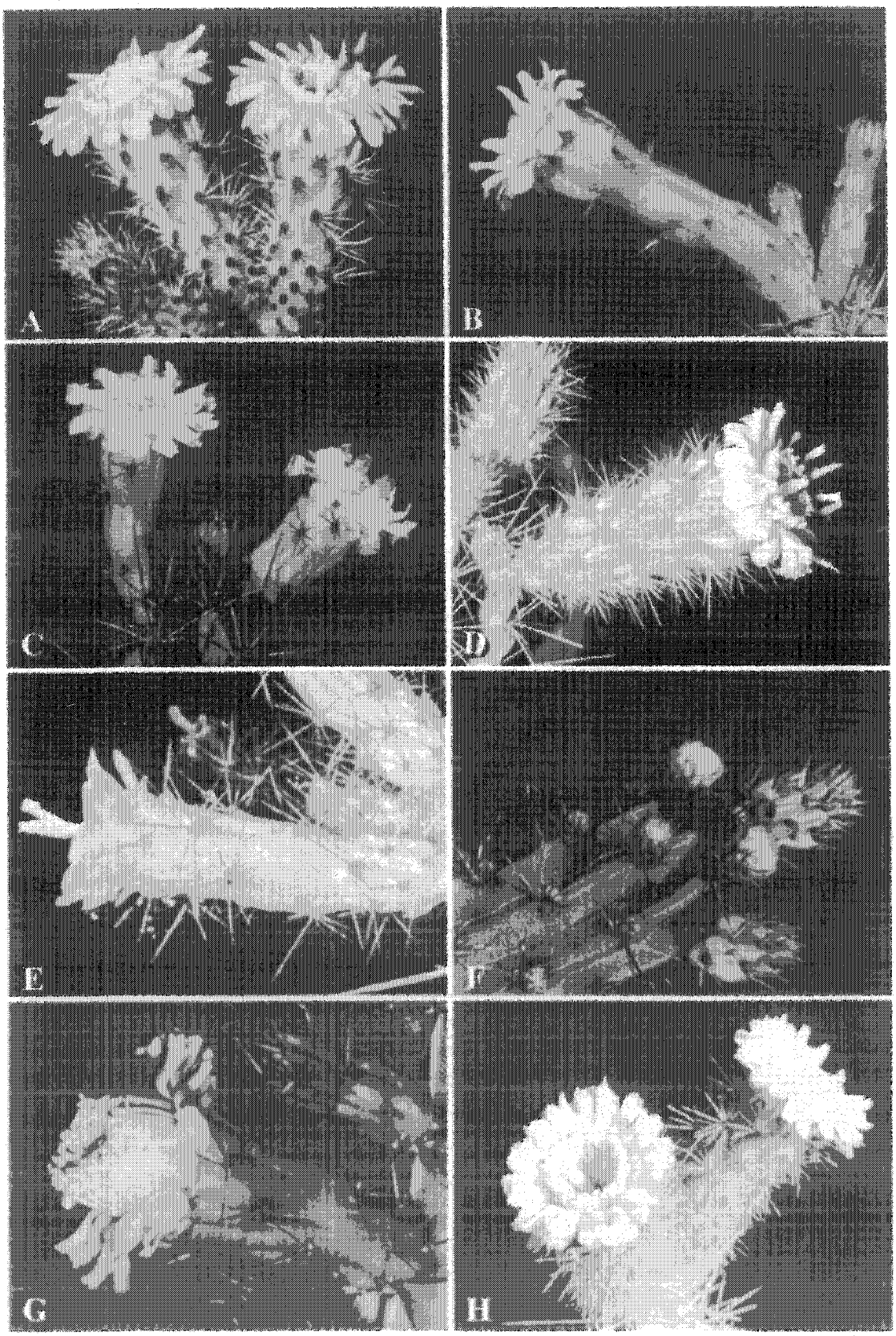

Plate 21.

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Plate 22. Flowers of *Leptocereus* spp. (III). All photographs are from the wild and/or cultivated material of original collections made by the author.

A, **B**. *Leptocereus wrightii* subsp. *wrightii*. **C**, **D**. *L. prostratus*. **E**. *L. scopulophilus*. **F**, **G**. *L. ekmanii*. **H**. *L. carinatus*. **I**. *L. sylvestris*. (A, B, from from Bahia Honda, Cuba —12 Dec 1993; C, D, from type locality at Sumidero, Pinar del Rio province, Cuba —5 Mar 1992; E, from type plant, summit of Somorrostro hill, Cuba —17 Apr 1976; F, G, from Sierra de Guane, Cuba —6 Jun 1984; H, from type plant, Sierra del Chorrillo, Najasa, Cuba —12 Sep 1990; I, from from Boca de Rio Las Puercas, Pilón, Cuba —4 May 1993).

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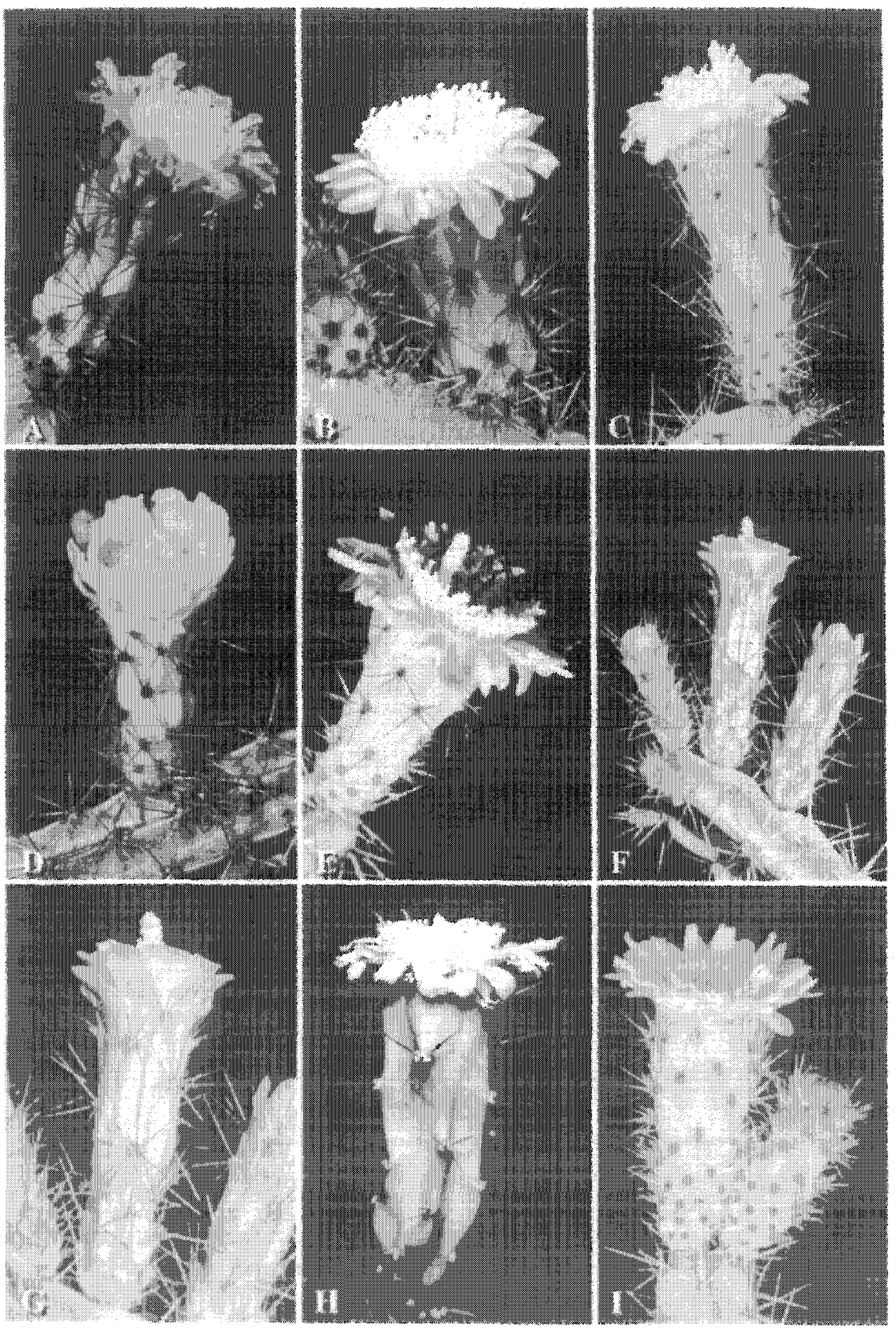

Plate 22.

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Plate 23. Flowers of *Leptocereus* spp. and *Samaipaticereus corroanus*. (IV). With the exception of *S. corroanus* (*Rose 20093, US*), all photographs are from the wild and/or cultivated material of original collections made by the author.

A. *Leptocereus leonii*. **B**. *L. albellus*. **C**. *L. carinatus*. **D**. *L. santamarinae*. **E**. *L. sylvestris*. **F**, **G**. *L. quadricostatus* subsp. *parvispinus*. **H**. *L. assurgens*. **I**. *Samaipaticereus corroanus*. (A, from type locality at Sierra de Anafe, Cuba —29 Oct 1975; B, from Sierra de San Carlos, Cuba —28 Mar 1992; C, from type plant, Sierra del Chorrillo, Najasa, Cuba —12 Sep 1990; D, from type plant, vicinity of Santa Lucía beach, Cuba —15 Apr 1990; E, from Boca del Rio Las Puercas, Pilón, Cuba —4 May 1993; F, G, from Bosque Estatal de Guánica, Puerto Rico —23 Feb 1994; H, from Ensenada de Valle, Viñales, Cuba —21 Feb 1979; I, from vicinity of Samaipata, Bolivia[4]).

[4] A cutting of the original plant from which *Rose 20093* was collected had been grown at The Huntington Botanical Gardens, San Marino, California under accesion number HNT 4980. Photograph is from a flower of this plant.

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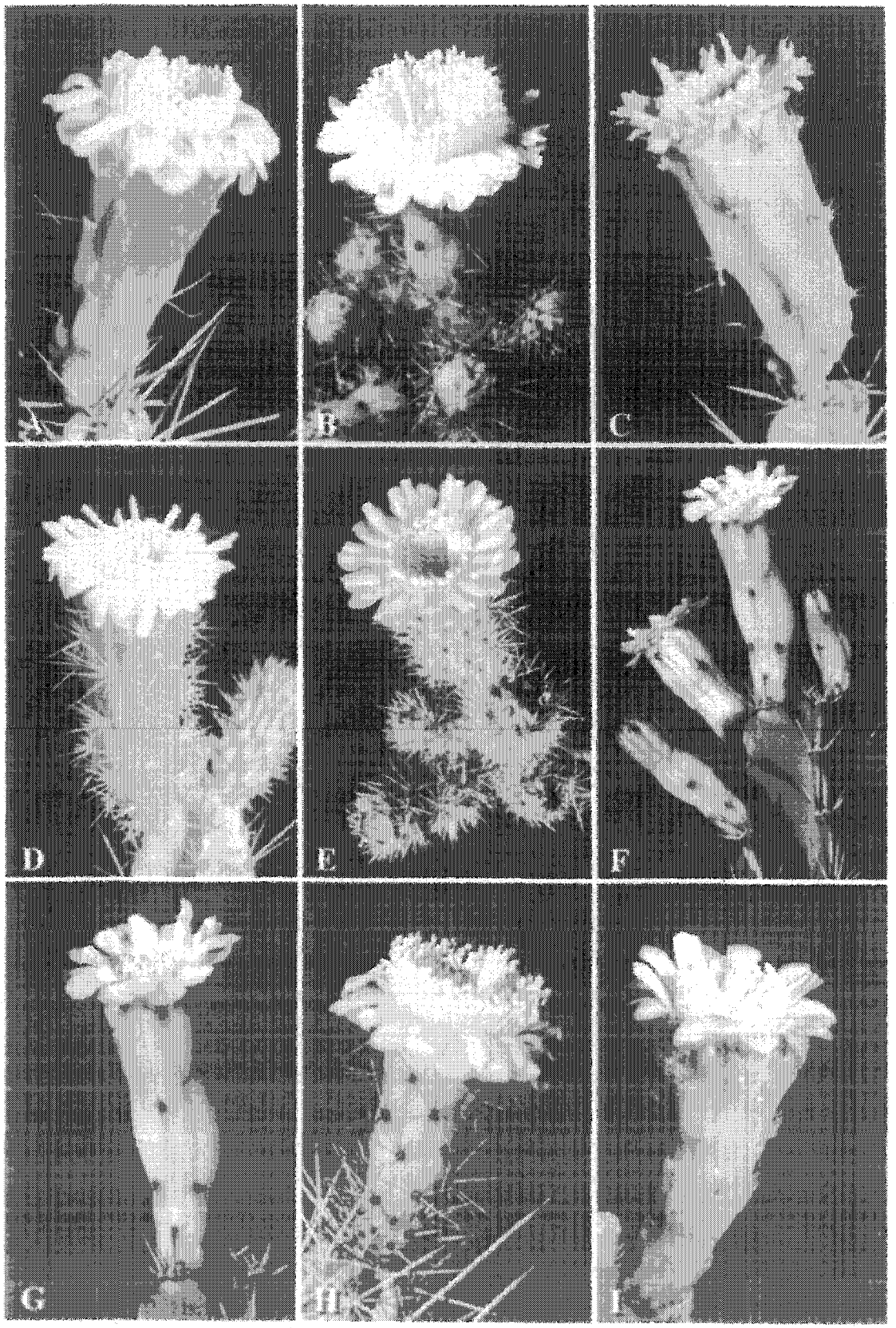

Plate 23.

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Plate 24. Flowers of *Leptocereus* spp., and callus of *L. grantianus* after micropropagation *in vitro* (V). All photographs are from the wild and/or cultivated material of original collections made by the author.

A. *Leptocereus paniculatus*. **B**. *L. weingartianus* subsp. *weingartianus*. **C**. *L. ekmanii*. **D**. *L. quadricostatus* subsp. *quadricostatus*. **E**. *L. ekmanii*. **F**. *L. assurgens*. **G**. Callus growth on sectioned stem of *L. grantianus* after being cultured in Murashige and Skoog medium containing 2, 4, D and kinetin. **H**. *L. assurgens*. (A, from La Descubierta, Dominican Republic —7 Jan 1995; B, from vicinity of Bayahibe, Dominican Republic —22 Jan 1991; C, E, from Sierra de Guane, Cuba —6 Jun 1984; D, from dry forests between Punta Melones and Laguna de Boquerón, Puerto Rico —13 Jun 1995; F, H, from Ensenada de Valle, Viñales, Cuba —21 Feb 1979; G, stem section from Culebra Island, Puerto Rico —8 Mar 1994).

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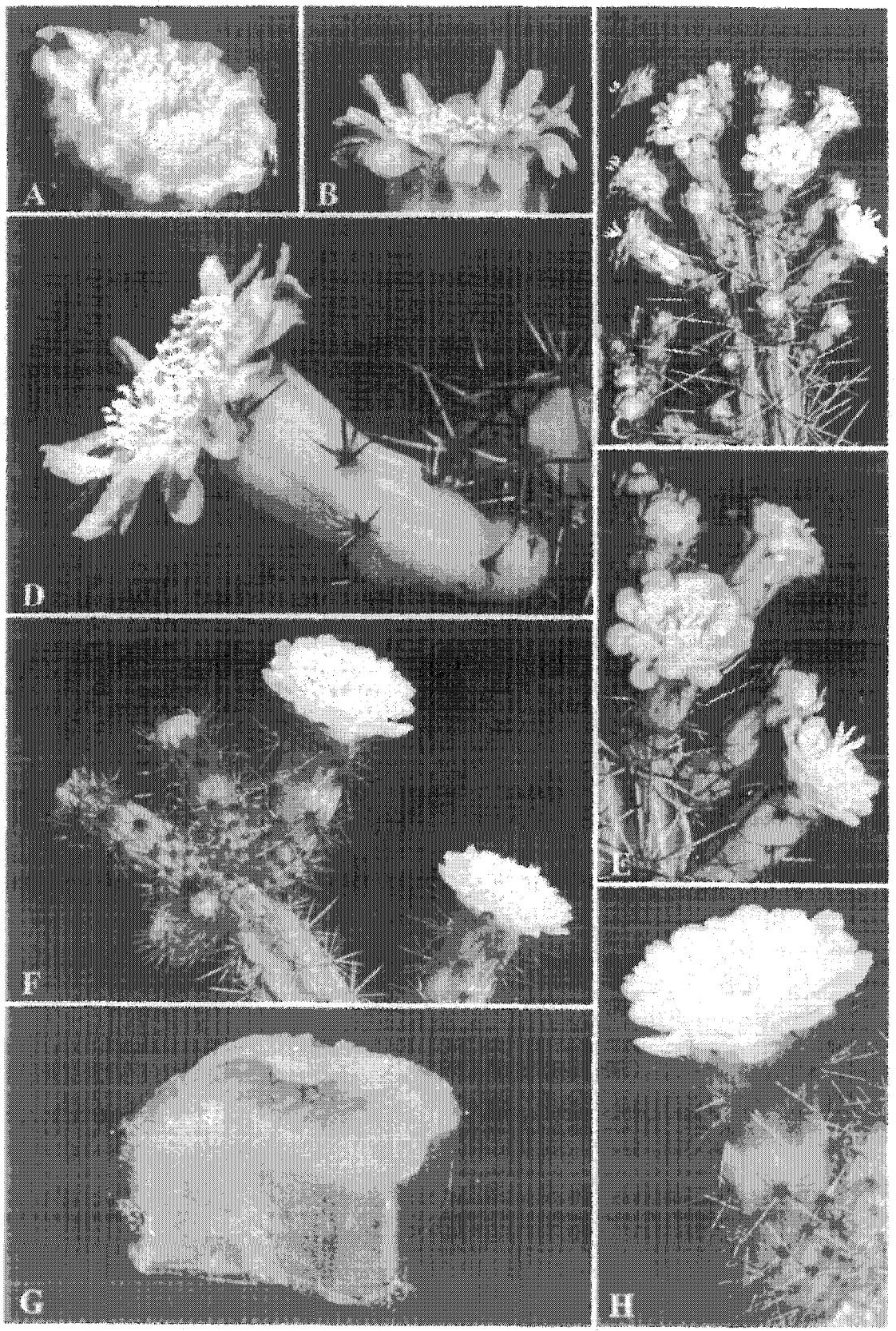

Plate 24.

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Plate 25. Arrangement of stamens in flowers of *Leptocereus* spp. (VI): A, B, C, F inserted; E, G, H, moderately exserted; D, with tight brush of stamens exserted four to six mm from receptacle-tube. All photographs are from the wild and/or cultivated material of original collections made by the author.

A. *Leptocereus arboreus*. **B**. *L. quadricostatus* subsp. *quadricostatus*. **C**. *L. sylvestris*. **D**. *L. chrysotyrius*. **E**. *L. leonii*. **F**. *L. weingartianus* subsp. *weingartianus*. **G**. *L. carinatus*. **H**. *L. wrightii* subsp. *wrightii*. (A, from Yaguanabo, Cuba —9 Jul 1993; B, from dry forests between Punta Melones and Laguna de Boquerón, Puerto Rico —13 Jun 1995; C, from from Boca de Rio Las Puercas, Pilón, Cuba —4 May 1993; D, from San Diego, Pinar del Rio province, Cuba —3 Nov 1976; E, from type locality at Sierra de Anafe, Cuba —29 Oct 1975; F, from vicinity of Bayahibe, Dominican Republic —22 Jan 1991; G, from type plant, Sierra del Chorrillo, Najasa, Cuba —12 Sep 1990; H, from Bahia Honda, Cuba —12 Dec 1993).

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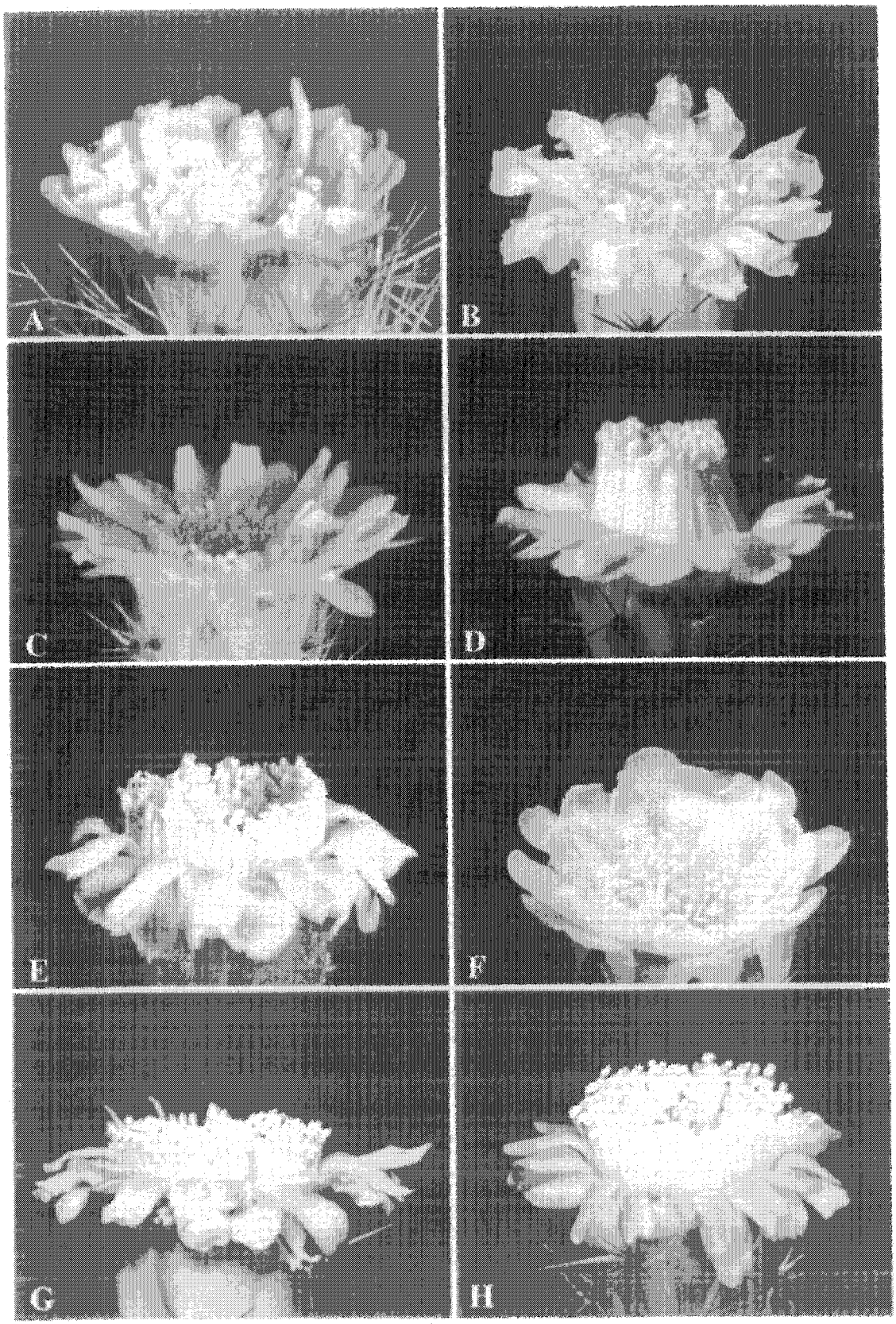

Plate 25.

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Plate 26. Flowers of *Cereus* (*Hamannia*) *fabiolae*. All photographs are from the type locality, in Haiti.

A, C, D, E. Fully expanded flowers of *Cereus* (*Hamannia*) *fabiolae* photographed four hours after sunset. **B.** Young, apiculate flower bud of the same species. (A-E, from from Môle St. Nicolas, Haiti —19 Jan 1995).

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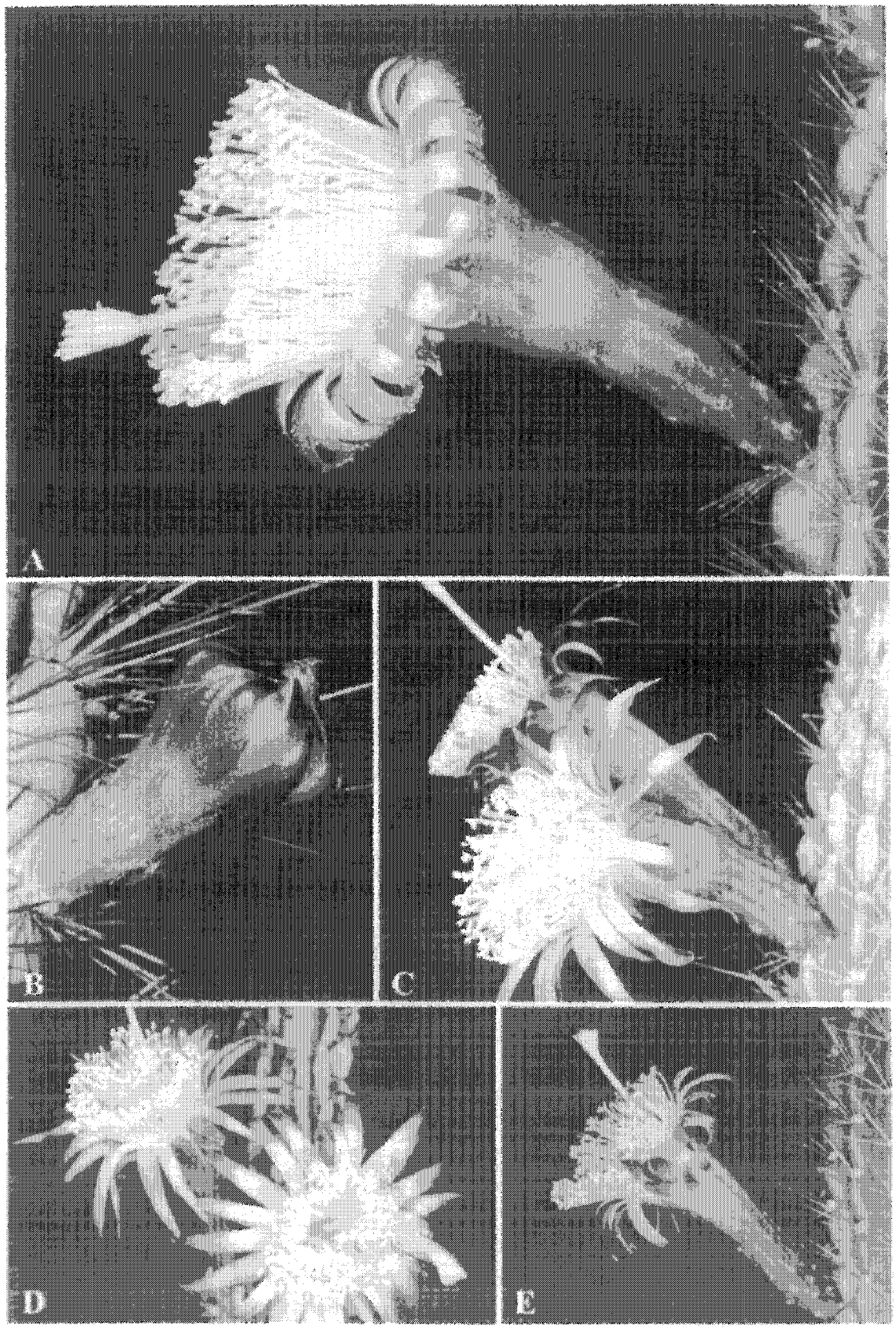

Plate 26.

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Table 9. Contrasted quantitative floral characters in *Leptocereus* and *Cereus* (*Hamannia*) *fabiolae*. LF, length of flower, from base to stigma or stamens —if exserted— (mm); DF, diameter of fully expanded flower (mm); DR, diameter of staminal ring (mm); WF, width of perianth limb at anthesis (mm); PD, proximal (maximum) diameter of receptacle-tube (mm); WP, width of pericarpel (mm).

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TAXON	LF	DF	DR	WF	PD	WP
L. assurgens	38-45	27-31	14-18	6-7	14-18	8-11
L. chrysotyrius	37-41	21-25	9-13	6-7	13-15	9-11
L. ekmanii	19-28	11-15	3-5	4-5	6-7	5-6
L. prostratus	37-40	22-27	9-13	7-8	11-13	8-10
L. albellus	46-54	32-36	21-25	5-7	20-23	10-17
L. wrightii						
subsp. *wrightii*	59-71	33-41	20-22	7-10	24-27	18-21
subsp. *gracilis*	57-70	34-42	18-21	7-9	25-27	18-20
L. scopulophilus	45-65	30-38	15-28	5-8	18-22	8-14
L. leonii	32-43	25-30	17-20	4-6	17-21	8-9
L. arboreus	58-77	29-38	18-21	6-9	22-27	19-21
L. carinatus	50-67	25-37	15-17	5-10	15-20	12-14
L. sylvestris	54-70	28-42	14-20	7-11	18-25	13-16
L. maxonii	50-62	27-35	14-16	7-9	14-18	10-15
L. santamarinae	57-72	31-36	15-17	8-10	20-23	11-19
L. weingartianus						
subsp. *weingartianus*	47-74	19-29	12-18	4-6	12-20	7-12
subsp. *demissus*	50-60	28-32	16-20	5-6	20-25	15-21
L. paniculatus	50-54	25-32	12-14	7-9	20-22	13-16
L. quadricostatus						
subsp. *quadricostatus*	40-47	26-35	10-19	8-9	15-16	9-12
subsp. *parvispinus*	46-53	22-30	11-13	7-9	14-17	9-11
L. grantianus	30-60	30-40	16-23	8-9	18-21	9-11
Cereus (*Hamannia*) *fabiolae*	89-115	46-72	31-40	15-20	28-38	12-14

Table 9.

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2.7. Fruits

The *Leptocereus* fruit is a conspicuous, usually globose, obovate, ellipsoid or fusiform, indehiscent berry, often with a thick pericarp armed with numerous spiny areoles. Because the axial tissue of the floral pericarpel —usually bearing spiny areoles— is involved in fruit formation, the pericarp of a typical *Leptocereus* fruit not only retains its original pericarpel spines, but also usually develops more while it grows. Most spiny of all *Leptocereus* fruits is the typically globose bur-like berry of *L. maxonii*, densely covered with persistent, yellow or brownish spines (Plate 27, B, C). There are some short-spined fruits, however, like those of *L. quadricostatus* subsp. *quadricostatus* (Plate 27, E), and of some obovoid or ellipsoid-obovoid forms of *L. weingartianus* subsp. *weingartianus* (Plate 29, B, C), but totally unarmed fruits are only found in *L. paniculatus* (Plate 28, H), and in *L. grantianus.* With occasional, thin, bristle-like scattered spines, the globose or globose-ovoid fruits of *L. leonii* may be considered nearly unarmed (Plates 27, D and 28, I). Fruits in *L. sylvestris* are at first heavily armed (Plate 29, A), but the spiny areoles often shed when the fruit is ripe leaving it partially or completely naked. *Leptocereus carinatus* has remarkable angled fruits; in this species the coalescence of the decurrent podaria in all pericarp orthostichies produces distinct vertical ribs, not unlike those of a typical stem segment (Plate 28, A). The presence of ribs in fruit can be interpreted as a plesiomorphic character state in the genus. In all species of *Leptocereus* the receptacle-tube stays attached to the fruit in the form of a dry, black, usually spiny remnant (Plate 28, E, F).

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Only occasionally, in *L. paniculatus*, the withered floral remains fall off leaving a well-defined umbilicus on the mature fruit.

Largest of all *Leptocereus* fruits is the ellipsoid to obovate ellipsoid fruit of *L. arboreus*; it may attain 10 cm long by seven cm wide (Plate 27, A). In many respects these large, spiny berries, with their relatively long pedicellate zone and elevated orthostichies, seem to represent the plesiomorphic condition in the genus. *Leptocereus santamarinae* and *L. sylvestris* also have relatively large fruits, up to 8 by 7 cm (Plates 27, H and 29, A, respectively). By contrast, the fruits of *L. leonii* are small, 2 to 4 cm in diameter. Although they rarely set fruit, members of subgenus *Leptocereus* section *Leptocereus* of western Cuba, seem to have the smallest fruits in the genus. The fruits of *Leptocereus chrysotyrius* and *L. albellus*, for example, are less than 2.5 cm long, while Britton and Rose (1919-1923) reported *L. prostratus* (another member of section *Leptocereus*) as having fruits about 1.5 cm in diameter.

There is not much variation in the color of *Leptocereus* fruits. In most species fruit color ranges from green to yellowish-green or yellow, but in *L. leonii* the fruits are entirely wine-red at maturity (Plates 27 D and 28 I). In some forms of the highly variable *L. weingartianus* subsp. *weingartianus* with ellipsoid-obovoid and fusiform fruits, these may be brownish, pinkish-green, or even pinkish (Plate 29, B-F). The fruits of *L. paniculatus* show streaks of pink or wine-red color on a greenish or greenish-yellow background. At maturity the pericarp of *Leptocereus* fruits, formed by the ovary wall and pericarpel, is usually green or greenish, more than 5 mm thick, and hard.

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However, in *L. leonii* and presumable in all species of subgenus *Leptocereus* series *Leptocereus*, it is relatively thin (less than 5 mm thick), and juicy. The numerous seeds in *Leptocereus* fruits are embedded in a firm, glutinous, greenish or grayish-green translucent pulp contrasting the color and texture of the pericarp rind, formed by the long funicles which are thickly intertwined in a mucilaginous mass.

The unarmed, elongated fruits of *Cereus* (*Hamannia*) *fabiolae*, with tiny bract scales bearing small tufts of white wool in their axils, are very different from those of *Leptocereus*, and do not support the idea of the Haitian "leptocereoid" *C. fabiolae* being phylogenetically close to this genus (Plate 29, G). When young, the fruits of *C. fabiolae* show 10 to 12 longitudinal keels that are separated by round grooves, and at maturity they become cylindrical or cylindric-obovate, and pendant. Likewise, the fruits of *Samaipaticereus corroanus* —another member of tribe Leptocereeae of Buxbaum— do not favor the hypothesis of this Bolivian taxon being phylogenetically close to *Leptocereus*. It is true that in the fruits of *S. corroanus* there is coalescence of the decurrent podaria in pericarp orthostichies, like in *L. carinatus*, but the vertical ribs produced are very different, *i.e.*, low, rounded at margin, and very numerous (Plate 29, H). After studying comparatively the essentially different seeds of *Leptocereus* and *Samaipaticereus* (see chapter 3: Seed Morphology), the presence of ribs in the fruits of both *L. carinatus* and *S. corroanus* (a presumable plesiomorphic condition) only seems to indicate that these genera may represent basal lineages in different, relatively unrelated groups.

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Plate 27. Fruits of *Leptocereus* spp. (I). All photographs are from the wild.

A. *Leptocereus arboreus*. **B, C**. *L. maxonii*. **D**. *L. leonii*. **E**. *L. quadricostatus* subsp. *parvispinus*. **F, G**. *L. quadricostatus* subsp. *quadricostatus*. **H**. *L. santamarinae*. (A, from Yaguanabo, Cuba —9 Jul 1993; B, C, from valley of Rio Tacre, Guantánamo, Cuba —21 Mar 1990; D, from type locality at Sierra de Anafe, Cuba —29 Oct 1975; E, from Bosque Estatal de Guánica, Puerto Rico —23 Feb 1994; F, G, from dry forests between Punta Melones and Laguna de Boquerón, Puerto Rico —13 Jun 1995; H, from type plant, vicinity of Santa Lucía beach, Cuba —15 Apr 1990).

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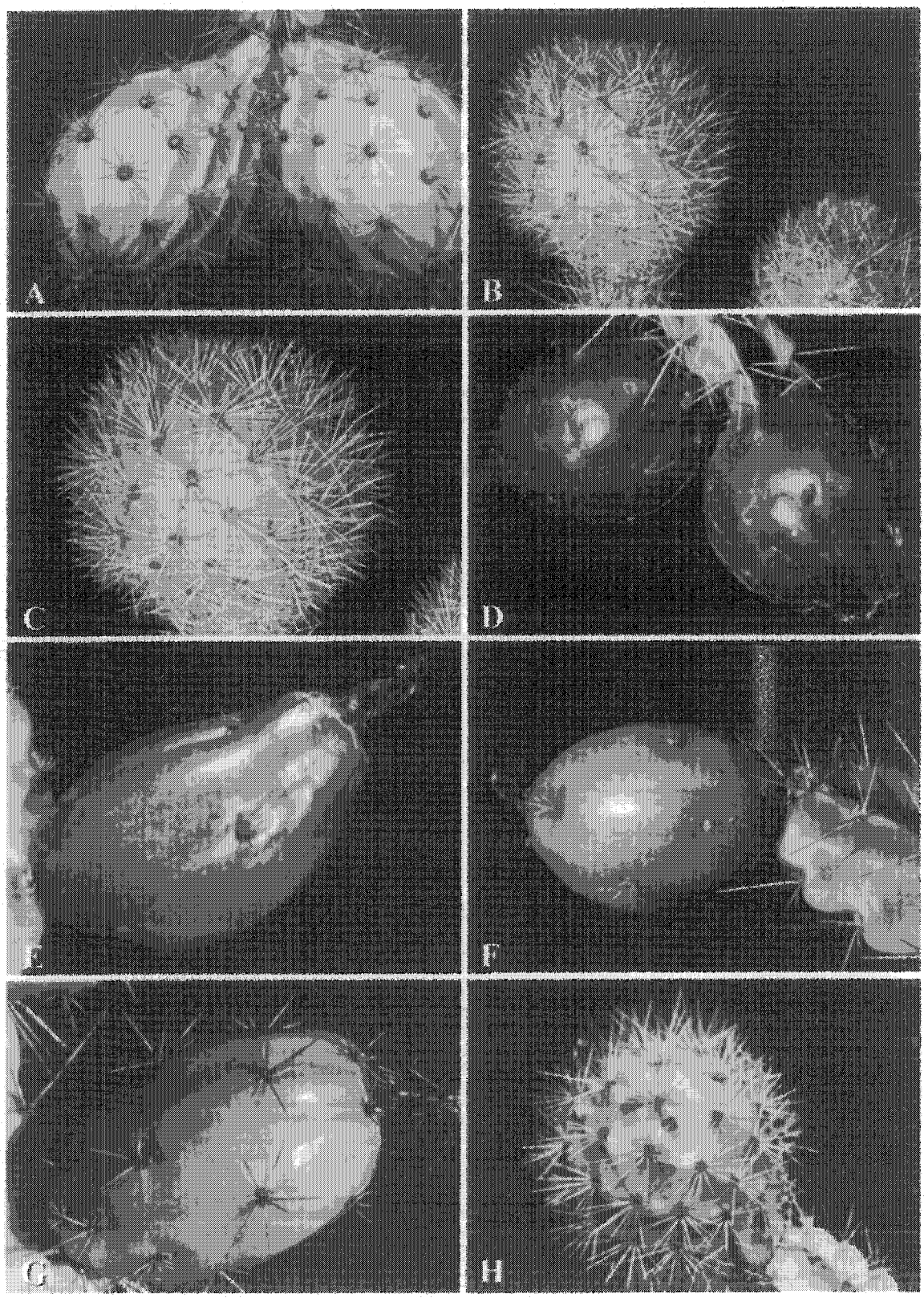

Plate 27.

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Plate 28. Fruits of *Leptocereus* spp. (II). All photographs are from the wild.

A. *Leptocereus carinatus*. **B, C.** Lateral fruits of *L. quadricostatus* subsp. *quadricostatus*, not produced in a cephalium **D.** Subapical fruit of the same subspecies. **E.** Withered floral remains on top of the fruit of the same subspecies. **F.** Young fruits of *L. weingartianus* subsp. *weingartianus*. **G.** Strongly armed fruit of *L. weingartianus* subsp. *demissus*. **H.** *L. paniculatus*. **I.** *L. leonii*. (A, from type plant, Sierra del Chorrillo, Najasa, Cuba —12 Sep 1990; B, C, D, E, from dry forests between Punta Melones and Laguna de Boquerón, Puerto Rico —13 Jun 1995; F, from Cabo Samaná, Dominican Republic —8 Jun 1991; G, from Pedernales, ca. Cabo Rojo, Dominican Republic —31 May 1991; H, from La Descubierta, Dominican Republic —7 Jan 1995; I, from type locality at Sierra de Anafe, Cuba —29 Oct 1975).

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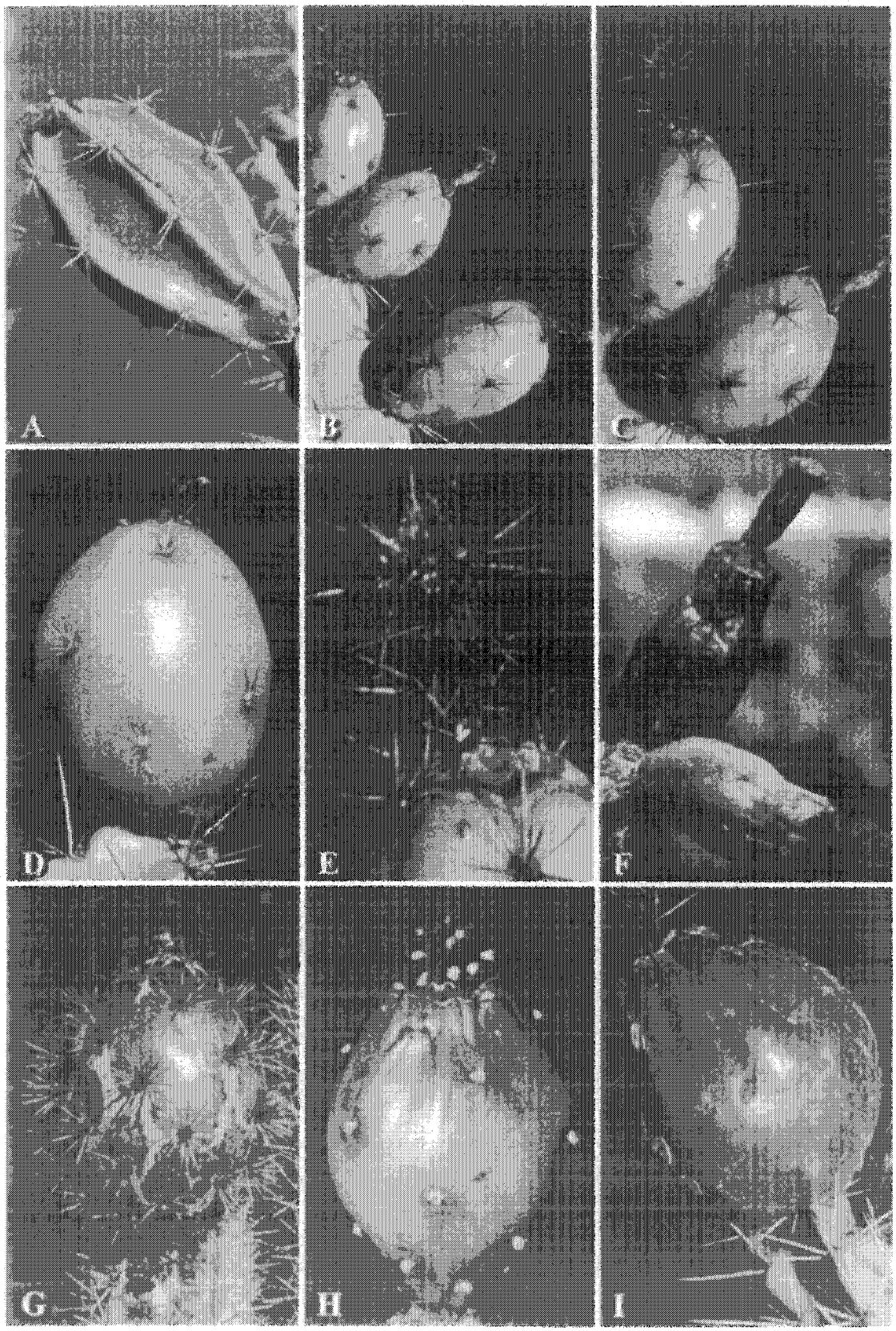

Plate 28.

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Plate 29. Fruits of *Leptocereus* spp., *Cereus* (*Hamannia*) *fabiolae*, and *Samaipaticereus corroanus* (III). Except for *Samaipaticereus corroanus* (*Rose 20093*), all photographs are from the wild.

A. *Leptocereus sylvestris*. **B-F**. *L. weingartianus* subsp. *weingartianus*. **G**. Immature fruit of *Cereus* (*Hamannia*) *fabiolae*. **H**. *Samaipaticereus corroanus*. (A, from Boca de Rio Las Puercas, Pilón, Cuba —4 May 1993; B, C, from vicinity of Bayahibe, Dominican Republic —22 Jan 1991; D, from Cabo Engaño, Dominican Republic —3 Jan 1995; E, F, from vicinity of Port-de Paix, Haiti —19 Jan 1995; G, from Môle St. Nicolas, Haiti —19 Jan 1995; H, from vicinity of Samaipata, Bolivia[5]).

[5] A cutting of the original plant from which *Rose 20093* was collected had been grown at The Huntington Botanical Gardens, San Marino, California under accesion number HNT 4980. Photograph is from a fruit of this plant.

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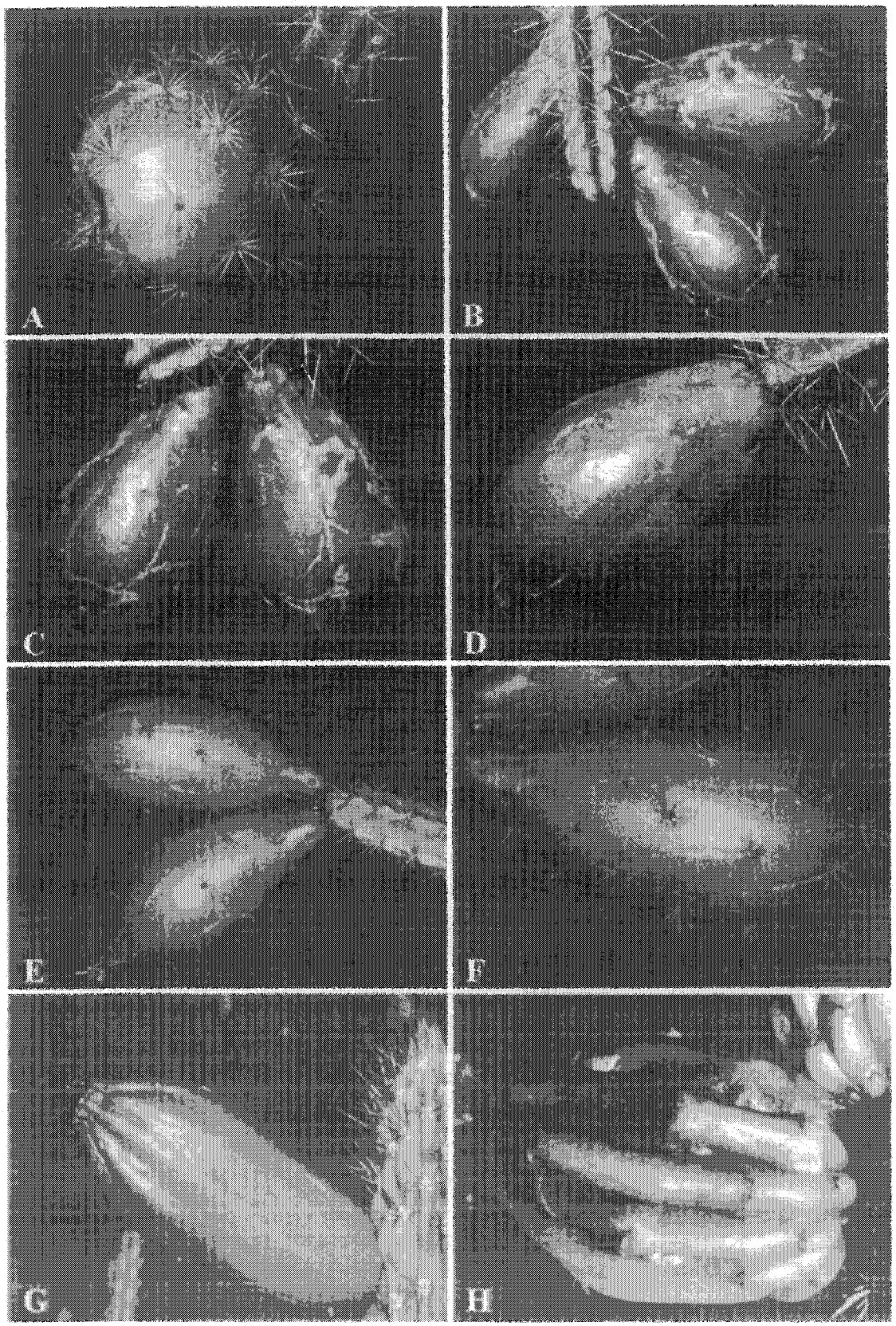

Plate 29

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3. SEED MORPHOLOGY

3. 1. Introduction

The seeds of the various cactaceous taxa differ appreciably, not only in size (from approximately 0.5 to 10 mm), but also in their shape, color, epidermal structure, and in appearance and position of the funiculus and micropyle (Barthlott and Voit, 1979). The overall shape of the cactus seed is highly variable and has unquestionable phylogenetic value. Depending upon the genus, cacti seeds may be rounded in outline, oblong, ovate, tear-, kidney-, or mussel-shaped, etc. In some species of *Echinopsis* the seed outline, which often resemble a knitted cap, has been described as a "bag gathered into a fine-meshed band or neck" (Friedrich and Glaetzle, 1983). The ultrastructure of the seed coat or exotesta, however, is where some of the most elegant discoveries of cactus structure have been made. Although more than eight decades ago Britton and Rose (1919-1923) used the external, easily identifiable seed characteristics as distinguishing features (*e.g.*, the seed color), it was Buxbaum (1958) who first studied and described the cactus seed coat under a low-power dissecting microscope. Following the studies of Buxbaum, observations using high-magnification photographs generated from the scanning electron microscope (SEM) have revealed that many groups of cacti have distinguishing seed features. Because most of these features correlate well with macro-morphological characters, they have proven useful in determining generic boundaries (*e.g.*, Taylor and Clark, 1983; Friedrich and Glaetzle, 1983; Glaetzle and Prestlé, 1986.).

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Viewing the exotesta at high magnification, many features appear that can be used for evaluating phylogenetic relationships. The exotesta, which develops out of the outer layer of the outer integument, consists of thick-walled, tanniferous cells (Haustein, 1986). The differences consist mainly in the varied construction of the individual exotesta cells. Besides their size and shape (isodiametric or elongate, with straight or variously indented anticlinal walls), the formation of the outer, periclinal cell-wall is crucial in determining the character of the exotesta, which can be one of these three different types:

1. FLAT. Usually very thickened (smooth, hard exotesta; when the wall thickening is completely reduced the exotesta is small-celled and soft).

2. CONVEX. Whereby either the entire outer wall is weakly to pronouncedly uneven (verrucose testa), or only one part develops usually excentric papillae or hair-like protrusions (*e.g.*, in the hairy seeds of some West Indian species of *Consolea*).

3. CONCAVE. As a result of the tendency of cohesion in the exotesta cells of the drying seed. This cohesive tendency affects a completely unthickened outer wall or one that is only so in a central area, causing it to curve inwards or even to split (pitted exotesta).

Further characteristics include depressed or elevated anticlinal walls and flat to crater-like depressions of the cell corners where three cells juxtapose (interstitial pits).

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The exotesta is also covered with a cuticle that often shows a complex and specific pattern of convolutions. Occasionally the cuticle is raised and visible to the naked eye as a wrinkled, whitish skin, sometimes wrongly termed the aril-membrane (Haustein, 1986). A thick and strongly wrinkled cuticle layer obscuring the exotesta cells is characteristic of some species of *Leptocereus*, particularly *L. paniculatus* (Plate 31, A-D). The fine cuticular folds exhibited by the seeds of the genus *Cereus* (*sensu stricto*), seem to be the plesiomorphic state of this character in sufamily Cactoideae (Zappi, 1994).

Exotesta characters have been widely used to make judgments about the placement of genera in the tribes and subtribes of subfamily Cactoideae, where the genus *Leptocereus* resides. In subtribe Stenocereinae of tribe Pachycereeae, for example, the striated seed coat ultrastructure is quite similar within the four genera of the subtribe and structurally quite different from the smooth seed coats found in subtribe Pachycereinae. Anderson and Boke (1969), and Anderson and Skillman (1984) have used seed coat morphology as one of many apomorphic features in evaluating the generic composition and relationships within tribe Cacteae. Other good examples are found in the tribes Notocacteae and Cereeae. The seeds of *Discocactus* closely resemble those of *Gymnocalycium*, an observation that helps in justifying their inclussion in Notocacteae. Both of these genera have seeds that are quite unlike those of *Melocactus*, which was formerly placed next to *Discocactus* because the cephalium of *Melocactus* superficially resembles the floriferous shoot tip of *Discocactus*. Instead,

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Melocactus has seeds that are quite similar to those of *Buiningia,* which is a genus of tribe Cereae (for detailed descriptions of *Melocactus* seeds, see Taylor 1991).

In many cactus genera funicular tissue grows out to build lignified arilloid structures or to form masses of non-lignified cells at the hilar end of the seed (strophioles). Strophiole cells may form a kind of collar around the hilum-micropylar zone or develop into an amorphous hump of cells. The strophiole is believed to have some function in seed dispersal and in water uptake prior to germination (Bregman and Bouman, 1983), and seems to be a derived condition. At least it is present in some highly specialized genera such as *Blossfeldia.* However, the presence of a strophiole apparently cannot be used to group taxa on the basis of a phylogenetic relationship because some species of the tribe Cacteae, for example, have a strophiole on the seed very similar to that of *Blossfeldia* and other related genera of the Notocacteae that are quite dissimilar in stem, flower, and fruit structure (Gibson and Nobel, 1986).

In the seeds of all the Cactaceae as a rule the endosperm is ultimately fully reabsorbed by the embryo, but as Bregman and Bouman (1983) indicated, endosperm remnants are sometimes present near the micropyle. It is a well-known fact that in *Pereskia* and some other primitive genera the perisperm, situated mainly between the cotyledons and the hypocotyl, is still copious, but in the more evolved groups of Cactaceae the perisperm has disappeared, its storage function having been taken over by the hypocotyl. Another important feature of cactus seeds that has been the subject of analysis is the thickness of the inner layer of the outer and inner integument layers plus

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nucellus, which may indicate the "evolutionary stage" of the taxon. In the Cactaceae the inner layer of the outer integument becomes crushed during seed development (Kapil and Prakash, 1969). The inner integument layers and the nucellus form a more or less thin membrane around the embryo ending in the micropyle (Bregman and Bouman, 1983).

As in other families of Centrospermae (Caryophyllales), the Cactaceae have developed interesting structural mechanisms of germination of seeds. First to report that in the early stages of germination of the seeds of *Echinocactus* and *Cereus,* "a piece is pushed off valve-like from the micropylar region," was Ganong (1898). Bernard (1967) also published some illustrations of cactus seeds in which an operculum is clearly seen, but it was Bregman and Bouman (1983) who contributed more to this subject. These authors distinguished eleven different types of germination mechanisms in the seeds of the Cactaceae, eight of which were without operculum formation.

Even though SEM studies of cactus seeds have only been published since the early 1970's, enough is now known about seed ultrastructure to compile a large atlas. Nothing has been published, however, on the ultrastructure and structural mechanisms of germination of the seed of the genus *Leptocereus*.

3.2. Materials and methods

Seeds of 11 species and 2 subspecies of *Leptocereus* obtained from fresh or dried

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material were studied. Also included were the seeds of the problematic Haitian cereoid (*Cereus fabiolae*), which was determined as a possible *Leptocereus* species by N. P. Taylor (*Leonard & Leonard* 13311, US), and *Samaipaticereus corroanus* Cárdenas, a Central-Andean taxon with small flowers resembling those of *Leptocereus*[6]. Most seeds were collected in the wild while others were obtained from herbarium material. *Leptocereus albellus, L. assurgens, L. carinatus, L. chrysotyrius, L. ekmanii, L. prostratus* and *L. wrightii* subsp. *gracilis* were not included in this study because their seeds were not available. The species and infraspecific taxa examined are listed in Table 10.

To separate the seeds from the mucilage and remains of pulp in which they were embedded, they were soaked in tap water for 24 hours and then washed repeatedly with deionized water with a few drops of industrial detergent (dil. to 1%). Then they were cleaned for 30 seconds in a 50% ethanol ultrasonic cleansing bath and dried overnight at room temperature in a calcium chloride chamber. All seeds were studied both under a stereo light microscope and a JEOL JSM-5410LV scanning electron microscope with integral digital scanning equipment. For SEM study the seeds were mounted on aluminum stubs with double-sided adhesive tape, and coated in a sputter coater for 5 minutes with a thin layer of gold. On average, 10 seeds were examined with light and scanning microscopy, and a typical specimen photographed under the SEM at 35×. For comparative purposes the whole seed was photographed at three different views: lateral (plate letters A, E, I), ventral (B, F, J), and dorsal (C, G, K). The ventral view shows in

[6] *Samaipaticereus* was placed in tribe Leptocereeae by Buxbaum (1958).

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detail the hilum-micropilar rim. Close-up photographs at 350× of the testa cells near the dorsal region of the seeds in lateral view were additionally taken (plate letters D, H, L). No artifacts were detected other than some cracking of the exotesta surface (in about 2% of samples), probably due to the effects of the strong dehydration of the seed within the sputter coater and the SEM's strong vacuum chamber.

TAXON	SOURCE
L. wrightii var. *wrightii*	*Areces* 6849, NY
L. scopulophilus	*León* 11446, NY
L. leonii	*Areces* 3292, NY
L. arboreus	*Cowell & Eagle* 10298, NY
L. sylvestris	*Britton, Cowell & Shafer* 13060, NY
L. maxonii	*León* 16761, GH
L. santamarinae	*Areces* 5341, MNHN
L. weingartianus weingartianus	*Areces* 5973, NY
L. weingartianus demissus	*Areces* 6812, NY
L. paniculatus	*Areces* 6386, NY
L. quadricostatus subsp. *quadricostatus*	*Areces* 6369, NY
L. quadricostatus subsp. *parvispinus*	*Areces* 6417, NY
L. grantianus	*Britton* 9725, NY
Cereus (*Hamannia*) *fabiolae*	*Areces* 6795, NY
Samaipaticereus corroanus	*Rose* 20093, US[7]

Table 10. List of taxa studied, and their sources.

[7] A cutting of the original plant from voucher *Rose 20093* has been grown at the Huntington Botanical Gardens, San Marino, California, under accesion number HNT 4980.

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To study the structural features of the early stages of germination in *Leptocereus* fresh seeds of two species were selected: *Leptocereus quadricostatus* and *L. sylvestris*. The seeds of the first one were collected in Boquerón, Puerto Rico (*Areces 6369*, NY) and correspond to subspecies *quadricostatus*, while those of *L. sylvestris* were obtained from my private collection at Hacienda Paraíso, Ponce, Puerto Rico (*Areces 6811*, cult. from Boca Río Las Puercas, Pilón, Cuba). Seeds were laid out to germinate in petri dishes over moist filter paper at room temperature (20-25° C), under a normal daylight regime (month October, at New York City latitude). Observations were made under a stereo light microscope.

The descriptive terminology of the seed is mostly that of Barthlott and Voit (1979). However, the simpler term "hilum" (in the sense of Friedrich and Glaetzle, 1983) is used instead of "hilum-micropylar zone," in German "Hilum-Micropylar-Bereich" (Barthlott and Voit, *op. cit.*), and "hilum-micropylar-rim" (Taylor and Clark, 1983), for the total non-clarified area consisting jointly of the proper hilum, and the micropyle, which is typical of most seeds of subfamily Cactoideae (Fig 5, A-1).

3.3. The seeds of *Leptocereus*: general remarks

In its basic characters, the seeds of typical *Leptocereus* are referable to a relatively common type in subfamily Cactoideae. These are laterally flattened and essentially mussel-shaped or cochleariform (miesmuschelförmige of Barthlott and Voit, 1979), although more unfamiliar tear-shaped forms and even subhemisphaerical forms are

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present (Fig 5, A). The profiles in outline are determined to a great extent by the size, position, and other characteristics of the hilum. The symmetry depends almost entirely on the relative angle that the hilum forms in relation to the long axis of the seed, which varies from –12° to 36°. Size varies from 1.1 to 1.8 mm long and 0.7 to 1.1 mm wide.

The ovule of *Leptocereus* is typically campylotropous. Its campylotropy explains why the micropyle and the hilum, together with the raphe and chalaza, form only a relatively small area of the seed surface. Unlike the Pereskioideae and some other Cactoideae genera (*e.g.*, *Echinocactus*, *Echinomastus*, *Coryphanta*, *Homalocephala*), in *Leptocereus* the micropyle and hilum are not separated by a zone of sclerotized exotesta cells. They are united to form a non-sclerotic zone of cells. There is no trace of arilloid structures, or strophioles derived from the funicular tissue. Depending upon the species, the hilum may be oblong or narrowly oblong, to narrowly oblong-lanceolate or triangular. Because *Leptocereus* seeds lack strophioles and arilloid structures, the hilum is sunken by the shrinkage of the funicular cells. This leads to the formation of a cavity that was described earlier in other genera of Cactoideae, called the "hillum cup" by Engleman (1960). The depth of this depression is provided by the so-called "funicular hump" (Engleman, 1960), which is formed at the junction of the raphe and the origin of the outer integument during seed development (Fig. 5, A-3). In most *Leptocereus* species examined, the hilum cup is relatively deep. The micropyle and funicle abscissions form two very unequal holes at opposite ends of the hilum cup (Fig. 5, A-2; A-9). The thickening of the funicle below the seed, coupled with a very unequal collar-

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like development leads to a hilum that is positioned obliquely[8] at the narrower end of the seed (Fig. 5, A-1). As *Leptocereus* seeds are laterally compressed, the more typical crater-like hilum is not formed. In this genus the characteristic hilum cup of the Cactoideae becomes a more or less elongated slit, the funicular hump forming an angular projection of 90-110°. The dorsal region of the hilum cup, opposite to the funicular hump, is particularly well developed in *Leptocereus*, forming an acute, obtuse or rounded but nevertheless projecting structure that I call a "rostrum." The dorsal line of the rostrum (as seen in lateral view) may be more or less straight, *e.g.*, in *Leptocereus quadricostatus* (Plate 30, A; E), or clearly upcurved, *e.g.*, in *Leptocereus maxonii* (Plate 32, A). The degree of development of the rostrum correlates well with macro-morphological characters, having potential value for use in phylogenetic analysis. I have noted the presence of this rostrate seed-type in *Dendrocereus,* another West Indian endemic genus of subfamily Cactoideae (Areces-Mallea, Revision of genus *Dendrocereus*, in prep.). No doubt that this character may support, to some extent, Backeberg's most criticized system of classification (1976). This author placed *Dendrocereus* and *Leptocereus* in the same Group "Leptocerei" (Tribe Cereae).

In *Leptocereus* the hilum may be offset at an acute or obtuse angle with respect to the rim that surrounds it, or may pass over into the outer surface of the hilum cup by means of a more or less rounded thickening. This is also a character of diagnostic

[8] Many authors describe the position of the hilum in species diagnosis as basal, subbasal, or lateral, terms that I consider meaningless since the hilum is, strictly speaking, the base of the seed. Therefore, I will refer to the hilum of most species of *Leptocereus* as oblique, since the longitudinal axis of the seed often cuts the hilum plane at an acute angle.

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importance to separate groups of species. In lateral view, where the seeds are seen from the side, the hilum may be undulate, straight or even slightly concave in profile. The testa cells of the hilum cup are very homogeneous and noticeably smaller than those of the lateral and dorsal regions, and lack the typical interstitial pits ("lacunae interstitiales") of the cell boundaries of those regions.

There is some variation in exotesta surface features of *Leptocereus.* Common to all species examined is the dark brown to nearly black color. In some species, for example *Leptocereus paniculatus,* this structure is almost entirely covered by thick, projecting cuticular folds that may obscure the contours of cells underneath (Plate 31, A-D). These seeds look grayish to the naked eye. Cuticular folds in *Leptocereus* may be classified as relatively fine, or regular (as in *L. wrightii, L. scopulophilus, L. leonii, L. arboreus, L. sylvestris, L. maxonii,* and *L. santamarinae*), coarse (as in *L. weingartianus, L. quadricostatus*, and *grantianus*), and very coarse (as in *L. paniculatus*). The exotesta is typically convex-verrucose, with the exotesta cells commonly round in outline. Only in the dorsal region of some species, *e.g.*, *Leptocereus scopulophilus*, are these oblong or elliptic-oblong (Plate 33, G). Usually there are well-marked interstitial pits between the verrucae, at the sites where three or four exotesta cells meet (Plate 33, H). According to its position in the seed, the verrucae may be classified as dorsal, lateral, and hilar, and their size in each region varies considerably (the dorsal verrucae are larger to much larger than the others, while the hilar ones are the smallest). Most often several parallel rows of larger verrucae run dorsally from the hilum to the apical region. In some species, for example *Leptocereus santamarinae,* these verrucae are so large that they

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Fig. 5. Seed and seedlings of *Leptocereus sylvestris*.

A. Longitudinal section of the seed; **B**. Transverse section of the seed; **C**. Seed shortly after germination, with the operculum being pushed aside by the growing embryo; **D**, and **E**. Later stages of germination of seed, the cotyledons still within the seed coat (the testa shell showing a typical dorsal crack); **F**, **G**, and **H**. Plantlets (different stages of growth), after releasing the seed coat. 1. Hilum (hilum-micropylar) zone; 2. Funicle remnant; 3. Funicular hump; 4. Cotyledons; 5. Perisperm; 6. Exotesta; 7. Embryo hypocotyl; 8. Embryo radicle; 9. Micropyle; 10. Inner integument and nucellus; 11. Inner layer of outer integument; 12. Outer layer of outer integument (exotesta); 13. Operculum; 14. First spines.

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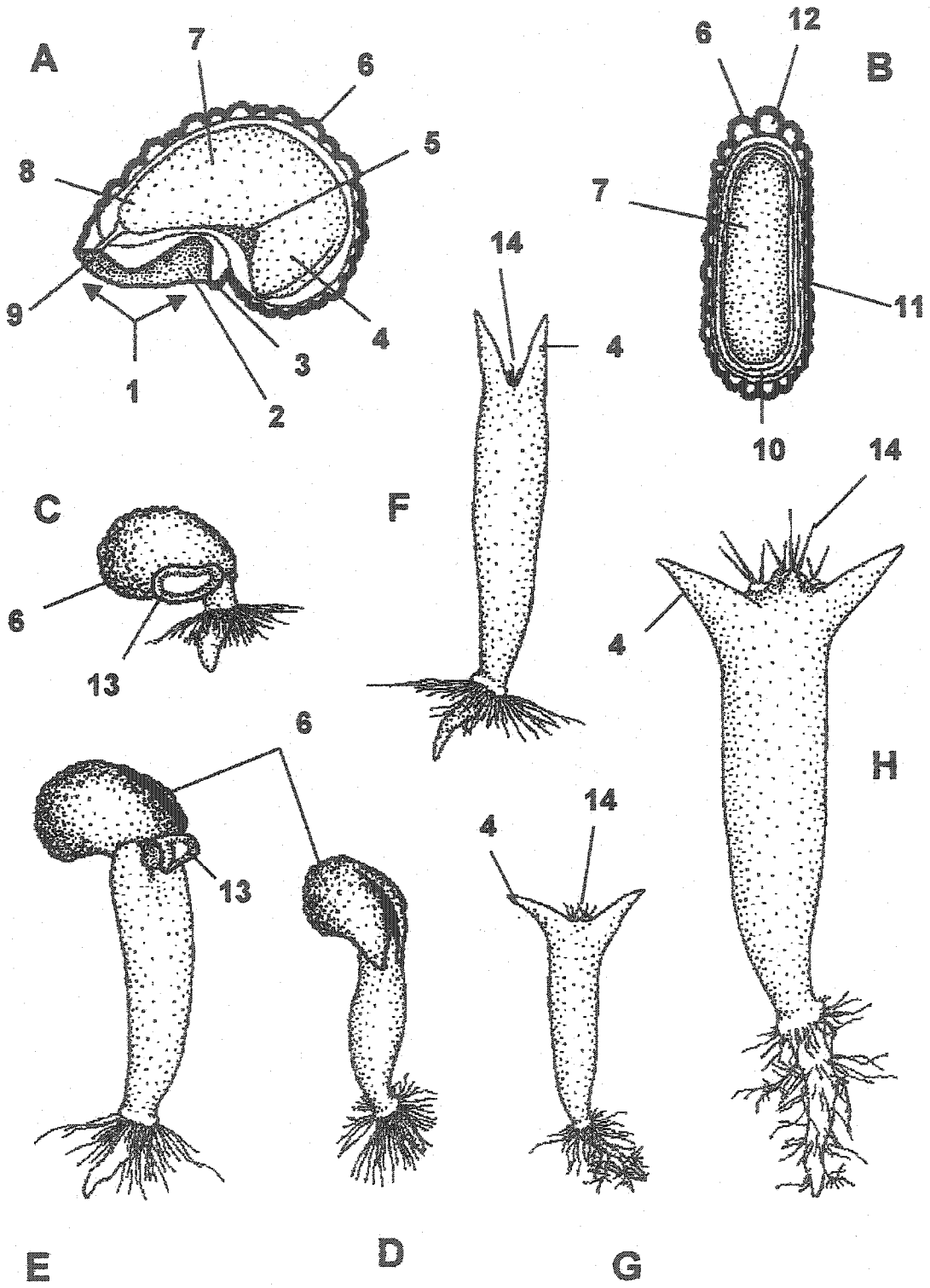

Figure 5.

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form a keel-like ridge in the dorsal region of the seed (Plate 32, E; G). Because it correlates with many other macroscopic plesiomorphic features of the plant body, *e.g.*, the tree-like habit and the spination and size of flowers and fruits, the plesiomorphic character state in relation to the size and covexity of dorsal exotesta cells seems to be the large, strongly domed (convex) ones. Groups of species can be delimited by their distinctive distinguishing verrucose patterns, which reflect species interrelationships judged on gross morphology.

The shape of the embryo within the seed depends largely on the shape of the seed itself. *Leptocereus* embryos are oblong, curved and relatively nonsucculent (Fig. 5, A). They possess a well-developed hypocotyl and reduced cotyledons (Fig. 5, A-4). No characters meriting evaluation for diagnostic purposes were recognized in the internal structure of the seed, which is fairly homogeneous in the entire genus (Fig. 5, A, B).

The problematic Haitian cereoid, hitherto described as *Cereus* (*Hamannia*) *fabiolae*, but referred to *Leptocereus* by some authors, has seeds that are also basically mussel-shaped, as in *Leptocereus* (*sensu stricto*), but with a narrower, more acute extreme. The general characters of the sunken hilum and hilum cup are also those of *Leptocereus*, but exotesta surface features vary significantly, the most important difference being its papillate (not verrucose) pattern (Plate 34, E-H). The seeds of *Samaipaticereus corroanus* Cárdenas from Bolivia (Plate 34, I-L) appear to be even more different when compared to those of *Leptocereus,* in most respects. Because there is not a narrower extreme, the shape of a *Samaipaticereus corroanus* seed resembles a

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short boomerang with its nearly bilaterally symmetrical profile. A massive dorsal keel is present, but contrary to the keel-like ridge formed by extremely large dorsal exotesta cells in some *Leptocereus* species, this one is a structural component of the seed body. In *Samaipaticereus corroanus* the hilum is very large and broad, and is surrounded by a massive straight rim that abruptly leads to the hilum-micropilar area as if cut off by a sharp instrument. The hilum tissue is not sunken by the shrinkage of the funicular cells and as a result this structure is not crater-like, but flat. No cavity is recognizable within the hilum area, other than the two rather small micropile and funicle abscission holes. The exotesta surface is brownish-black and very glossy. Under the scanning electron microscope its surface looks very smooth; cuticular folds are very thin to totally absent, and the anticlinal exotesta cell walls, which are hardly discernible, lack the typical transverse microsculpturing of *Leptocereus*.

3.4. Germination

After 10 days of water uptake, cracking of the rigid exotesta led to the appearance of the radicule tip of the growing embryo (Fig. 5, C). The radicule tip never protruded through the micropyle itself in any of the seeds of the two species studied. The membrane formed by the inner integument and the nucellus was penetrated, in both cases, next to the endostome. Swelling of the embryo and spliting of the seed membrane is an important event in *Leptocereus*, but the most significant one is the cracking pattern of the exotesta shell, because it distinguishes to which germination variant the genus belongs. In both *Leptocereus* species examined, a large dorsal crack

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occurred at the boundary of two of the main rows of dorsal cells (Fig.5, E, D). Simultaneously, two other lateral cracks form at the hilum cup, extending to the ventral side of seeds. As a result the whole hilum-micropilar region is pushed aside by about 90-100°, or sometimes even completely detached by the protruding embryo (Fig. 5, C; F). Cracks also cut between adjacent cells at the borderline exotesta-hilar cup. Because in some cases the hilum crack appears following strong dehydration of the seed (*e.g.*, for SEM studies —see Plates 31, J, and 32, B), the area of lateral cracks that forms the hilar "operculum" seems somewhat predetermined. Although Bregman and Bouman (1983) did not study *Leptocereus*, they reported this germination type, which they called "the *Cereus* variant" in a large number of other genera within subfamily Cactoideae, particularly South American genera. These authors found that the *Cereus* variant was the only germination type present in the examined species of *Corryocactus, Erdisia, Eulychnia, Neocardenasia, Neoraimondia* and *Philippicereus*, all members of tribe Leptocereeae of Buxbaum (1958).

Another feature examined in both *Leptocereus* species studied was the relationship between cotyledons and testa. Because the cotyledons escape readily from the entire testa shell after germination, *Leptocereus* seedlings may be described as typical phanerocotylar (Fig 5, D, E, H). As in most phanerocotylar species, the germination pattern is epigeal (Duke, 1965).

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Plate 30. SEM photographs of *Leptocereus* seeds (I).

A-D. *Leptocereus quadricostatus* subsp. *quadricostatus*. (*Areces 6369*, NY); **E-H**. *L. quadricostatus* subsp. *parvispinus*. (*Areces 6417*, NY); **I-L**. *L. grantianus*. (*Britton 9725*, NY).

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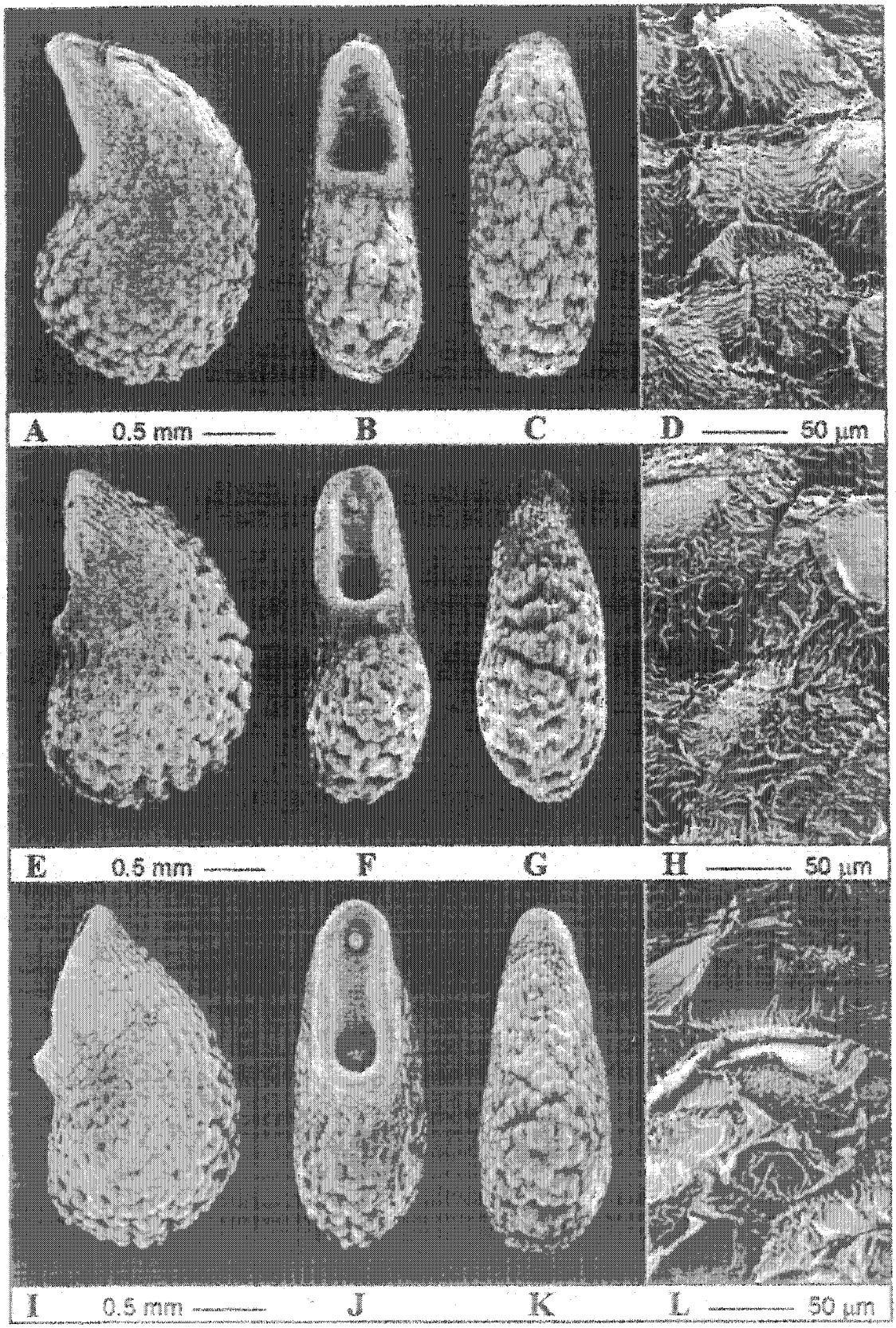

Plate 30.

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Plate 31. SEM photographs of *Leptocereus* seeds (II).

A-D. *Leptocereus paniculatus*. (*Areces 6386*, NY); **E-H**. *L. weingartianus* subsp. *weingartianus*. (*Areces 5973*, NY); **I-L**. *L. weingartianus* subsp. *demissus*. (*Areces 6812*, NY).

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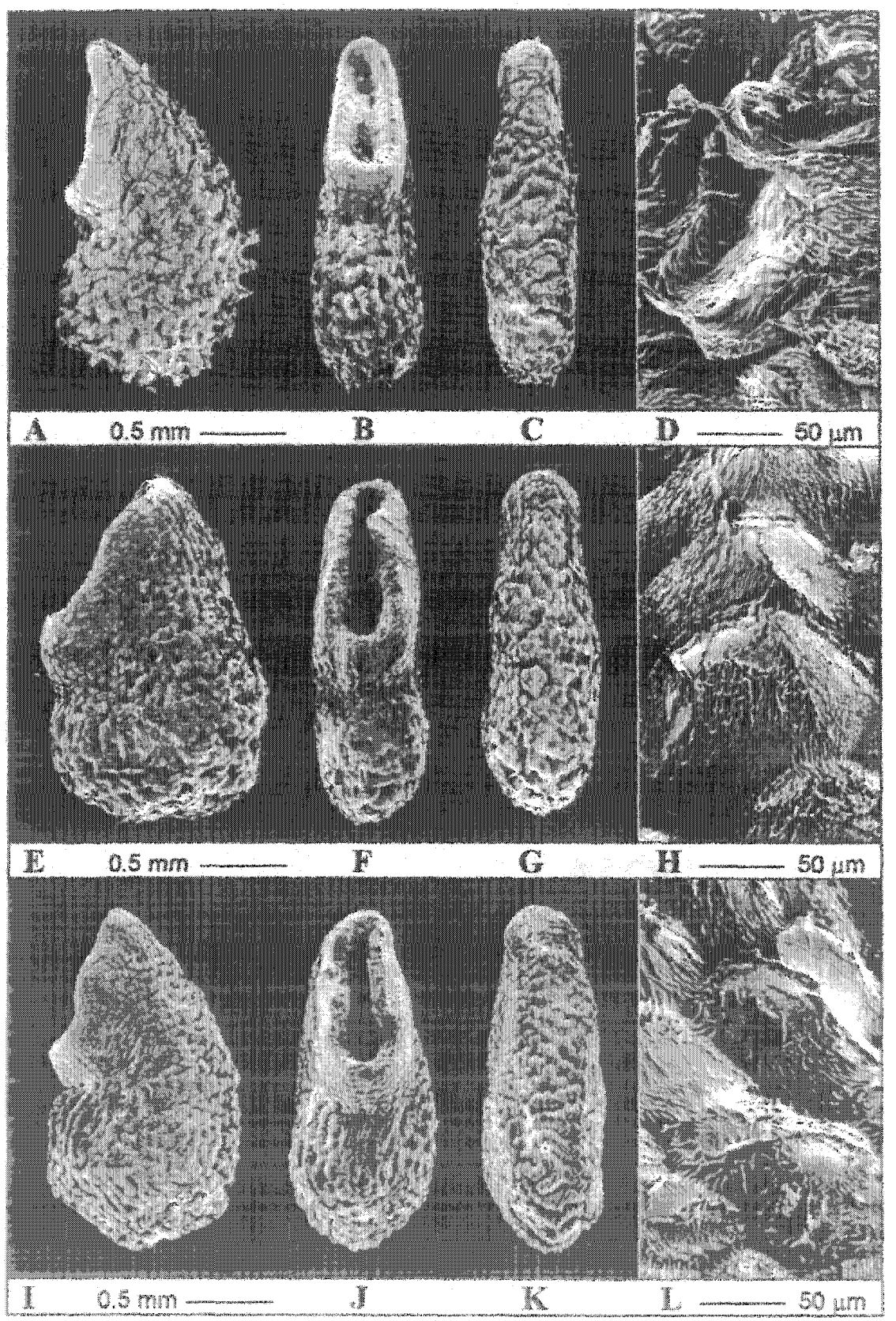

Plate 31.

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Plate 32. SEM photographs of *Leptocereus* seeds (III).

A-D. *Leptocereus maxonii*. (*León 16761*, GH); **E-H**. *L. santamarinae*. (*Areces 5341*, MNHN); **I-L**. *L. sylvestris*. (*Britton et. al. 13060*, NY).

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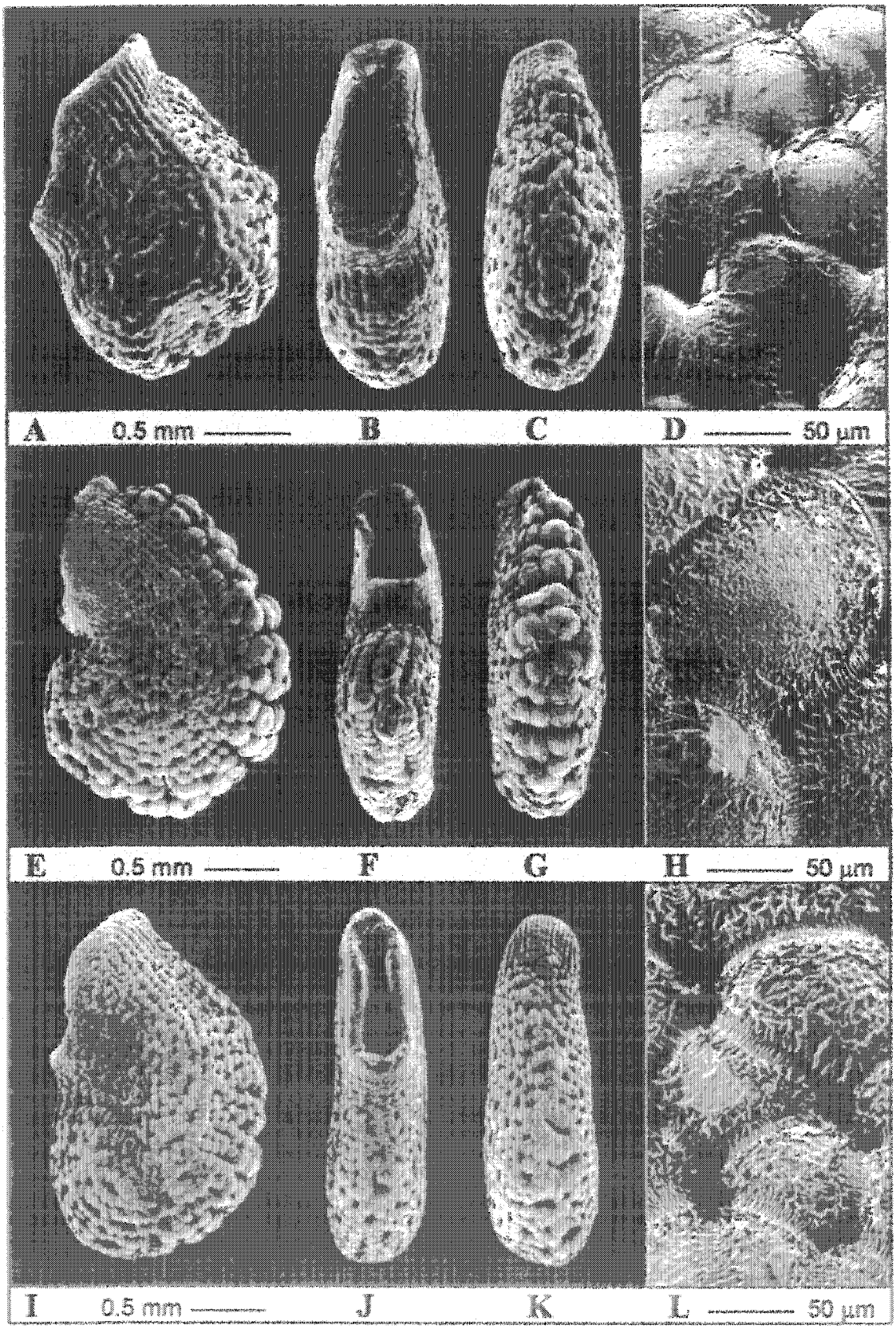

Plate 32.

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Plate 33. SEM photographs of *Leptocereus* seeds (IV).

A-D. *Leptocereus leonii*. (*Areces 3292*, NY); **E-H**. *L. scopulophilus*. (*León 11446*, NY); **I-L**. *L. wrightii* subsp. *wrightii*. (*Areces 6849*, NY).

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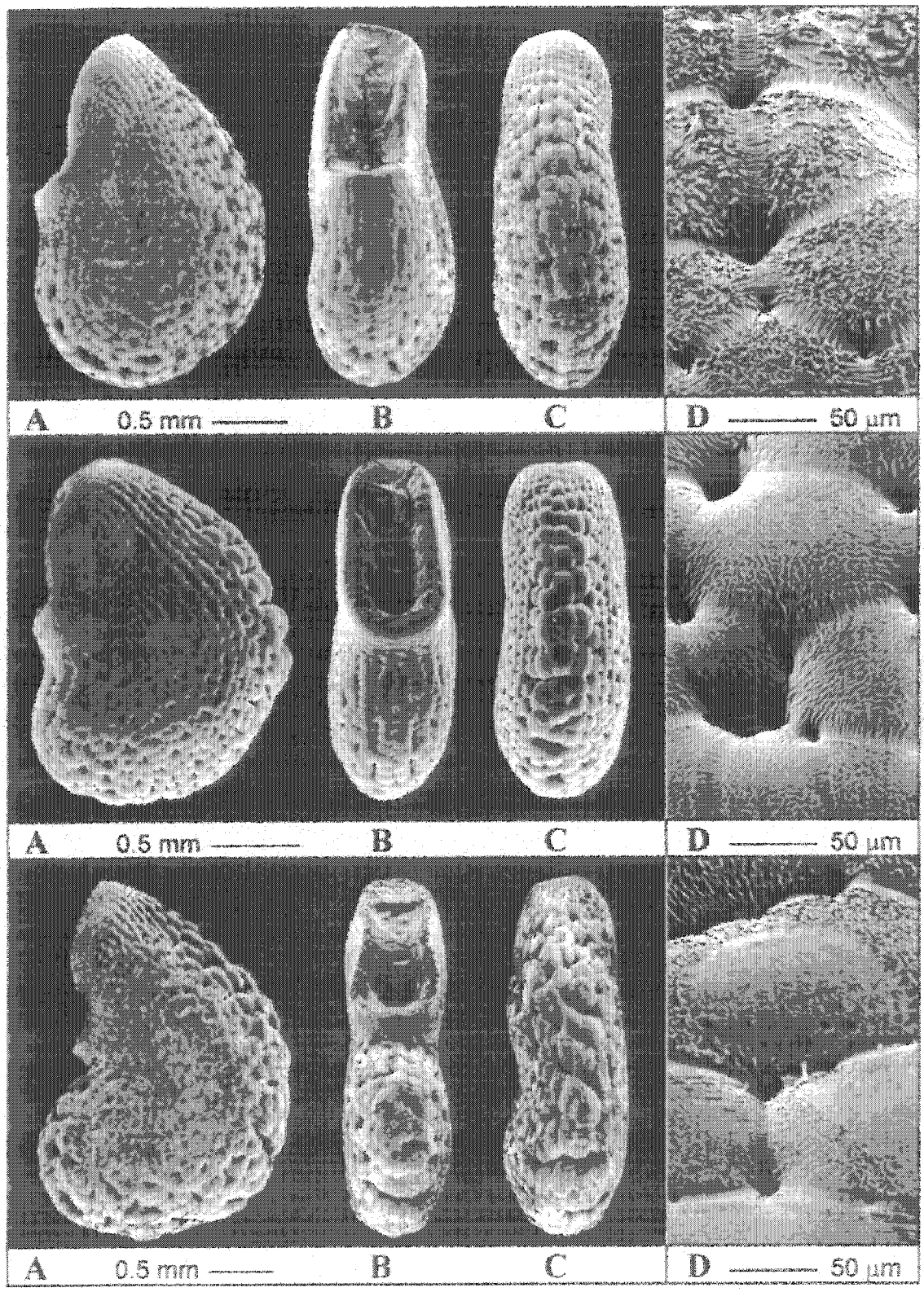

Plate 33.

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Plate 34. SEM photographs of *Leptocereus, Cereus* (*Hamannia*) *fabiolae,* and *Samaipaticereus corroanus* seeds (V).

A-D. *Leptocereus arboreus*. (*Cowell & Eagle 10298*, NY); **E-H.** *Cereus* (*Hamannia*) *fabiolae*, the puzzling new cereoid species from Haiti. (*Areces 6795*, NY); **I-L.** *Samaipaticereus corroanus*. (*Rose 20093*, US).

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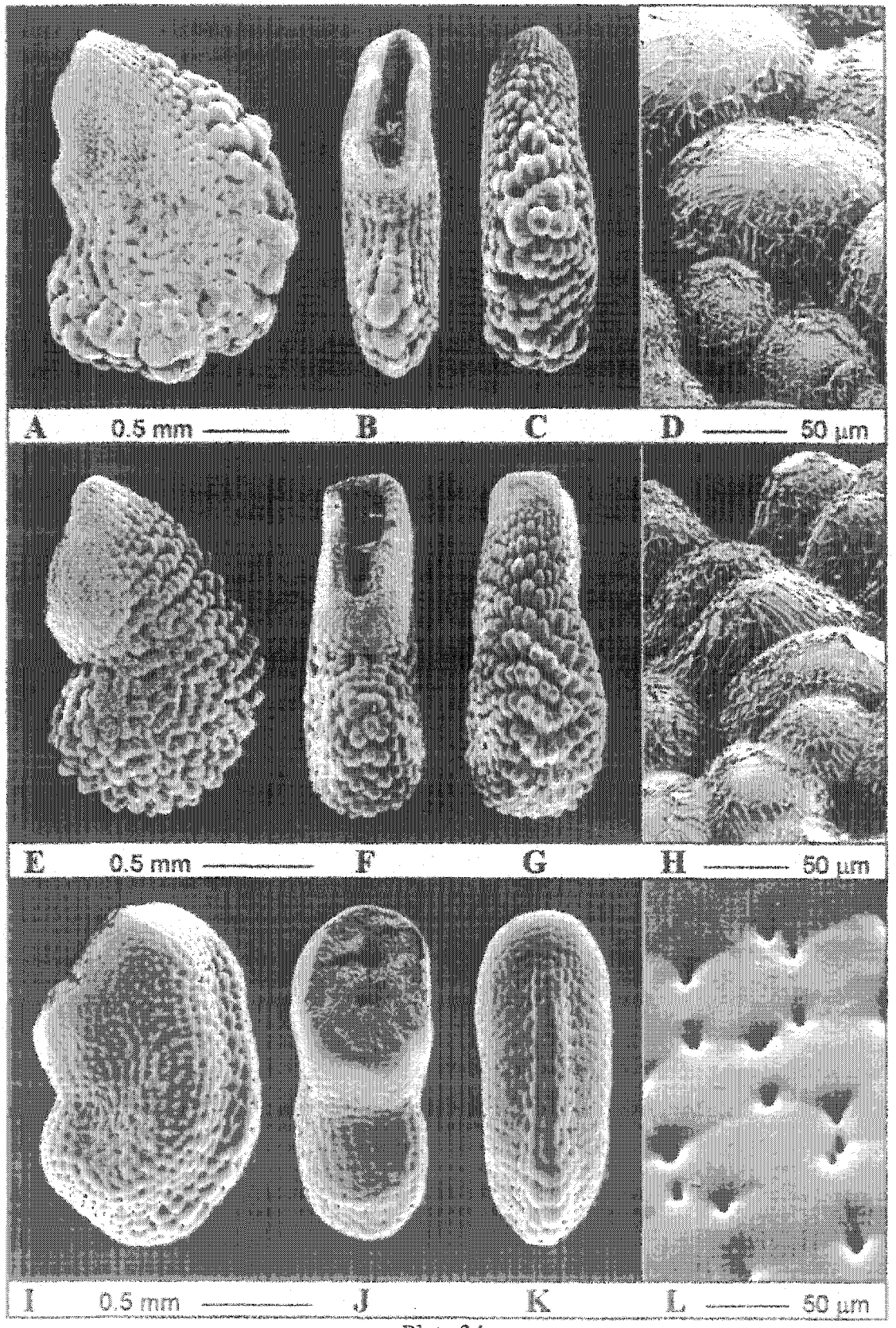

Plate 34.

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3.5. Species grouping by seed characters

With the exception of the problematic Haitian taxon *Cereus fabiolae*, the seeds of all *Leptocereus* taxa studied have many features in common and seem to define a natural group. On account of the great variation of seed morphology in subfamily Cactoideae, the fact that *Leptocereus* (*sensu stricto*) shows a more or less homogeneous seed morphology is yet another indication of the monophyletic origin of the genus. Although the assessment of variation is limited, considering that in most cases only 10 seeds of each taxon were measured within the genus, however, a number of groups of characters became apparent. These well-defined groups bear a direct relationship with other macro-morphological and geographical features of *Leptocereus.* In the case of *L. paniculatus, L. wrightii* subsp. *wrightii*, and *L. weingartianus* subsp. *demissus*, where more seeds were examined (up to 20), the only inference that could be drawn on infraspecific variability was that seed size and shape vary a little more. Exotesta surface features were very consistent, and practically no variation was observed by doubling the number of seeds examined. On the basis of seed morphology *Samaipaticereus corroanus* does not bear enough resemblance to any *Leptocereus* (*sensu stricto*) to be considered a coherent member of this genus. Likewise, due to its papillate exotesta, the Haitian "leptocereoid" (*Cereus fabiolae*) is also left aside, and its position within the genus *Cereus*, reasserted.

For the seed characters evaluated I have used some of the abbreviations of Friedrich and Glaetzle (1983). These characters are listed as follows:

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L. —Length of seed, in μm (average).

B. —Breadth of seed, in μm (average).

L/B. —Ratio length to breadth.

W. —Width of seed, in μm (average).

HL. —Length of hilum measured internally (excl. rim), in μm (average).

HW. —Width of hilum at middle (excl. rim), in μm (average).

LA. —Lateral exotesta cell, μm (average).

LD. —Largest dorsal exotesta cell, in μm (average).

LD/LA. —Ratio dorsal to lateral exotesta cell diameter.

A. —Angle, hilum plane to longitudinal axis, in degrees (average).

The quantitative expression of these characters is contrasted in Table 11. Some of the numerical indices shown in the table are of practical value for grouping species, especially when used with other non-quantitative features. The combined set of characters used to define taxonomic and geographical units will be discussed briefly in each recognized seed group:

GROUP 1: Seeds of the Cuban taxa, all included in subgenus *Leptocereus* (Plate 32, A-L; Plate 33, A-L; Plate 34, A-D). L: 1,267-1812 μm; B: 868-1,065 μm; L/B: 1.4-1.7; W: 437-554 μm; HL: 348-589 μm; HW: 85-263 μm; LA: 38-57 μm; LD: 104-196 μm; LD/LA: 1.8-4.8; A: –7 to 32°

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TAXON	L	B	L/B	W	HL	HW	LA	LD	LD/LA	A
L. wrightii subsp. *wrightii*	1,812	1,065	1.7	466	546	263	42	163	3.9	–7°
L. scopulophilus	1,302	937	1.4	501	543	217	38	157	4.1	11°
L. leonii	1,496	993	1.5	554	550	211	38	128	3.4	32°
L. arboreus	1,295	868	1.5	437	504	154	41	196	4.8	17°
L. sylvestris	1,501	913	1.6	497	589	85	54	130	2.4	26°
L. maxonii	1,267	889	1.4	516	549	193	57	104	1.8	31°
L. santamarinae	1,522	978	1.6	478	348	152	37	174	4.7	7°
L. weingartianus subsp. *weingart.*	1,294	783	1.7	446	537	113	48	61	1.3	31°
L. weingartianus subsp. *demissus*	1,282	750	1.7	478	489	196	39	49	1.3	18°
L. paniculatus	1,324	707	1.9	402	456	81	41	50	1.2	–6°
L. quadricostatus subsp. *quadricost.*	1,457	869	1.7	510	483	199	61	83	1.4	–12°
L. quadricostatus subsp. *parvisp.*	1,587	913	1.7	598	459	198	59	85	1.4	–8°
L. grantianus	1,270	783	1.6	522	630	152	43	65	1.5	20°
Cereus (*Hamannia*) *fabiolae*	978	542	1.8	341	374	137	39	59	1.5	19°
Samaipaticereus corroanus	996	624	1.6	380	431	328	35	91	2.6	36°

Table 11. Contrasted quantitative characters of the seed of *Leptocereus* spp., *Cereus (Hamannia) fabiolae*, and *Samaipaticereus corroanus*.

The seeds of the Cuban taxa are more mussel-shaped, less elongated (L/B: 1.4-1.7) than those of Group 2, with a less developed and less acute rostrum as well. Because the development of the hilum-cup that leads to the rostrum is less unequal, the hilum plane rarely cuts the longitudinal axis of the seed at negative angles. As seen in lateral

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view the hilum is always undulate, and instead of passing over into the outer surface of the cup by a rounded thickening, the hilum margin is offset at an angle (acute or obtuse) to the sclerified exotesta. This angle is particularly acute in *Leptocereus wrightii* (Plate 33, J). The exotesta cells of the dorsal region of the seed, often elongated and exceeding 100 μm diameter, are strongly differentiated from those of the lateral regions. Commonly, the convex periclinal walls of these exotesta cells are somewhat flattened, although some strongly hemispheric forms are known as well. Cuticular folds are more discrete and never run between cell boundaries; interstitial pits and anticlinal walls, with their characteristic transverse microsculpture, are clearly seen, especially in the lateral region of the seed.

The species of this group, which are also individually recognizable by means of their seed morphology, may be divided further into two main subordinate groups, namely subgroups 1a and 1b, based on the shape of the rostrum tip:

SUBGROUP 1a: Seeds of species with a western and central distribution in Cuba (sections *Roseiflori* and *Costanthus*): *Leptocereus wrightii, L. scopulophilus, L. leonii,* and *L. arboreus* (Plate 33, A-L; Plate 34, A-D).

The hilum cup of the seeds of *Leptocereus wrightii, L. scopulophilus, L. leonii,* and *L. arboreus* shows a straight to broadly rounded dorsal wall. Although the rostrum tip of seeds may be acute, obtuse, or rounded (as seen in lateral view), their profile is essentially symmetrical. Within this subgroup, *Leptocereus arboreus* separates readily

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from other species because of its nearly globose dorsal exotesta cells and narrowly oblong hilum (Plate 34, A-D). *Leptocereus wrightii, L. scopulophilus*, and *L. leonii* bear more flattened dorsal cells and their hilum is typically oblong, more than 200 μm broad (Plate 33, A-L).

SUBGROUP 1b: Seeds of species with an eastern distribution in Cuba (section *Spinosissimus*): *Leptocereus sylvestris, L. maxonii,* and *L. santamarinae* (Plate 32, A-L).

Because the dorsal wall of the hilum cup is abruptly recurved in all members of this subgroup, the general profile of the rostrum tip is asymmetrical. This important diagnostic character correlates with other vegetative and floral features of the subgroup. According to seed morphology within the subgroup, *Leptocereus sylvestris* and *L. maxonii* are more closely related than *L. santamarinae* is with any of them.

GROUP 2: Seeds of the Hispaniolan-Puerto Rican taxa, all included in subgenus *Weingartianea* (Plate 30, A-L; Plate 31, A-L). L:1,270-1,587 μm; B: 707-913 μm; L/B: 1.6-1.9; W: 402-598 μm; HL:456-630 μm; HW: 81-199μm; LA: 39-61μm; LD:49-85 μm; LD/LA: 1.2-1.5; A: –12 to 31°

This group is distinguished by its rather elongated seeds (L/B: 1.6-1.9). The well developed rostrum, which is fairly acute in profile (as seen in lateral view), often gives the seed a "tear drop" shape. Due to the very unequal development of the hilum cup

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that leads to this long rostrum, the hilum plane sometimes cuts the longitudinal axis of the seed at negative angles. In lateral view the hilum is concave, straight or nearly so, or slightly undulate. It passes over into the outer surface of the rim cup by a rounded thickening. The exotesta cells of this group are isodiametric and relatively homogeneous in size and shape; there is not a strong differentiation between those of the dorsal and lateral regions of the seed. Periclinal walls of the dorsal exotesta cells are strongly convex. The most distinctive character of this group, however, is the thick, coarse cuticle that covers almost entirely the exotesta cell surface. Projecting cuticular folds may run between the cell boundaries obscuring the sunken anticlinal walls and the interstitial pits. The species of this group, which are all individually recognizable by means of their seed morphology, may be further divided into two subordinate groups:

SUBGROUP 2a: Seeds of the non cephalium-producing species of Hispaniola (section *Tenuicaulis*): *Leptocereus weingartianus* (Plate 31, E-L).

Leptocereus weingartianus is often characterized by a discrete constriction at the hilum-cup insertion level. Sometimes a slight but nevertheless perceptible narrowing of the entire hilum-cup occurs. This effect is often coupled with a more or less abrupt flattening of the exotesta cells on the cup side. Cuticular folds of exotesta cells are coarse. No significant morphological differences were found on the seed of the two recognized varieties of this species.

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SUBGROUP 2b: Seeds of the cephalium-producing species of Hispaniola and Puerto Rico (section *Cephaliphora*): *Leptocereus paniculatus, L. quadricostatus* and *L. grantianus* (Plate 30, A-L; Plate 31, A-D).

The seeds of this subgroup lack a constriction or narrowing of the hilum-cup. Flattening of exotesta cells towards the hilum rim is gradual. This subgroup includes the two very closely related species of Puerto Rico and adjacent islands (*L. quadricostatus* and *L. grantianus*), with relatively similar seed morphology, and the Hispaniolan *L. paniculatus*. The seeds of the latter are easily distinguished from the Puerto Rican species by means of their lower L/B index, and the very coarse cuticular folds forming extensive scale-like pleats that completely obscure exotesta cell walls and interstitial pits. The hilum of *L. paniculatus* is also linear, not oblong as in the Puerto Rican species, and convex in lateral profile.

For practical purposes it may be useful to contrast, in key form, the diagnostic seed characters of all *Leptocereus* species examined:

KEY TO THE SPECIES OF *LEPTOCEREUS* EXAMINED, BASED ON SEED MORPHOLOGY

1. Seeds with reduced cuticular folds, never running between exotesta cell boundaries; largest exotesta cells of dorsal region strongly differentiated from laterals in size and shape, often elongated, > 100 μm diam.; hilum surrounded by a more or less

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angular rim (subgenus *Leptocereus*)

2. Dorsal wall of hilum cup slightly incurved to nearly straight in outline

3. Hilum oblong, > 200 μm broad; dorsal exotesta cells more or less flattened (section *Roseiflori*)

4. Seeds 1.7-1.9 mm long; hilum rim with a sharp edge, slightly narrowed at middle ..... *L. wrightii*

4'. Seeds < 1.6 mm long; hilum rim without a sharp edge, not narrowed at middle

5. Seeds subhemispherical in outline; hilum positioned parallel to the longitudinal axis of seed or, if oblique, at < 15° angle; rostrum tip broadly rounded ..... *L. scopulophilus*

5'. Seeds mussel-shaped in outline; hilum positioned obliquely at 25-35° angle at the narrower end of seed; rostrum tip angular or subangular ..... *L. leonii*

3'. Hilum narrowly oblong, to 170 μm broad; dorsal exotesta cells nearly globose (section *Costanthus*) ..... *L. arboreus*

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2'. Dorsal wall of hilum cup recurved, its tip abruptly bending backwards (section *Spinosissimus*)

6. Seeds large, commonly > 1.5 mm long; L/B index 1.6

7. Hilum plane cutting the longitudinal axis of seed at 20-35° angle; dorsal exotesta cells narrowly elongated, not markedly large and not forming a keel-like ridge; LD/LA index < 3 ..... *L sylvestris*

7'. Hilum plane cutting the longitudinal axis of seed at 1-15° angle; dorsal exotesta cells broadly elongated to nearly rounded, very large, forming a keel-like ridge; LD/LA index > 4 ..... *L. santamarinae*

6'. Seeds relatively short, < 1.4 mm long; L/B index < 1.5 ..... *L. maxonii*

1'. Seeds with thick cuticular folds, often running between exotesta cell boundaries; largest exotesta cells of dorsal region slightly or nearly not differentiated from laterals, essentially isodiametric, < 100 μm diam.; hilum surrounded by a curved rim (subgenus *Weingartianea*).

8. Seeds slightly narrowed or with a discrete constriction at the hilum-cup insertion level, the exotesta cells more or less abruptly flattened on the cup side (section

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Tenuicaulis) ..... *L. weingartianus*

8'. Seeds not narrowed or constricted at the hilum-cup insertion level, the exotesta cells not abruptly flattened on the cup side (section *Cephaliphora*)

9. Cuticular folds forming extensive scale-like pleats; L/B index > 1.8; hilum linear, less than 90 μm broad and convex in profile (lateral view) .... *L. paniculatus*

9'. Cuticular folds not forming extensive scale-like pleats; L/B index < 1.8; hilum oblong to narrowly oblong-lanceolate, > 100 μm broad at middle, straight or slightly undulate in profile (lateral view)

10. Seeds > 1.4 mm long; hilum plane most often cutting the longitudinal axis of seed at negative angles (to –20°) ..... *L. quadricostatus*

10'. Seeds < 1.4 mm long; hilum plane cutting the longitudinal axis of seed at positive angles (5-25°) ..... *L. grantianus*

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3.6. Discussion

As in *Notocactus, Ferocactus, Echinopsis* and other genera of cacti, seed characters have proven to be a good basis for delimiting infrageneric groups in *Leptocereus*. Of course, seed morphology itself cannot be used to make taxonomic divisions, or determine phylogenetic connections among different populations, because the number of characters that can be evaluated is too small to yield conclusive natural groupings. However, if the characters provided by seed morphology are taken in conjunction with other vegetative and reproductive characteristics of plants, and with ecological and geographical data as well, the whole picture would make a much more reliable basis for taxonomic conclusions. If I am not proposing an infrageneric treatment of *Leptocereus* based solely on the morphological features of its seeds, at least the following conclusions may be considered clear and indisputable:

1. The genus *Leptocereus*, as circumscribed in this paper, seems to be a natural, monophyletic group, characterized by its mussel- and tear-shaped elongated seeds with an operculate germination type. These laterally flattened seeds, with compressed hilum cups, all have a well-developed rostrum (dorsal region of hilum cup), and a funicular hump with an angular projection of 90-110°. The exotesta is typically convex, verrucose, and the periclinal walls of its cells have definite cuticular folds.

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2. It is possible to distinguish individual species in the selected taxa studied, on the basis of seed characters. This indicates that species delimitation is approximately correct, because it is based on phenetic discontinuities in both gross and micro-morphology.

3. Two main subgroups are easily recognizable within the genus: an "eastern group", distributed in Hispaniola, Puerto Rico and Culebra island, and a "western" group, restricted to Cuba. The seeds of the eastern group have thick cuticular folds, isodiametric exotesta cells that are poorly differentiated into dorsal and laterals, and a curved hilum rim. By contrast, the seeds of the western group have much more reduced cuticular folds, strongly differentiated exotesta cells (the dorsal ones being larger and more elongated than the laterals), and an angular hilum rim. These characters correlate well with the presence (western group) vs. absence (eastern group) of a pigment that strongly blackens the stem if wounded, and of a dense fibrous reticule in the cortex. The discontinuities in gross morphology as well as in seed morphology between these two geographically separated groups justify the division of *Leptocereus* into two subgenera: subgenus *Leptocereus*, and subgenus *Weingartianea.*

4. The so-called "eastern" group of *Leptocereus* taxa (see above), which corresponds to subgenus *Weingartianea*, may in turn be divided into two discrete subgroups on the basis of their seed characters. Most important of these subgroups is the one with seeds not narrowed or constricted at the hilum cup insertion level. Within the

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subgroup, this character correlates with other important features of gross morphology, particularly the relatively low number of ribs (3-5), and the presence of a cephalium on fertile stems. This subgroup, which corresponds to section *Cephaliphora*, includes *Leptocereus paniculatus* from Hispaniola, *L. quadricostatus* from Puerto Rico, and *L. grantianus* from Culebra Island. The 5-7-ribbed *L. weingartianus*, only representative of the other subgroup (section *Tenuicaulis*), lacks cephalia and acts more like a connecting-link between eastern and western main groups. Having established the division of these subgroups within *Leptocereus* (as sections of subgenus *Weingartianea*), some suggestions of which components display primary or derived characters seem desirable. Assuming that the non-cephalium-producing form of *Pereskia* is representative of the ancestral type, it is not unreasonable to suppose that *L. weingartianus* is less derived than the three cephalium-producing species of the eastern group. If I have evaluated this feature correctly, another idea seems to follow: that in this group there is a trend to reduce the number of ribs, to group flowers in specialized terminal stems (cephalia), and to produce more rostrate seeds with thicker cuticular folds.

5. The "western" or Cuban group of *Leptocereus* is sharply divided into two distinct subgroups by means of a single but significant seed character: the shape of the dorsal wall of the hilum. These two subgroups occupy different geographic areas within the island of Cuba. For example, occurring in east Cuba, with the dorsal wall of the hilum cup abruptly recurved, we distinguish section *Spinosissimus* including *L. sylvestris, L. maxonii,* and *L. santamarinae.* These species are all strict night-

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bloomers. Although more heterogeneous, the other subgroup is also distinguished by its seed morphology. It includes *L. wrightii, L. scopulophilus, L. leonii* (section *Roseiflori*), and *L. arboreus* (section *Costanthus*), all distributed in central and western Cuba. This entire subgroup is characterized by seeds with a broadly rounded to nearly straight dorsal wall of the hilum. A trend towards the transition from strict night-flowering species, to daytime flowering, is recognizable in some of the above mentioned species. In the "western" or Cuban group (subgenus *Leptocereus*) there is a general tendency towards derived character states comprising the reduction in diameter of dorsal exotesta cells, and the flattening of their periclinal walls. This trend has been observed independently in both aforementioned subgroups.

6. Seed characters do not support the problematic Haitian "leptocereoid" (*Cereus fabiolae*) as being a candidate for a possibly new species of *Leptocereus*. This taxon has a papillate exotesta, as opposed to the verrucose exotesta of all studied members of the genus *Leptocereus*.

7. The seeds of *Samaipaticereus corroanus* are morphologically very different from those of *Leptocereus*, and do not favor the assumption of this Bolivian member of tribe Leptocereeae being closely related to the progenitor of *Leptocereus*, from which all species later evolved.

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8. The *Cereus* germination variant found in the seeds of *Leptocereus quadricostatus* and *L. sylvestris* poses and interesting biogeographical question. As Bregman and Bouman (1983) demonstrated, cactus species with operculate seeds are relatively rare in Mexico and the southeastern United States. Conversely, the seeds of most South American cacti form an operculum when germinating. If variants derived from operculate forms are not taken into consideration (*e.g.*, *Frailea, Gymnocalycium, Melocactus*), then the only seeds lacking opercules in South America are basically those of the primitive subfamily Opuntioideae. This fact favors the hypothesis that the closest relatives to *Leptocereus* are to be found in South America. At first glance the 4-ribbed, small-flowered *Samaipaticereus corroanus* from the central Andes seemed the perfect candidate to share a common ancestor with the Caribbean genus *Leptocereus*, but the seeds of *Samaipaticereus* are fundamentally different. Another interpretation can be made, however, based on the presence of the relatively large number of small, relict genera of subfamily Cactoideae that are endemic to Mexico, *e.g.*, *Leuchtenbergia* and *Homalocephala*. According to Bregman and Bouman (1983) most of these taxonomically relict Mexican genera have seed germination types that are precursors to the operculate "*Cereus* variant." Accordingly, the advent of an operculum in *Cereus*-like seeds may have begun in Mexico and followed in the Caribbean and South America. In this case, a *Leptocereus* relative should be more likely looked for in Mexico, perhaps among the *Pachycereeae*, and not in South America, but maybe this interesting question should be resolved with the aid of molecular techniques.

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4. PALYNOLOGY

4.1. Introduction

Pollen morphology has been widely used in plant systematics and in many cases it has prooven to be very helpful in ellucidating taxonomic problems. The palynology of the Cactaceae received considerable attention after Kurtz (1948) demonstrated in his classic study of the pollen grains of cacti native to Arizona, that the genera, subgenera, and sometimes the species can be distinguished by the size, sculpturing of exine, and number and position of apertures. In 1963 this same author produced a more thorough study of the pollen grains of about 700 species and 110 genera, based on Britton and Rose's system (1919-1923). In his work, however, all exine and aperture characters are presented in comparative tabular form, with no further comments on the relationships of the many taxa studied. Erdtman (1952) also gave a description of the pollen grains of the family indicanting its range of variability. However, Tsukada (1964) was the first to reveal evolutionary lineages in the Cactaceae based on very detailed studies of the pollen grains of a selection of genera and species. Analysing palynological characters of 37 species distributed in 14 genera, and the results of Kurtz's first paper, Tsukada (*op. cit.*) distinguished eight basic pollen types and suggested three evolutionary tendences within the family. Tsukada and Kurtz were pioneers who showed the basics of cactus palynology using only light-microscopy methods; they revealed many important features of the pollen grains of the Cactaceae, such as the striking difference between subfamilies Opuntioideae and Cactoideae.

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Nowicke (1975), Skvarla and Nowicke (1976) and Nowicke and Skvarla (1979) have reviewed the palynology of Cactaceae in a survey of the Caryophyllales (Centrospermae), while Anderson and Stone (1971), Kozar (1974), Barthlott (1974, 1975), Barthlott and Rauh (1974, 1975) and Jarvis (1981) have published papers on pollen grain morphology of small groups of taxa or individual species. The most complete and comprehensive contribution to the study of the pollen grains of the Cactaceae is that of Leuenberger (1976a, 1976b). In fact, covering 630 species from 157 of the 160 genera in Buxbaum's (1962) system, Leuenberger examined pollen size, number, position and character of apertures, quality and density of exine surface, and exine structural elements using both light microscopy and SEM. He described the pollen grains of *Leptocereus* as being irregularly hexacolpate, with an exine of the "Cereus type," and numerous, slender columelles in the ektexine layer.

Palynological characters, which are essentially a special type of morphological character, may or may not be taxonomically useful, depending upon the group of plants studied. Leuenberger (1976a) was able to show that the variations in pollen grain structure are fairly uniform in each tribe (recognized by Buxbaum, 1962), and on this basis some genera that had been placed in the wrong tribe were easily identified. Anderson and Stone (1971) could even demonstrate that in *Lophophora williamsii* it is possible to differentiate geographical races. In the genus *Rhipsalis* —another example— closely allied species can be distinguished by means of their pollen grains, in most cases at least (Barthlott, 1974), whereas these are of little help in determining

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generic relationships in the Borzicactinae (Jarvis, 1981). Certainly, palynology confirms the isolated and phylogenetically derived position of subfamily Opuntioideae, but in general has had a rather limited influence on the current classification of the Pereskioideae and Cactoideae (Barthlott and Hunt, 1993). Barthlott and Rauh (1975) believe that palynological data must be interpreted with great circumspection because many convergences of pollen grain characters can lead to untenable phylogenetic speculations. Systematically valid statements about the Cactaceae can probably be made —according to these authors— within relatively small groups of closely allied taxa, and then again for the distinction of groups in a higher taxonomic level, such as at the rank of subfamilies. *Leptocereus*, being a small group of morphologically and geographically isolated taxa, we can expect to find taxonomically useful characters in the pollen grains of its species.

4.2. Pollen grains of the Cactaceae

Pollen grains in family Cactaceae are medium-sized, *e.g.*, *Gymnocalycium* sp., with 36 μm in diameter (Barthlott and Hunt, 1993), to very large, up to 120 μm in diameter, *e.g.*, *Opuntia* sp., and some members of subfamily Cactoideae (Barthlott and Hunt, *op. cit.*, and Leuenberger 1976b, respectively). With the exception of *Pseudorhipsalis himantoclada* and *P. alata*, which have tetrads, cactus pollen consists of isopolar or rarely heteropolar monads. With respect to their shape, these are spheroidal to subprolate, rarely suboblate, with a number of apertures that vary from 3, 6, or 12, to more, rarely 15 or 31. In Cactaceae triaperturate pollen is always

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zonotremous, and hexa- to 31-aperturate (polyaperturate) is pantotremous. Apertures can be furrows (colpi) or pores, but never colpores. In Pereskioideae pollen grains are tri- to polycolpate, which is surprising because this subfamily exhibits most plesiomorphic characters of the Cactaceae (in angiosperms polycolpate and polyporate pollen grains are presumed to be derived with respect to the tricolpate type). However, reduction of aperture number in the Cactaceae cannot be excluded as a possibility, considering that many species (*e.g.*, *Leptocereus* spp., with 3-colpate and 6-colpate pollen grains) show variations in the number of apertures within the same flower.

In subfamily Opuntioideae, polyporate pollen grains are typical, the lowest aperture number being 6 (*Opuntia macbridei* and *O. glaucescens*), and the highest corresponding to the genus *Pereskiopsis*, with up to 31 pores (Leuenberger, 1976b). According to Leuenberger (*op. cit.*), these 6-pantoporate grains of *Opuntia macbridei* and *O. glaucescens* represent reduction forms of the 12-pantoporate grains common to most platyopuntias. In subfamily Cactoideae, which accounts for more than 80% of all cacti, variation in pollen size is relatively high, and the number of apertures is 3 to 15(-18), mostly colpi, rarely pores. Leuenberger (1976a, 1976b) records a few species with ill-defined apertures (irregular or asymetrical colpi). He observed a single band-like furrow (2-syncolpate pollen grain) in *Leptocladodia elongata* var. *stella-aurata*. These syncolpate or irregularly-aperturated pollen grains were, in several cases, a consequence of polyploidy (*e.g.*, in *Mammillaria prolifera* and *Notocactus submammulosus*).

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The exine in the Cactaceae is semi-tectate (the tectum may be reduced to simple muri in some opuntias) or fully tectate. The nexine and endexine layers are presumably fused with each other (Barthlott and Hunt, 1993), while the sexine is well differentiated into columellae and tectum. The columellae are up to twice as high as the thickness of the tectum; they are usually evenly dispersed, or may follow a reticuloid pattern. With a few exceptions where its surface is verrucose, or just flat, the tectum bears spinules varying in height from 0.3 to 3.0 μm., and is perforated. Leuenberger (1967a, 1967b) distinguishes with the term *puncta* (pl. *punctae*) those tectum perforations that are less than 1 μm in diameter, while he uses the name *foveola* (pl. *foveolae*) for those with more than 1μm in diameter. This distinction has only a practical value; there are, in fact, infinite transition forms in the exine of the Cactaceae, from essentially punctate, to foveolate, to reticulate (*e.g.*, in most opuntioids).

4.3. Materials and methods

Sixteen pollen samples from *Leptocereus* and one sample from the Haitian species *Cereus fabiolae* covering 18 species and one subspecies are studied. Pollen from the South American *Samaipaticereus corroanus* (*Rose 20093*, US) was also checked for resemblance with *Leptocereus*, but not described in detail. The pollineferous material was processed for both light microscopy (LM) and scanning electron microscopy (SEM) studies (40 SEM photographs of selected taxa are presented in Plates 35-39). All samples were collected by the author from liquid-preserved material of wild or cultivated specimens except for *L. maxonii* (*Britton & Cowell 12657,* NY), which was

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collected from a herbarium specimen. The cultivated specimens of *Leptocereus* that yielded flowers for palynological studies were also collected by the author in the wild (as cuttings). Fresh *Samaipaticereus* pollen was obtained from a clone of the original plant from which *Rose 20093* was collected. This clone had been grown at The Huntington Botanical Gardens, San Marino, California, under accesion number HNT 4980. All the examined taxa are listed in Table 12 with their corresponding voucher information.

For LM, pollen samples were acetolized using Erdtman's (1960) acetolysis method. Standard slides mounted in glycerine jelly were made and their coverslips sealed with paraffin. General observations including number of colpi, and measurements of exine thickness, apocolpium diameter, and distance between ends of adjacent ectocolpi were made at 1000× magnification using a Leitz Wetzlar Dialux Microscope with an apochromatic oil immersion objective. Because acetolysis destroyed the colpus membrane of *Leptocereus* and deformed the grains, measurements of polar and equatorial diameter were made on unacetolyzed pollen mounted in generous amounts of glycerine jelly without sealing the coverslips (temporary slides). For the same reason, the polliniferous material intended for SEM was not subjected to acetolysis treatment. Samples for SEM studies were mounted on aluminum stubs with double-sided adhesive tape, and coated in a sputter coater for three minutes with a thin layer of gold. Observations of the outer sculpturing of the exine were made on a JEOL JSM-6300 SEM microscope. In all LM samples 20 pollen grains of each taxon were measured, while in samples for SEM studies at least 10 grains of each taxon were

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investigated. The descriptive terminology is mostly that of Erdtman (1969). For all palynological characters lending themselves to quantitative expression in Table 13, I have used the following abbreviations (all meassurements in μm):

PD. —Polar diameter.

ED. —Equatorial diameter.

PE. —Ratio polar axis (mean)/equatorial axis (mean).

AD. —Apocolpium diameter.

EA. —Distance between ends of adjacent ectocolpi.

PuDi. —Diameter of punctae.

WR. —Width of puncta ring.

PuDe. —Puncta density (number of punctae per 100 μm^2).

AI. —Apocolpium index (ratio of the mean distance between ends of adjacent ectocolpi of a zonocolpate pollen grain, to its mean equatorial diameter).

ET. —Exine thickness.

SpH. —Spinule height.

SpW. —Spinule width.

SpD. —Spinule density (number of spinules per 100 μm^2).

4.4. Results

All samples of *Leptocereus* taxa studied yielded pollen grains of the same basic type, corresponding to the 3-zonicolpate spinulate type of Tsukada (1964: 52), and the

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TAXA	LOCALITY	SOURCE
L. albellus	Sierra de San Carlos, Cuba	Areces 6343, NY
L. assurgens	Viñales, Cuba	*Areces 6789*, NY
L. chrysotyrius	San Diego, Cuba	*Areces 4547*, NY
L. prostratus	Sumidero, Cuba	*Areces 6344*, NY
L. wrightii wrightii	Bahía de Ortigosa, Cuba	*Areces 6414*, NY
L. scopulophilus	Somorrostro, Cuba	*Areces 4601*, NY
L. leonii	Sierra de Anafe, Cuba	*Areces 3292*, NY
L. carinatus	Najasa, Cuba	*Areces 5489*, NY
L. sylvestris	Pilón, Cuba	*Areces 5385*, NY
L. maxonii	Daiquirí, Cuba	*Britton & Cowell 12657*, NY
L. santamarinae	Santa Lucía, Cuba	*Areces 5341*, NY
L. weingartianus weingart.	Bayahibe, Dom. Rep.	*Areces 6348*, NY
L. paniculatus	La Descubierta, Dom. Rep.	*Areces 6788*, NY
L. quadricostatus quadr.	Ballena Bay, Puerto Rico	*Areces 6415*, NY
L. quadricostatus parvisp.	Guánica, Puerto Rico	*Areces 6417*, NY
L. grantianus	Culebra Island	*Areces 6377*, NY
Cereus (Hamannia) fabiolae	Môle St. Nicolas, Haiti	*Areces 6795*, NY
Samaipaticereus corroanus	Samaipata, Bolivia	*Rose 20093*, US

Table 12. List of taxa studied, and their sources.

Cereus type of Leuenberger (1976a, 1976b). They are spheroidal, their size most often varying from 55 to 75 µm, with a range of polar diameter of 43.1 to 79.6 µm, and a range of equatorial diameter of 44.0 to 80.7 µm (PE ratio 0.97-1.03). The equatorial ambitus (outline) is circular/subcircular. Based on the study of two species, *L.*

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weingartianus (as *L. maxonii*) and *L. quadricostatus*, Leuenberger (1976a) stated that the pollen grains of *Leptocereus* were essentially 6-colpate, but my investigations demonstrate that these are commonly 3-colpate, or 3-colpate with a minor representation of 6-colpates. Only one species showed dominance of of 6-colpates (58%) over 3-colpate grains (*i.e.*, *Leptocereus weingartianus* subsp. *weingartianus*). Rarely 12-colpate or 9-colpate grains occur, and very rarely 2-colpate (1-2 % or less). Leuenberger (1976a) recorded some inaperturates in *L. weingartianus* (as *L. maxonii*). The colpi are rather long and very sharply pointed at either end, and a colpus membrane is always present (in unacetolyzed pollen). The apocolpium diameter varies from 14.6 to 45.2 μm, and the apocolpium index is within the rank of 0.35 to 0.54.

The exine of *Leptocereus* is 1.3 to 3 μm thick and fully tectate, the tectum being supported by numerous, closely spaced, regularly distributed, columellae that are up to 0.6 to 0.8 μm in diameter and simple. The surface of the tectum is spinulose and minutely perforated by 0.2 to 0.9 μm wide punctae, each of them surrounded by a 0.1 to 0.3 μm wide raised ring. The spinules are most often conical, sometimes blunt at their tip, their height varies from 0.3 to 1.4 μm, and their width at base varies from 0.3 to 1.3 μm. The range of spinules per 100 μm^2 of tectum surface is 3 to 17, while the range of puntae is higher, *i.e.*, 6 to 56. Table 13 shows some contrasted quantitative characters of the pollen grains of *Leptocereus*, in the 16 taxa selected for this study. The Haitian cereoid taxon is also included in Table 13 (as *Cereus fabiolae*).

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In general, the morphology of the pollen grains of *Leptocereus* is fairly homogeneous, showing only minor differences. In fact, there are more significant palynological dissimilarities between *Leptocereus* spp. and *Cereus fabiolae*, for example, than between any *Leptocereus* species (Table 13). These minor differences correlate with the overall size of the grain, the relative proportions between 3-colpate and 6-colpate grains, the length of the colpi, the thickness of the exine, and the character and density of spinules and punctae, all of which have a solely quantitative expression. Depending upon the taxa, the spinules may be relatively high or low, acute or blunt at tip, and abundant to sparse. The punctae differ slightly in their abundance and diameter, and in the width of the rim that surrounds them. The vast majority of these differences are not discrete, and in practical terms they fail to define groups of taxa bearing direct relationship with morphological and geographical features. Only two exceptions apply: the Puerto Rican cephalium-bearing taxa (*L. quadricostatus* and *L. grantianus*), which correlate with the grains that have the thinnest exines, and the yellow-flowered species of western Cuba (*L. assurgens, L. chrysotyrius* and *L. prostratus*), which correlate with the lowest rates of spinule density. Even though the quantitative differences among the pollen grains of *Leptocereus* are not suitable for phylogenetic analysis, they may serve the purpose of distinguishing species or groups of very closely related species.

Largest of all pollen grains studied are those of *Leptocereus santamarinae*, with diameters up to 80 μm (mean 69.5 × 69.7 μm). The smallest pollen pertain to *L. chrysotyrius* (Plate 37, E-H), with an average size of 54.8 × 55.9 μm. *Leptocereus*

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Table 13. Contrasted palynological characters of selected species of *Leptocereus* and *Cereus* (*Hamannia*) *fabiolae*. PD, polar diameter; ED, equatorial diameter; PE, ratio polar axis/equatorial axis; AD, apocolpium diameter; EA, distance between ends of adjacent ectocolpi; ET, exine thickness; SpH, spinule height; SpW, spinule width; SpD, spinule density (no. of spinules per 100 μm^2); PuDi, diameter of punctae; WR, width of puncta ring; PuDe, puncta density (no. of punctae per 100 μm^2); AI, apocolpium index. All measurements in μm.

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TAXA	PD	ED	PE	AD	EA	ET	SpH	SpW	SpD	PuDi	WR	PuDe	AI
L. assurg	58.9-69.4	59.2-69.6	0.99	16.5-37.9	16.1-28.7	2.2-3.0	0.5-1.2	0.5-1.0	4-7	0.2-0.5	0.2	12-18	0.35
L. chryso	43.1-66.6	44.0-67.8	0.98	21.3-34.7	19.7-30.9	2.5-3.0	0.5-1.3	0.7-1.1	4-8	0.2-0.4	0.2-0.3	11-17	0.45
L. prostr	56.8-71.3	59.9-72.6	0.98	25.7-32.3	20.2-32.4	2.2-3.0	0.6-0.8	0.4-0.9	3-9	0.2-0.8	0.2	14-20	0.40
L. albell	58.4-73.4	58.3-74.0	0.99	25.7-39.2	23.7-33.9	2.3-3.0	0.5-1.0	0.5-1.0	5-9	0.2-0.4	0.1-0.2	6-13	0.44
L. wri wri	60.8-77.1	60.4-78.1	0.99	19.9-38.5	17.5-29.7	2.0-2.8	0.4-0.8	0.4-0.8	5-10	0.3-0.5	0.1	15-20	0.34
L. scopul	56.5-70.8	55.4-76.2	0.97	27.5-45.2	25.7-40.2	2.0-2.5	0.5-0.9	0.4-0.9	5-9	0.3-0.5	0.1	15-22	0.50
L. leonii	55.9-72.2	57.3-79.1	0.95	28.1-47.1	28.0-41.6	2.0-2.5	0.4-0.9	0.4-0.8	5-10	0.3-0.6	0.1	17-21	0.51
L. carinat	52.6-68.3	52.8-68.9	0.99	27.6-40.4	24.3-37.5	2.0-2.5	0.3-0.7	0.3-0.8	9-13	0.2-0.6	0.2	14-20	0.51
L. sylvest	55.8-73.5	55.5-75.0	1.03	21.7-35.2	20.9-29.1	2.3-3.0	0.5-1.4	0.5-1.3	8-10	0.3-0.6	0.1	18-22	0.54
L. maxon	54.1-67.7	54.6-70.2	0.98	19.8-35.4	17.8-28.2	2.3-3.0	0.7-1.4	0.8-1.3	10-14	0.2-0.3	0.2-0.3	40-56	0.37
L. santam	59.4-79.6	58.7-80.7	0.99	17.4-33.0	16.1-31.0	2.0-2.5	0.5-0.9	0.5-0.9	7-9	0.3-0.5	0.1-0.2	17-24	0.34
L. wei wei	53.3-64.9	53.0-65.4	1.00	18.3-35.8	15.9-27.1	2.0-2.5	0.5-1.1	0.5-1.0	8-11	0.3-0.4	0.1-0.2	25-32	0.36
L. panicu	50.9-62.7	46.6-63.0	1.03	14.6-26.2	16.1-22.7	2.0-3.0	0.6-1.2	0.5-1.3	13-17	0.2-0.4	0.1	25-33	0.35
L. qua qua	62.4-74.9	64.0-75.3	0.99	25.3-40.5	22.6-37.3	1.2-2.0	0.4-0.7	0.4-0.8	6-9	0.3-0.9	0.1	14-19	0.43
L. qua par	62.5-76.2	65.6-76.1	0.98	23.9-39.3	22.9-36.8	1.3-2.0	0.5-0.8	0.5-0.8	7-9	0.3-0.8	0.1	15-20	0.42
L. grantia	60.8-75.0	63.7-75.8	0.98	24.1-38.5	22.4-36.9	1.3-2.0	0.4-0.7	0.4-0.8	6-9	0.3-0.8	0.1	15-20	0.43
C. fabiol	37.0-55.1	36.2-55.2	1.01	20.3-32.1	17.1-27.5	2.5-3.3	1.5-2.0	1.5-2	4-10	0.2-0.3	0.2-0.3	20-23	0.49

Table 13.

paniculatus (Plate 38, E-H) also has relatively small grains (mean 56.8 × 54.8 μm) that contrast with the larger grains of other members of the Hispaniolan-Puerto Rican group that bear cephalia (*L. quadricostatus* and *L. grantianus*). The polar axis/equatorial axis (PE) ratio of *L. paniculatus* is slightly above 1.00, a rare condition in *Leptocereus* shared only with *L. sylvestris* (Plate 36, E-H). Relatively high values of PE index (above 1.00) may indicate a trend towards the flattening of the grains, but in *L. paniculatus* and *L. sylvestris* these values are far from being high enough to be described as oblate.

The number of colpi in *Leptocereus* is another interesting aspect of their pollen morphology. Most species have 3-colpate pollen grains, which is believed to be the ancestral condition in angiosperms (Leuenberger, 1976b). Some species, however, show dominance of 3-colpate grains in my samples, but in smaller proportions another aperturate type, or types, may also be present. For example, *L. sylvestris* has 94% of 3-colpate grains and only 6% of 6-colpate grains. *Leptocereus assurgens* has a more diversified pollen spectrum: 80% 3-colpate, 17% 6-colpate, 2% 12-colpate, and 1% 2-colpate. On the other hand, in my sample *L. weingartianus* subsp. *weingartianus* has essentially 58% 6-colpate, with admixture of 36% 3-colpate, 5% 9-colpate and 1% 12-colpate. With respect to the length of colpi, *L. leonii* has the shortest colpi, and consequently the largest apocolpium diameter (37.6 μm, average), the longest distance between ends of ectocolpi (34.8 μm, average), and one of the highest values of apocolpium index (0.51, average). The colpi of *L. paniculatus*, by contrast, extend deeply into the poles leaving less room for a large apocolpium (AD is only 20.4 μm,

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average). As a result, the average distance between the apices of adjacent ectocolpi in this species is very reduced (19.4 μm), and its apocolpium index is low: 0.35 (Plate 38, E-H).

Exine thickness seems to be inversely correlated with pollen size in *Leptocereus*. The smallest grains (*L. chrysotyrius*, Plate 37, E-H) show the thickest exines (2.5 to 3 μm). Conversely, the Puerto Rican group of cephalium-producing taxa, *L. quadricostatus* subsp. *quadricostatus* (Plate 39, F-H), *L. quadricostatus* subsp. *parvispinus*, and *L. grantianus*, with relatively large grains up to 75 or 76 μm in diameter, have the thinnest exines (1.2 to 2.0 μm). This Puerto Rican group and the Cuban species *L. carinatus* and *L. wrightii* subsp. *wrightii* share the smallest tectal spinules: 0.3 to 0.8 μm × 0.3 to 0.8 μm (see Table 13 and Plate 36, A-D). The largest spinules are those of *L. maxonii* (0.7 to 1.4 μm × 0.8 to 1.3 μm), a species that also has a high spinule density: 10 to 14 spinules/100 μm^2 (Plate 35, A-D). This spinule density index (SpD) of *L. maxonii* is only surpassed by the Hispaniolan species *L. paniculatus* (13-17 spinules/100 μm^2). The lowest SpD range (3-9 spinules/100 μm^2) is that of the western Cuban species *L. assurgens*, *L. chrysotyrius* (Plate 37, E-H), and *L. prostratus* (Plate 39, C-E), all with yellow flowers.

Although the pollen grains of *Leptocereus* and of the Haitian "leptocereoid" *Cereus fabiolae* exhibit the same basic features of Leuenberger's "Cereus type" (1976a), there are some significant differences between them that confirm their position in separate generic lineages. *Cereus fabiolae* has relatively small grains, smaller than

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those of *Leptocereus* but with a thicker exine, and the tectum spinules are nearly twice as large (Table 13 and Plate 35, E-H). Likewise, a brief look at the oblate pollen grains of *Samaipaticereus corroanus* —another member of tribe Leptocereeae Buxbaum and a possible candidate for a *Leptocereus* lineage— suggest that this South American genus is not a close relative to the Antillean taxon (Plate 39, A, B). For practical purposes it may be useful to contrast in key form some important differences among the pollen grains of the species of *Leptocereus* studied, along with those of *Cereus fabiolae* and *Samaipaticereus corroanus*:

KEY TO THE TAXA (OR GROUPS OF TAXA) OF *LEPTOCEREUS* EXAMINED, BASED ON POLLEN MORPHOLOGY

(Incl. *Cereus fabiolae* and *Samaipaticereus corroanus* for comparison)

1. Pollen oblate, the polar axis significantly shorter than the equatorial one (Plate 39, A, B) ..... *Samaipaticereus corroanus*

1'. Pollen spheroidal, or nearly so

2. Tectum spinules 1.5-2 μm high and 1.5-2 μm wide at base (Plate 35, E-H) .... *Cereus* (*Hamannia*) *fabiolae*

2'. Tectum spinules < 1.5 μm high and < 1.5 μm wide at base

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3. Tectum with 40-56 punctae per 100 μm^2 (Plate 35, A-D) ..... 12. *L. maxonii*

3'. Tectum with < 40 punctae per 100 μm^2

4. Exine rather thin, most often < than 2.0 μm thick [16a. *L. quadricostatus* subsp. *quadricostatus* (Plate 39, F-H), 16b. *L. quadricostatus* subsp. *parvispinus*, and 17. *L. grantianus*] ..... *L. quadricostatus* sp. group

4'. Exine 2.0 μm thick, or more

5. Exine to 2.5-2.8 μm thick

6. Ratio polar axis/equatorial axis 0.95-0.97; maximum distance between ends of adjacent ectocolpi 40-42 μm [7. *L. scopulophilus*, and 8. *L. leonii* (Plate 37, A-D)] ..... *L. leonii* sp. group

6'. Ratio polar axis/equatorial axis 0.99-1.00; maximum distance between ends of adjacent ectocolpi 27-38 μm

7. Mean apocolpium index 0.51 (Plate 36, A-D) ..... 10. *L. carinatus*

7'. Mean apocolpium index 0.34-36

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8. Largest grains 77-81 μm in diameter; tectum with 15-24 punctae per 100 μm^2

9. Apocolpium diameter to 39 μm; punctae rings 0.1 μm thick ..... 6a. *L. wrightii* subsp. *wrightii*

9'. Apocolpium diameter to 33 μm; punctae rings to 0.2 μm .... 13. *L. santamarinae*

8'. Largest grains to 65 μm in diameter; tectum with 25-32 punctae per 100 μm^2 ..... 14a *L. weingartianus* subsp. *weingartianus*

5'. Exine to 3.0 μm thick

10. Mean apocolpium index 0.35

11. Tectum with 4-7spinules per 100 μm^2 ..... 1. *L. assurgens*

11'. Tectum with 13-17 spinules per 100 μm^2 (Plate 38, E-H) .... 15. *L. paniculatus*

10'. Mean apocolpium index > 0.35

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12. Mean apocolpium index 0.40-0.45

13. Smallest grains 43-45 μm in diameter (Plate 37, E-H) .....

..... 2. *L. chrysotyrius*

13'. Smallest grains 57-60 μm in diameter

14. Mean apocolpium index 0.40; tectum with 14-20 punctae per 100 μm^2 (Plate 39, C-E) ..... 4. *L. prostratus*

14'. Mean apocolpium index 0.44; tectum with 6-13 punctae per 100 μm^2 (Plate 38, A-D)..... 5. *L. albellus*

12'. Mean apocolpium index 0.54 ..... 11. *L. sylvestris*

4.5. Discussion

Pollen morphology is considered to be a conservative feature of a species. Potentially, it can provide significant insight into evolutionary relationships of plants at the species level and above, and is capable of playing a critical role is establishing different taxonomic groupings. Pollen characters in the Cactaceae have proven to be taxonomically useful in some cases, in other instances not. In those genera of subfamily

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Plate 35. Pollen grains of *Leptocereus maxonii* and *Cereus* (*Hamannia*) *fabiolae*.

A-D. *Leptocereus maxonii*: **A**. Polar view. **B**. Equatorial view. **C**. Detail of colpus. **D**. Detail of exine surface. **E-H**. *Cereus* (*Hamannia*) *fabiolae*: **E**. Equatorial view. **F**. Transverse section of pollen wall showing tectum and columellae. **G**. Detail of colpus. **H**. Detail of exine surface.

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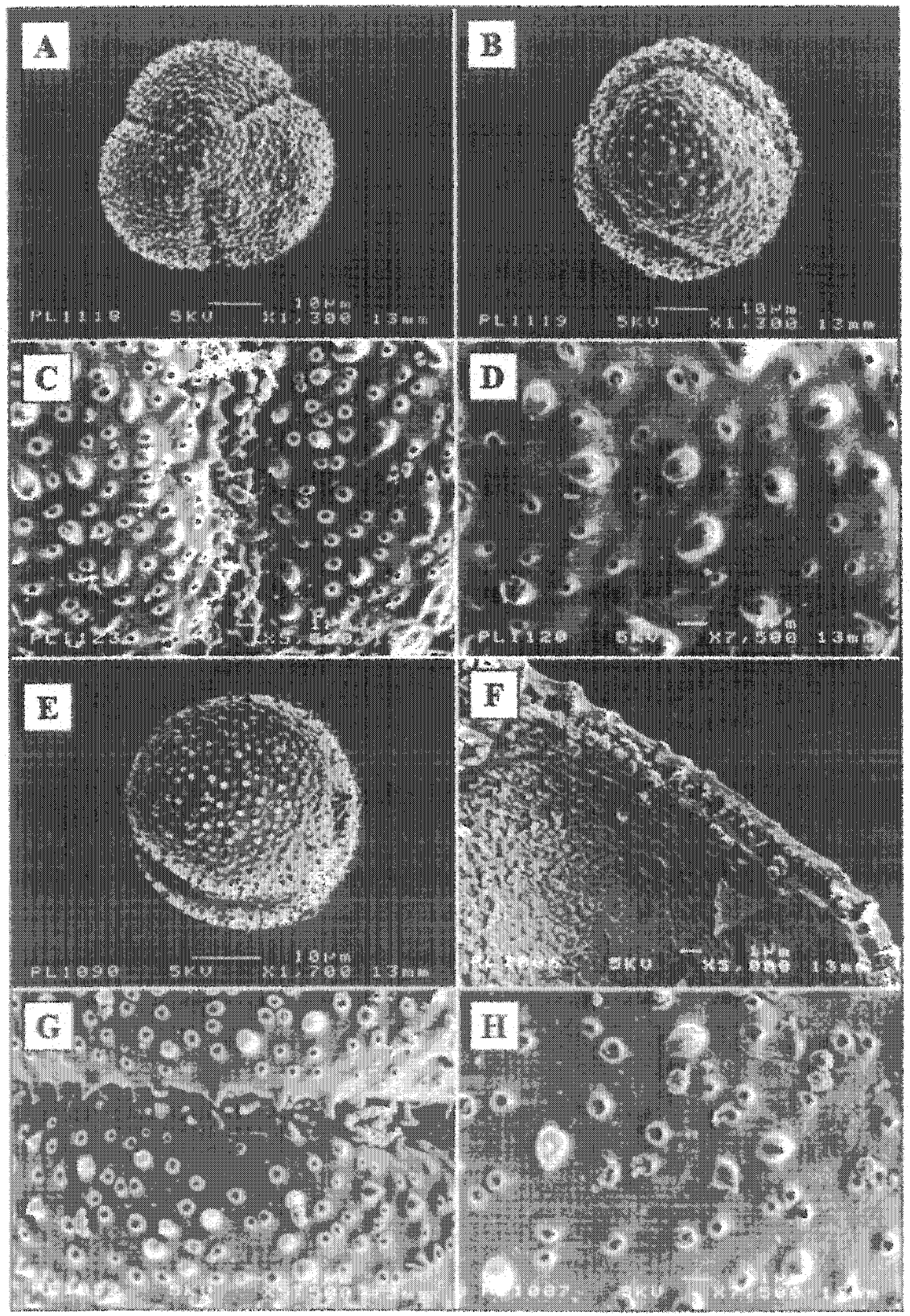

Plate 35.

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Plate 36. Pollen grains of *Leptocereus carinatus* and *L. sylvestris*.

A-D. *Leptocereus carinatus*: **A.** Polar view. **B.** Equatorial view. **C.** Detail of colpus. **D.** Detail of exine surface. **E-H.** *L. sylvestris*: **E.** Polar view. **F.** Equatorial view. **G.** Detail of colpus. **H.** Detail of exine surface.

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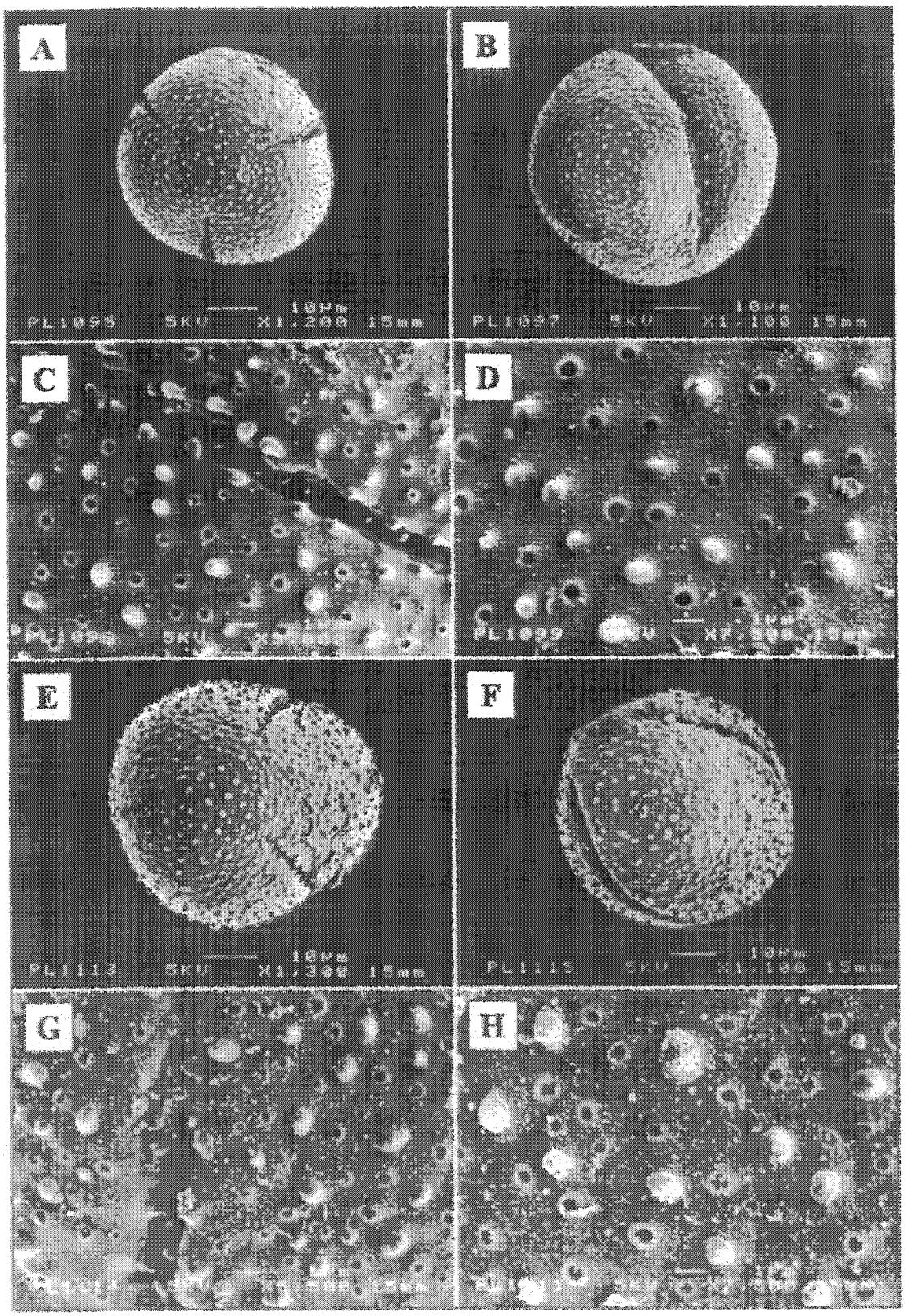

Plate 36.

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Plate 37. Pollen grains of *Leptocereus leonii* and *L. chrysotyrius*.

A-D. *Leptocereus leonii*: **A**. Polar view. **B**. Equatorial view. **C**. Detail of colpus. **D**. Detail of exine surface. **E-H**. *L. chrysotyrius*: **E**. Polar view. **F**. Equatorial view. **G**. Detail of colpus. **H**. Detail of exine surface.

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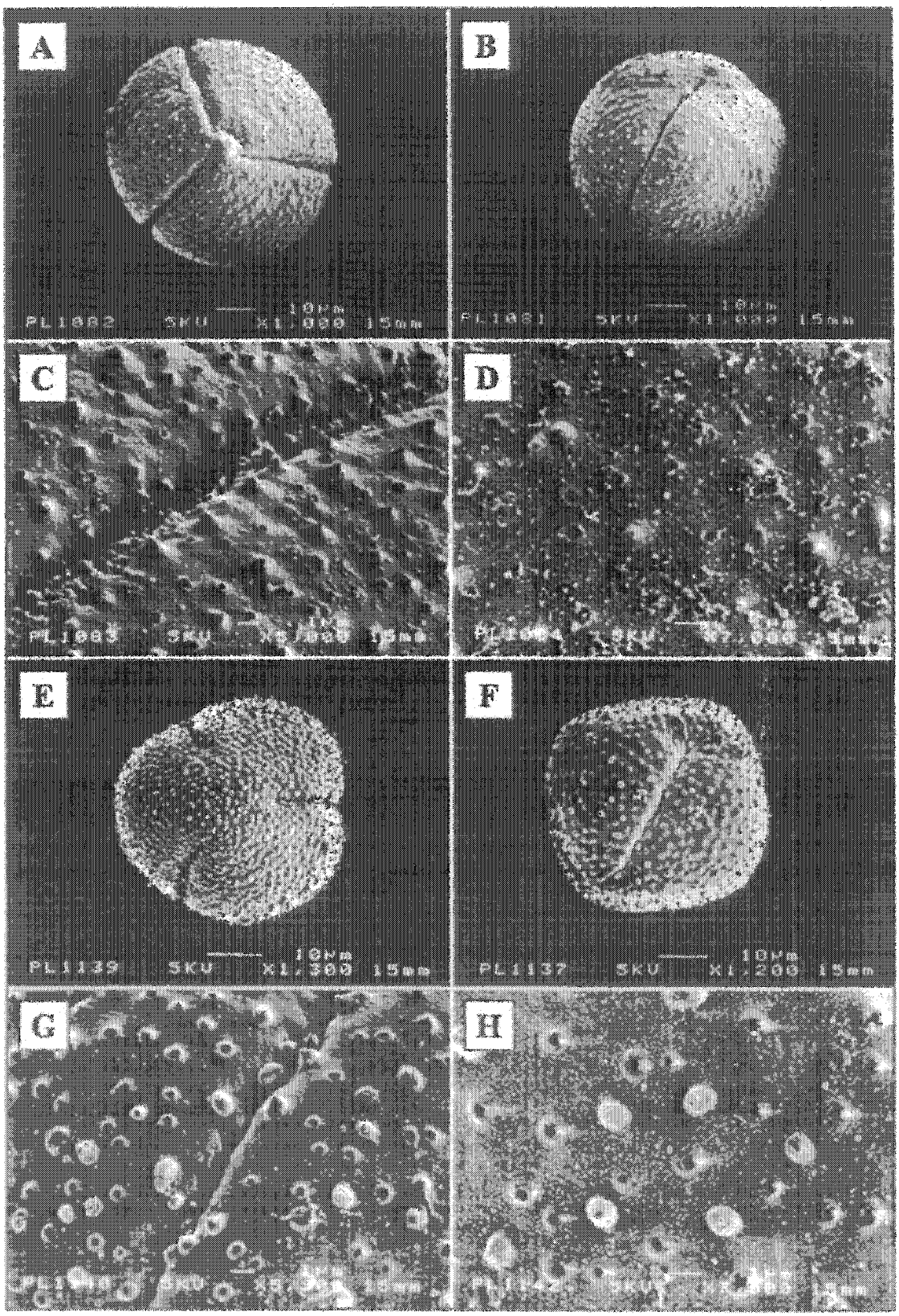

Plate 37.

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Plate 38. Pollen grains of *Leptocereus albellus* and *L. paniculatus*.

A-D. *Leptocereus albellus*: **A**. Polar view. **B**. Equatorial view. **C**. Detail of colpus. **D**. Detail of exine surface. **E-H**. *L. paniculatus*: **E**. Polar view of a 3-colpate grain. **F**. View of a 12-colpate grain. **G**. Detail of colpus. **H**. Detail of exine surface.

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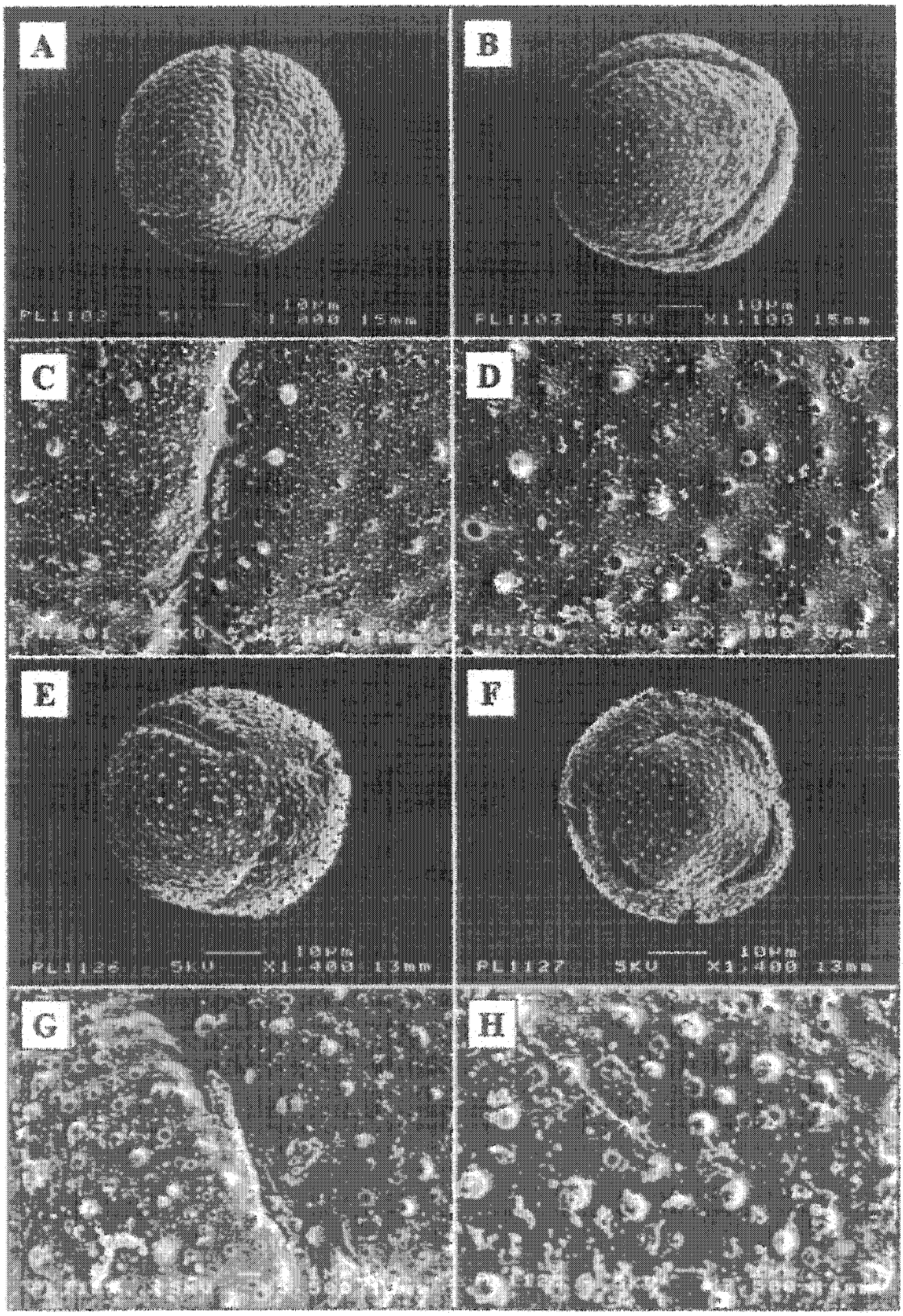

Plate 38.

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Plate 39. Pollen grains of *Samaipaticereus corroanus*, *Leptocereus prostratus*, and *L. quadricostatus* subsp. *quadricostatus*.

A, B. *Samaipaticereus corroanus*: **A.** Equatorial view of a typical oblate grain. **B.** Detail of short colpus. **C-E.** *Leptocereus prostratus*: **C.** Detail of exine surface. **D-E.** Equatorial views of pollen grains. **F-H.** *L. quadricostatus* subsp. *quadricostatus*: **F.** Equatorial view. **G.** Polar view. **H.** Detail of exine surface.

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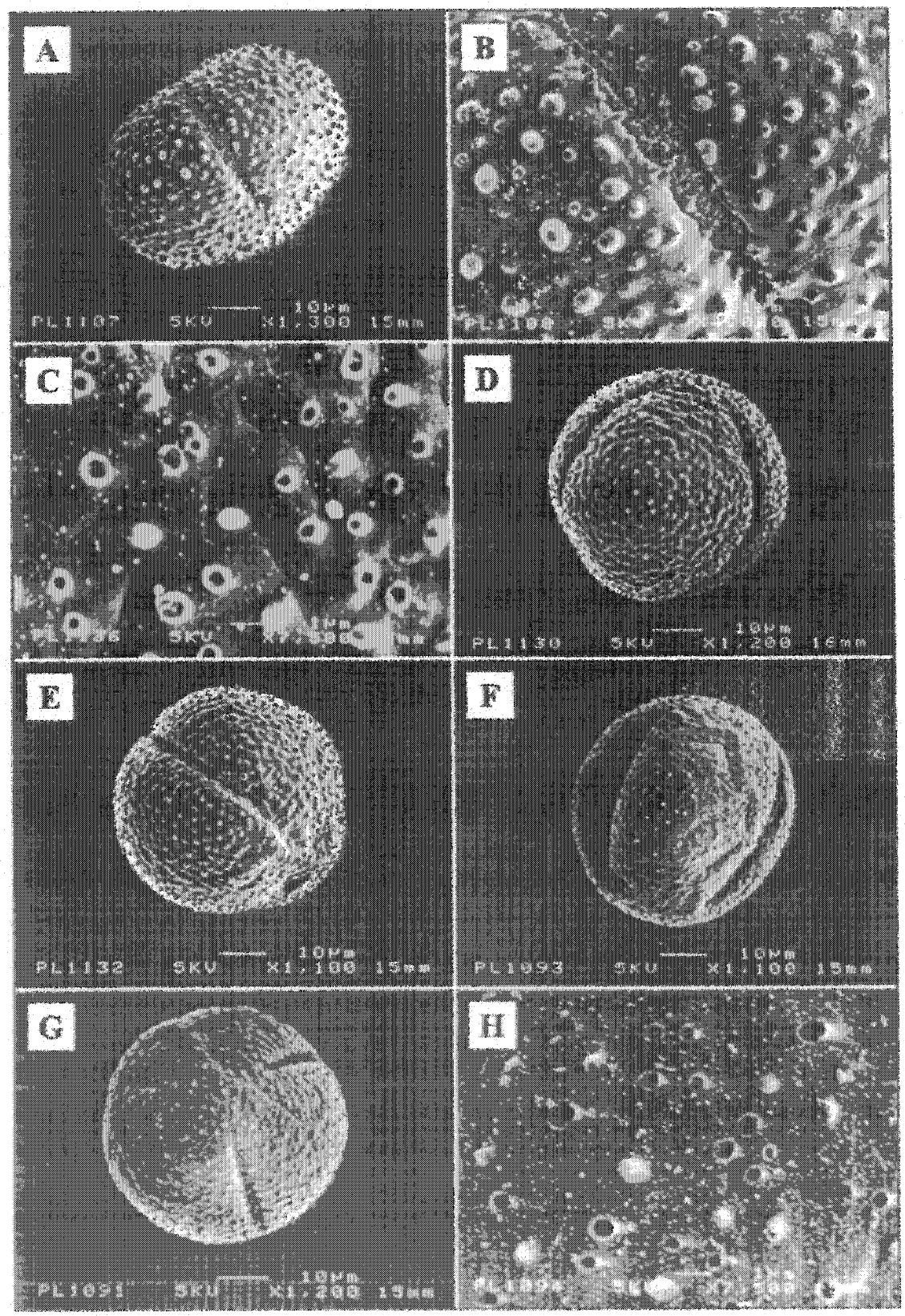

Plate 39.

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Cactoideae that exhibit the rather widespread 3-colpate "Cereus type," pollen morphology has often been of little use in elucidating phylogenetic relationships at the species rank. In *Leptocereus* it can be used to distinguish some species (as circumscribed here), although some very closely related taxa are too similar, *e.g.*, those of the *Leptocereus quadricostatus* species group. Unlike seed characters, palynological characters do not define more than two small groups of species bearing direct relationship with morphological and geographical features, probably because the number of characters that can be evaluated, and the rate of their variation, were to small to yield conclusive natural groupings. However, the following conclusions may be considered clear and valid:

1. As circumscribed in this work, the genus *Leptocereus* seems to define a natural, monophyletic group, characterized by medium-sized, isopolar, spheroidal pollen grains with nearly circular equatorial outline and numerous, small spinules and punctae. The number of colpi is most often three, rather long, and very sharply pointed at either end. The columellae are also numerous, and regularly distributed.

2. This study does not support Leuenberger's (1976a) statement (based on only two species) that the pollen grains of *Leptocereus* are esentially 6-colpate. In my samples, only one species out of 16 examined (*L. maxonii*) had more than 50% of 6-colpate grains. The dominant pollen type in *Leptocereus* is 3-colpate, sometimes with an important admixture of 6-colpates and the eventual presence of 9-colpates

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and 12-colpates. The 2-colpate, 4-colpate, and inaperturate grains are too rare to consider them standard pollen types of the genus.

3. On the basis of quantitative pollen characters, it is possible to distinguish most individual species of *Leptocereus*. As with seed characters, this indicates that the species delimitation is approximately correct because it is based on phenetic discontinuities in both gross and micromorphology. Some very closely related species, however, are practically undistinguishable by means of their pollen grains [*e.g.*, *Leptocereus quadricostatus* (Plate 39, F-H) and *L. grantianus*, and also *L. leonii* (Plate 37, A-D) and *L. scopulophilus*].

4. Pollen morphology is of very little help in grouping species of *Leptocereus* by their phylogenetic affinities. Pollen character differences bear no direct relationships to macromorphological and geographical features. Exceptions are the indistinguishable Puerto Rican group of cephalium-producing taxa, which all have grains with the thinnest exines, and the yellow-flowered species of western Cuba, with the lowest rates of spinule density.

5. Palynology does support placement of the Haitian "leptocereoid" taxon in a separate genus. The gross morphology of this taxon superficially resembles *Leptocereus* probably because of a convergent event, but most anatomical features indicate affinities with the South American genus *Cereus*. This species, hitherto described as *Cereus* (*Hamannia*) *fabiolae*, has relatively small grains, smaller than those of any

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Leptocereus but with a thicker exine, and the tectum spinules are nearly twice as large as those exhibited by *Leptocereus*.

6. The striking suboblate pollen of *Samaipaticereus corroanus*, with its short colpi and large spinules is far removed from that of *Leptocereus* in actual relationship. Thus, palynology does not seem to favor the assumption that this Central Andean "leptocereoid" is phylogenetically close to the ancestor of *Leptocereus*, from which all Antillean species later evolved.

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5. ANATOMY

5.1. Introduction

The ability of cacti to adapt to extreme environmental conditions can be attributed in great part to their anatomy. Stem succulence is one adaptation to survival during long, physiologically xeric periods, but there are other adaptative features for withstanding drought conditions, such as loss of leaves, general reduction of surface area (lack of surface area greatly reduces transpirational water loss), and thickening of epidermal cuticle. The cuticle is made of cutin, an impermeable substance secreted by the cells that repels surface water and prevents water vapor from escaping from the plant. This explains why the most striking anatomical features of the Cactaceae are found in the so-called skin complex, the cortex, and the wood.

The cactus covering, or skin complex, usually consists of two different layers: the epidermis, which is coated by the waxy cuticle, and the hypodermis, made of thick-walled collenchyma cells. The outer (periclinal) wall of a typical epidermal cell is flat or convex; very rarely it bears minute, nipple-like projections called papillae (*e.g.*, *Opuntia basilaris*). In many species of subfamilies Opuntioideae and Cactoideae epidermal cells contain druses of calcium oxalate (Haustein, 1986). Because the stem of most cacti is the principal photosynthetic organ, the epidermis has numerous stomata that may be evenly distributed over the entire stem or, on a ribbed plant, occur only on the sides of the ribs and not on the ridges and grooves (Gibson and Nobel, 1986). The

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stomata may run at right angles or parallel to the axis of the stem, or appear in a completely irregular fashion, but are largely constant within each genus and therefore taxonomically significant (Haustein, 1986).

The continuous layer of collenchyma below the epidermis, called hypodermis, is a supportive tissue of living cells with unevenly thickened walls that contain high concentrations of pectin and hemicellulose, but no lignin (Gibson and Nobel, 1986). Because pectin attracts water, which fills the walls and makes them flexible, a cactus stem can expand and contract without experiencing cell damage or rupture of the epidermis. The hypodermis, which can be over one millimeter thick in some gigantic columnar cacti, is only interrupted beneath the stomata where air passageways (substomatal canals) occur for gas exchange.

Vesque (1881, 1889) was first to notice the usefulness of epidermal features in establishing taxonomic relationships, particularly those related with the stomatal apparatus. Using electron microscopy techniques, Barthlott and Ehler (1977) reaffirmed that epidermal features are very varied in angiosperms and can be used to assess phylogenetic relationships. Specifically oriented towards cactus taxonomy, Gibson and Horak (1978) demonstrated that skin-complex anatomy was of important taxonomic value in cereoid cacti. After a certain number of studies, epidermal features of cacti have proven largely constant in each genus (Mauseth, 1984). Within the last three decades the epidermis (and often the inner collenchymatous hypodermis) of about 700

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species of cacti have been examined by different investigators, most of them searching for features to use in reconstructing evolutionary relationships.

Cortex morphogenesis in the Cactaceae has evolved not merely to produce a massive tissue containing water-storing cells. In addition, the outer cortex forms a "palisade" structure consisting of essentially radial rows of columnar chlorenchyma cells. The cells of each column are slightly separated from those of neighboring columns so the "palisade" cortex resembles the typical leaf palisade mesophyll of a normal leafy dicotyledons (Mauseth, 1995). Because chlorophyll is absent, the color of deeper cell layers in the cortex is opalescent, white, pinkish or yellow, but not green. Within the cortex there is an extensive network of cortical bundles that extend from the stele bundles to the base of the palisade cortex (Mauseth, 1995). In a central position there is also a ring of vascular cambium that produces a cylinder of wood (secondary xylem) surrounding the parenchymatous central pith. In young shoots the individual vascular bundles that produce the woody cylinder are arranged in circle, separated by broad medullary rays that connect the cortex with the pith. Additional medullary bundles can be observed in the pith of many species of subfamily Cactoideae, but not in the Pereskioideae and Opuntioideae (Gibson and Nobel, 1986). In many species of cacti we can also observe throughout the cortex clear, mucilage-bearing cells.

Typically, the wood of *Pereskia* and also of all tree-like members of subfamily Cactoideae, shows a matrix of narrow, thick-walled fibers and small clusters of medium-sized vessels surrounded by scanty paratracheal parenchyma. There is no

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apotracheal parenchyma in the wood of the Cactaceae and the rays are narrow, consisting of small, lignified cells (Mauseth, 1995). However, the highly modified wood of small, globular Cactoideae lacks fibers and its matrix consists of parenchyma and wide-band tracheids, or just parenchyma cells (Mauseth, 1995).

Anatomical studies of the Cactaceae have been conducted by many authors, including Bailey (1961, 1962, 1964), Gibson (1973), Gibson and Horak (1978), Gasson (1981), Eggli (1984), Mauseth (1995, 1996), and Mauseth and collaborators (1988, 1997a, 1997b, 1998a, 1998b). Detailed anatomical descriptions have been made for *Pereskia, Pereskiopsis* and *Quiabentia* by Bailey (*op. cit.*), while extensive anatomical surveys of the wood of many columnar Cactoideae have been provided by Gibson (1973) and Gibson and Horak (1978). More recently, Mauseth (*op. cit.*) began a program to study the anatomy of the most relictual genera of subfamily Cactoideae, in coordination with the International Organization for Succulent Plant Study (IOS). Some anatomical features of *Leptocereus* have been described by Gibson (1973), Mauseth and Ross (1988), Eggli (1984), Mauseth (1996), Mauseth and Plemons-Rodriguez (1998a), and Mauseth *et al.* (1998b), but the genus has not been studied thoroughly. Only six species of *Leptocereus* out of 17 (35%) have been considered in these purely descriptive studies. The present study is an attempt to assess the taxonomic potential of anatomical characters in *Leptocereus*, especially those derived from epidermis examination, for delimitation of species, or groups of species within the genus.

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5.2. Materials and methods

All material examined was taken from the wild or from mature living specimens vegetatively propagated from wild-collected plants, in my collections at Puerto Rico, Lehman College (City University of New York), and The New York Botanical Garden. Observations of periderm formation were made directly in the field on all *Leptocereus* taxa. For transverse sectioning of the stem *L. grantianus* was selected, a species that has never been studied before. For epiderm studies using the SEM, samples from all *Leptocereus* taxa except *L. albellus*, and from *Cereus* (*Hamannia*) *fabiolae*, were examined. A summary of the species investigated, and their sources, is given in Table 14.

Materials for transverse sections of epidermis and cortex, and for SEM studies were collected from mature, one to two year-old stem segments that had not yet formed bark. They were all liquid-preserved in formalin-acetic acid-ethanol fixative solution for at least 48 hours before processing. Portions of the stem of *Leptocereus grantianus* deprived of areoles were dehydrated, embedded in paraffin, and stained with safranine and fast green by standard histological techniques (Mauseth *et. al.*, 1984). These were later sectioned on a sledge microtome at thickness between 30 and 40 μm to prepare microscope slides. For SEM surface examination of epidermis small rectangular portions of fixed material taken from the ribs were dehydrated in an ethanol series and subsequently washed in chloroform, acetone and xylene to remove the resistant wax covering. This material was allowed to air-dry overnight at room temperature, mounted on aluminum stubs with double-sided adhesive tape, and plated in a sputter coater for

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TAXA	LOCALITY	SOURCE
L. assurgens	Viñales, Cuba	*Areces 6789*, NY
L. chrysotyrius	San Diego, Cuba	*Areces 4547*, NY
L. ekmanii	Sierra de Guane, Cuba	*Areces 6793*, NY
L. prostratus	Sumidero, Cuba	*Areces 6344*, NY
L. albellus	Sierra de San Carlos, Cuba	*Areces 6343*, NY
L. wrightii wrightii	Cojímar, Cuba	*Areces 6849*, NY
L. wrightii gracilis	San Diego, Cuba	*Areces 5777*, NY
L. scopulophilus	Somorrostro, Cuba	*Areces 4601*, NY
L. leonii	Sierra de Anafe, Cuba	*Areces 3292*, NY
L. arboreus	Yaguanabo, Cuba	*Areces 6120*, NY
L. carinatus	Najasa, Cuba	*Areces 5489*, NY
L. sylvestris	Pilón, Cuba	*Areces 5385*, NY
L. maxonii	Valley of Rio Tacre, Cuba	*Areces 5412*, NY
L. santamarinae	Santa Lucía, Cuba	*Areces 5341*, NY
L. weingartianus weingartianus	Bayahibe, Dom. Rep.	*Areces 6348*, NY
L. weingartianus weingartianus	Samaná, Dom. Rep.	*Areces 5973*, NY
L. weingartianus demissus	Pedernales, Dom. Rep.	*Areces 6812*, NY
L. paniculatus	El Limón, Dom. Rep.	*Areces 6386*, NY
L. quadricostatus quadricostatus	Ballena Bay, Puerto Rico	*Areces 6415*, NY
L. quadricostatus parvispinus	Guánica, Puerto Rico	*Areces 6417*, NY
L. grantianus	Culebra Island	*Areces 6377*, NY
Cereus (Hamannia) fabiolae	Môle St. Nicolas, Haiti	*Areces 6795*, NY

Table 14. List of taxa studied, and their sources.

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five minutes with a thin layer of gold. No significant bending of the rectangles occurred because portions of parenchymatic tissue were left underneath the epidermis before dehydration. All samples were examined with a JEOL JSM-5410LV scanning electron microscope with integral digital scanning equipment. Maximum length and width of epidermal cells refer to measurements of 20 cells randomly selected in each sample, while the maximum number of stomata/mm^2 is the result of 10 counts per surface unit in 10 different areas. Although some measurements were taken, this study was basically designed to search for qualitative, rather than quantitative differences among species, because sufficient number of field collections of each taxon could not be made to do adequate statistical analyses. All evaluations of epidermal characters and character states are shown in Tables 15 and 16.

5.3. The skin complex: epidermis and hypodermis

The skin complex of *Leptocereus* is relatively long-lived, and in some cases, *e.g.*, *L. ekmanii*, it may persist in a healthy state over the main stem, branches, and ultimate segments for the lifetime of the plant (this is not unusual in the Cactoideae and Opuntioideae, but does not occur in the Pereskioideae). The skin growth of *Leptocereus* adjusts to the growth of each stem segment by continuous division, a process that could take six months to 2 to 3 years to complete (in other genera of large columnar cacti it may take decades).

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Table 15. Contrasted epidermal characters of *Leptocereus* and *Cereus* (*Hamannia*) *fabiolae* (I). NS, maximum number of stomata/mm^2; SC, maximum number of subsidiary cells in stomatal apparatus; OS, orientation of stomata with respect to stem axis (0: randomly oriented; 1: longitudinally oriented); PS, position of stomatal apparatus with respect to epidermis surface (0: superficial; 1: slightly sunken; 2: sunken); NF, presence of non-functional stomatal apparatus (0: essentially non-existent; 1: 10 to 25 % of total number of stomata); CW, convexity of periclinal walls of epidermal cells (0: convex; 1: essentially flattened).

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TAXON	NS	SC	OS	PS	NF	CW
L. assurgens	47	5	0	2	0	0
L. chrysotyrius	28	5	0	0	0	0
L. ekmanii	40	(5) 6	0	1	0	0
L. prostratus	20	(5) 6	0	0	0	0
L. wrightii						
subsp. *wrightii*	32	5	0	0	0	0
subsp. *gracilis*	49	5	0	0	0	0
L. scopulophilus	34	5-6	1	0	0	1
L. leonii	24	5-6	0	0	0	0
L. arboreus	37	5-6	0	0	0	0
L. carinatus	23	(5) 6	0	0	0	0
L. sylvestris	29	5-6	0	0	0	0
L. maxonii	25	4-5	0	0	0	0
L. santamarinae	30	5-6	0	0	0	0
L. weingartianus						
subsp. *weingartianus* (Bayahibe)	34	5-6	0	0	1	0
subsp. *weingartianus* (Samaná)	38	5-6	0	0	1	0
subsp. *demissus*	31	5-6	0	0	1	0
L. paniculatus	36	5-6	0	0	1	1
L. quadricostatus						
subsp. *quadricostatus*	34	(5) 6	0	0	0	0
subsp. *parvispinus*	30	(5) 6	0	0	0	0
L. grantianus	27	(5) 6	0	0	0	0
Cereus (*Hamannia*) *fabiolae*	11	6	0	0	0	0

Table 15. Contrasted epidermal characters of *Leptocereus* and *Cereus* (*Hamannia*) *fabiolae* (I).

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Table 16. Contrasted epidermal characters of *Leptocereus* and *Cereus* (*Hamannia*) *fabiolae* (II). SD, presence of secondary divisions in epidermal cells (0: absent, or nearly so; 1: few; 2: many); AW, anticlinal walls of epidermal cells (0: straight or nearly so; 1: undulated; 2: dentated, with cells alternating dentils at boundaries); IU, amplitude of undulation/dentation of anticlinal walls (0: slightly manifested; 1: strongly manifested; na: not applicable); CB, epidermal cell boundaries (0: with acute, V-shaped groove; 1: with U-shaped groove 3.5 to 11 μm wide); ML, maximum length of epidermal cells, in μm; MW, maximum width of epidermal cells, in μm.

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TAXON	SD	AW	IU	CB	ML	MW
L. assurgens	2	1	1	0	53	34
L. chrysotyrius	1	1	1	0	61	36
L. ekmanii	0	1	1	0	83	69
L. prostratus	1	1	1	0	50	28
L. wrightii						
subsp. *wrightii*	2	0	–na–	0	66	24
subsp. *gracilis*	2	0	–na–	0	69	22
L. scopulophilus	0	1	0	0	86	33
L. leonii	1	1	0	0	78	29
L. arboreus	0	1	0	0	75	25
L. carinatus	0	1	0	0	86	40
L. sylvestris	2	1	0	0	83	26
L. maxonii	0	1	0	0	110	25
L. santamarinae	1	1	1	0	75	28
L. weingartianus						
subsp. *weingartianus* (Bayahibe)	1	2	0	1	65	34
subsp. *weingartianus* (Samaná)	1	2	0	1	61	33
subsp. *demissus*	1	2	0	1	64	31
L. paniculatus	0	2	0	1	97	39
L. quadricostatus						
subsp. *quadricostatus*	2	1	0	0	67	32
subsp. *parvispinus*	2	1	0	0	68	35
L. grantianus	2	1	0	0	53	28
Cereus (*Hamannia*) *fabiolae*	1	1	0	0	200	93

Table 16. Contrasted epidermal characters of *Leptocereus* and *Cereus* (*Hamannia*) *fabiolae* (II).

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The epidermis of all examined species of *Leptocereus* consists of tabular cells with a maximum length of 50 to 110 μm, and a maximum width of 22-69 μm. Their profile is fairly low compared to their overall dimensions (those of *L. grantianus* are only 13 to 16 μm tall when seen in cross-section). In the vast majority of species these cells are oblong or suboblong in outline, but in *L. maxonii* they are narrowly oblong, a character of diagnostic value (Plate 42, K, L). The epidermis of *L. grantianus* is uniformly unistratose, as are those of *L. quadricostatus* and *L. weingartianus*, but not *L. paniculatus*, which, according to Mauseth *et al.* (1998b) is irregularly multistratose. Crystals, as small rhomboidal bodies, are present in some epidermal cells of *L. grantianus*.

The anticlinal walls of the epidermal cells of *Leptocereus* are thickened and usually undulate. However, in some species undulation may be feeble (*e.g.*, *L. grantianus*, Plate 43, J, K), or virtually non-existent (*e.g.*, *L. wrightii*, Plate 42, A-D). The inner periclinal walls of *L. grantianus* are also thickened, and uniform, as seen in cross-section. The outer periclinal walls of *Leptocereus* have no papillae or projections of any kind, yet in most taxa they slightly curve outward in a simple, convex manner (Plate 40, F). In *L. scopulophilus*, however, these walls are remarkably flat (Plate 41, L, M). Some species (*i.e.*, *L. sylvestris*) have cells with uneven periclinal cell surfaces, slightly bulging when seen under the SEM. This is apparently due to the existence of one to four secondary divisions within each epidermal cell (Plate 42, I, J). In these cases the individual epidermal cells become clusters of two to five cells, the internal divisions being formed after the primary anticlinal walls of cells have been shaped. The

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Plate 40. Scanning electron photomicrographs of the epidermis of *Leptocereus* (I).

A, **B**. *L. weingartianus* (Bayahibe), showing a multistratose hypodermis below the epidermis (**B**). **C**. Slightly sunken stomata of *L. ekmanii*. **D**. *L. paniculatus*. **E**, **F**, **G**. As in most *Leptocereus* species, the outer periclinal wall of the cells of *L. weingartianus* (Samaná) is a little convex (**F**). This species has functional and non-functional stomata lacking guard cells (**E**, **G**). **H**. Stomatal apparatus of *L. santamarinae*.

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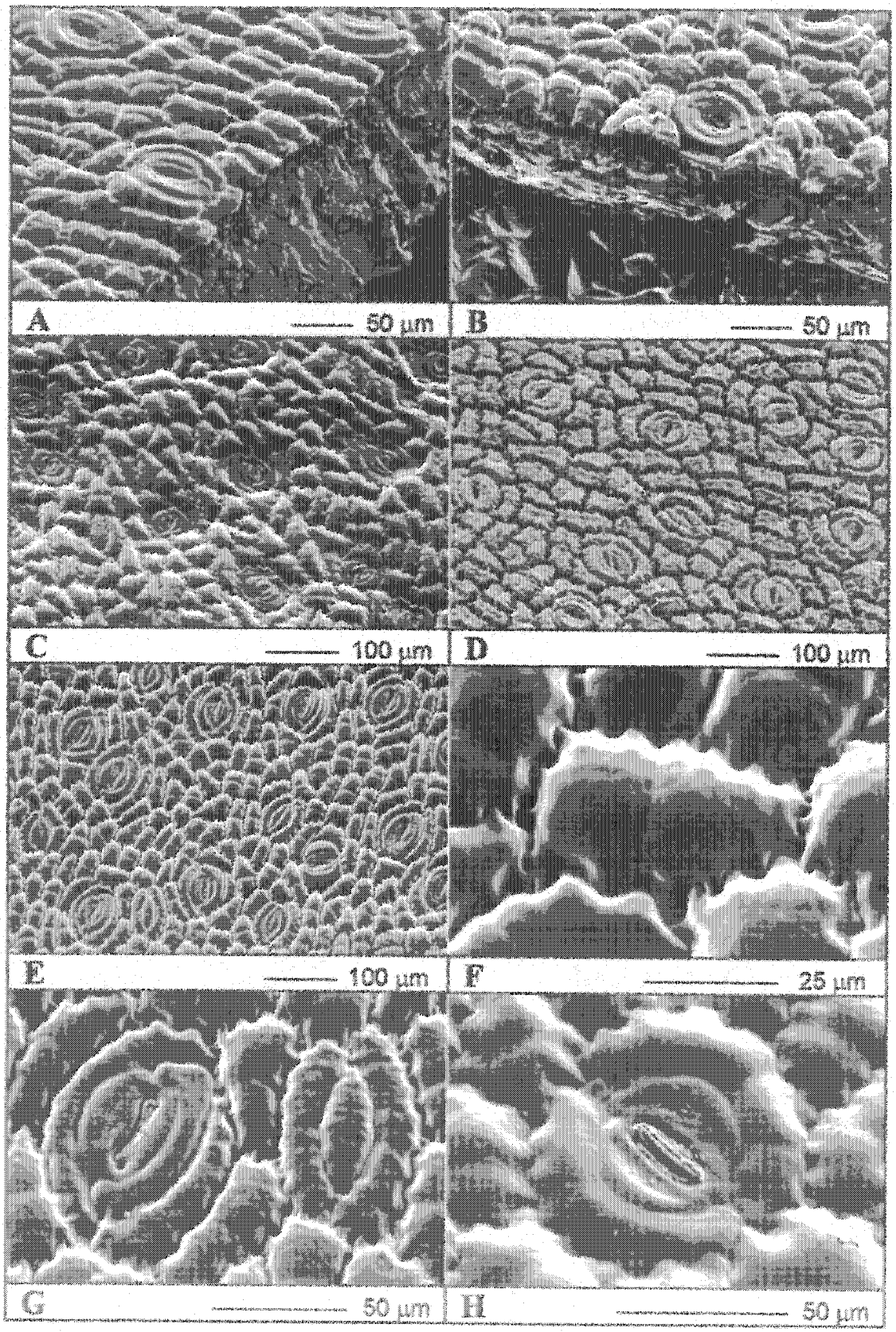

Plate 40.

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Plate 41. Scanning electron photomicrographs of the epidermis of *Leptocereus* (II).

A, B. Slightly sunken stomata of *L. ekmanii*, with flattened subsidiary cells. **C, D, E.** Sunken stomata of *L. assurgens*. **F, G.** *L. prostratus*. **H, I.** *L. chrysotyrius*. **J, K.** *L. leonii*. **L, M.** The characteristic epidermal cells of *L. scopulophillus* are markedly flat, a clear distinction with its closest relative *L. leonii*. **N, O.** *L. carinatus*.

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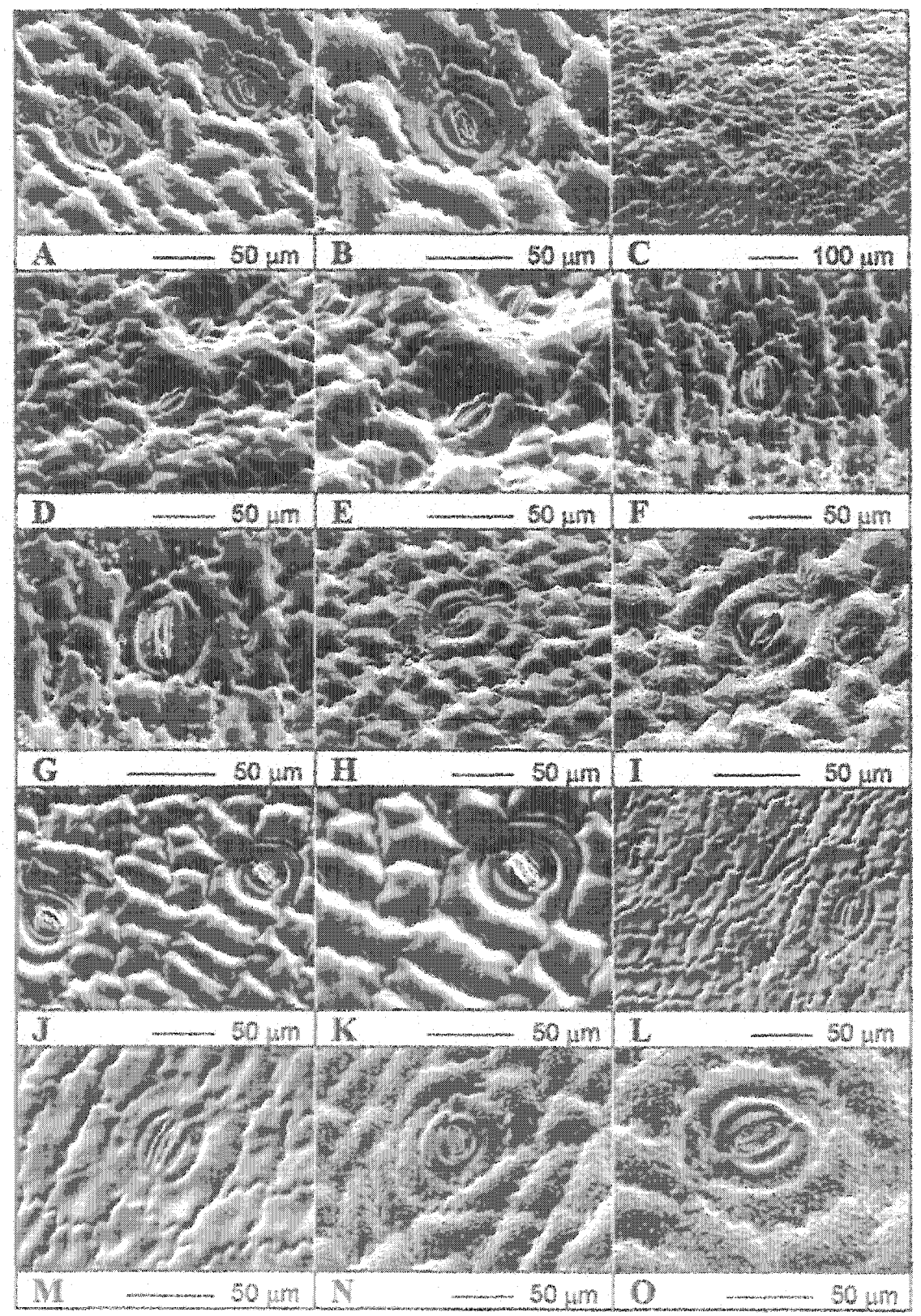

Plate 41.

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Plate 42. Scanning electron photomicrographs of the epidermis of *Leptocereus* (III).

A, **B**. *L. wrightii* subsp. *wrightii*. **C**, **D**. *L. wrightii* subsp. *gracilis*. cannot be distinguished from the typical subspecies on epidermal grounds. **E**, **F**. *L. arboreus*. **G**, **H**. *L. santamarinae*. **I**, **J**. *L. sylvestris*. **K**, **L**. *L. maxonii*. **M**, **N**. *L. weingartianus* subsp. *demissus*. **O**. *L. weingartianus* subsp. *demissus*. This taxon exhibits practically identical epidermal features than the typical subspecies.

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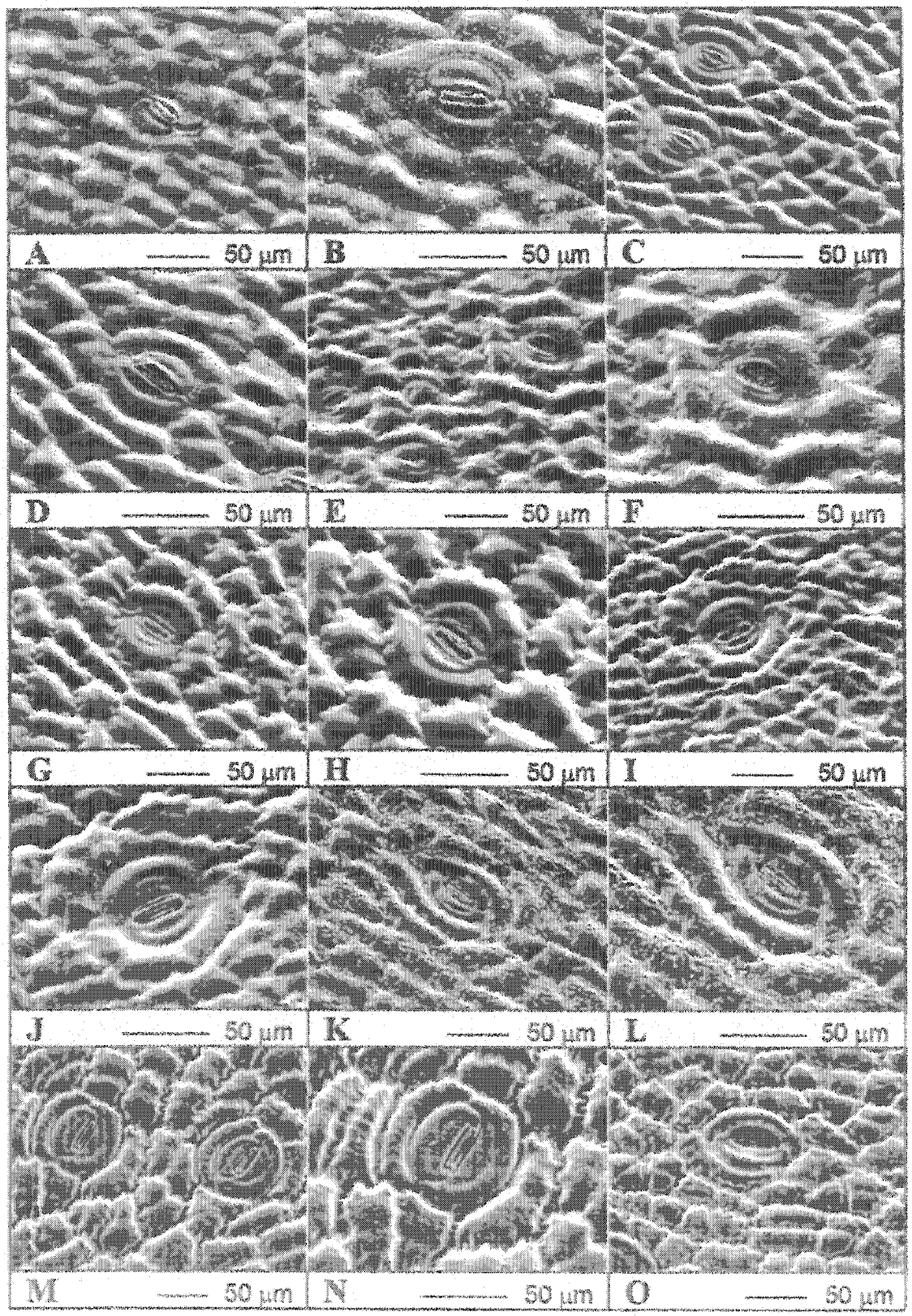

Plate 42.

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Plate 43. Scanning electron photomicrographs of the epidermis of *Leptocereus* and *Cereus* (*Hamannia*) *fabiolae* (IV).

A. *L. weingartianus* subsp. *weingartianus* (Bayahibe). **B**, **C**. *L. weingartianus* subsp. *weingartianus* (Samaná). **D**, **E**. The epidermal cells of *L. paniculatus* have grooved anticlinal boundaries. **F**, **G**. *L. quadricostatus* subsp. *quadricostatus*. **H**, **I**. *L. quadricostatus* subsp. *parvispinus*, with a nearly identical epiderm as subspecies *quadricostatus*. **J**, **K**. *L. grantianus*. Being closely related with *L. quadricostatus*, the epidermal features of both species are quite similar. Undulation of anticlinal walls of cells, however, is less pronounced in *L. grantianus*. **L-O**. *Cereus* (*Hamannia*) *fabiolae*, with its large angular cells, seems far from *Leptocereus* in actual relationship.

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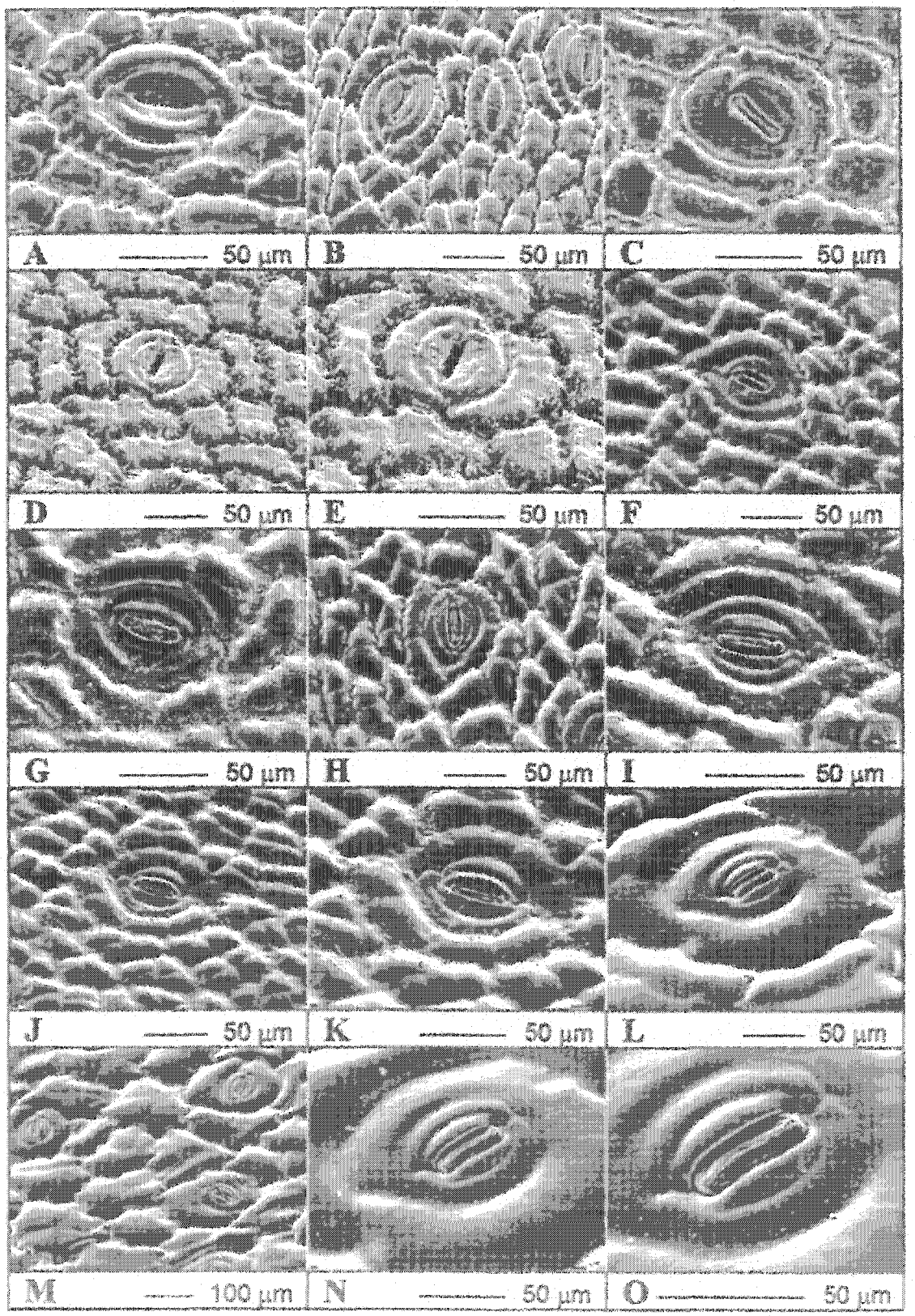

Plate 43.

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primary anticlinal walls of *Leptocereus* may be undulate or nearly straight, but are always thick, whereas the walls of later divisions are invariably straight and thinner. Because the new cell cluster is slightly larger than the primary cell, we might expect that it would become elevated due to the increase in volume, thereby forming a bullate micro-relief.

The cuticle layer of the epidermal cells of *Leptocereus* varies greatly in thickness, depending upon the species. In *L. grantianus* it was found to be rather thin (approximately 3 μm thick), whereas in *L. weingartianus* and *L. paniculatus* Mauseth *et al.* (1998b) reported a cuticle thickness of 14 and 20 μm, respectively. In addition to the cuticle, the epidermis outer surface is covered by a layer of wax, which in *L. paniculatus* (Plates 8, C, and 9, I) and *L. weingartianus* (Plate 10, D, E) imparts a grayish hue to the stem (epidermal waxes are also responsible for the far more attractive white bloom of young shoots of another genus of West Indian columnar cacti, *Pilosocereus*).

The stomatal apparatus of *Leptocereus* is typically of the parallelocytic type, with a series of 4-6, usually C-shaped subsidiary cells gradually increasing in size from the center outwards. Within the series, the outer subsidiary cells, which may have transverse secondary divisions (*e.g.*, *L. quadricostatus* subsp. *parvispinus*, Plate 43, H), partially overlap the ends of the inner ones. If the anticlinal walls of epidermal cells are undulated, then the convex side of the outer subsidiary cells are also undulated (*e.g.*, *L. santamarinae*, Plate 40, H).

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The stomata in *Leptocereus* are evenly distributed over the entire rib surface, and in most cases, they are randomly oriented (Plate 40, D). As an exception, *L. scopulophilus* has a tendency to orient its stomata parallel to the stem axis (Plate 41, L, M). The maximum number of stomata in each square millimeter varies from 20 (*L. prostratus*) to 49 (*L. wrightii* subsp. *gracilis*). A majority of *Leptocereus* species show superficial stomata, where the whole stomatal apparatus is at the same level as the epidermis (*e.g.*, Plate 42, M, N). The exceptions to this rule are *L. ekmanii* and *L. assurgens*. In *L. ekmanii* the stomatal apparatus, with its outer subsidiary cells remarkably flattened, is slightly lowered in position with respect to the neighboring epidermal cells (Plate 41, A, B). Because in this case the inner subsidiary cells are lower than the outer ones, the sinking of the occlusive cells is gradual. In *L. assurgens* there are patches of epidermal surface where the stomata are confined to small depressions (Plate 41, C, E). Stomata in sunken zones like those of *L. assurgens* have been documented in a small number of cacti, *e.g.*, *Opuntia cylindrarticulata* and *Aporocactus flagelliformis* (Eggli, 1984).

The hypodermis of *Leptocereus grantianus*, which is the lower stratum of its skin complex, consists of three to four, rarely five layers of flattened, non-lignified collenchymatous cells. It is approximately 45 to 55 μm thick and no crystals are present. Other *Leptocereus* species, namely *L. quadricostatus*, *L. weingartianus*, and *L. paniculatus*, have been reported with a 63, 34, and 213 μm thick hypodermis (Mauseth *et al.*, 1998b). These authors (*op. cit.*) found that the thick hypodermis of *L. paniculatus*

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(referred to as *Neoabbottia paniculata*) had prismatic crystals like those commonly found in epidermal cells.

For practical purposes it may be useful to contrast in key form some important differences among the species of *Leptocereus* related to the skin complex, particularly, the epidermis:

KEY TO THE SPECIES OF *LEPTOCEREUS* BASED ON EPIDERMAL MORPHOLOGY

(Incl. *Cereus fabiolae* for comparison)

1. Epidermis with less than 15 stomata/mm^2; epidermal cells 76-93 μm wide; longitudinal diam. of stomatal apparatus 195-225 μm (Plate 43, L-O) .... *Cereus* (*Hamannia*) *fabiolae*

1'. Epidermis with more than 15 stomata/mm^2; epidermal cells less than 70 μm wide; longitudinal diam. of stomatal apparatus 43-134 μm.

2. Epidermis with 10-25 % of non-functional stomata lacking guard cells; anticlinal walls of epidermal cells dentated, their boundaries with U-shaped grooves

3. Epidermal cells with few secondary divisions; periclinal walls convex; anticlinal boundaries with 3.5-7 μm wide grooves (Plates 40, A, B, E-G; 42,

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M-O; 43, A-C) ..... 14. *L. weingartianus*

3'. Epidermal cells usually lacking secondary divisions; periclinal walls essentially flattened; anticlinal boundaries with 9-11 μm wide grooves (Plates 40, D; 43, D, E) ..... 15. *L. paniculatus*

2'. Epidermis with nearly 100 % functional stomata; anticlinal walls of epidermal cells straight or undulated, their boundaries with acute V-shaped grooves

4. Anticlinal walls of epidermal cells straight (Plate 42, A-D) ..... 6. *L. wrightii*

4.' Anticlinal walls of epidermal cells undulated

5. Anticlinal walls of epidermal cells strongly undulated

6. Epidermis with more than 35 stomata/mm^2; stomatal apparatus essentially sunken

7. Epidermal cells with numerous secondary divisions; stomatal apparatus often in sunken zones (crypts), usually with 5 convex subsidiary cells (Plate 41, C-E) ..... 1. *L. assurgens*

7'. Epidermal cells without secondary divisions or nearly so; stomatal

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apparatus slightly sunken, usually with 6 flattened subsidiary cells (Plates 40, C; 41, A-B) ..... 3. *L. ekmanii*

6'. Epidermis with less than 35 stomata/mm^2; stomatal apparatus superficial

8. Largest epidermal cells less than 65 μm long

9. Stomatal apparatus 57-68 μm in diam., usually with 5 subsidiary cells; largest epidermal cells 35 μm wide or more (Plate 41, H, I) ..... 2. *L. chrysotyrius*

9'. Stomatal apparatus 70-82 μm in diam., usually with 6 subsidiary cells; largest epidermal cells less than 30 μm wide (Plate 41, F, G) ..... 4. *L. prostratus*

8'. Largest epidermal cells exceeding 70 μm long (Plates 40, H; 42, G, H) ..... 13. *L. santamarinae*

5'. Anticlinal walls of epidermal cells moderately to very slightly undulated

10. Periclinal walls of epidermal cells flattened or slightly concave; stomata transversely oriented in stem (Plate 41, L, M) ..... 7. *L. scopulophilus*

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10'. Periclinal walls of epidermal cells convex; stomata randomly oriented in stem

11. Epidermal cells most often lacking secondary divisions

12. Epidermal cells narrowly oblong, the largest ones to 110 μm long; stomatal apparatus distinctly elongated, its longitudinal diam. 122-134 μm, the outermost subsidiary cell ending in acute point (Plate 42, K, L) ..... 12. *L. maxonii*

12'. Epidermal cells oblong, the largest ones less than 90 μm long; stomatal apparatus almost circular, its longitudinal diam to 100 μm, the outermost subsidiary cell not ending in acute point

13. Largest epidermal cells 75 ×25; longitudinal diam. of stomatal apparatus 61-73 μm; margin of subsidiary stomatal cells obscurely undulate (Plate 42, E, F) .... 9. *L. arboreus*

13'. Largest epidermal cells 85 ×40; longitudinal diam. of stomatal apparatus 84-100 μm; margin of subsidiary stomatal cells distinctly undulate (Plate 41, N, O) .... 10. *L. carinatus*

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11'. Epidermal cells with distinct secondary divisions

14. Secondary divisions of epidermal cells occurring sporadically; longitudinal diam. of stomatal apparatus 63-79 μm (Plate 41, J, K) ..... 8. *L. leonii*

14'. Secondary divisions occurring in the vast majority of epidermal cells; longitudinal diam. of stomatal apparatus 84-126 μm

15. Epidermal cells with an irregular, bulging periclinal surface; longitudinal diam. of stomatal apparatus 84-98 μm (Plate 42, I, J) ..... 11. *L. sylvestris*

15'. Epidermal cells without a bulging periclinal surface; longitudinal diam. of stomatal apparatus 105-126 μm

16. Anticlinal walls of epidermal cells distinctly undulated (Plate 43, F-I) ..... 16. *L. quadricostatus*

16'. Anticlinal walls of epidermal cells obscurely undulated (Plate 43, J, K) ..... 17. *L. grantianus*

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5.4. Periderm formation

As in all members of the cactus family, *Leptocereus* may form phellogen from the skin complex, after its epidermal cells activate to undergo periclinal divisions (in most plants other than cacti, phellogen commonly forms from old cortical cells). Green tissue is then replaced by yellowish-brown patches (young periderm), and ultimately, by thick grayish or brown bark.

Periderm formation in *Leptocereus* is a common event that occurs in old branches and stems of all members of subgenus *Weingartianea*, and in all members of sections *Roseiflorei*, *Costanthus*, and *Spinosissimus* of subgenus *Leptocereus*. By contrast to this group of 12 species with "normal" periderm formation, I distinguish a small group of five-species with "retarded" periderm formation: section *Leptocereus* of subgenus *Leptocereus*. In this group, the formation of periderm is not necessarily a consequence of aging. The stems of the dwarf *L. ekmanii*, for example, may undergo aging remaining nearly as green and photosynthetic as they where when their growth ceased. Other species of section *Leptocereus*, *e.g.*, the procumbent or dangling *L. prostratus* and *L. albellus*, may produce bark at the very base of their main stems, many years after sexual maturity has been attained. Because in this case ribs often remain green and functional, and activation of epidermal cells to produce phellogen seems to be the mere consequence of covering the fissures opened by the expansion of the basal shoot stele after undergoing secondary growth. In the cephallium-bearing species of Hispaniola

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and Puerto Rico, a phellogen layer can arise very precociously on the specialized flowering tips, or cephalia (Plate 19, A-D).

Normal and retarded periderm formation in *Leptocereus* usually follows two distinct patterns. It may be continuous, the phellogen initiating its activity in a fairly continuous, single narrow band along the stem grooves, wherever the skin was subject to tension or had split (Plate 44, A-E). This type is always related with production of secondary xylem. Periderm formation may be also patchy (maculate), the rather thin and translucent phellem layers often occurring in numerous, small, 1 to 2 mm rounded patches on the stem grooves, or ribs, later merging by accretion to cover extensive areas (Plate 44, F). Sometimes large, essentially rounded patches of periderm appear on the ribs of old stem segments, *e.g.*, in *L. paniculatus* (Plate 44, H), with no apparent relation to the secondary growth of stele. In this patchy type of periderm formation, rupture of skin at the stem grooves and covering of the fissures by bark, is an event that usually comes after the replacement (with peridermis) of the whole primary epidermis of the stem. (Plate 44, G). The two patterns of periderm formation (continuous and patchy) are of taxonomic value, since the patchy type is restricted to members of section *Cephaliphora* of subgenus *Weingartianea*, which includes the cephalium-bearing species of Hispaniola and Puerto Rico.

5.5. The cortex

Beneath the epidermis of *Leptocereus* there is a relatively thin cortex composed of

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Plate 44. Periderm formation in *Leptocereus*.

A-E. Continuous type of periderm formation along the stem grooves, following secondary growth of stele. In this type, ribs usually remain green and photosynthetically active long after the grooves have been fissured and covered with bark. **F-H.** Patchy (maculate) type of periderm formation, where the phellem layers occur in small rounded patches (**F**) that will merge by accretion to cover wider areas (**G**). Sometimes large patches appear on the ribs of old stem segments (**H**), with no apparent relation to the secondary production of xylem. **A.** *L. arboreus*. **B.** *L. carinatus*. **C.** *L. leonii*. **D.** *L. prostratus*. **E.** *L. wrightii* subsp. *wrightii*. **F.** *L. quadricostatus* subsp. *parvispinus*. **G.** *L. quadricostatus* subsp. *quadricostatus*. **H.** *L. paniculatus*. (A, from Yaguanabo, Cuba —9 Jul 1993; B, from type plant, Sierra del Chorrillo, Najasa, Cuba —12 Sep 1990; C, from Sierra de Anafe, Cuba —29 Oct 1975; D, from type locality at Sumidero, Pinar del Río province, Cuba —5 Mar 1992; E, from Bahia Honda, Cuba —12 Dec 1993; F, from Bosque Estatal de Guánica, Puerto Rico —23 Feb 1994; G, from dry forests between Punta Melones and Laguna de Boquerón, Puerto Rico —13 Jun 1995; H, from La Descubierta, Dominican Republic —7 Jan 1995.

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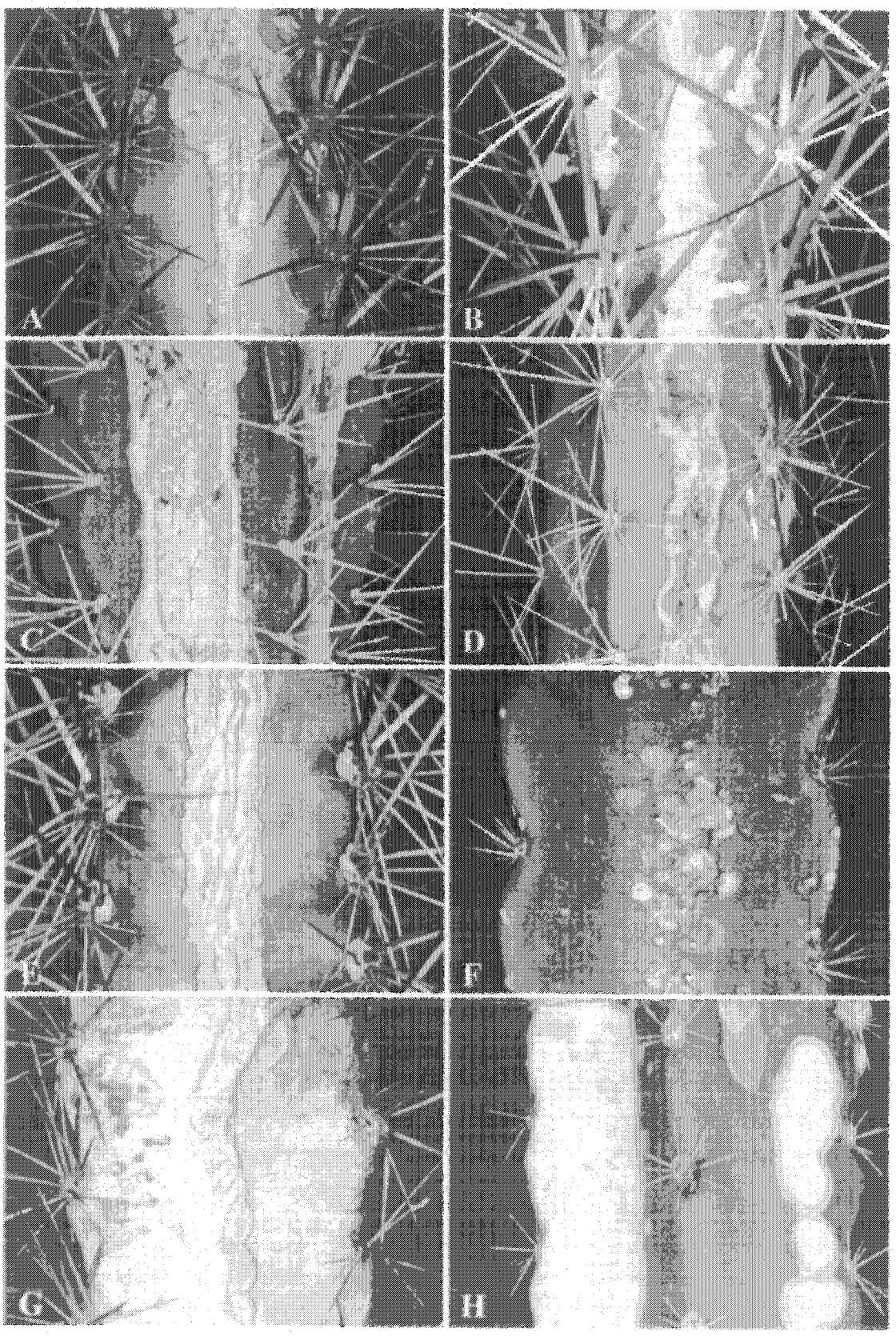

Plate 44.

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water-filled parenchyma cells. The outer 0.5 to 1 millimeter (palisade cortex) corresponds to green, photosynthetically active parenchyma, while the yellowish-white inner area lacks chloroplasts. The chlorophyll-rich cells of the palisade cortex occur in distinct columns. In *L. grantianus* (and presumably in other species of *Leptocereus* as well), chloroplasts are of ordinary size and shape. Mucilage cells were observed in both, the palisade and inner cortex, but no crystal druses occurred in the palisade area. Mauseth *et al.* (1998b) reported presence of mucilage cells in the palisade cortex of *L. quadricostatus*, and absence in *L. weingartianus* and *L. paniculatus*.

Because the cortex is so thin, especially in arborescent and large shrubby forms, the exomorphic structure of *Leptocereus* is not particularly accentuated by succulence. Most genera of columnar cacti (and large globular Cactoideae as well) produce a rather thick cortex, not comparable to that of *Leptocereus*. Since there is no cortex in *Pereskia*, its presence in subfamily Cactoideae could be interpreted as a derived condition. Likewise, within the cortex-producing Cactoideae, a thin cortex such as that of *Leptocereus* seems to be plesiomorphic with respect to the thick cortex of a barrel or globular cactus, *e.g.*, *Melocactus* (Figs. 2, 3).

In cross-section, *Leptocereus grantianus* exhibits numerous cortical, bundles than contain both xylem and phloem. These collateral bundles branched frequently, forming an extensive network within the cortex. They have no relation with areole traces and usually end as narrow tips in the innermost layers of the palisade cortex. No bundle sheath or endodermis surrounding the vascular tissues was observed in this species.

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Mauseth and Ross (1988), who studied in detail the cortical bundles of *L. quadricostatus* —the closest relative to *L. grantianus*— found tracheary elements with scalariform-helical secondary walls, accompanied by 5 to 14 tracheids (as seen in cross-section). These authors also described a phloem complex consisting of sieve tube members, companion cells, and non-conductive parenchyma. Caps of primary phloem fibers seem to occur irregularly within the genus *Leptocereus*. Mauseth *et al.* (1998b) found them in *L. weingartianus* but not in *L. quadricostatus* and *L. paniculatus*.

5.6. The stele

The vascular cylinder (stele) of the ultimate stem segments of *Leptocereus* is rather thin in comparison to the stele of most columnar cacti. Its diameter ranges from 2 mm in *L. ekmanii* (Fig. 2, H1, H2) to 13 mm in *L. wrightii* subsp. *gracilis* (Fig. 3, A). With such narrow stele, the stellar diameter/shoot diameter ratio (stelar index) of *Leptocereus* is one of the lowest in subfamily Cactoideae, varying from 0.130 to 0.225 (a clear distinction with *Cereus fabiolae*, which has a stelar index of 0.32 to 0.67).

In all but one species of *Leptocereus*, namely *L. prostratus*, the vascular cylinder is positioned always in the geometrical center of the shoot. In the procumbent *L. prostratus* old stems may show a slight differentiation between their dorsal and ventral sides, old steles are sometimes a little excentrical. Due to differences in the growth rate of secondary xylem, the dorsal and ventral walls of the vascular cylinder in these prostrate shoots may be of different thickness. Cambium cells apparently proliferate

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faster in the dorsal side of stele, than in the ventral side. These differences are only noticeable in older plants; after a three-year growth period, the dorsal cylinder wall of *L. prostratus* could be 63% thicker than the ventral wall (Fig. 2, E2).

In harmony with its thin stele, the pith of *Leptocereus*, which is the central succulent tissue of the stem, is narrow (1.8 to 12 mm) as compared with other columnar cacti. In cross-section, the pith of *L. grantianus* consists of a groundmass of parenchymatous cells traversed by medullary bundles similar to the cortical bundles described earlier. No cap of primary phloem fibers was observed in the medullary bundles of this species. By contrast, Mauseth *et al.* (1998b) found phloem fiber caps in *L. weingartianus*, but not in *L. quadricostatus* and *L. paniculatus*. In addition to the medullary parenchyma and vascular bundles, the pith of *L. grantianus* contains mucilage cells and small druses.

No attempt was made to study the secondary xylem of *Leptocereus*, because in Cactaceae wood characters are remarkably uniform and not particularly correlated with environmental factors (Mauseth and Plemons-Rodríguez, 1998b). However, some important aspects of the secondary xylem of this genus provided by Mauseth and Ross (1988), and Mauseth *et al.* (1998b) will be summarized, as follows:

The secondary xylem of *Leptocereus* consists of vessels, scanty paratracheal parenchyma, and thick-walled libriform fibers, which are nucleate and septate. In *L. quadricostatus*, the vessel elements have scalariform-helical bordered pitting and

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simple, round to oval perforations. Over 50% of them occur in clusters of two or three vessels (Mauseth and Ross, 1988). Where these vessels are accompanied by libriform fibers, there is scanty paratracheal parenchyma, not sufficient to encase a vessel completely. In fact, most of the vessels are in contact with fibers, not parenchyma cells (Mauseth *et al.* 1998b).

Xylem rays in *Leptocereus quadricostatus* shoots are tall and narrow, 8 to 10 cells wide. The cells are very heteromorphic, and have thick (2.5 μm), lignified secondary walls. In contrast to fibrous wood, parenchymatous wood lacking fibers occurred in the cephalia of *L. quadricostatus* and *L. paniculatus* (Plate 19, A-D). The matrix of this soft, parenchymatous wood is composed of parenchyma cells, and ray cells are mere round parenchyma cells with thin, unlignified walls. Vessels occur in large clusters (Mauseth *et al.* 1998b).

5.7. Discussion

The study of anatomical characters in *Leptocereus* has revealed that many of these characters can be used to distinguish species and groups of closely related species. As in the assemblages defined by seed characters (see Chapter 3, page 129), those demarcated by anatomical characters bear direct relationship with other macromorphological and geographical features. Some anatomical features of *Leptocereus* are associated with the morphologically primitive Pereskioideae, and seem

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relictual in subfamily Cactoideae. Based on the set of anatomical data provided by this and earlier works, the following conclusions seem inevitable:

1. *Leptocereus* seems to circumscribe a natural group, anatomically characterized by a uniseriate epidermis (sometimes with multiseriate patches) consisting of thin-walled cells with prismatic crystals, and a 2 to 6-layered collenchymatous hypodermis (the cephalium epidermis, however, consists of small cubelike cells with very thick walls). Its cortex is not too widely expanded, and has a typical external palisade region and a system of collateral cortical bundles. Mucilage cells and druses are abundant. The vascular cylinder is thin (2 to 13 mm in diameter), and the stellar index (0.13 to 0.225) is one of the lowest in subfamily Cactoideae. There is a narrow mucilaginous pith with collateral medullary bundles lacking secondary sclereids. The wood is typically fibrous; only in the apical cephalia of *L. quadricostatus, L. grantianus,* and *L. paniculatus* is there parenchymatous wood.

2. The thin-walled epidermal cells of *Leptocereus* are very similar to those of *Pereskia* and most genera of subfamily Cactoideae considered relictual by the International Organization for Succulent Plant Studies (IOS) consensus. The IOS consensus proposed Group 1a to contain six heteromorphic genera (Hunt and Taylor, 1990): *Acanthocereus, Echinocereus, Harrisia, Leptocereus, Peniocereus,* and *Pseudoacanthocereus.*

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3. A remarkable characteristic of the epidermis of *Leptocereus* is the presence of prismatic crystals. These structures are absent from epidermal cells of almost all members of subfamily Cactoideae, but occur in three genera of IOS Group 1a: *Acanthocereus*, *Leptocereus*, and *Peniocereus* (Mauseth *et al.* 1998b). Because *Pereskia* epidermis lacks crystals, this character may be relictual for all cacti.

4. *Leptocereus paniculatus* is unusual among members of genus *Leptocereus* in having a uniseriate epidermis, with patches of multiseriate (multistratose) epidermis and hypodermal crystals (prisms). These structures are almost uniformly absent from IOS Group 1a and the rest of subfamily Cactoideae.

5. *Leptocereus paniculatus* and *L. weingartianus*, both members of subgenus *Weingartianea* occurring in Hispaniola, exhibit 10% to 25% of non-functional stomata lacking guard cells. These two species have also typical U-shaped grooves at the boundaries of the anticlinal walls of epidermal cells, a character not exhibited by other *Leptocereus* species.

6. Two of the yellow-flowered species of subgenus *Leptocereus*, section *Leptocereus* of western Cuba, *L. assurgens* and *L. ekmanii*, have unusual sunken stomata. However, in the former species the stomatal apparatus, usually with six flattened subsidiary cells, is only slightly sunken, while in the latter species the apparatus, commonly with five convex subsidiary cells, occurs in shallow crypts.

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7. Periderm formation in all members of section *Leptocereus* (subgenus *Leptocereus*) of western Cuba is very retarded, and not necessarily a consequence of aging. As a matter of fact, the epidermal cells of the stems of some species may never activate to produce phellogen (*e.g.*, *L. ekmanii*).

8. Subdivision of subgenus *Weingartianea*, as circumscribed in this work, is strongly supported by fine anatomical characters. Within this subgenus, two groups corresponding to sections *Tenuicaulis* and *Cephaliphora* are clearly defined by the presence or absence of: (1) primary phloem fiber caps on cortical bundles, (2) xylary fibers in medullary bundles, and (3) terminal cephalia for flower production on mature stem segments. Section *Tenuicaulis*, which consists of *L. weingartianus*, has fiber caps on its cortical bundles, and a complex medullary bundle structure with xylary fibers, but lacks cephalia. Conversely, section *Cephaliphora*, consisting of *L. paniculatus*, *L. quadricostatus*, and *L. grantianus*, has cephalia but lacks cortical fiber caps and medullary xylary fibers. Additional support to these sections is given by the characteristics of periderm formation in each group, the "patchy" type, which is restricted to Hispaniola and Puerto Rico, occurring only in section *Cephaliphora*. It is in all members of this section that a phellogen layer arises very precociously on the specialized terminal portion of the stem, to produce a cephalium.

9. On the basis of stem anatomy, the Haitian "leptocereoid" *Cereus* (*Hamannia*) *fabiolae* bears no close relationship to *Leptocereus*. Epidermal cells of this species,

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for example, are very large (100–200 × 76–93 μm) and strongly angular in outline; its vascular cylinder and pith are much wider, and its stellar index (0.32 to 0.67) falls off the limits of *Leptocereus*.

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6. MOLECULAR SYSTEMATICS

6.1. Introduction

As some researchers have recently pointed out (*e.g.* Wallace, 1995), the Cactaceae represents an assemblage of structurally diverse plants that manifest a remarkable series of morphological and habit parallelisms, in addition to expressing extreme levels of specialization in vegetative, floral, and other morphological characters. Because of these evolutionary parallelisms and convergences, the phylogenetic analysis of this group is very difficult particularly at taxonomic ranks above the genus. The Cactaceae is a family of plants with high environmentally induced plasticity in which the loss of certain characters due to specialization seems to have occurred more than once throughout its evolutionary history, in different, not closely related groups. In fact, the likelihood of occurrence of morphological parallelisms in distinct evolutionary lineages within the Cactaceae is high by virtue of many of these lineages having evolved in similar habitats, under similar biotic and abiotic factors. It was by no means impossible that in those relatively unrelated lineages, selective pressures have favored similar strategies to adapt successfully to habitat. Not surprisingly, problems related to convergence in growth habit, pollination syndrome, and dispersal mechanisms have plagued Cactaceae systematics since the 17th century. North American saguaros (*Carnegia gigantea*), for example, look very similar to some *Trichocereus* species from Argentina, but they are not closely related. The morphologically similar bat-pollinated flowers of *Acanthocereus* and *Dendrocereus* can exemplify convergence in pollination

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syndrome. Modern phylogeneticists always have to cope with the unavoidable dilemma of deciding whether a morphological character state observed in more than one lineage is homologous (a requirement for proper phylogenetic analysis), or just the result of parallel evolution, or convergence. The many problems associated with the development of a phylogenetically based classification of the Cactaceae have been addressed by a number of authors, such as Gibson *et al.* (1986); Gibson and Nobel (1986); Hunt and Taylor (1986); Barthlott (1988); Brathlott and Hunt (1993), and Wallace (1995).

To circumvent the problems that have influenced Cactaceae systematics over the centuries, a type of relatively "morphologically-independent" source of data has been chosen lately by some investigators. This new source of data uses various laboratory techniques collectively named "molecular biology" to study molecular variation. Through the use of molecular variation to infer relationships, the problems associated with parallel evolution and morphological complexity in the Cactaceae have been reduced significantly, since it is assumed that molecular characters are not as subject to the same external forces that can influence or determine morphology (Wallace, 1995). Molecular data lend themselves particularly well to cladistic analysis, since the determination of an hypothesis of how each character changes is not as subject to *a priori* interpretation error as are morphological characters. In morphological studies, assessment of homology (developmental similarity) and possible homoplasy (parallelisms) are often quite problematic. The analytic methods used in molecular systematics have been repeatedly found to be reliable in their ability to construct

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evolutionary hypotheses (cladograms) from the data, and computer algorithms to accomplish these analyses are readily available and designed to apply to molecular data sets.

6.2. Chloroplast DNA

The chloroplast DNA (cpDNA) molecule is a closed, circular loop of double-stranded DNA found within the plastids of green plants, and it is presumed to be of endosymbiotic origin. Structurally, it contains four "regions," namely a large single copy region (LSC), a small single copy region (SSC), and two inverted repeat regions (IR), which contain exact copies of the same sequence but are inverted in an opposite orientation (Shinozaki *et al.*, 1986). Because gene content and gene order are relatively conserved in plants, the rate of evolutionary change within this molecule has been demonstrated to be appropriate to address questions at virtually all taxonomic levels, depending upon the region that is chosen for these studies (Palmer, 1986, 1987; Palmer *et al.*, 1988). Variations (nucleotide substitutions and indels) found within the chloroplast DNA molecule may be used to infer evolutionary relationships between plants. The rate of nucleotide substitution has been shown to vary between lineages and between genes or regions of the chloroplast genome. Empirical sequence examination of the group to be studied, to detect these substitutions, is (at present) the only way to determine the appropriateness of a particular gene or molecule region to resolve phylogenetic questions for the taxa being investigated. Methods for sequence examination are well established and are proven to be very reliable (Wallace, 1995).

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One reason why the chloroplast DNA molecule is well suited to easy structural characterization is because it has a relatively high density of identified genes. The availability of well-studied "reference" genomes (*e.g.*, tobacco), which have been fully sequenced (Shinozaki *et al.*, 1986), has also helped. Changes in gene order or content due to structural rearrangements of the chloroplast DNA molecule are uncommon, resulting in a relatively high level of gene order conservatism. These rearrangements may occur in various forms, such as inversions, deletions, insertions, and translocations. However, the most precise estimates of DNA variation for taxonomic purposes are made, as mentioned above, through determining its primary sequence of nucleotides. A great number of comparative cpDNA sequencing studies have examined the chloroplast encoded gene for the large subunit of the enzyme *RUBISCO* (*rbc*L) in a relatively large number of plant families, and there are a remarkable number of sequences already determined for this 1428 bp gene (Chase *et al.*, 1993).

Full-length *rbc*L gene sequences for over 45 representative taxa from throughout the Cactaceae have been completed by Wallace (1995), who examined the cladistic relationships shown among the various groups of taxa. This analysis provides empirical evidence for the relationships among the major lineages within the Cactaceae (*i.e.*, subfamilies Opuntioideae and Cactoideae, plus *Pereskia* and *Maihuenia*) at the most basal node (polychotomy). Judging from the results obtained by Wallace (1995), rates of *rbc*L sequence evolution make this gene appropriate for subfamilial or perhaps tribal studies within the Cactaceae, but it does not vary sufficiently among groups to permit

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its use at lower taxonomic levels. For example, while the *rbc*L gene sequence data provide strong support for monophyletic lineages of the subfamilies Opuntioideae and Cactoideae, subfamily Pereskioideae is not well supported as being monophyletic. Other lineages within subfamily Cactoideae, such as those of tribes Hylocereeae, Cacteeae, Rhipsalideeae, and Notocacteeae are supported by unique nucleotide substitutions. However, the columnar taxa in tribes Cereeae, Browningieae, Trichocereeae, Pachycereeae, and Leptocereeae are less well resolved. Because the resolution within the clade of columnar Cactaceae (to which the genus *Leptocereus* belongs) using the *rbc*L data can be considered inconclusive, we should not expect this gene to provide good phylogenetic resolution among the subordinate taxa of *Leptocereus*.

Despite the broad taxonomic spectrum for which *rbc*L sequences can provide meaningful data, it seems obvious that it will not resolve many important questions of cactus phylogeny. We need to compare faster, more rapidly evolving genes or DNA segments to resolve interspecific relationships within *Leptocereus* in order to explore its patterns and processes of speciation. My goal was to investigate this genus with particular reference to the examination of whether the genus is monophyletic, the identification of infrageneric groups, and the development of a phylogeny to be interpreted in a morphological and biogeographical context. To accomplish these objectives a non-coding chloroplast DNA region was studied —the intron between the 5' exon and the 3' exon of *trn*L (UAA)— in 10 selected taxa of *Leptocereus*. In non-coding regions such as the *trn*L intron, the reliability of small and medium-sized indels

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(insertion/deletions) as taxonomic markers for inferring global groupings of closely related taxa (populations, species, or genera) has been demonstrated by van Ham *et al.* (1994). The intron of the *trn*L (UAA) gene has proved useful in the Crassulaceae where, as in *Leptocereus*, it has a length of approximately 600 bp. (van Ham *et al.*, 1994). Most of the selected *Leptocereus* taxa represent different subgroups, highlighted by the cladistic analysis discussed earlier in this work using solely morphological and anatomical data. The *trn*L intron was also sequenced in selected members of tribes Cereeae and Hylocereeae of columnar Cactoideae (*sensu* Buxbaum, 1958), and in some representatives of subfamilies Opuntioideae and Pereskioideae. In the present study, gene sequence data can contribute to answering the fundamental questions:

A. Is *Leptocereus* a monophyletic group? Is it monophyletic with or without the cephalium-producing species of Hispaniola and Puerto Rico?

B. What is *Leptocereus* related to? Is it close to *Dendrocereus* and/or other members of tribe Hylocereeae, or is it related to tribe Cereeae?

C. What are the delimitations of the species and their relationship within the genus *Leptocereus*?

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6.3. Materials and methods

DNAs from 19 accessions of the Cactaceae were isolated from West Indian native cacti collections, and one accession (*Pereskia saccharosa*) from northern Argentina (Table 17) These are representatives of the three traditionally recognized subfamilies of Cactaceae, and three important tribes of subfamily Cactoideae —Leptocereeae, Cereeae, and Hylocereeae— *sensu* Buxbaum (1958). Tribe Leptocereeae was represented by 10 taxa of genus *Leptocereus* (nine species and one subspecies) from Cuba, Hispaniola, and Puerto Rico. In addition, two species of *Pereskia* (Pereskioideae) and two species of Opuntioideae (genera *Opuntia* and *Consolea*) were selected as outgroup taxa. All of these were vouchered as either pressed herbarium specimens or spirit-preserved material.

Total genomic DNA was extracted from fresh chlorenchymatous tissues of stem cortex previously frozen or dried in silica gel. All Cactoideae and Opuntioideae material was obtained from the chloroplast-rich region of cortex closest to the collenchymatous hypodermis, after peeling off epidermis and associated tissues. In the leafy cacti *Pereskia saccharosa* and *P. quisqueyana*, fresh leaves were used instead of cortex. Between 0.3 and 0.5 g of dried material of each taxon was placed in Bio 101 Lysing Matrix tubes and pulverized for 10 seconds using a Bio 101 FastPrep machine at speed 5. Five hundred µl of lysis buffer (2 g CTAB, 8.18 g NaCl, 0.745 g EDTA, 10 ml 1 M Tris/HCl, plus Nanopure water [18.3 megohm-cm] to 100 ml, autoclaved or dissolved while in a microwave, cooled down, verified to pH 9.5, 1g PEG 4000 added

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TAXA	LOCALITY	ACCESSION DATA
Subfamily **PERESKIOIDEAE**		
1. *P. saccharosa*	Salta, Argentina (cult P. Rico)	17 (*Areces 6783* NY)
2. *P. quisqueyana*	Bayahibe, Dominican Rep.	14 (*Areces 6346* NY)
Subfamily **OPUNTIOIDEAE**		
3. *Opuntia acaulis*	El Galeón, Dominican Rep.	40 (*Areces 6385* NY)
4. *Consolea nashii*	Saint Croix, USVI	38 (*Areces 6784* NY)
Subfamily **CACTOIDEAE**		
Tribe CACTEEAE		
5. *Melocactus intortus*	Vieques Isl., Puerto Rico	39 (*Areces 6351* NY)
6. *Pilosocereus royenii*	Cabo Rojo, Puerto Rico	24 (*Areces 6413* NY)
Tribe HYLOCEREEAE		
7. *Harrisia gracilis*	Great Pedro Bluff, Jamaica	44 (*Areces 6785* NY)
8. *Dendrocereus undulosus*	Barahona, Dominican Republic	34 (*Areces 6345* NY)
9. *D. nudiflorus*	Varadero, Cuba (cult. USVI)	11 (*Areces 6786* NY)
Tribe LEPTOCEREEAE		
10. *Leptocereus arboreus*	Yaguanabo, Cuba	29 (*Areces 6120* NY)
11. *L. carinatus*	Najasa, Cuba	25 (*Areces 5488* MNHN)
12. *L. sylvestris*	Pilón, Cuba	30 (*Areces 5385* NY)
13. *L. maxonii*	Rio Tacre, Cuba	26 (*Areces 5412* NY)
14. *L. santamarinae*	Santa Lucia, Cuba	22 (*Areces 5341* MNHN)
15. *L. weingartianus* subsp. *weingartianus*	Samaná, Dominican Rep.	33 (*Areces 5973* NY)
16. *L. paniculatus*	Enriquillo, Dominican Rep.	19 (*Areces 6386* NY)
17. *L. quadricostatus* subsp. *parvispinus*	Guánica, Puerto Rico	3 (*Areces 6417* NY)
18. *L. quadricostatus* subsp. *quadricostatus*	Cabo Rojo, Puerto Rico	28 (*Areces 6411* NY)
19. *L. grantianus*	Culebra Isl., Puerto Rico	27 (*Areces 6377* NY)

Table 17. Plant specimens used in chloroplast DNA variation study of *Leptocereus*. Tribal classification based upon Buxbaum, 1958.

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when cool). Then 75 µl ß-mercaptoethanol was added to each tube, and were then incubated for 20-80 min at 74° C, and shaken occasionally. Cell debris was spun down using a Brinkmann Eppendorf Centrifuge 5415C at 14,000 rpm for ca. 30 seconds, and 400 µl of the supernatants were transferred to new tubes containing 10 µl glass milk (Bio 101). Tubes were shaken gently for 5 minutes and then spun for 5 seconds (as above); the supernatants were discarded, and 800-1000 µl of ice-cold New Wash solution (Bio 101) was added to each tube and the glass milk pellet redissolved. The centrifugation and washing steps were repeated a total of six times using only 150 µl of New Wash for the final wash. After the last centrifugation, all traces of New Wash solution were removed using fine pipette tips. The pellets were resuspended in 50 µl of autoclaved 10 mM TRIS, incubated for 2 to 3 minutes at 45-55° C, centrifuged for 30 sec (as above), and the supernatants (*i.e.*, DNA-containing solutions) transferred to new tubes for storage at –20° C.

6.3.1. PCR amplification and sequencing

The *trn*L intron was amplified using primers designed by Taberlet *et al.* (1991), a 25 µl reaction mixture (2.5 µl 10X buffer [Boehringer Mannheim], 9.8 µl autoclaved Nanopure water, 1 µl 25 mM $MgCl_2$ [Perkin Elmer], 2.5 µl 0.04 % BSA [New England Biolabs], 2.5 µl 2.5 mM dNTPs [Boehringer Mannheim], 1 µl 20 mM each primer, 2.5 µl 0.1 mM TMACl [Sigma], 0.2 µl Taq polymerase [Boehringer Mannheim], and 2 µl DNA template), a P-E Applied Biosystems 9600 PCR machine, and the following cycling program: 95° C, 50 seconds; 60° C, 50 seconds; 50 ° C, 1 minute 50 seconds;

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repeat 30 cycles; hold 4° C. PCR products were isolated from a 2% low-melt agarose gel (Fisher Biotech), resuspended in 300 µl autoclaved Nanopure water, and second PCR amplifications were made from the gel-isolated products using the same PCR program. The resulting double-stranded amplified products were purified using a Bio 101 GeneClean II kit and the following protocol: 18 µl of the PCR reactions was added to tubes containing 4µl glass milk and 60 µl NaI solution; these were allowed to stand or were shaken slowly for 20 minutes to 2 hours, and then spun down for 30 seconds using a model 5415C Brinkmann Eppendorf Centrifuge at 14,000 rpm; the supernatants were discarded, and 200 µl of ice-cold New Wash solution were added to each tube and the glass milk pellet redissolved. The centrifugation and washing steps were repeated a total of three times using only 150 µl of New Wash for the final wash. After the final centrifugation, all traces of New Wash solution were removed using fine pipette tips and two additional centrifugations. The pellets were resuspended in 10 µl autoclaved Nanopure water, incubated for 10 minutes at 55–60° C, and centrifuged for 5 min (as above), and the supernatants (*i.e.*, DNA-containing solutions) transferred to new tubes for storage at –20° C.

The cleaned PCR products were subsequently run through a cycle-sequencing reaction using a 7 µl reaction mixture (1 µl dRhodamine Terminator Cycle Sequencing Ready Reaction [P-E Applied Biosystems], 2 µl Half-term [GENPAK Limited], 1.5 µl 10mM primer, and 2.5 µl DNA template), a P-E Applied Biosystems 9600 PCR machine and the following program: hold 95° C, 1 minute; cycle 96° C, 10 seconds; 50 ° C, 5 seconds; 60° C, 3 minutes; 32 cycles; hold at 4° C. The cycle sequencing

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products were cleaned using Princeton Separations Centri-Sep 100 columns (following the manufacturer's protocol). Both DNA strands were sequenced (as recommended by the manufacturer) using a P-E Applied Biosystems ABI 377 automated DNA sequencer and associated software. Sequences were edited using the software program Sequencher 3.0 (GeneCodes).

6.3.2. Alignment and phylogenetic analysis

Phylogenetic analyses were conducted using the parsimony algorithm of the software package PAUP (Phylogenetic Analysis Using Parsimony, version 3.1.1: Swofford, 1993). With these types of analyses, character changes were scored and polarized to the observed condition in more distantly related outgroup taxa. Excluding the primer sites and doubtful sequences at the ends of the intron, all bp positions (680) were used. The sequences were easily aligned (using Sequencher 3.0 with hand adjustments), and a nucleotide by nucleotide comparison was made for all taxa, where similar nucleotide substitutions at each position were interpreted as a synapomorphic cladistic character. Inferred insertions/deletions (indels) were coded as question marks and were not treated further. The data matrix contained 19 taxa and 680 characters. Heuristic tree searches were executed of 1000 random taxon-addition replicates under the non-additive parsimony criterion (Fitch, 1971), unordered with equal weights. Only two equally parsimonious trees were generated, from which a strict consensus was derived. These trees are the hypothetical solution for the data, which require the

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minimum number of character changes (steps) to explain the variation within the data, by lineage.

Appropriate treatment of independent data sets is the source of controversy at the moment. Some authors (*e.g.*, Swofford, 1991; Cracraft and Helm-Bychowski, 1991) favor keeping different types of data separate and performing a consensus analysis, to maximize independence of characters, to prevent swamping of morphological characters by the vastly more numerous molecular ones, because it is difficult to compare a nucleotide base with a complex character such as placentation, and because they feel phylogenetic decisions can be made by determining the amount of support offered by different data sets for the same taxonomic relationships. Separate data sets can also be used in reciprocal scrutiny: results from one may allow us to reexamine assumptions made in the other. Kluge and Wolf (1993), Donoghue and Sanderson (1992), Barret *et al.* (1991), and Miyamoto (1985) maintain a different point of view. These authors advocate combining data into a single "total evidence" matrix to avoid having to choose between conflicting trees, to use the maximum amount of data to provide the (presumably) most reliable cladogram, and to require making the fewest *ad hoc* assumptions.

In the current study the morphological and molecular data sets were used separately to test competing hypotheses of relationships, and also combined into one unweighted matrix to determine how the data interact. These analyses suggested answers for the questions posed earlier, and also indicated the level of confidence we

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should have in the results (based on conflicts in trees as well as on analyses intended to determine the robustness of the trees). The combined morphological and molecular data set was prepared for *Leptocereus* using *Pereskia* and *Cereus* as outgroup taxa. Because the phylogenetic analysis based on morphological and anatomical data was conducted using the software package Winclada version 1.00.08 (Nixon, 2002), the combined morphological and molecular data set was analyzed using this same program. This combined matrix of 779 columns generated four equally parsimonious trees from which a strict consensus tree of 433 steps was produced.

6.4. Results

Of the 680 characters in the molecular data matrix, 395 were invariant and 153 were variable in two or more taxa. Equally weighted tree searches resulted in two trees of 84 steps. These trees are characterized by a consistency index (CI) of 0.917 and a retention index (RI) of 0.925 (the consistency index excluding uninformative characters is equal to 0.854). One of the two most parsimonious trees is shown as Fig. 6, while the strict consensus of both parsimonious trees is depicted as Fig. 7.

Current concepts of subfamilial relationships of Cactaceae are, for the most part, widely accepted by systematists. Two members of subfamily Pereskioideae (*Pereskia saccharosa* and *P. quisqueyana*), and two members of subfamily Opuntiodeae (*Opuntia acaulis* and *Consolea nashii*) were included in this study to provide a broad sampling of variation within the cactus family. Rooting the trees with *Pereskia*, which exhibits

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Fig. 6. Most parsimonious tree (1 of 2 trees) determined from phylogenetic analysis of chloroplast *trn*L intron sequence data.

Length of tree: 84; consistency index (CI): 0.917; consistency index (CI) excluding uninformative characters: 0.854; retention index (RI): 0.925. The clade representing the genus *Leptocereus* is defined at level "A."

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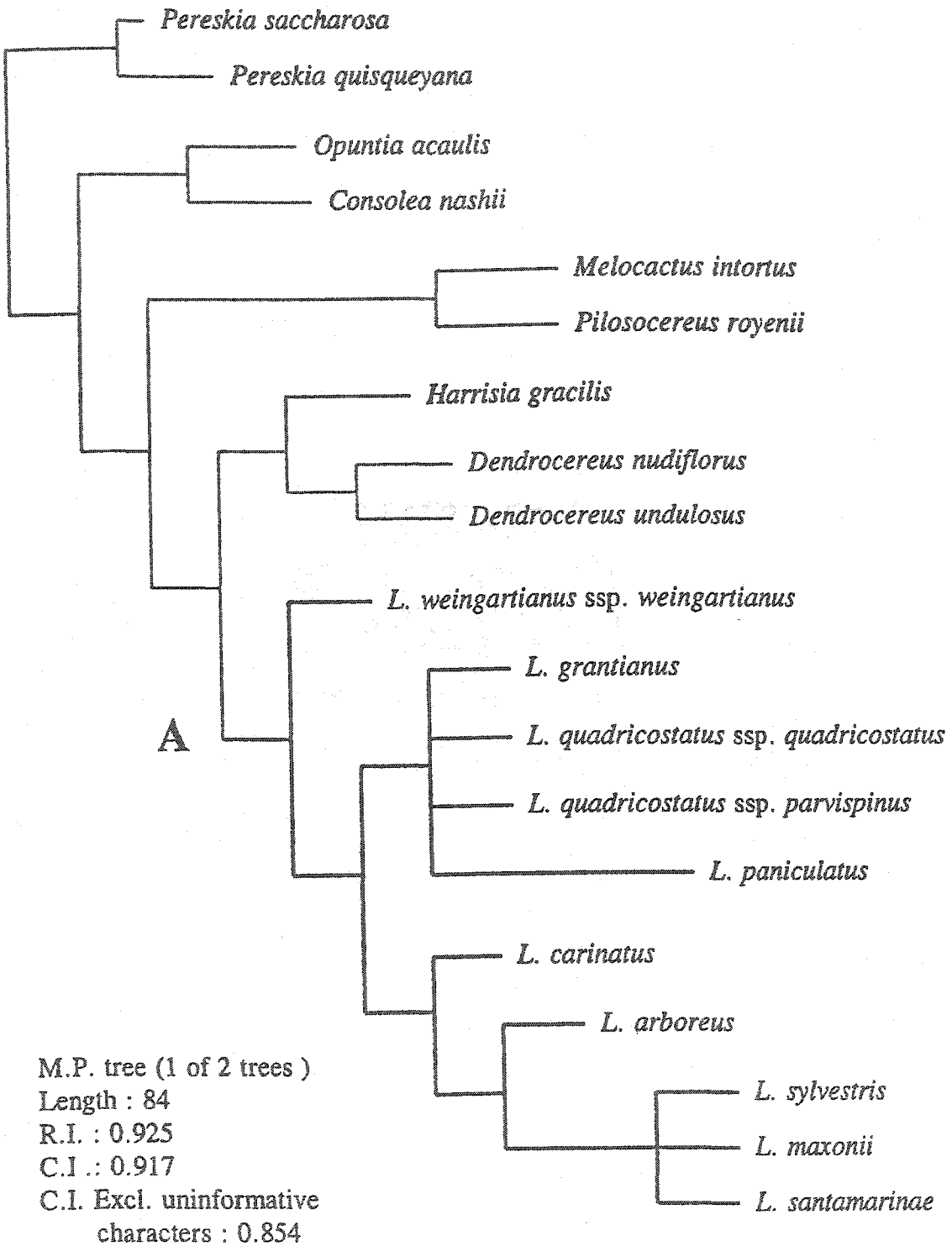

Figure 6.

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Fig. 7. Strict consensus tree determined from phylogenetic analysis of chloroplast *trn*L intron sequence data.

Length of tree: 84; consistency index (CI): 0.917; consistency index (CI) excluding uninformative characters: 0.654; retention index (RI): 0.925. The clade representing the genus *Leptocereus* is defined at level "A."

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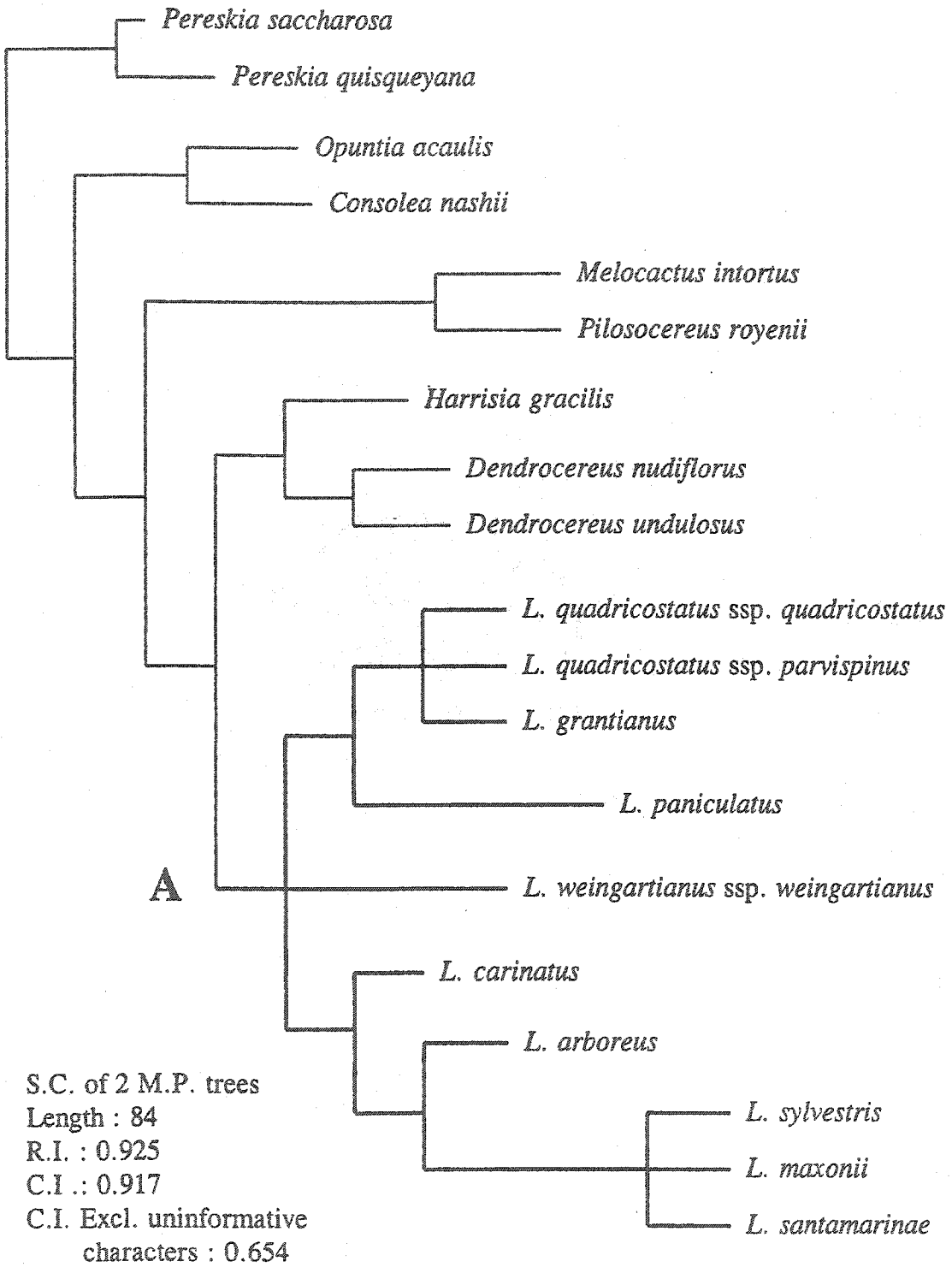

Figure 7.

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most of the plesiomorphic characters of the Cactaceae, members of subfamily Opuntioideae form a sister group to the Cactoideae. Wallace's (1995) cladogram using *rbc*L sequence data and a non-cactaceous outgroup found similar relationships, but while he obtained strong support for monophyletic lineages of the Opuntioideae and Cactoideae, the subfamily Pereskioideae was not well supported as being monophyletic by *rbc*L data.

In this *trn*L-based analysis strong support was found for clades including all sequenced members of subfamily Cactoideae, tribes Cereeae and Hylocereeae (*Harrisia gracilis*, *Dendrocereus nudiflorus* and *D. undulosus*) along with all of *Leptocereus*. Three putative deletions of 6, 2 and 14 bp and a small insertion of 4 bp in the intron of the *trn*L gene readily distinguishes the "tribe Cereeae" from the "tribe Hylocereeae" clades. The strong relationship shown between *Melocactus intortus* (P. Miller) Urban and *Pilosocereus royenii* (L) Byles and Rowley in the "Cereeae clade," supports the point of view of the International Organization for Succulent Plant Studies (IOS) Working Party (Hunt and Taylor, 1990), in relation to the position of genus *Melocactus*. According to the IOS group (Hunt and Taylor, *op.cit.*), *Melocactus* should not be considered part of tribe Notocacteae, but a derived member of the Cereeae. Likewise, *Harrisia* and *Dendrocereus* (this latter included in *Acanthocereus* by some authors), had been placed in tribe Hylocereeae by Gibson and Nobel (1986), and in an approximately equivalent group (Group I-A) by the IOS team (Hunt and Taylor, *op.cit.*). In this *trn*L cladogram both *Harrisia gracilis* (P. Miller) Britton, and the two *Dendrocereus* species, namely *D. nudiflorus* (Engelmann ex Sauvalle) Britton and

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Rose, and *D. undulosus* (A. P. de Candolle) Britton and Rose, are sister groups within the "Hylocereeae clade" and thus, support this point of view. However, *Harrisia* has also been referred to tribe Echinocereeae by Barthott and Hunt (1993). Surprisingly, *rbc*L sequence data (Wallace and Forquer, 1995) also provide "compelling evidence" that the controversial *Harrisia* is more closely related to members of tribe Trichocereeae. The relationship demonstrated here between *Harrisia* and *Dendrocereus* seems to agree with their placement in the same tribal group as shown in both the Gibson and Nobel system (1986) and the IOS taxonomic arrangement (1990).

Another interesting point of view of the IOS party is that tribe Leptocereeae is untenable because various "primordial" genera basal to other tribes had been placed in this group, making it paraphyletic. Considering that (1) *Dendrocereus* and *Leptocereus* share the same rare, diffuse branching type, as opposed to the characteristic candelabriform, verticillate or columnar branching pattern of most tree-like Cactoideae (see chapter II), and (2) that the "Hylocereeae clade" of this *trn*L study is the sister group to all sequenced *Leptocereus*, it is by no means impossible that this fairly primitive genus that exhibits so many plesiomorphic states within subfamily Cactoideae may represent the basal lineage of Group I of the IOS taxonomic arrangement (tribes Leptocereeae Buxbaum, 1958, in part, Echinocereeae Buxbaum, 1958 *sensu* Barthlott, 1988, and Hylocereeae Buxbaum, 1958 *sensu* Barthlott, 1988). However, there is yet insufficient data to provide full support for this hypothesis.

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6.5. Phylogeny of *Leptocereus*

The phylogeny generated from *trn*L sequence data provides evidence for the monophyly of genus *Leptocereus* as well as support for some smaller groups within the genus. Perhaps most striking is the support of the only group of *Leptocereus* taxa that is characterized by having terminal cephalia, which not only includes *L. paniculatus* —formerly known as *Neoabbottia paniculata*— but also *L. quadricostatus*, and *L. grantianus* as well. This cephalium-bearing group of three Puerto Rican taxa and one Hispaniolan species was shown to form an unresolved monophyletic lineage within the *Leptocereus* clade.

Another interesting group within the *Leptocereus* clade is that entirely confined to Cuba. This Cuban lineage is correlated with the presence of significant anatomical and phytochemical features that are absent in the Hispaniolan-Puerto Rican group, *e.g.*, presence of a reticle of fibers in the stem cortex, strong darkening of stem tissues upon injury probably due to air oxidation of the aglycone of Lemairin, a relatively common glucoside of columnar Cactaceae, and presence in the seed of an angular hilum rim and strong differentiation of exotesta cells. According to the *trn*L consensus cladogram, *Leptocereus carinatus* (Areces-Mallea, 1993a), with ribbed flowers and fruits —a plesiomorphic character state— is the basal sister group to all other Cuban *Leptocerei* considered in this study. The next most basal lineage is represented by *L. arboreus*, a tree-like species with relatively large bat-pollinated flowers. This species is the sister taxon of an unresolved assemblage of three morphologically related, albeit distinct

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species, restricted to eastern Cuba: *L. sylvestris*, *L. maxonii* and *L. santamarinae*. The other *Leptocereus* taxon sequenced for this study, *L. weingartianus* ssp. *weingartianus* from Hispaniola, is shown in the tree in an unresolved position within the *Leptocereus* clade.

The single tree resulting from the phylogenetic analysis of 100 morphological, anatomical and palynological characters (264 character states) is essentially congruent with the *trn*L consensus cladogram. The *Leptocereus* clade, however, represented in this tree by more taxa, showed a better resolution (Fig. 8). It is noteworthy the correspondence of the morphological/anatomical tree with the taxonomic division of the genus as proposed in this work, most sections being supported by a clade (see Tables 3 and 4 of chapter 1). All characters and character states evaluated, and the resulting data matrix, are given in Tables 18 to 22 at the end of this chapter.

For the combined molecular and morphological analysis, 24 taxa were considered, and 780 characters, analyzed (the matrix of combined data is presented in Table 23 at the end of this chapter). As expected, the strict consensus tree, with a CI = 0.74 and a RI = 0.77, is for the most part in agreement to the proposed taxonomic circumscription of *Leptocereus* (Fig. 9). In this combined tree that used three species of *Pereskia* as outgroup taxa, *Cereus fabiolae* is basal with respect to the *Leptocereus* clade. Within this *Leptocereus* clade two main groups are delimited: a Hispaniolan-Puerto Rican group, and a strictly Cuban assemblage. *Leptocereus weingartianus* occupies a basal position in the Hispaniolan-Puerto Rican group, while in the Cuban kin two subordinate

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Fig. 8. Single tree (as phylogram) determined from phylogenetic analysis of morphological, anatomical and palynological data.

Length of tree: 241; consistency index (CI): 0.66; retention index (RI): 0.66; number of characters evaluated: 100; character states: 264. The clade representing the genus *Leptocereus* is defined at level "A." Subordinate clades such as those corresponding to sections *Leptocereus* and *Roseiflori* (subgenus *Leptocereus*), and *Tenuicaulis* and *Cephaliphora* (subgenus *Weingartianea*), support the infrageneric division of the genus presented in this work.

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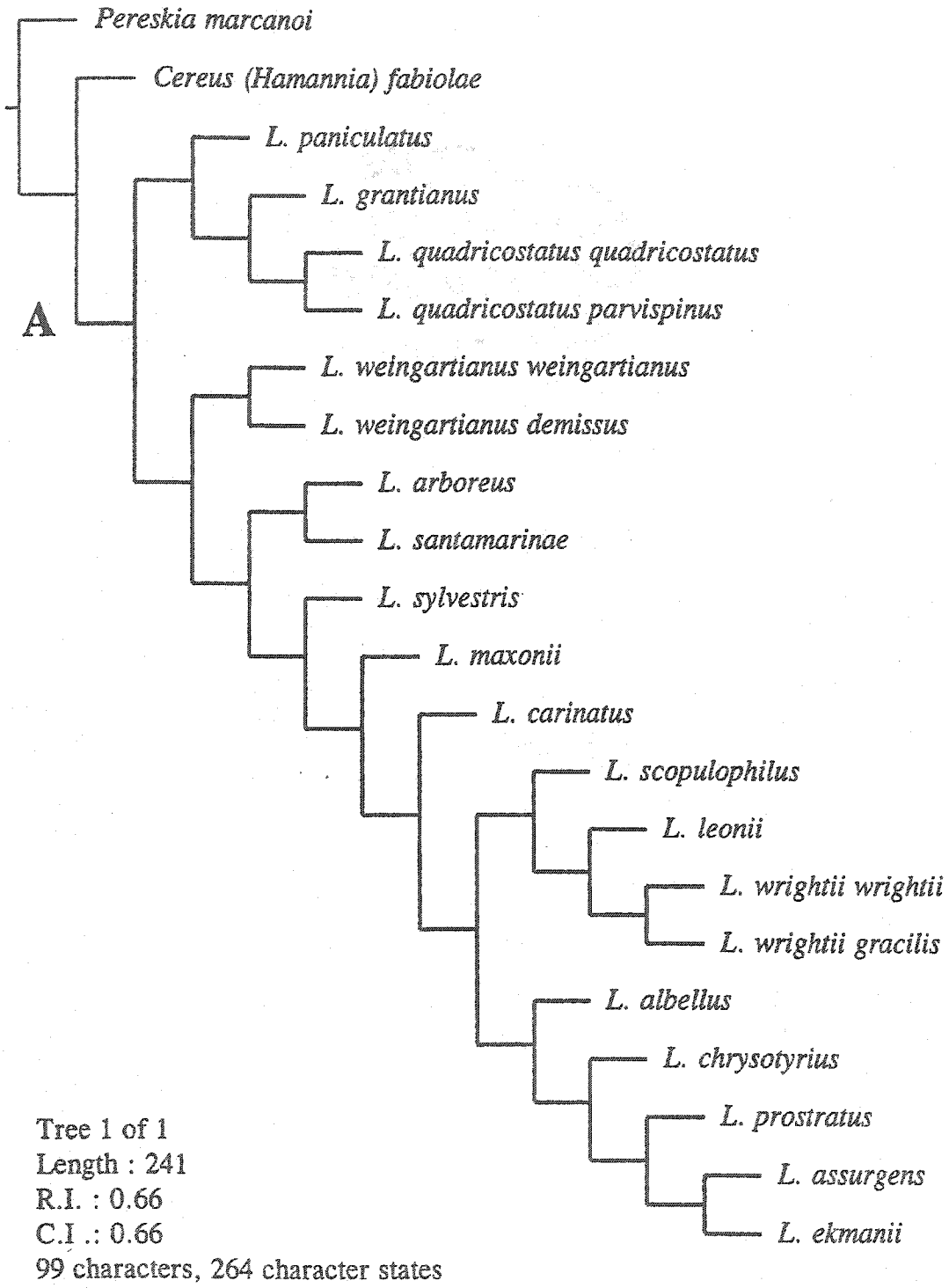

Figure 8.

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Fig. 9. Strict consensus tree (as phylogram) determined from parsimony analysis of combined morphological and molecular data.

Length of tree: 433; consistency index (CI): 0.74; retention index (RI): 0.77; number of morphological characters evaluated: 100; character states: 264; number of *trn*L intron bases sequenced: 680. The clade representing the genus *Leptocereus* is defined at level "A." Subordinate clades such as those corresponding to sections *Leptocereus*, *Roseiflori*, and *Spinosissimus* (subgenus *Leptocereus*), and *Tenuicaulis* and *Cephaliphora* (subgenus *Weingartianea*), support the infrageneric division of the genus presented in this work.

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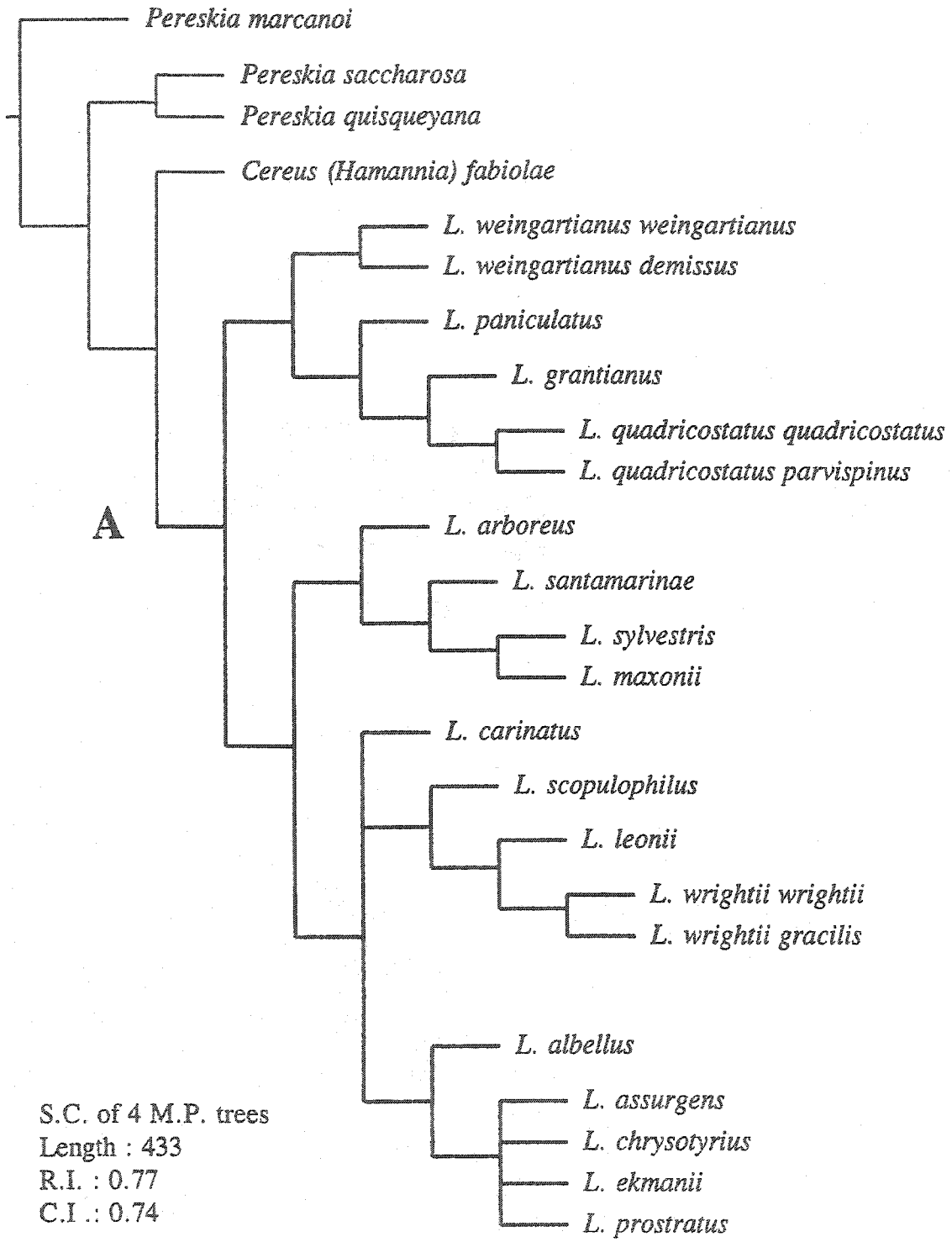

Figure 9.

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groups are recognized. One of these, with the white-flowered *L. carinatus* positioned at the base, includes two sister clusters distributed in western Cuba: one with pinkish to orange perianth segments in the flowers, and another with white or yellow flowers mostly visited by bees and butterflies. In the Hispaniolan-Puerto Rican clade the three cephalium-producing species are grouped together. *Leptocerus grantianus* and the two subspecies of *L. quadricostatus*, all of which are endemic to Puerto Rico (including some neighboring islands), come together at the end of this clade. Among other things, these tree taxa have in common two- to four- ribbed stem segments, and the presence of flower-producing cephalia.

6.6. Phylogenetic and biogeographic patterns

As discussed in earlier chapters, *Leptocereus* is endemic to Cuba, Hispaniola, Puerto Rico and the adjacent island of Culebra. This island-pattern is very well reflected in the phylogenetic analysis of the genus, with some clades representing islands or small groups of islands. The fact that (1) no species is endemic to more than one island, (2) 13 out of a total number of 17 species are endemic to the single island of Cuba, and (3) no species are found in Jamaica and other islands that were completely submerged during the Late Eocene or Early Oligocene, strongly suggests that over-water dispersal is not achieved by the species of this genus. This distribution pattern supports Rosen's (1976, 1985) hypothesis of the geohistory of the Greater Antilles, and his vicariance model.

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Leptocereus seems to make an ideal group for testing vicariance models of West Indian biogeography, because (1) it is a member of a Central and North American mainland group (tribe Hylocereeae *sensu* Gibson and Nobel, 1986, or Group I of IOS tribal arrangement, Hunt and Taylor, 1990), and (2) it does not appear to disperse readily over water; it is not "island prone" in the sense of Perfitt and Williams (1989). The phylogeny of *Leptocereus*, as interpreted from sequences of chloroplast gene *trn*L is consistent with Caribbean vicariance models and provides a step towards resolving biogeographical questions of the Greater Antilles. Invoking vicariance is at least a heuristic assumption, because it predicts a pattern to be found in other unrelated plant or animal taxa endemic to the Antilles that have North American continental sister groups. The phylogeny and biogeography of the melastome and legume genera *Mecranium* and *Poitea*, respectively, like that of *Leptocereus*, are consistent with Rosen's vicariance model. Other phylogenetic studies on Antillean Poeciliid fishes (Rauchenberger, 1988), Anole lizards (Guyer and Savage, 1986), Boid snakes (Tolson, 1987) and Carabid beetles (Liebherr, 1988), likewise suggest that Hispaniola and Cuba are compound landmasses because they each contain diverse assemblages of relatively unrelated lineages.

6.7. Conclusions

The application of established molecular systematic techniques to resolve questions on the evolution, classification, and biogeography of the Cactaceae has proven to be very useful by providing a morphologically-independent source of data,

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from which hypotheses can be made regarding the relationships within and among the various groups of cacti. This limited but nevertheless interesting molecular study in *Leptocereus* demonstrate that (1) the chloroplast *trn*L region can provide a valuable set of characters for addressing medium to high level phylogenetic questions in columnar Cactoideae, and (2) that the resulting phylogenetic results can be congruent with those obtained from morphological data sets. However, the amount of variation in *trn*L sequence data is not sufficient to resolve relationships among closely related species, and subspecies.

The phylogeny generated from *trn*L sequence data provides evidence for the monophyly of *Leptocereus*, and support for some smaller groups within the genus. Distinction of two subordinate clades, a Cuban clade and Hispaniolan-Puerto Rican clade, gives some room for analysis of its biogeographic history. Although *Leptocereus* appears to be more closely related to the Hylocereeae alliance than to tribe Cereeae, a much more thorough sampling of tribes pertaining to the Cactoideae is still needed to resolve the tribal affiliation of the genus within subfamily Cactoideae. It is also necessary to include the remaining taxa of *Leptocereus* in the phylogenetic analysis derived from molecular data to further resolve the relationships. After suggesting the monophyly of *Leptocereus* by means of molecular techniques, and in consequence, its validity as a well delimited natural group (including the cephalium-producing species), it became obvious that the genus itself contains some of the greatest diversity of body structure of any genus in subfamily Cactoideae. *Leptocereus* represents an excellent

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example of the degree to which plant structures are capable of evolving within a single genus, and which features are beneficial in certain environments.

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Table 18. The 100 characters (CH) and 264 character states (CHS) used in the morphological data matrix.

CH. 0 ***Habitat:*** CHS. 0: xeric; 1: mesic.

CH. 1 ***Growth habit:*** CHS. 0: tall trees up to 8-10 m; 1: small trees up to 3 - 5 m; 2: large shrubs up to 4 m: 3: medium-size shrubs 1.5 - 3 m: 4: suffruticose, less than 1.5 m; 5: scandent or trailing; 6: procumbent; 7: dangling.

CH. 2 ***Branching pattern:*** CHS. 0: diffuse; 1: candelabriform.

CH. 3 ***Tuberous roots:*** CHS. 0: absent; 1: present.

CH. 4 ***Dorsi-ventral differentiation of stem:*** CHS. 0: absent; 1: present.

CH. 5 ***Leaves:*** CHS. 0: present; 1: absent.

CH. 6 ***Succulent stems:*** CHS. 0: absent; 1: present.

CH. 7 ***Cortex:*** CHS. 0: fibrous; 1: nonfibrous.

CH. 8 ***Diameter of pith:*** CHS. 0: 1 to 7 mm in diameter; 1: 10-18 mm in diameter.

CH. 9 ***Strong darkening reaction of stem upon injury:*** CHS. 0: absent; 1: present.

CH. 10 ***Ribbed stems:*** CHS. 0: absent; 1: present.

CH. 11 ***Rib margin:*** CHS. 0: crenate or dentate; 1: sinuate.

CH. 12 ***Minimum number of ribs:*** CHS. 0: no ribs; 1: 3 ribs; 2: more than 3 ribs.

CH. 13 ***Maximum number of ribs:*** CHS. 0: 16; 1: 9-10; 2: 8; 3: 6-7; 4: 4-5; 5: 0.

CH. 14 ***Maximum rib height:*** CHS. 0: 0 mm; 1: 5-9 mm; 2: 11-12 mm; 3: 13-14 mm; 4: 15-17 mm; 5: more than 20 mm.

CH. 15 ***Minimum rib height:*** CHS. 0: 0 mm; 1: 2-8 mm; 2: more than 8 mm.

CH. 16 ***Minimum rib width:*** CHS. 0: 0 mm; 1: 2 mm; 2: 3-6 mm; 3: 7-8 mm.

CH. 17 ***Small notch in rib margin halfway between areoles:*** CHS. 0: present; 1: absent.

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CH. 18 ***Stem sinuses:*** CHS. 0: acute; 1: rounded.

CH. 19 ***Periderm formation in stem:*** CHS. 0: normal; 1: retarded.

CH. 20 ***Type of periderm formation:*** CHS. 0: continuous; 1: patchy.

CH. 21 ***Color of stem epidermis:*** CHS. 0: green; 1: bluish- or greyish-green.

CH. 22 ***Luster of stem epidermis:*** CHS. 0: glossy; 1: dull.

CH. 23 ***Size of epidermal cells (longitudinal axis):*** CHS. 0: less than 100 μm long; 1: more than 120 μm long.

CH. 24 ***Epidermal cell boundaries:*** CHS. 0: with U-shaped groove 35 μm wide or more; 1: with narrow V-shaped groove.

CH. 25 ***Anticlinal walls of epidermal cells:*** CHS. 0: sinuate; 1: straight or nearly so.

CH. 26 ***Anticlinal sinuses of epidermal cells:*** CHS. 0: to 12 μm broad; 1: 14-27 μm broad; 2: 27-41 μm broad.

CH. 27 ***Epidermal groundmass:*** CHS. 0: flat; 1: elevated.

CH. 28 ***Number of stomata per 10,000 square μm in stem:*** CHS. 0: less than 3; 1: 3-6; 2: more than 6.

CH. 29 ***Stomate type in stem:*** CHS. 0: parallelocitic; 1: "opuntioid."

CH. 30 ***Presence of non-functional stomata:*** CHS. 0: nearly non-existent (less than 2 %); 1: 10-30 % of total number of stomata.

CH. 31 ***Minimum distance between areoles in stem:*** CHS. 0: 20 mm or more; 1: less than 20 mm.

CH. 32 ***Areole level in orthostichy:*** CHS. 0: at rib margin level; 1: elevated; 2: sunken in deepest part of rib sinus; 3: sunken but not in deepest part of rib sinus.

CH. 33 ***Density of thrichomes in areole:*** CHS. 0: trichomes densely set, fairly tortuous; 1: trichomes loosely set, slightly tortuous.

CH. 34 ***Length of trichomes in areole:*** CHS. 0: 1 mm long or more; 1: less than 1mm long.

CH. 35 ***Color of trichomes in areole:*** CHS. 0: creamy to tawny; 1: brown to dark reddish-brown; 2: light gray or pale brown.

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CH. 36 ***Maximum number of spines in each areole:*** CHS. 0: 4; 1: 5-19; 2: 20-24.

CH. 37 ***Maximum length of spines in each areole:*** CHS. 0: 1-5 mm; 1: 10-30 mm; 2: 35-45 mm; 3: 50-70 mm; 4: more than 70 mm.

CH. 38 ***Position of spines in areole:*** CHS. 0: spreading; 1: adaxially oriented; 2: radially oriented.

CH. 39 ***Color of young stem spines:*** CHS. 0: yellow; 1: pinkish to brownish yellow; 2: dark brown to nearly black.

CH. 40 ***Differentiation of spines in areole:*** CHS. 0: subequal in length, to slightly unequal; 1: markedly unequal.

CH. 41 ***Production of secondary spines in areoles:*** CHS. 0: retarded (areoles with dormancy); 1: precocious (areoles without a dormant period).

CH. 42 ***Shape of cells of spine surface:*** CHS. 0: cylindrical; 1: expanded at their ends (bone-shaped).

CH. 43 ***Cell boundaries in spine surface:*** CHS. 0: cells in close contact, or nearly so; 1: cells separated by 2-5 μm grooves.

CH. 44 ***Floral arrangement:*** CHS. 0: less than 10 flowers/buds in each branch; 1: 10 or more flowers/buds in each branch.

CH. 45 ***Terminal cephalium:*** CHS. 0: absent; 1: present.

CH. 46 ***Ramification of cephalium:*** CHS. 0: cephalium always simple; 1: cephalium occasionally ramified.

CH. 47 ***Width of cephalium:*** CHS. 0: 0 mm; 1: 4-9 mm; 2: 10-25 mm.

CH. 48 ***Color of cephalium:*** CHS. 0: creamy; 1: dark brown to nearly black.

CH. 49 ***Flower buds:*** CHS. 0: rounded at apex; 1: acute or apiculate at apex.

CH. 50 ***Flower insertion:*** CHS. 0: stalked; 1: sessile.

CH. 51 ***Presence of receptacle tube:*** CHS. 0: perianth segments free; 1: perianth segments for the most part fused forming a tube.

CH. 52 ***Maximum length of flower:*** CHS. 0: less than 30 mm; 1: 30-60 mm; 2: 61-77 mm; 3: more than 80 mm.

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CH. 53 ***Flower shape:*** CHS. 0: narrowly tubular; 1: campanulate; 2: obconical; 3: cylindrical; 4: rotate.

CH. 54 ***Pericarpel:*** CHS. 0: ribbed; 1: smooth.

CH. 55 ***Podaria of pericarpel:*** CHS. 0: with tufts of white wool; 1: without tufts of white wool.

CH. 56 ***Constrictions above and below nectar chamber:*** CHS. 0: receptacle tube distinctly constricted; 1: receptacle tube not constricted.

CH. 57 ***Ribs on receptacle tube:*** CHS. 0: present; 1: absent.

CH. 58 ***Color of upper receptacle tube:*** CHS. 0: green; 1: yellow; 2: wine-colored; 3: tawny to yellowish-olive.

CH. 59 ***Podaria of upper receptacle tube:*** CHS. 0: tawny or brownish; 1: wine-colored; 2: green or greenish-yellow.

CH. 60 ***Presence of bracts in flower:*** CHS. 0: flower with leafy bracts; 1: flower with triangular bract-scales; 2: flower lacking bracts or bract-scales.

CH. 61 ***Presence of spines in flower:*** CHS. 0: spines absent; 1: spines present in very few areoles; 2: spines present in nearly all areoles.

CH. 62 ***Maximum number of spines per areole in flower:*** CHS. 0: none; 1: 4 spines; 2: 5 spines; 3: 8 spines; 4: 10-12 spines; 5: 20-25 spines; 6: 30 or more spines.

CH. 63 ***Color of growing base of spine in flower:*** CHS. 0: creamy; 1: green; 2: pink or pinkish; 3: greenish-yellow.

CH. 64 ***Rigidity of floral spines:*** CHS. 0: spines straight, more or less pungent; 1: spines very weak, frequently bended.

CH. 65 ***Perianth limb:*** CHS. 0: inflexed; 1: slightly reflexed; 2: strongly reflexed; 3: essentially flat, extending at 90 degrees with respect to the floral axis.

CH. 66 ***Enclosure of perianth segments:*** CHS. 0: segments almost enclosed in the spine lattice of tube; 1: segments spreading freely.

CH. 67 ***Length of perianth segments:*** CHS. 0: up to 20 mm; 1: more than 20 mm.

CH. 68 ***Abaxial surface of outermost perianth segments:*** CHS. 0: pink, reddish, or wine-colored; 1: greenish-white; 2: yellow; 3: brownish.

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CH. 69 ***Color of inner perianth segments:*** CHS. 0: white to creamy; 1: pink or whitish-pink; 2: pinkish-orange; 3: yellow.

CH. 70 ***Apex of perianth segments:*** CHS. 0: obtuse or rounded, to emarginate or truncate; 1: acuminose.

CH. 71 ***Diameter of fully expanded flowers:*** CHS. 0: to 15 mm; 1: 19-42 mm; 2: more than 45 mm.

CH. 72 ***Flower throat:*** CHS. 0: to 5 mm in diameter; 1: more than 8 mm in diameter.

CH. 73 ***Position of stamens with respect to flower throat:*** CHS. 0: inserted or very little exserted (not more than 3 mm); 1: to 5-9 mm exserted; 2: more than 10 mm exserted.

CH. 74 ***Stamen arrangement:*** CHS. 0: stamens more or less loosely set; 1: stamens grouped altogether to form a compact column.

CH. 75 ***Style/stigma exsertion index:*** CHS. 0: less than 3; 1: 3-6; 2: 6.1-9; 3: more than 9.

CH. 76 ***Number of stigma lobes:*** CHS. 0: more than 10; 1: less than 10.

CH. 77 ***Position of fruits:*** CHS. 0: fruits nearly always terminal in stem; 1: fruits either terminally or laterally produced; 2: fruits only lateral in stem.

CH. 78 ***Fruit shape:*** CHS. 0: depressed-globose; 1: globose to elliptical or obovate; 2: cylindrical.

CH. 79 ***Surface texture of fruit:*** CHS. 0: smooth and even; 1: with elevated orthostichy lines; 2: strongly ribbed; 3: with leafy bracts.

CH. 80 ***Fruit color:*** CHS. 0: uniformly green or yellowish green; 1: lemon-colored (citrinus); 2: yellowish green, with tips of podaria wine-colored; 3: reddish- to olive green; 4: uniformly wine-colored.

CH. 81 ***Fruit spination:*** CHS. 0: fruit spineless; 1: fruit with short spines less than 5 mm long; 2: fruit with thin bristles 10 mm long or more; 3: fruit with stiff spines 10 mm long or more.

CH. 82 ***Density of spines in fruit:*** CHS. 0: fruit densely covered by a continuous lattice of spines; 1: spines scarcely overlapping by their tips; 2: spines separated by wide spaces; 3: spines absent.

CH. 83 ***Areole persistence in fruit:*** CHS. 0: areoles persistent at maturity; 1: areoles often dropping off at maturity.

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CH. 84 ***Spine/bristle persistence in fruit:*** CHS. 0: spines/bristles persistent in mature fruit; 1: spines/bristles commonly dropping off in mature fruit.

CH. 85 ***Fruit at maturity:*** CHS. 0: pendulous; 1: not pendulous.

CH. 86 ***Persistence of floral remains in fruit:*** CHS. 0: fruit without marcescent floral remains; 1: fruit crowned by the marcescent flower.

CH. 87 ***Depth of fruit umbilicus:*** CHS. 0: umbilicus broad, flat; 1: umbilicus narrow, deep.

CH. 88 ***Ratio length to breadth in seeds:*** CHS. 0: less than 1.4; 1: 1.4-1.7; 2: 1.8; 3: more than 1.8.

CH. 89 ***Surface of seed exotesta:*** CHS. 0: smooth; 1: verrucose; 2: papillate.

CH. 90 ***Cuticular folds of seeds:*** CHS. 0: absent; 1: thin; 2: thick; 3: very thick, forming scale-like pleats.

CH. 91 ***Hilum-cup (HC) of seed:*** CHS. 0: seeds narrowed/constricted at the HC insertion level; 1: seeds not narrowed/constricted at the HC insertion level.

CH. 92 ***Width of hilum-cup:*** CHS. 0: 0.2 mm broad, or more; 1: less than 0.2 mm broad.

CH. 93 ***Hilum-micropilar region:*** CHS. 0: surrounded by a curved rim; 1: surrounded by an angular rim.

CH. 94 ***Dorsal keel-like ridge in seed:*** CHS. 0: seeds with a keel-like ridge of large exotesta cells; 1: seeds without a keel-like ridge.

CH. 95 ***Diameter of exotesta cells of seed:*** CHS. 0: largest cells exceeding 100 μm in diameter; 1: largest cells less than 100 μm in diameter.

CH. 96 ***Presence of dorsal megacells in seed coat:*** CHS. 0: with dorsal megacells 180-200 μm in diam.; 1: without dorsal megacells 180-200 μm in diameter.

CH. 97 ***Percentage of 6-colpate pollen grains:*** CHS. 0: more than 50%; 1: less than 50%.

CH. 98 ***Height of exine spinules in pollen grains:*** CHS. 0: 1.5 μm, or more; 1: less than 1.5 μm.

CH. 99 ***Number of punctae in pollen tectum per 100 square μm:*** CHS. 0: 6-33 punctae/100 square μm; 1: 40-56 punctae/100 square μm.

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100 CHARACTER BPA MATRIX FOR MORPHOLOGICAL DATA (I) : CHARACTERS 0 to 24

TAXA: 22

CHARACTERS	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
TAXA																									
Pereskia marcanoi	0	0	0	0	0	0	0	1	0	0	0	-	0	5	0	0	0	-	-	0	0	0	0	0	1
Cereus (*Hamannia*) *fabiolae*	0	0	1	0	0	1	1	1	1	0	1	0	2	0	1	1	2	1	0	1	0	0	0	1	1
Leptocereus assurgens	1	3	0	0	0	1	1	0	0	1	1	0	2	1	1	1	1	1	0	1	0	0	0	0	1
L. chrysotyrius	1	3	0	0	0	1	1	0	0	1	1	0	2	3	3	1	2	1	0	1	0	0	0	0	1
L. ekmanii	1	4	0	0	0	1	1	0	0	1	1	0	2	3	1	1	1	1	0	1	0	0	0	0	1
L. prostratus	1	6	0	0	1	1	1	0	0	1	1	0	2	2	1	1	3	1	1	1	0	0	0	0	1
L. albellus	1	7	0	0	0	1	1	0	0	1	1	0	2	3	3	2	3	1	0	1	0	0	0	0	1
L. wrightii subsp. *wrightii*	0	1	0	0	0	1	1	0	0	1	1	0	2	4	5	2	3	1	1	1	0	0	0	0	1
L. wrightii subsp. *gracilis*	1	1	0	0	0	1	1	0	0	1	1	0	2	4	5	2	3	1	1	1	0	0	0	0	1
L. scopulophilus	1	3	0	0	0	1	1	0	0	1	1	0	2	3	2	1	3	0	1	1	0	0	0	0	1
L. leonii	1	1	0	0	0	1	1	0	0	1	1	0	2	2	2	2	3	1	0	1	0	0	0	0	1
L. arboreus	0	0	0	0	0	1	1	0	0	1	1	0	2	3	5	2	3	0	0	1	0	0	0	0	1
L. carinatus	1	3	0	0	0	1	1	0	0	1	1	1	2	3	4	1	3	1	0	1	0	0	1	0	1
L. sylvestris	0	1	0	0	0	1	1	0	0	1	1	0	2	3	4	2	3	1	0	1	0	0	0	0	1
L. maxonii	0	3	0	0	0	1	1	0	0	1	1	0	2	3	4	1	3	1	0	1	0	1	1	0	1
L. santamarinae	0	0	0	0	0	1	1	0	0	1	1	0	2	3	5	2	3	1	0	1	0	0	0	0	1
L. weingartianus subsp. *weingartianus*	0	0	0	1	0	1	1	1	0	0	1	0	2	3	2	1	3	1	1	1	0	1	1	0	0
L. weingartianus subsp. *demissus*	0	5	0	1	0	1	1	1	0	0	1	0	2	3	1	1	3	1	1	1	0	1	1	0	0
L. paniculatus	0	0	0	0	0	1	1	1	0	0	1	0	2	3	5	2	3	1	0	1	1	1	1	0	0
L. quadricostatus subsp. *quadricostatus*	0	2	0	0	0	1	1	1	0	0	1	0	1	4	5	2	3	1	0	1	1	0	0	0	1
L. quadricostatus subsp. *parvispinus*	0	2	0	0	0	1	1	1	0	0	1	0	1	4	5	2	3	1	0	1	1	0	0	0	1
L. grantianus	0	2	0	0	0	1	1	1	0	0	1	0	1	4	5	2	3	1	0	1	1	0	0	0	1

Table 19.

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100 CHARACTER BPA MATRIX FOR MORPHOLOGICAL DATA (II) : CHARACTERS 25 to 49

TAXA: 22

CHARACTERS	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
TAXA																									
Pereskia marcanoi	?	?	0	0	1	0	1	0	?	0	0	0	1	0	2	0	0	?	?	0	0	-	0	-	0
Cereus (*Hamannia*) *fabiolae*	0	2	0	1	0	0	1	2	1	0	0	2	2	0	0	0	1	0	0	?	0	-	0	-	1
Leptocereus assurgens	0	0	1	2	0	0	1	2	0	1	1	1	1	0	1	0	0	1	1	1	0	-	0	-	0
L. chrysotyrius	0	1	0	2	0	0	1	2	0	1	0	1	3	0	1	1	0	1	1	1	0	-	0	-	0
L. ekmanii	0	0	0	2	0	0	1	2	0	1	1	1	2	0	1	1	0	1	1	1	0	-	0	-	0
L. prostratus	0	0	0	2	0	0	1	1	0	1	1	2	3	0	1	1	0	1	1	1	0	-	0	-	0
L. albellus	0	0	0	2	0	0	1	2	0	1	1	1	1	0	1	0	0	1	1	1	0	-	0	-	0
L. wrightii subsp. *wrightii*	1	-	0	2	0	0	1	2	0	1	1	2	2	0	1	0	0	1	1	0	0	-	0	-	0
L. wrightii subsp. *gracilis*	1	-	0	2	0	0	1	2	0	1	1	1	1	1	1	0	0	1	1	0	0	-	0	-	0
L. scopulophilus	0	0	0	2	0	0	1	2	0	1	1	1	3	0	2	1	0	1	1	0	0	-	0	-	0
L. leonii	0	0	0	2	0	0	1	2	0	1	1	1	1	0	2	0	0	1	1	0	0	-	0	-	0
L. arboreus	0	0	0	2	0	0	1	2	0	1	0	1	2	0	0	0	0	1	1	0	0	-	0	-	0
L. carinatus	0	0	0	2	0	0	1	3	0	1	1	1	3	0	2	1	0	1	1	0	0	-	0	-	0
L. sylvestris	0	0	0	2	0	0	1	2	0	1	1	2	2	0	0	0	0	1	1	0	0	-	0	-	0
L. maxonii	0	0	0	2	0	0	1	2	0	1	1	2	3	0	2	1	0	1	1	0	0	-	0	-	0
L. santamarinae	0	0	0	2	0	0	1	2	0	1	0	2	1	0	0	0	0	1	1	0	0	-	0	-	0
L. weingartianus subsp. *weingartianus*	0	0	0	2	0	1	1	2	0	1	0	2	2	0	0	0	0	1	1	0	0	-	0	-	0
L. weingartianus subsp. *demissus*	0	0	0	2	0	1	1	0	0	1	0	2	1	0	0	0	0	1	1	0	0	-	0	-	0
L. paniculatus	0	0	0	2	0	1	1	2	0	1	0	2	1	0	1	0	0	1	1	0	1	0	2	0	0
L. quadricostatus subsp. *quadricostatus*	0	0	0	2	0	0	0	2	0	1	0	1	2	0	2	0	0	1	1	0	1	1	1	1	0
L. quadricostatus subsp. *parvispinus*	0	0	0	2	0	0	0	2	0	1	0	1	1	1	2	0	0	1	1	0	1	1	1	1	0
L. grantianus	0	0	0	2	0	0	0	2	0	1	1	0	0	2	2	0	0	1	1	0	1	1	1	1	0

Table 20.

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100 CHARACTER BPA MATRIX FOR MORPHOLOGICAL DATA (III) : CHARACTERS 50 to 74

TAXA: 22

CHARACTERS	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74
TAXA																									
Pereskia marcanoi	0	0	0	4	1	1	-	-	-	-	0	0	0	-	-	0	1	0	0	1	-	1	-	-	0
Cereus (*Hamannia*) *fabiolae*	1	1	3	0	1	0	1	1	0	2	1	0	0	0	0	2	1	1	0	0	1	2	1	2	0
Leptocereus assurgens	1	1	1	3	1	1	1	1	1	2	2	2	4	0	0	1	1	0	2	3	0	1	1	1	0
L. chrysotyrius	1	1	1	3	1	1	1	1	2	1	2	2	4	0	0	3	1	0	2	3	0	1	1	1	1
L. ekmanii	1	1	0	3	1	1	1	1	1	2	2	2	4	0	0	1	1	0	2	3	0	0	0	0	0
L. prostratus	1	1	1	3	1	1	1	1	1	2	2	2	4	0	0	1	1	0	2	3	0	1	1	1	0
L. albellus	1	1	1	2	1	1	1	1	0	2	2	2	4	0	0	1	1	0	1	0	0	1	1	1	0
L. wrightii subsp. *wrightii*	1	1	2	1	1	1	1	1	2	1	2	2	5	2	0	1	1	0	0	2	0	1	1	1	0
L. wrightii subsp. *gracilis*	1	1	2	1	1	1	1	1	2	1	2	2	4	2	0	1	1	0	0	2	0	1	1	1	0
L. scopulophilus	1	1	1	2	1	1	1	1	0	1	2	2	4	1	0	1	1	0	0	1	0	1	1	1	0
L. leonii	1	1	1	2	1	1	1	1	2	1	2	1	1	2	1	1	1	0	0	1	0	1	1	1	0
L. arboreus	1	1	2	3	0	1	1	1	0	2	2	2	6	1	0	1	0	0	1	0	0	1	1	0	0
L. carinatus	1	1	2	3	0	1	1	0	0	2	2	2	4	0	0	1	1	0	1	0	0	1	1	0	0
L. sylvestris	1	1	2	3	1	1	1	1	3	0	2	2	5	0	0	1	1	0	3	0	0	1	1	0	0
L. maxonii	1	1	2	3	1	1	1	1	3	0	2	2	5	0	0	1	1	0	3	0	0	1	1	0	0
L. santamarinae	1	1	2	3	1	1	1	1	3	0	2	2	5	0	0	1	1	0	0	0	0	1	1	0	0
L. weingartianus subsp. *weingartianus*	1	1	2	0	1	1	0	1	0	0	2	2	3	0	0	1	1	0	0	0	0	1	1	0	0
L. weingartianus subsp. *demissus*	1	1	1	0	1	1	0	1	0	0	2	2	3	0	0	1	1	0	0	0	0	1	1	0	0
L. paniculatus	1	1	1	3	1	1	1	1	0	1	2	0	0	-	-	1	1	0	0	0	0	1	1	0	0
L. quadricostatus subsp. *quadricostatus*	1	1	1	0	1	1	0	1	0	2	2	2	3	3	0	1	1	0	1	0	0	1	1	0	0
L. quadricostatus subsp. *parvispinus*	1	1	1	0	1	1	0	1	0	2	2	2	2	3	0	1	1	0	1	0	0	1	1	0	0
L. grantianus	1	1	1	2	1	1	0	1	0	2	2	0	0	-	-	1	1	0	1	0	0	1	1	0	0

Table 21.

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100 CHARACTER BPA MATRIX FOR MORPHOLOGICAL DATA (IV) : CHARACTERS 75 to 99

TAXA: 22

CHARACTERS	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99
TAXA																									
Pereskia marcanoi	-	1	0	0	3	0	0	3	0	-	0	0	0	0	0	0	1	0	?	1	1	1	?	?	?
Cereus (*Hamannia*) *fabiolae*	0	0	2	2	0	1	0	3	0	-	0	1	1	2	2	1	1	0	?	1	1	1	1	0	0
Leptocereus assurgens	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0
L. chrysotyrius	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0
L. ekmanii	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0
L. prostratus	1	1	1	1	0	0	3	1	0	0	1	1	1	?	?	?	?	?	?	?	?	?	1	1	0
L. albellus	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0
L. wrightii subsp. *wrightii*	2	1	1	1	0	0	3	1	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0
L. wrightii subsp. *gracilis*	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
L. scopulophilus	1	1	1	1	0	0	3	1	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0
L. leonii	3	1	1	1	0	4	2	2	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0
L. arboreus	3	1	1	1	1	0	3	1	0	0	1	1	1	1	1	1	1	1	1	0	0	0	1	1	0
L. carinatus	3	1	1	1	2	0	3	2	0	0	1	1	1	?	?	?	?	?	?	?	?	?	1	1	0
L. sylvestris	3	1	1	1	0	0	3	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0
L. maxonii	3	1	1	1	0	0	3	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1
L. santamarinae	3	1	1	1	1	0	3	1	0	0	1	1	1	1	1	1	1	1	1	0	0	1	1	1	0
L. weingartianus subsp. *weingartianus*	3	1	1	1	0	3	1	2	0	0	1	1	1	1	1	2	0	1	0	1	1	1	0	1	0
L. weingartianus subsp. *demissus*	3	1	1	1	0	3	3	1	0	0	1	1	1	1	1	2	0	1	0	1	1	1	?	?	?
L. paniculatus	3	1	0	1	0	2	0	3	0	0	1	1	1	3	1	3	1	1	0	1	1	1	1	1	0
L. quadricostatus subsp. *quadricostatus*	3	1	1	1	0	0	3	2	0	0	1	1	1	1	1	2	1	1	0	1	1	1	1	1	0
L. quadricostatus subsp. *parvispinus*	3	1	1	1	0	0	1	2	0	0	1	1	1	1	1	2	1	1	0	1	1	1	1	1	0
L. grantianus	3	1	1	1	0	0	0	3	0	0	1	1	1	1	1	2	1	1	0	1	1	1	1	1	0

Table 22.

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Table 23. BPA matrix for combined morphological and molecular data (24 taxa, 780 characters).

Pereskia marcanoi. ..... 00010001000-05000--000001??001010?00010200??00-0-0000411----000--01001-1—
0-10030030-00000010?111???
??
??
??
??
??

Cereus fabiolae. ..... 00110111101020112101000110201001210022000100?0-0-1113010110210000211001212 0
002201030-01122110?111100???
??
??
??
??
??

Leptocereus assurgens. 13010110011021111101000010012001201111010011 10-0-0111311111222400110230 11
1011?????????????????????110???
??
??
??
??
??

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L. chrysotyrius. ..... 13010110011023312101000010102001201013011011 10-0- 01113111121224003102301111111??????????????????????110??????????????????????

L. albellus. 17010110011023323101000010002001201111010011 10-0011121111022240011010011
1011??????????????????????110???
??
??
??
??
??

L. wrightii wrightii. 01010110011024523111000011-020012011220100110 0-0-011211111212252011002011 10
211100310011111111110111 0??
??
??
??
??
??

L. wrightii gracilis. ..... 11010110011024523111000011-020012011111100110 0-0-011211111212242011002011 1021??
??
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??
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L. scopulophilus. ..... 13010110011023213011000010002001201113021011 00-0-011121111012241011001011101111003100111111111101110??????????????

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L. carinatus. 13010110011123413101001010002001301113021011
00-0-01123011002224001101001100311120320011?????????1100211303023032200011301300232000013331000331020200 0
11132200330030000032224100311320211001311334444444400000000000442100000004002023310200021002003000020000 4
42200022321020201310002200233233130010003202233201323213232331330300200444433133110310000131100300000000 0
42223000210303012302320010030310003203300320100111200111232123040311230333444444403030303033303304444 3
00313203003132444444003344130443333030300303200303200030303033044430000302030033130313000300000333340200 3
03200032000004333030320000003220020033333222330320031203311002332000000200310003033103330131101023132030 2
03133332002001320330033220120200320020302023111233130103231003013201001000200033303023002022007031123120 1

L. sylvestris. 01010110011023423101000010002001201122000011 0
0-0-01123111130225001103001100311100311011111111110111002113030230322000113013002320000133310003310202000 0
11132200330030000032224100311320211001311334444444400000000000442100000004002023310200021002003000020000 4
42200022321020201310002200233233130010003202233201323213232331330300200444433133110310000131100300000000 0
42223000210303012302320010030310003203300320100111200111232123040311230333444444403030303033303304444 3
00313203003132444444003344130443333030300303200303200030303033044430000302030033130313000300000333340300 3
03200032000000333030320000003220020033333222330320031203311002332000000200310003033103330131101023132030 2
03133332002001320330033220120200320020302023111233130103231003013201001000200033313023002022007031123120?

L. maxonii. 03010110011023413101011010002001201123021011 0
0-0-01123111130225001103001100311100300011111111110111102113030230322000113013002320000133310003310202000 0
11132200330030000032224100311320211001311334444444400000000000442100000004002023310200021002003000020000 4
42200022321020201310002200233233130010003202233201323213232331330300200444433133110310000131100300000000 0
42223000210303012302320010030310003203300320100111200111232123040311230333444444403030303033303304444 3
00313203003132444444003344130443333030300303200303200030303033044430000302030033130313000300000333340300 3
03200032000000333030320000003220020033333222330320031203311002332000000200310003033103330131101023132030 2
03133332002001320330033220120200320020302023111233130103231003013201001000200033313023002022007031123120 1

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L. santamarinae. 0001011001102352310100001000200120102100001100-0-0112311113022500110000110031111031001111111110011100211307023032200011301300232000013331000331020200011132200330030000032224100311320211001311334444444000000000044210002000400202331020002100200300002000040220002232102020131000220023323313001000320223320132321323233133030020044443313311031000013110030000000042223000210303012302320010030310003203300320100111200111231212304031123033344444403030303033333030444430031320300313244444400334413044333030300303200303200030303033044430000302030033130313000330000333340300303200000033303032000000322002003333322233032003120331100233200000020031000303310333013110102313203020313333200200132033003322012020032002030202311123313010323100301320100100020003331302300202200003112312010

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L. paniculatus. ..... 0001011100102352310111100000201120102101001101020011131111012001—11000011003101020300111313110111110301130302303220041132130013200001333100033101020001113220033003000003222410031132021100131133344424444400000000044210000003400222331020002100200300002000040422000223210202013100022002332331300100032022332013232132323313303002004444331331103100001311003000000000422230002103030123023200100303100032033003201001112001112301230403112303334444440303030303330333033044443003132030031324444440033441304433330303003032003032000303030330444300003020300331303130003000003333402003032000330000003330303200000032200200333332223303200312033110023320000002003100030331033301311010231320302031333320020013203300332201202003200203020231112331301032310020132010010002030333130230020220004311131201

L. quadricostatus quadricostatus. 0201011100101452310110001000200020101202001101111011001014523101100010002000201012020011011132200330030000032224100311320211001311333442444440000000004421000000340022233102000210020030000200004422000223210202013100022002332331300100032022332013232132323313303002004444331331103100001311003000000000422300021030301230232001003031000320330032010011120011123012304031123033344444403030303033303330403000313203003132444444003344130443333030300303200303200030303033044430000302030033130313000300000333402003032000330000003330303200000032200200333332223303200312033110023320000002003100030331033301311010231320302031333320020013203300332201202003200203020231112331301032310030132010010002000333130230020220004311131201

L. quadricostatus parvispinus. 0201011100101452310110001000200020101112001101111011001014523101100010002000201011120011011132200330030000032224100311320211001311333442444440000000004421000000340022233102000210020030000200004422000223210202013100022002332331300100032022332013232132323313303002004444331331103100001311003000000000422300021030301230232001003031000320330032010011120011123012304031123033344444403030303033303330403000313203003132444444003344130443333030300303200303200030303033044430000302030033130313000300000333402003032000330000003330303200000032200200333332223303200312033110023320000002003100030331033301311010231320302031333320020013203300332201202003200203020231112331301032310030132010010002000333130230020220007311231201

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L. grantianus. ..... 0201011100101452310110001000200020110022001101111012110102200—1101001100311100030011111211011111002113030230322000113013002320000133310003310202000111322003300300000322241003113202110013113334442444440000000004421000000340022233102000210020030000200004422000223210202013100022002332331300100032022332013232132323313303002004444331331103100001311003000000000422230002103030123023200100303100032033003201001112001112301230403112303334444444030303033033033030444430031320300313244444400334413044333030300303200303200030303033044430000302030033130313000300000333340200303200000033303032000000322002003333222330320031203311002332000000200310003033103330131101023132030203133033003220120200320020302023111233130103231003013201001000200033313023?020220000311231201

Pereskia saccharosa. ..... 00000001000-05000--000101??001000?0214020 0??00-0-0000411----000--01101-2--0-10130030-10000010?1111??02113030230322000113013002320000133310003310202000 111322003300300000322241003113202110013113333331444440000000004421000000340022233102100210020030000000000 022000223210202013100022002332331300100032222332013232132323313303002004444331331103100001311003000000004 422230002103030123023200130303100032033003201001112003112444430403112303333344444030303030304444444444443 003132030031324444440033034404433330303003032003032000303030330444300003020300331303130003000003333302003 032000320000003330303200000032200200333032223303200312033110023320000002003100030331033301311030231320302 031333320020003203300312201202003200203020231112331301032310030132010010032000333030230020220000311231201

Pereskia quisqueyana. ..... 00010001000-05000--000001??001010?0201010 0??00-0-0000411----000--01101-2--0-10130030-10000010?1111??02113030230322000113013002320000133310003310202000 111322003300300000322241003113202110013113333332444400000000004421000000340022233102000210020030000000000 022000223210202013100022002332331300100032222332013232132323313303002300000331331103100001311003000000000 422230002103030123023200130303100032033003201001112003112444430403112303333333333303030303030304444444443 003132030031324444440033034404433030303003032003032000303030330444300003020300331303130003000003333402003 032000320000003330303200000032200200333032223303200312033110023320000002003100030331033301311030231320302 031333320020003203300312201202003200203020231112331301032310030132010010032000333030230020220000311231201

7. ECOLOGY AND PHYTOGEOGRAPHY

7.1. Distribution

The genus *Leptocereus* is confined to the Greater Antilles, with the exception of Jamaica (Plate 45, A). It extends not only to the main Antillean islands but to the neighboring cays of northeastern Cuba (Cayo Sabinal, Plate 47, A, B), and to Culebra, a small islet West of Puerto Rico (Plate 48, C). In Cuba it ranges from the haystack mountains of Sierra de Guane in the western part of Pinar del Rio province (ca. 22°12' N, 84°3' W, Plates 45, C, and 46, A), throughout most of the limestone chains and coastal terraces of the island as far as the arid southern coast of the province of Guantánamo (ca. 20°4' N, 74°30' W, Plates 46, B, and 47, A, B). In Hispaniola it occurs from near Port-à-Pimente in the southwestern peninsula of Haiti (ca. 18°17' N, 74°8' W), to Cabo Engaño, the eastern end of the Dominican Republic (ca. 18°36' N, 68°20' W, Plate 48, A). The easternmost overall distribution of *Leptocereus* corresponds to a rocky shore near Punta Melones, in the Puerto Rican island of Culebra (ca. 18°19' N, 65°17' W, Plate 48, C). The genus is also known from the Cabo Rojo and Guánica areas in southwestern Puerto Rico.

Since the Greater Antilles is an arc of islands that extends West to East, the overall latitudinal distribution of *Leptocereus* is, in conformity, very narrow (less than 6°). The farthest north it gets is the rocky coastal terraces of Havana province, Cuba (ca. 23°10' N), while the lowest latitude at which it can be found is ca. 17°20' N (dry thickets near

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Oviedo, province of Pedernales, Dominican Republic, Plate 48, A). Altitudes recorded for localities range from sea level (*e.g.*, Bahía Honda and Cabo Engaño, in Cuba and the Dominican Republic, respectively) to nearly 600 m in Sierra de Viñales, Cuba.

Throughout its range there is a significant concentration of species in western Cuba (Plate 45, B), where 9 species out of 17 occur (53%). Except for *Leptocereus weingartianus* subsp. *weingartianus* and *L. paniculatus*, which extend to both Haiti and the Dominican Republic, nearly all *Leptocereus* taxa occur in relatively small, isolated populations. Some narrow endemics, for example, *L. grantianus* and *L. ekmanii*, are as yet known only from their type localities at Culebra Island (Puerto Rico), and Sierra de Guane (western Cuba), respectively. Because the rather polymorphic *L. weingartianus* sensu lat. has the greatest ecological plasticity, it has the largest distributional range in southern Hispaniola, stretching more than 640 km from the vicinity of Port-à-Pimente (Haiti) to Cabo Engaño (Dominican Republic). While capable of prospering in an area with only 422 mm of average annual precipitation (Cabo Rojo), this species also thrives in places with 1200 mm of annual rainfall in southeastern Dominican Republic (Plate 48, A). Second in range after *L. weingartianus* is *L. paniculatus*, extending 165 km from near Port-au-Prince eastwards to the dry forests West to Azua (Dominican Republic), and from here 285 km to Baie de Henne in northwestern Haiti (Plate 48, A). Cuban and Puerto Rican species have a much more limited distribution. The most widespread Cuban taxa are *L. santamarinae*, with 164 km of distributional range in the coasts of northeastern Cuba, and *L. wrightii* sensu lat. (Plates 46, A, B, and 47, A, B). This latter extended its range 85 km in western Cuba, from Ortigosa, near Bahía Honda,

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Plate 45. Geographic distribution of *Leptocereus* (I).

A. Area covered by *Leptocereus* in the Greater Antilles. **B**. Centers of concentration of species in Cuba. **C**. Distributional range of *Leptocereus* in the limestone backbone of Pinar del Rio province, western Cuba.

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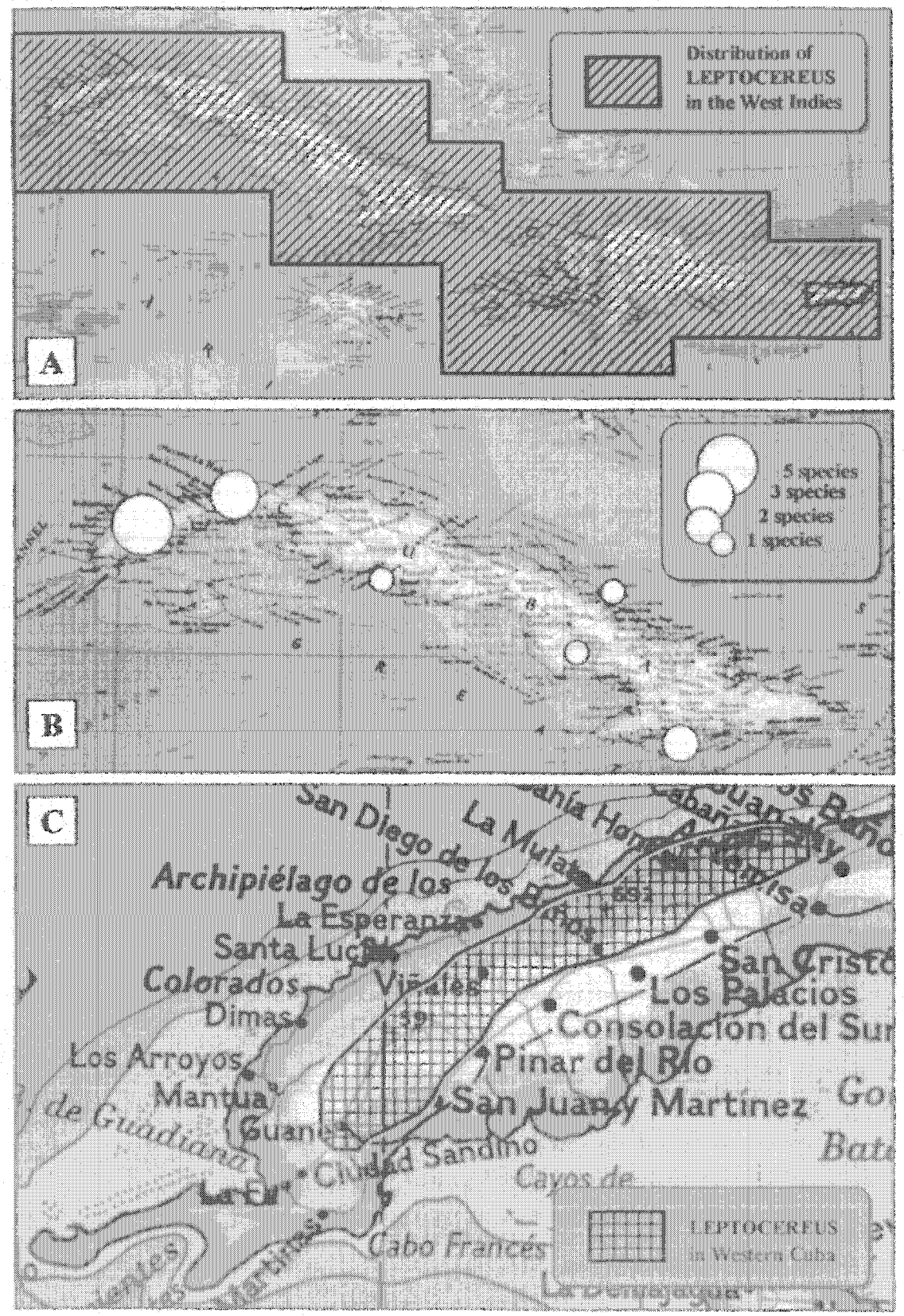

Plate 45.

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Plate 46. Geographic distribution of *Leptocereus* (II).

A. Distribution of *Leptocereus* in western Cuba. **B**. Distribution of *Leptocereus* in central Cuba.

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Plate 46.

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Plate 47. Geographic distribution of *Leptocereus* (III).

A. Distribution of *Leptocereus* in east central Cuba. B. Distribution of *Leptocereus* in eastern Cuba.

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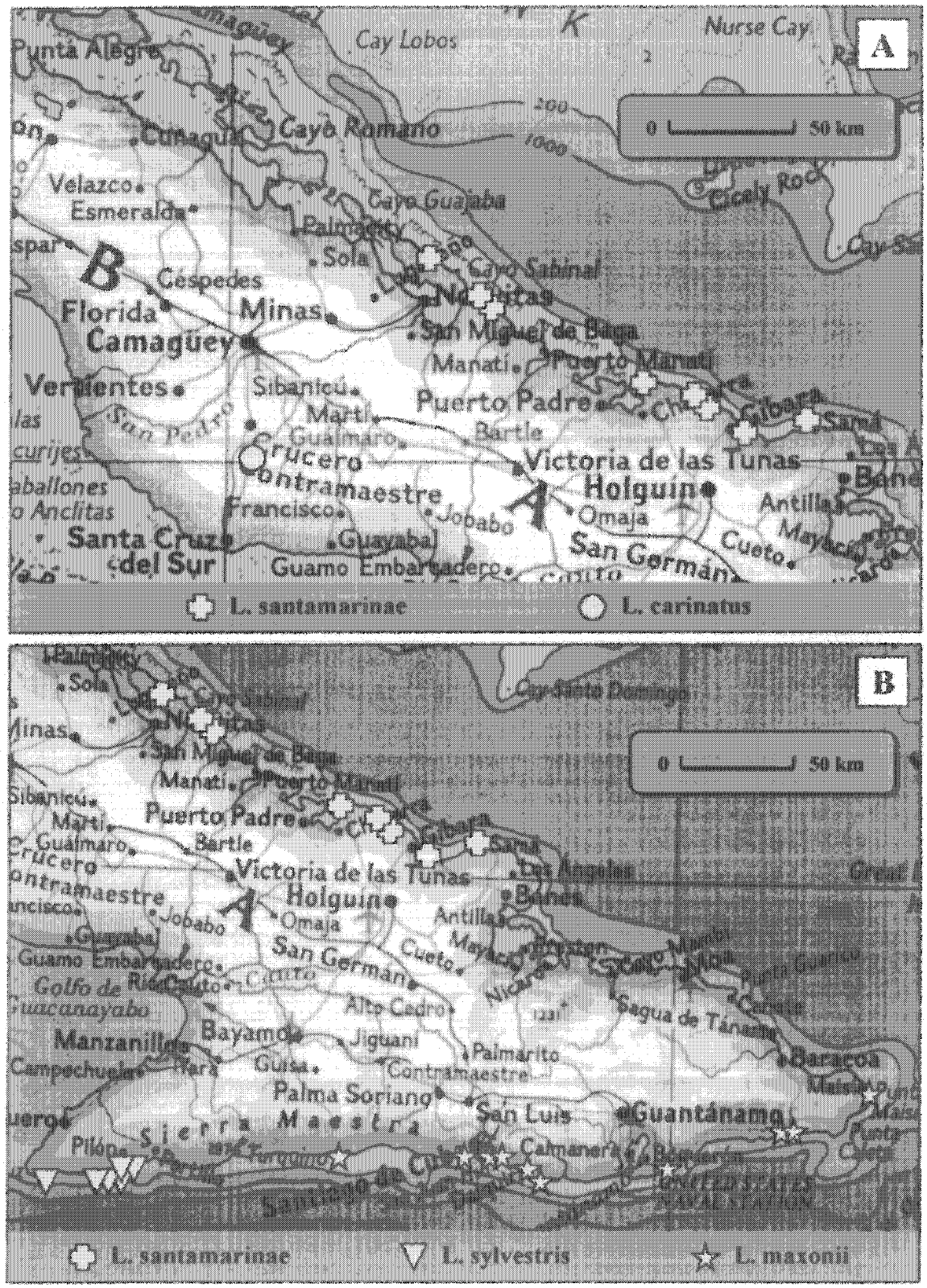

Plate 47.

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Plate 48. Geographic distribution of *Leptocereus* (IV).

A. Distribution of *Leptocereus* in Hispaniola. **B**. Distribution of *Leptocereus* in northwestern Haiti. **C**. Distribution of *Leptocereus* in Puerto Rico.

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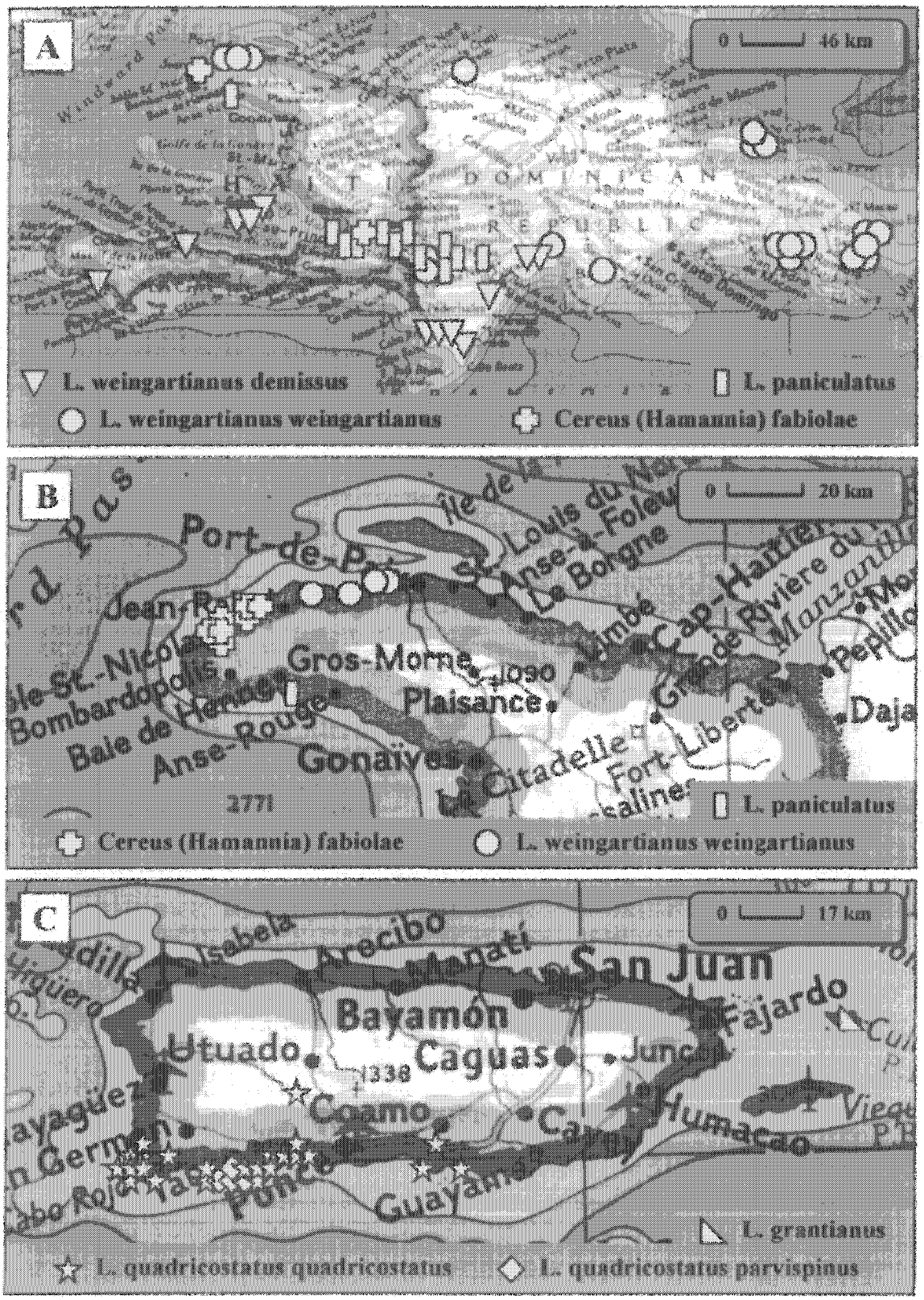

Plate 48.

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to Cojímar, and from here 125 km inland to a disjunct area in San Diego, province of Pinar del Río.

Only two species of *Leptocereus* have overlapping ranges of distribution, the widespread *L. weingartianus* sensu lat., and *L. paniculatus*, both in Hispaniola. However, no naturally occurring hybrids between these two taxa are known. All other species of Cuba and Puerto Rico are allopatric, suggesting that the general process of speciation within the genus occurred via geographic isolation and subsequent differentiation (Table 24). This explains the presence of allopatric pairs of closely related taxa sharing unique morphological features (*e.g.*, *L. assurgens* and *L. ekmanii*; *L. albellus* and *L. prostratus*; *L. leonii* and *L. scopulophilus*; *L. quadricostatus* and *L. grantianus*). This process is still at work in most of the geographic subunits in which the genus can be divided, each representing a definite evolutionary tendency (*e.g.*, in sections *Leptocereus* and *Roseiflori* of western Cuba, and in sections *Spinosissimus* and *Cephaliphora* of eastern Cuba and eastern Greater Antilles, respectively).

7.2. Phytogeography

Leptocereus is a member of a family of neotropical origin occurring around the central part of its range, which extends from 56°15' North latitude in British Columbia to 50° South latitude in Patagonia. The genus is restricted to the Caribbean phytogeographic province of the Caribbean floristic region (Good, 1954). If we follow Borhidi's system (1996) for a more detailed placement, then *Leptocereus* would stretch

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out into three island-provinces (Cuba, Hispaniola, and Puerto Rico) of the Antillean floristic sub-region, which is one of the two phytogeographical units that conform the Caribbean region. Although each of these provinces has its own floristic unity, there are four endemic genera restricted to the whole set of three islands, the largest of which is *Leptocereus*, with 17 species. The other three genera are *Ditta* (Euphorbiaceae, 2 species), *Ottoschultzia* (Icacinaceae, 3 species), and *Torralbasia* (Celastraceae, 2 species). Probably because Borhidi thought that *Leptocereus* was also native to Jamaica, he did not consider the genus to be endemic of Cuba, Hispaniola and Puerto Rico alone (see Tables 32, 33 in Borhidi, 1996).

7.3. Habitat

Stebbins (1952) pointed out that a dry environment stimulates speciation. The ecological characteristics of most of the Greater Antillean endemics provide evidence for this phenomenon. In general, the largest number and highest density of endemics may be observed in the arid zones (coastal areas, semi-deserts) and in the physiologically dry habitats, *i.e.*, serpentines, limestone karsts, and siliceous sands (Areces-Mallea, 1997). The 17 endemic species of *Leptocereus* are no exception, being all distributed in coastal or subcoastal areas, semi-deserts, and in open karstic forests. No *Leptocereus* taxon, however, occurs on serpentine outcrops, or on siliceous sands.

Eight species of *Leptocereus* are restricted to coastal and subcoastal areas, and dry inland semi-deserts. They are common vicariant associates of dry evergreen forests,

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Table 24. Sympatric analysis of *Leptocereus*. Within subgenus *Leptocereus* (1-14, box enclosed by double lines) there are no sympatric taxa. This suggests that the process of speciation occurred by means of strong isolation mechanisms. In subgenus *Weingartianea* (15-20) representatives of its two sections, *Tenuicaulis* and *Cephaliphora*, may be found sympatric (i.e., *L. weingartianus* subsp. *weingartianus* and *L. paniculatus*), while another two members of section *Cephaliphora* (i.e., *L. quadricostatus* subsp. *quadricostatus* and *L. quadricostatus* subsp. *parvispinus*) are of sympatric occurrence (as indicated by the two lower boxes at the right). S = sympatric occurrence; • = allopatric occurrence.

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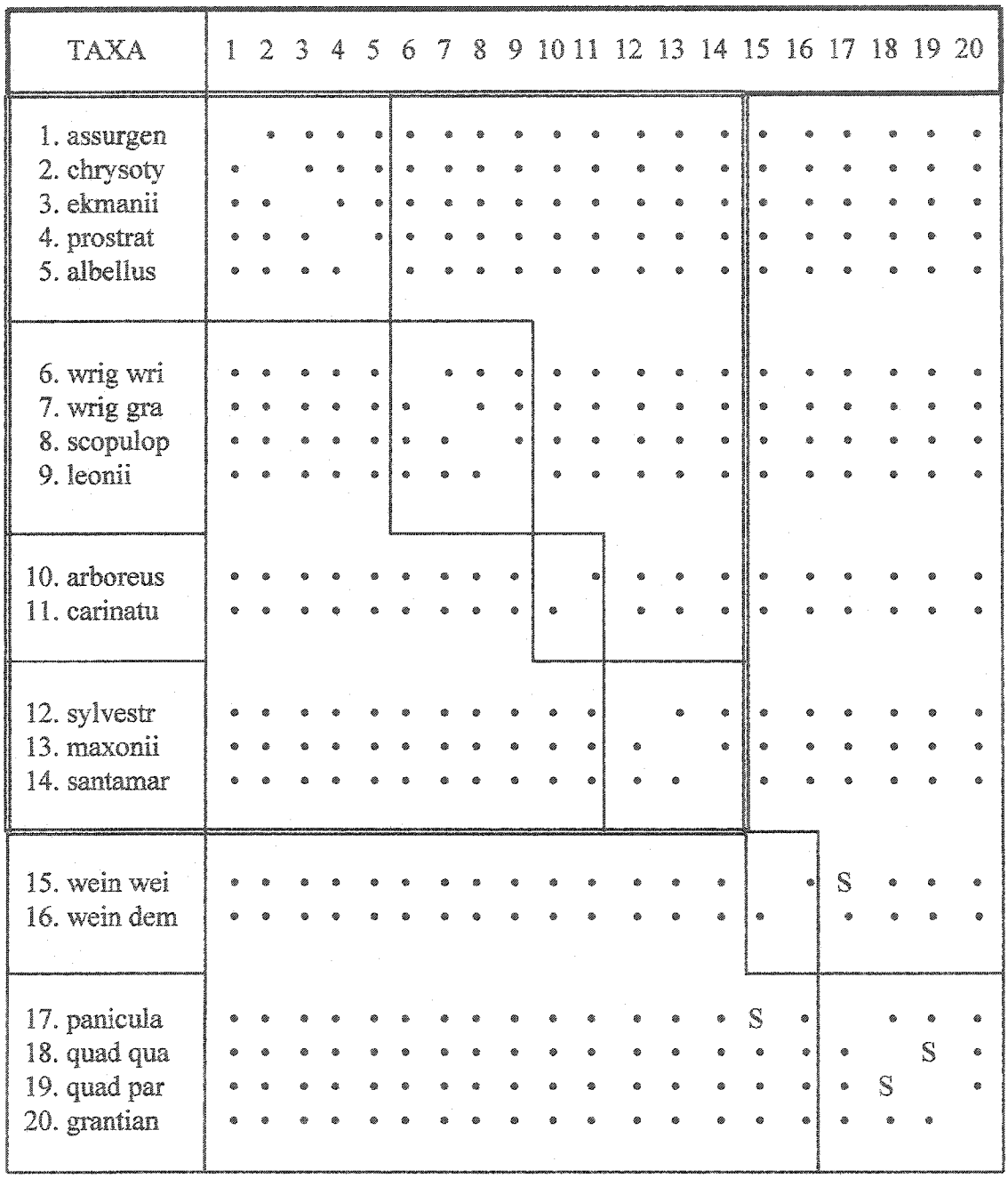

Table 24.

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evergreen and drought-deciduous shrubwoods and shrublands, and semi-desert scrubs occupying well-drained, usually rocky substrates. Relatively extensive semi-desert vegetation —unique open association of spiny, usually microphyllous shrubs, small, trees, and cacti— exist along the leeward coasts of eastern Cuba and Hispaniola; three *Leptocereus* species thrive in them.

Another eight species of *Leptocereus* are confined to the karstic forests of Cuba that occur inland, on isolated mountain ranges. They associate with limestone-based forests and open shrubwoods composed of primarily deciduous species with seasonal flowering (Areces-Mallea *et al.*, 1999). *Leptocereus wrightii* is unique among the species of this genus in having one subspecies in the karstic forests near San Diego de Los Baños (western Cuba), and another in the coastal thickets of Havana and Pinar del Rio provinces. Important ecological and floristic aspects of all these habitats on coastal and subcoastal terraces, dry inland areas, and karstic ranges are discussed as follows.

7.3.1. Evergreen/drought-deciduous shrubwoods and dry evergreen forests

Leptocereus wrightii subsp. *wrightii*, endemic to northwestern Cuba, thrives in the shrubwoods and dry forests on Pliocene and Quaternary limestone that abound on Caribbean coastal areas. These vegetation types are usually composed of thorny, sclerophyllous, small-leaved trees and shrubs that prosper on nearly bare rocks of dry limestone terraces, most often on the inland side of the coastal rock pavement vegetation. (Areces-Mallea *et al.*, 1999). The typical Caribbean coastal shrubwood

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consists of a single, 2 to 3 m high shrub layer with scattered, 5 to 6 m tall "rod-like" emergent individuals, or groups of individuals. Not only diffuse-branched *Leptocereus* species, but also columnar cacti (*Stenocereus hystrix, Pilosocereus* spp.) may occur in these vegetation types under a loose canopy, or intermingled with shrubs in denser, nearly impenetrable communities. They are often seen at the edges of cliffs and exposed rock surfaces (Plate 49, A, B). If the climate is dry enough, these coastal shrubwoods and dry forests may extend inland several kilometers, *e.g.*, in Cabo Rojo, near the southern tip of Pedernales province, southwestern Dominican Republic, where the historical average rainfall is 420 mm per year (SEA/DED, 1990). It is in this dry area of Pedernales, and in southern Haiti as well, where *Leptocereus weingartianus* subsp. *demissus* is commonly found, along with a dwarf form of the opuntioid cactus *Consolea moniliformis* (Plate 49, F). In Hispaniola there is also an extensive stand of dry shrubwoods and forests in areas below sea level in the Enriquillo Valley and Cul-de Sac region, giving way to succulent sea coast vegetation, with *L. weingartianus* subsp. *weingartianus*, *Melocactus lemairei* and *Mammillaria prolifera*. The climate in this hot basin is typically xerothermic, with a mean annual rainfall of 700-800 mm (SEA/DED, 1990, Areces-Mallea, 1997). A much smaller flora of spiny shrubs and dry forests with the endemic *Leptocereus quadricostatus sensu lato* exists along the leeward coast of Puerto Rico, whereas *L. grantianus* occurs in the dry shrublands along a rocky shoreline on the southwestern part of Culebra, a little island off the northeastern coast of Puerto Rico. Being located barely 8 to 10 m from high tide, this *L. grantianus* population, the only one yet known for the species, is very susceptible to damage from heavy storm surges.

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Flat karsts, cliffs and rocky hills are often seen in the coast ranging from Bahia Honda to Cojímar, the domain of *L. wighthii* subsp. *wrightii*. This region, characterized by many drought-tolerant endemic species like *Gochnatia sagraeana* and *Coccothrinax borhidiana*, receives a yearly rainfall of 1000-1400 mm (Borhidi, 1996).

Similar to the Cuban northwestern coast and also with skeletal humic-carbonated soils is the coastal area between Cienfuegos and Trinidad, the realm of the vicariant species *Leptocereus arboreus* (Plate 46, B). Subject to a winter drought of 5 to 6 months and with an annual rainfall of 1000 to 1200 mm, the dry evergreen forests at this site are characterized by large succulents, *i.e.*, the aforementioned *L. arboreus*, *Dendrocereus nudiflorus*, *Pilosocereus brooksianus*, and *Pereskia zinniiflora*. The other two Cuban coastal-bounded *Leptocereus* species occur in even drier areas: the northern coralline terraces and islands of Camagüey, Las Tunas and Holguín provinces (*L. santamarinae*, Plate 47, A), and the coastal belt and terraces of southeastern *Cuba* (*L. sylvestris* and *L. maxonii*, Plate 47, B). The flat dogtooth limestone where *L. santamarinae* is found, for example, is under a seasonal bixeric climate (5 to 8 dry months), and the Puerto Padre-Playa Herradura area —the richest in endemics— is the driest part of the range; its annual rainfall can drop to 700 mm in years of extreme drought (Borhidi, 1996). *Leptocereus sylvestris* inhabits the Pliocene lower coastal terraces between Cabo Cruz and Pilón (province Granma) with 700 to 1,200 mm of yearly rainfall, while *L. maxonii* receives *about* the same precipitation within the

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evergreen shrublands on the rocky coasts of Santiago province, but much less in the semi-deserts of Guantánamo.

7.3.2. Semi-deserts

Three *Leptocereus* taxa, namely *L. weingartianus* subsp. *weingartianus*, *L. maxonii*, and *L. paniculatus* may occur in some open cactus scrubs that from a physionomical standpoint are considered to be true semi-deserts (Areces-Mallea *et al.*, 1999). This vegetation type is characterized by small trees and shrubs that are co-dominated or even dominated by succulents —mainly cacti— in both shrub and canopy layers. Most conspicuous elements are the large columnar and tree-shaped cacti (*Pilosocereus* spp., *Leptocereus paniculatus*, *Stenocereus hystrix*, *Dendrocereus* spp., and/or *Consolea* spp.) sometimes represented by local vicariant endemics in Cuba and the Dominican Republic (Plate 50, E). Open cactus scrubs are conditioned by an extremely arid climate with nine to eleven dry months and usually 300 to 800 mm of annual rainfall (Areces-Mallea *et al.*, 1999). In eastern Cuba they form an unbroken stretch along the coast from Guantánamo Bay to Imías. From Imías to the East end of the island (Maisí) smaller fragments occur, mainly on sandy deposits. Although *L. maxonii* may be present in these areas, the species is not as abundant in these open scrubs as it is coastal shrublands where it seems to reach its ecological climax.

In the Enriquillo Valley and the Cul-de-Sac area (southwestern Dominican Republic and southern Haiti) there is an impressive semi-desertic landscape with the

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tree-like *L. paniculatus* extended to the alternating salt rock and gypsum outcrops on the slopes of the abutting mountain ranges. *Leptocereus paniculatus* is a codominant species in the canopy layer of these scrubs, along with *Stenocereus hystrix*, *Prosopis juliflora*, and *Consolea moniliformis* (Plate 49, D). Between 300 and 600 individuals per hectare of *L. paniculatus*, for example, were reported by García and Castillo (1994) in three randomly selected areas between Azua and Lake Enriquillo, with an annual rainfall ranging from 673.8 mm (Azua) and 871 mm (Cabral). *Leptocereus weingartianus* subsp. *weingartianus* is also present in the Enriquillo-Cul-de-Sac cactus scrub, yet it exhibits a more disseminated distribution pattern. In northwestern Haiti there are other stands of semi-desertic vegetation with *L. weingartianus* subsp. *weingartianus*, *Stenocereus hystrix*, *Harrisia* sp., and the local endemic opuntioid *Consolea falcata*, but no *L. paniculatus*. Selective clearing of the *Prosopis* trees and other hardwoods for charcoal production (*e.g.*, in north central Haiti) has often led to the establishment of unique cacti savannas (Plate 50, G, H).

7.3.3. Montane karstic forests

Leptocereus ekmanii, *L. assurgens*, *L. prostratus*, *L. chrysotyrius*, *L. albellus*, and *L. wrightii* subsp. *gracilis* are endemic to the Sierra de los Organos limestone complex of western Cuba. They inhabit tower-like karstic hills known as "haystack mountains," or simply "mogotes," composed of hard Upper Jurassic rocks. The highest peak of Los Organos, named "Pan de Azúcar," is 591 m. Due to the gradual weathering of these old limestone rocks, freestanding cliffs (Plate 49, C), deep gorges, and wide sinkholes are

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common. Deep, long valleys separating the "sierras" —and with them the vicariant *Leptocereus* species— extend in a general NE-SW direction (Plate 50, A, B). The climate is tropical seasonal with a dry winter season extended for 1 to 2 months in the southern and eastern ranges, and for 3 to 4 months in the western and northern chains. The annual precipitation varies between 1500 and 2200 mm (Borhidi, 1996).

The surface and edges of the haystack mountains, where *Leptocereus* occurs, is usually bare eroded rock with pockets of skeletal, humic-carbonated rendzina soils. The culminant forests have a 4 to 9 m open canopy layer, underneath which not only *Leptocereus* but also other cactus genera such as *Opuntia*, *Harrisia*, *Mammillaria*, *Selenicereus*, *Hylocereus* and *Rhipsalis* prosper as well, thanks to the intense illumination of the understory. All these cacti taxa are part of an ancient and highly specialized karstic flora with 40% of endemics, including various taxonomically isolated relicts such as the monospecific genera *Microcycas* (Zamiaceae), *Euchorium* (Sapindaceae) and *Ancistranthus* (Acanthaceae). Specifically, the Los Organos range constitutes a secondary center of diversity and endemism for the genus *Leptocereus*, where an entire section of five species has originated (section *Leptocereus* of subgenus *Leptocereus*).

East of the Sierra de Los Organos ridges, in Havana province, there are two younger limestone ranges with endemic *Leptocereus* species: Sierra de Anafe —with *L. leonii*— and the more disperse Bejucal-Madruga-Limonar group, with *L. scopulophilus* on top of Somorrostro Hill. Although Sierra de Anafe receives between 1400 and 1600

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mm of annual rainfall (the climate is seasonal, with 3 to 4 dry months in the winter), due to the karstic factor the top of the range (to 275 m) is covered with dry evergreen forests. Curiously, *L. leonii* does not inhabit the top but the steep slopes of the range. As opposed to the Anafe endemic, the vicariant *L. scopulophilus* is primarily a top dweller; nearly all collected specimens of this species come from the eroded limestone summit of Somorrostro Hill (Areces-Mallea, 1993b).

The easternmost *Leptocereus* species to be found on inland karstic ridges is *L. carinatus*, endemic to the limestone heights of Sierra de Najasa (highest peak 301 m) in Camagüey province, eastern Cuba (Areces-Mallea, 1993a). With about 1800 mm of annual rainfall and a dry winter season that lasts 3 to 4 months, the climate of Sierra de Najasa is not very different from that of the occidental karstic ranges (Borhidi, 1996). Like most inland *Leptocereus* species of western Cuba, *L. carinatus* associates with semideciduous forests on shallow humic-carbonated soils, but these communities lack the floristic richness of the older haystack mountains of Pinar del Río province.

Although tropical karstic ranges and eroded limestone plateaus also exist outside Cuba, *e.g.*, in Jamaica in the Cockpit Country (Plate 50, C, D), in Los Haitises (Dominican Republic), and in the mogotes region of northern Puerto Rico, no *Leptocereus* species have yet evolved in these geologically younger areas to thrive in the specialized karstic habitat.

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Plate 49. Habitats of *Leptocereus* (I).

A. Fringe of *Stenocereus hystrix* at the edge of a coastal cliff. **B**. Idem, with a close-up view of the columnar cactus *S. hystrix*. **C**. Vertical limestone cliff in a typical karstic range of western Cuba; the hard, crystalline rock is of Jurassic age. **D**. Open cactus scrub (semi-desert) on sandy soil in southwestern Hispaniola, with *Leptocereus paniculatus* (left) and *Consolea moniliformis* (right) in the foreground. **E**. A stand of semi-desertic vegetation dominated by *Stenocereus hystrix*, in northwestern Haiti. In the horizon, a series of limestone coastal terraces only 77 km away from those of Maisí in Cuba's East End. **F**. Dry shrublands in southwestern Dominican Republic, with a dwarf form of the opuntioid cactus *Consolea moniliformis*. (A, B, from Guantánamo Bay, Cuba —2 Oct 2000; C, from Viñales Valley, western Cuba —21 Feb 1979; D, from the Lake Enriquillo area, Dominican Republic —8 Jan 1995; E, from Môle St. Nicolas, Haiti —19 Jan 1995; F, from vicinity of Cabo Rojo, Pedernales, Dominican Republic —31 May 1991).

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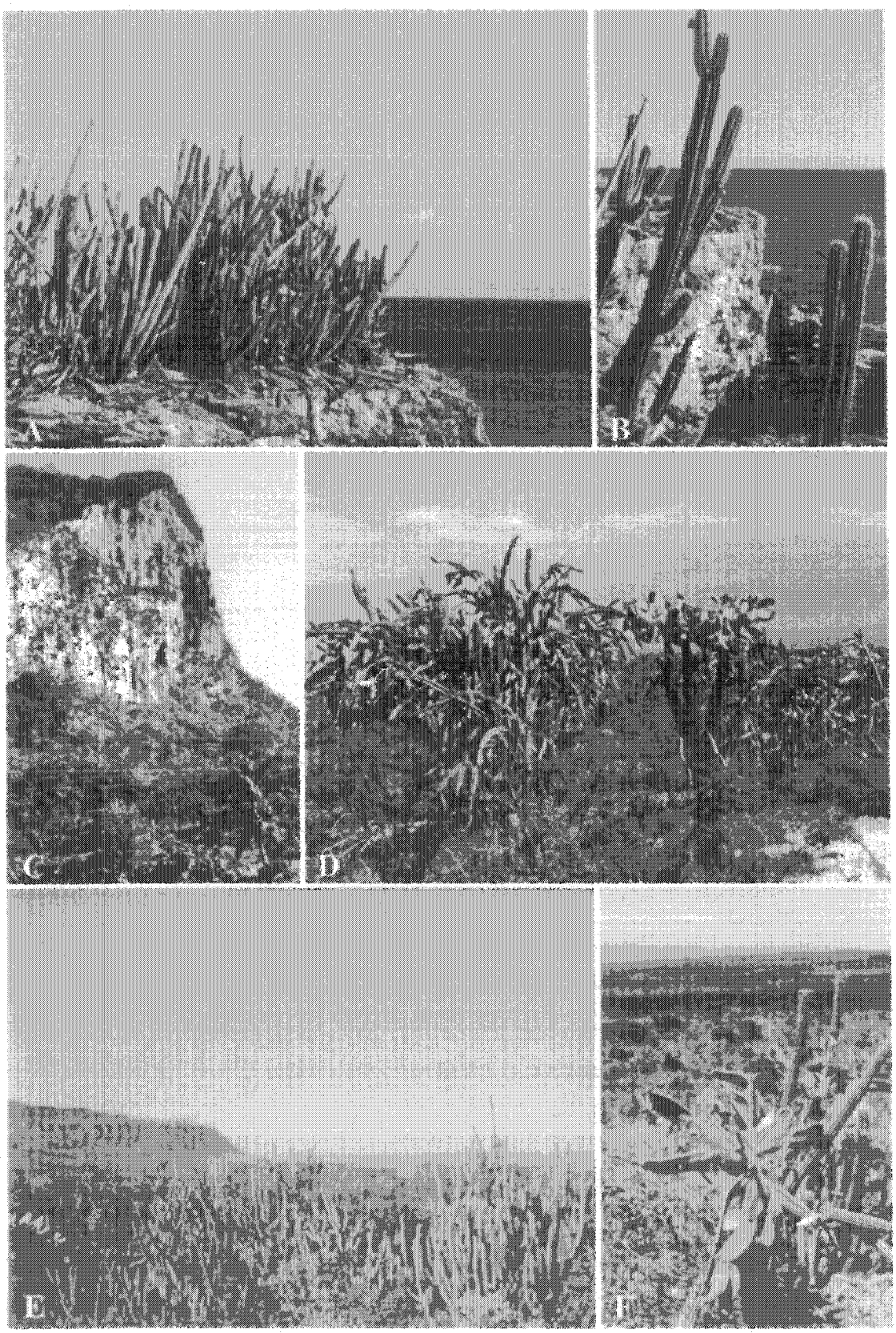

Plate 49.

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Plate 50. Habitats of *Leptocereus* (II).

A. Ranges of haystack mountains in Pinar del Río province, western Cuba. **B**. Close-up view of a haystack mount with very steep walls covered with vegetation. **C**, **D**. Karstic relief in an eroded Cenozoic limestone plateau in central Jamaica. Although mounts and cliffs are present, no *Leptocereus* has yet been discovered in this rather unexplored area. **E**. Open cactus scrubs (semi-deserts) of southeastern Cuba dominated by the columnar cactoid *Stenocereus hystrix*. **F**. Dry stream bead crossing a cactus scrub dominated by *Prosopis juliflora* in southern Hispaniola. Two sympatric *Leptocereus* species occur in this area: *L. paniculatus*, and *L. weingartianus* subsp. *weingartianus*. **G**, **H**. *Stenocereus hystrix* (**G**) and *Consolea moniliformis* (**H**) savannas. Selective clearing of the *Prosopis* trees and other hardwoods for charcoal production has led to the establishment of cacti savannas in Haiti. (A, B, from Los Jazmines, Viñales Valley, Cuba —21 Feb 1979; C, D, from the Cockpit Country near Ramgoat Cave, Jamaica — 24 Jan 1995; E, from the windward side of Guantánamo Bay, Cuba —4 Oct 1996; F, from semi-deserts West to Azua, Dominican Republic —4 Jan 1995; G, H, from vicinity of Gonaïves, Haiti —26 Dec 1998).

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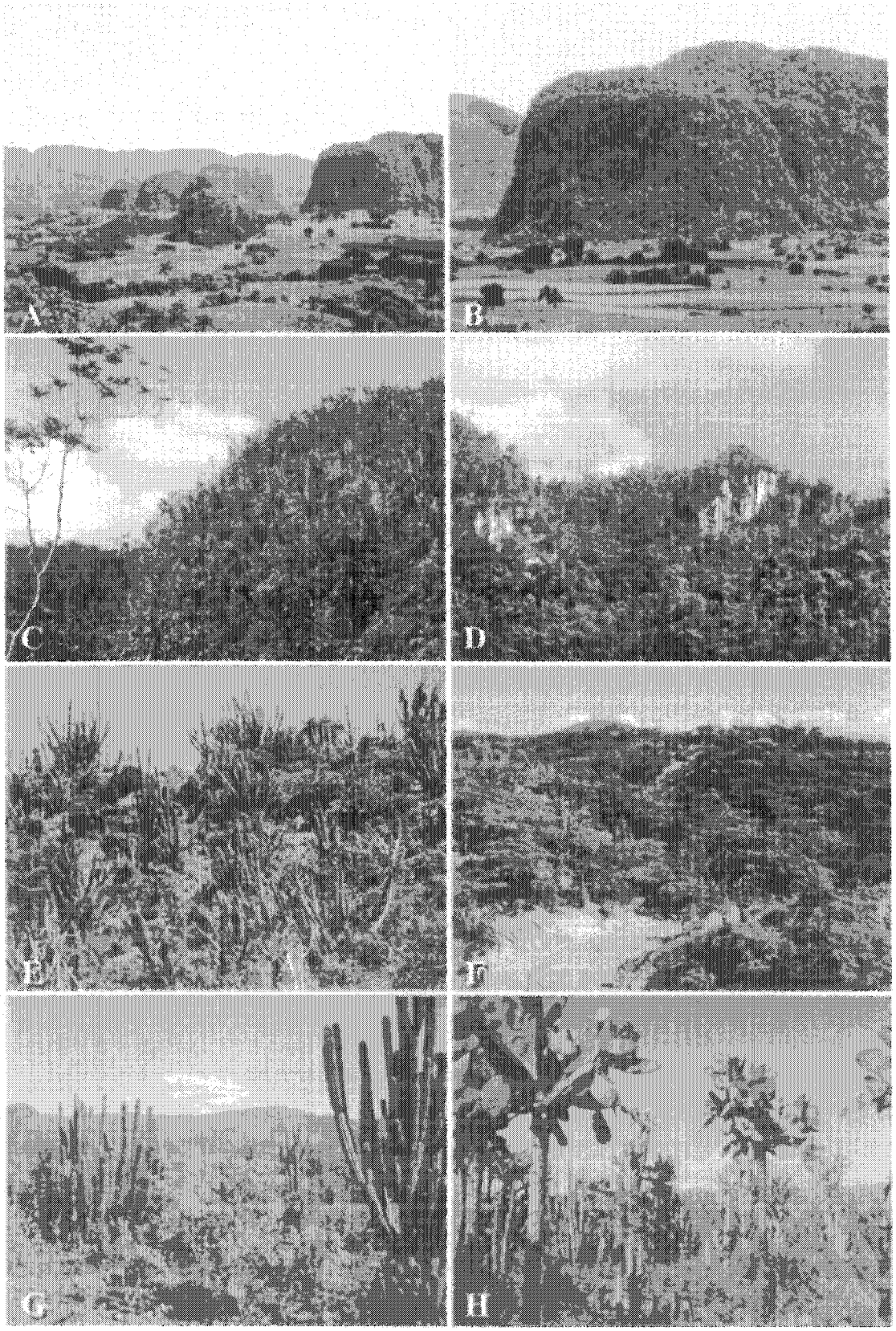

Plate 50.

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8. REPRODUCTIVE BIOLOGY

Although the first thorough research on pollination mechanisms in the Cactaceae was made more than sixty years ago (Porsch, 1938-39), the reproductive biology of the family, particularly the breeding systems, are still poorly known. Studies are few, not very well documented, and most of them refer to subfamily Opuntioideae, mainly to North American species of the genus *Opuntia*. However, in recent years there has been more interest in subfamily Cactoideae, and some excellent papers dealing with the pollination ecology of globular and columnar cacti are now available (*e.g.*, Schlindwein and Wittmann, 1995; Locatelli *et al.*, 1997). No investigations on the reproductive biology of *Leptocereus* have been made prior to this study.

Because genetic recombination of parental genotypes leads to maximum genetic variability in the progeny, the vast majority of the Cactaceae are typical outcrossers (Gibson and Nobel, 1986). As a result, they are highly dependent on biotic pollinators to transfer their pollen from one plant to another. There is also a tendency towards developing morphological features that favor outcrossing. Herkogamy, for example, the spatial separation of stigma and stamens, is the normal condition of the flowers of all self-compatible cacti that are not autogamous or cleistogamous. Herkogamy and floral syndromes act together in the Cactus family to promote outcrossing.

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8.1. Floral syndromes

From medicine the useful term "syndrome" has been expanded for use in biology to designate groups of morphological features (not necessarily all appearing together) that characterize specific adaptations, diseases, or abnormal genetic conditions. In pollination ecology, for example, a "bat syndrome" stands for a flower possessing most of a series of characters that collectively pre-adapt it for bat pollination, for example, that of *Pilosocereus* spp. In the Cactaceae, very rarely is a flower visited exclusively by one species alone, but among the visitors it is common that a group of animals —or even one single animal—is selected by its size, form and behavior as principal pollinator. Because many cactus flowers are adapted to various degrees to the body characteristics and *modus operandi* of an animal (or animal group) acting as principal pollinator, a co-evolution system between them is presumed. The adaptation of the flower involves: floral morphology (size and shape), color, presence or absence of scent (and type, if present), time and duration of anthesis, amount of pollen and nectar production (including sugar composition and concentration of nectar), and all functional structures such as stamens, pollen, style, stigma, etc. (Faegri and Van der Pijl, 1979; Grant and Grant, 1979; Cota, 1993). Insects, birds, and bats make up the vast majority of pollinator groups in the Cactaceae. Thus, it is expected that the four major floral syndromes reported in this family are: (1) bee-syndrome (Plate 51, G); (2) hawkmoth-syndrome (Plate 52, A, B); (3) bird-syndrome (Plate 52, C); and (4) bat-syndrome (Plate 52, F, H). A fifth but not less important category has been included for

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those unselective floral types that lack preferences for any particular pollinator. This category is typified by the rather unspecialized flower of *Pereskia* (Plate 51, F), from which all the four above mentioned floral syndromes seem to have evolved (Rowley, 1980). Figure 10. illustrates schematically the adaptations of the cactus flower to its different pollinators.

Because bees are more generalists and do not require highly specific morphological adaptations of flowers, most authors consider bee pollination —by far the most common pollination system in the family— to be very close to the primitive condition (Cota, 1993). According to Grant and Grant (1979), who studied the pollination spectrum of the cactus flora of southwestern U. S., hawkmoth, bird, and bat pollination involve up only 6.5% of the family in that area. These apparently derived pollination types are more circumscribed to certain groups of columnar cacti of Central and South America, such as the Pachycereeae and Trichocereeae tribes (Grant and Grant, 1979; Gibson and Nobel, 1986; Cota, 1993).

Most cactus scholars agree that despite the frequency of bright yellows and red colors in their flowers, there is little evidence for a butterfly syndrome in the Cactaceae (Rowley, 1980). However, some poorly known species of *Leptocereus* from western Cuba —particularly *L. ekmanii* and *L. chrysotyrius*— have partially evolved towards attracting diurnal lepidoptera, and they do so by means of an indisputable attribute for promoting butterfly pollination: the salverform flower. The presence of this floral type

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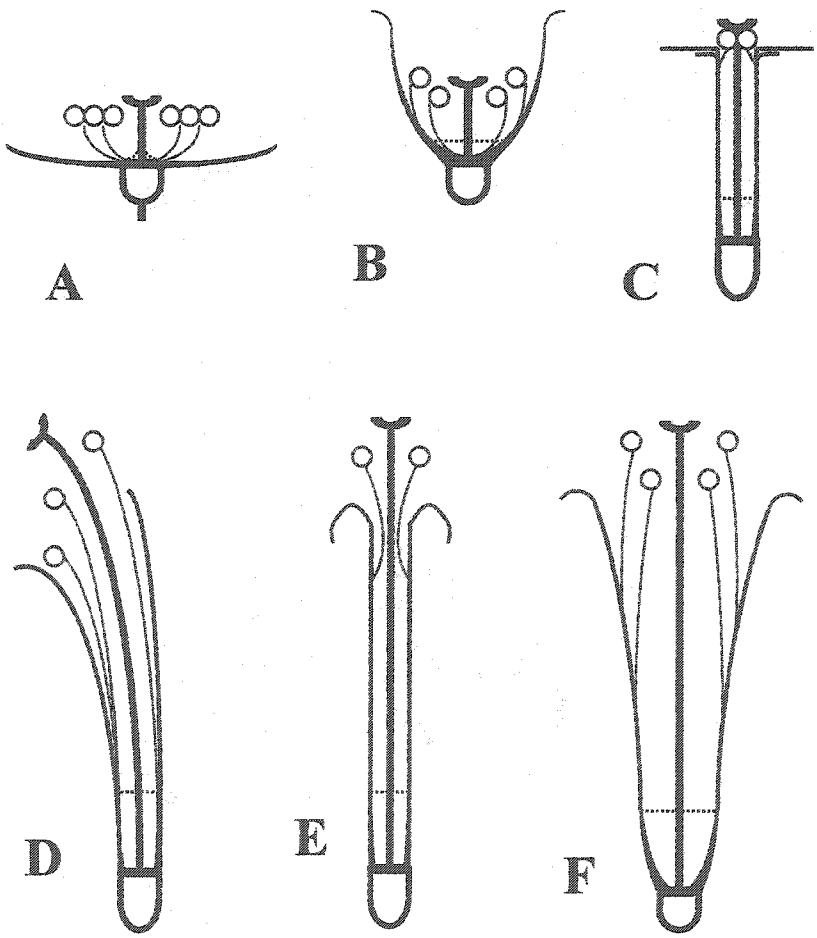
Fig. 10. Schematic profiles of cactus flowers (longitudinal sections), exhibiting the morphological set of characters that identifies each pollination syndrome. **A.** Unselective flower (*e.g.*, *Pereskia* spp.; some *Opuntia*). **B.** Bee flower (*e.g.*, most *Opuntia*; *Ferocactus* spp. *Echinocactus* spp.). **C.** Butterfly flower (*e.g.*, *Leptocereus ekmanii*; *L. chrysotyrius*). **D.** Bird flower (*e.g.*, *Schlumbergera* spp.; *Cleistocactus* spp.). **E.** Hawkmoth flower (*e.g.*, *Epiphyllum* spp.; *Pigmaeocereus* spp.; *Discocactus placentiformis*). **F.** Bat flower (*e.g.*, *Pilosocereus* spp.; *Pachicereus* spp.; *Cipocereus* spp.).



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has strongly influenced the results of my field observations. If we examine the recorded spectrum of animal visitors in these Cuban *Leptocereus* taxa (Tables 34 and 35), we will notice a significant dominance of rhopaloceroid insects. This may well indicate, beyond any reasonable doubt, that butterflies are presumably their main or at least most reliable agents of cross-pollination. Based on these considerations, I will include the butterfly-syndrome to the list of floral syndromes reported to occur in the Cactaceae (Rowley, 1980). These may be better summarized in key form, and characterized by some of the best known examples that I have come across:

KEY TO POLLINATION SYNDROMES IN THE CACTACEAE

(adapted from Rowley, 1980)

A Flowers diurnal, usually medium to small-sized and brightly colored (vivid yellow, orange, pink or red); scent faint or none

B Flowers flattened or nearly so, at maximum anthesis usually wider than longer, with abundant pollen and nectar (if present) freely exposed (*e.g.*, *Pereskia quisqueyana*, Plate 51, F) ..... 1. UNSELECTIVE

B' Flowers commonly not flattened, most often longer than wider, with nectar more or less hidden at the base of the tubular, cup- or bell-shaped perianth

C Flowers tubular, stiff and unyielding, with watery nectar in a distinct chamber at the base of an essentially long and often narrow tube

D Flowers mostly yellow, actinomorphic; perianth segments spreading at right

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angles to the straight tube forming a more or less flat dish-like landing stage (*e.g.*, *Leptocereus ekmanii*, Plate 24, C) ..... 2. BUTTERFLY FLOWERS

D' Flowers mostly red and commonly zygomorphic, the limb often oblique; tube usually vaulted or with a faint S-bend (*e.g.*, *Schlumbergera truncata*, Plate 52, C) ..... 3. BIRD FLOWERS

C' Flowers cup- or bell-shaped, half to wide opening, perianth not stiff or rigid, with concentrated nectar in a rather indistinct nectar chamber (*e.g.*, *Opuntia dillenii*, Plate 51, G) ..... 4. BEE FLOWERS

A' Flowers nocturnal, medium to large-sized, inner perianth segments white, the outer ones gloomy and lusterless (usually greenish, dull yellowish-brown, or wine-colored); scent if present then at night only

E Flowers narrow funnel-shaped to cylindrical, with an essentially flat or refexed limb and narrow tube; scent often intense and sweet; usually sufrutescent or shrubby plants (*e.g.*, *Epiphyllum phyllanthus*, Plate 52, A, B) ..... 5. HAWKMOTH FLOWERS

E' Flowers stout, funnel-shaped, the tube more or less thick, often (but not always) with a large brush of exserted stamens; scent usually unpleasant, like onions or overripe fruits; tree-like plants (*e.g.*, *Pilosocereus brooksianus*, Plate 52, H) ..... 6. BAT FLOWERS

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Plate 51. Pollination syndromes in the Cactaceae (I).

A-D. Bees, butterflies, and hummingbirds visit the flowers of *Consolea moniliformis*: **A**. Pollen and nectar are freely exposed in the flower. **B**. Honeybee (*Apis mellifera*) gathering pollen. **C**. *Siproeta stelenes stelenes* (Lepidoptera: Nymphalidae) on a flower. **D**. Green Mango *Anthracothorax viridis* (Aves: Trochilidae), the common large hummingbird of Puerto Rico, taking advantage of a cultivated, blooming *Consolea*. **E**. The flowers of *Consolea picardae* open orange-yellow and become red with senescence, perhaps to attract different pollinators (red flowers are still capable of releasing fertile pollen). **F**. Unselective bloom of *Pereskia quisqueyana*, with its characteristic flat profile. These open flowers are wasteful of pollen, which is accessible to both pollinators and robbers; from them other more specialized floral types presumably evolved. **G**. The yellow cup-shaped flowers of *Opuntia dillenii* are typical bee flowers. **H**. *Xylocopa brasiliorum* (Apidae: Xylocopinae) visiting an *Opuntia* sp. flower. Bee pollination is the most common pollination system in the Cactaceae. (A, from Azua, Dominican Republic —4 Jan 1995; B-D, from Pedernales, near Cabo Rojo, Dominican Republic —5 Jan 1995; E, from road to Bayahibe, Dominican Republic —2 Jan 1995; F, from Bayahibe, Dominican Republic —2 Jan 1995; G, from Isla de Pinos, Cuba —8 Nov 1990; from lowlands South to Spanish Town, Jamaica —26 Jan 1995).

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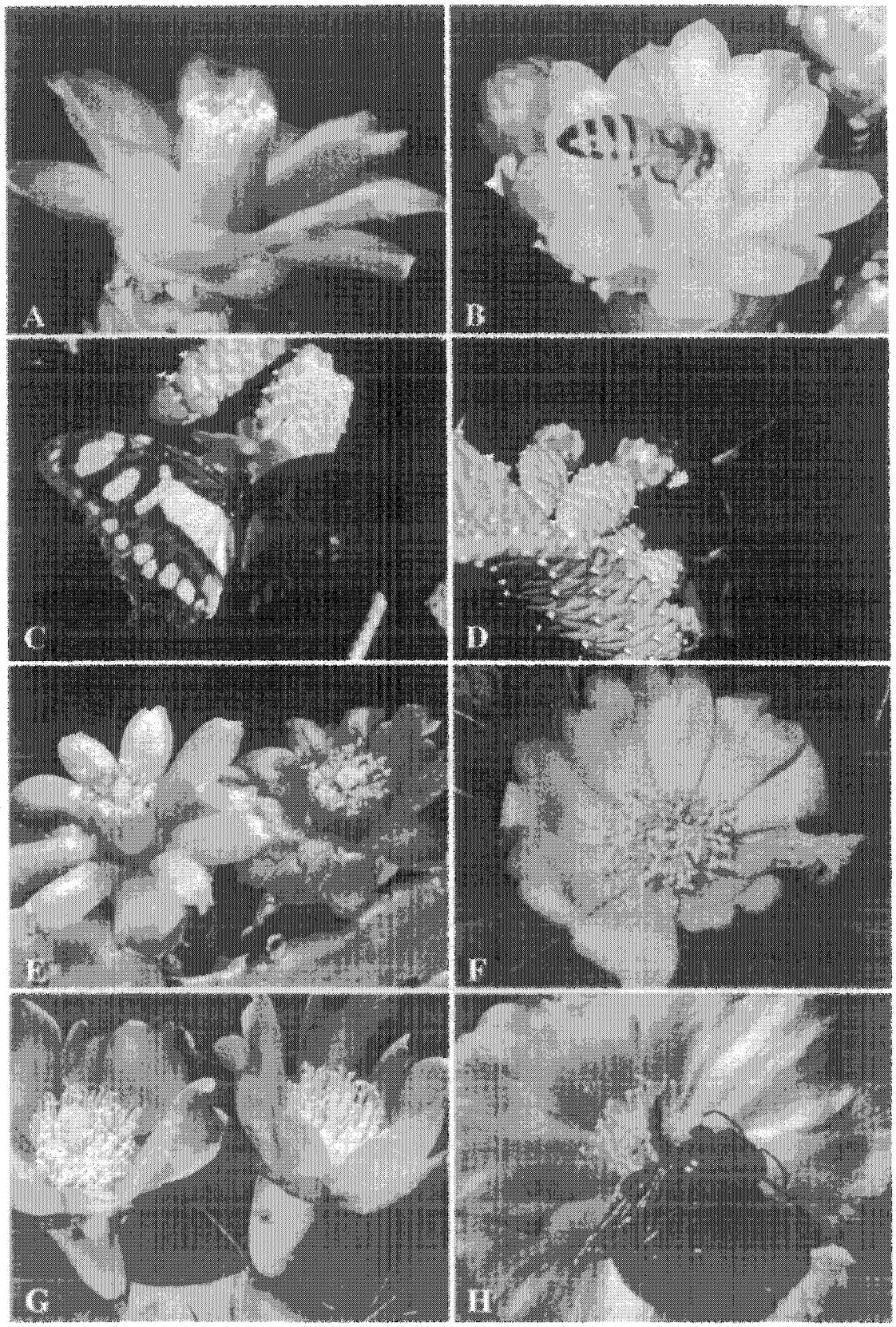

Plate 51.

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Plate 52. Pollination syndromes in the Cactaceae (II).

A-B. *Epiphyllum phyllanthus* typically exhibits the hawkmoth pollination syndrome: **A**. Close-up of flowers showing the long-exserted stamens and style. **B**. Long narrow tube of same flower. **C**. Perianth segments are oblique in a typical bird flower (*Schlumbergera truncata*), giving zygomorphic symmetry to the flower. Herkogamy is clearly manifested (anthers are well positioned below the stigma). **D**. The bright pink flowers of *Melocactus intortus* are attractive to hummingbirds. **E**. Probably to avoid pollen and nectar robbers, the flowers of *Mammillaria jamaicensis* are concealed beneath a lattice of radial spines. A hummingbird's beak, however, can easily penetrate the spine framework. **F**. Large, stout flowers of the bat-pollinated *Dendrocereus nudiflorus*. **G**. *Harrisia taylorii* exhibits a combination of bat and hawkmoth pollination syndromes. **H**. The flowers of *Pilosocereus brooksianus* —typically bat pollinated— produce an unpleasant scent that evokes rotten onions. (A, B, from Cayman Brac, Cayman Islands, B.W.I. —November 1991; C, from a cultivated plant at Longwood Gardens, Pennsylvania — November 1994; D, from Culebra Island, Puerto Rico —28 May 1995; F, G, H, from Guantánamo Naval Station, Guantánamo Bay, Cuba —9 Oct 1996).

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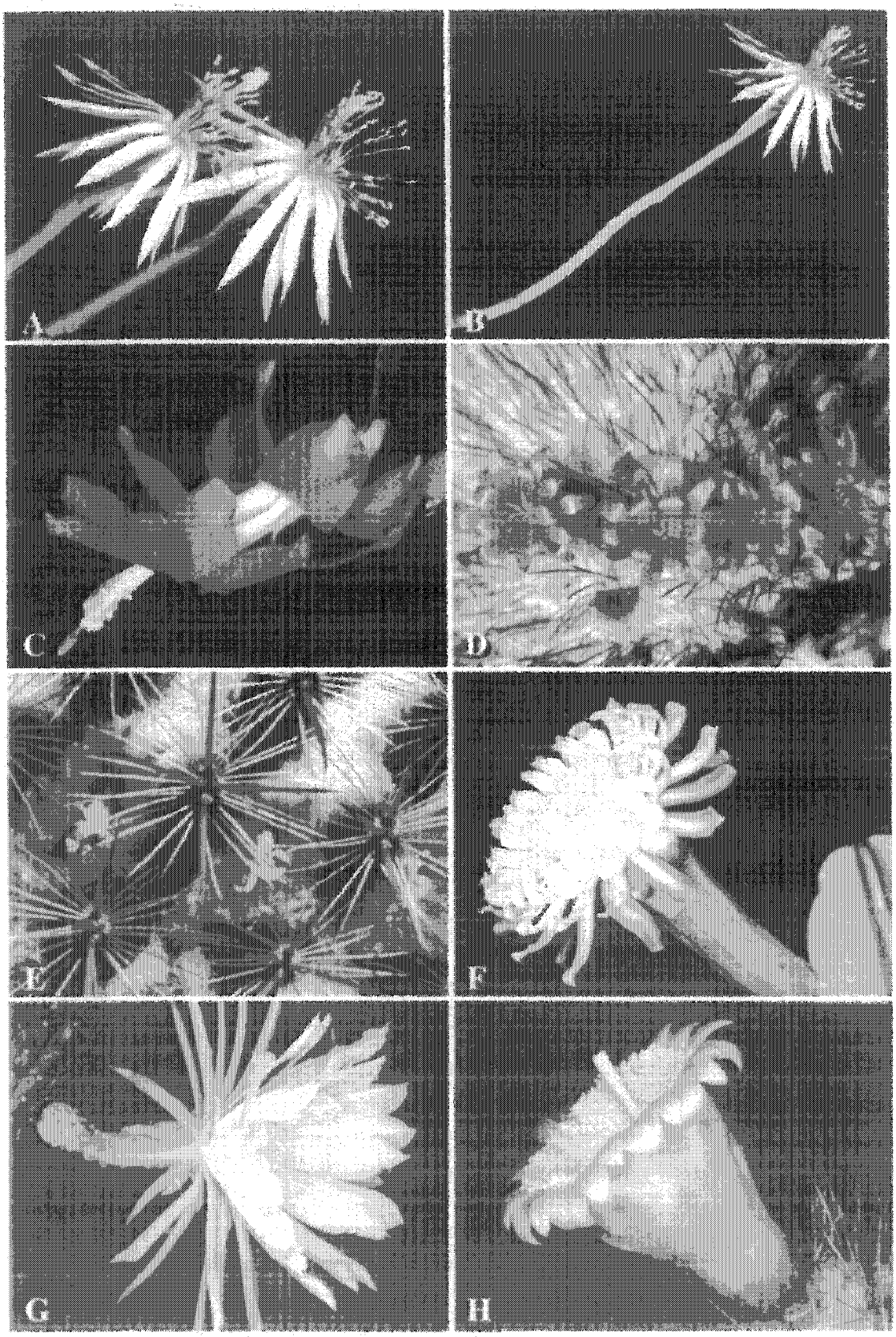

Plate 52.

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8.2. Self-incompatibility

Self-incompatibility (SI) in flowering plants is the inability of a fertile hermaphroditic plant producing functional pollen and ovules to produce zygotes after self-pollination. SI is common in angiosperms and is a major mechanism for enforcing outbreeding in plant populations. It is therefore instrumental in determining the genetic structure of populations, and is of considerable evolutionary significance. Many members of the Cactaceae are self-fertile and set seed in the absence of pollinators; others, however, require cross-pollination for fruit and seed production. In SI Cactaceae, mating between close relatives is expected to reduce the number and/or vigor of offspring by virtue of the so-called "inbreeding depression." The relative fitness of inbred versus outbred progeny in rare and endangered cacti is an important thing to be determined, to assess whether outcross pollination will be necessary for *ex situ* and *in situ* conservation management programs (Negrón-Ortiz, 1998).

The first major review of the reproductive systems of the Cactaceae is that of Ganders (1976) who reported SI in 15 genera of subfamily Cactoideae. His paper was soon followed by that of Taylor (1976), with the addition of 9 more genera of cactoids to the list of "unselfings." At present, SI appears to be widespread in the Cactus family. Since cacti have trinucleate pollen, it is likely that the mechanism of SI is sporophytically controlled (Ganders, 1976). Maybe the diploid sporophyte synthesizes recognition proteins in the tapetum of the anther and in the stigmatic papillae, as it has

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been well documented in the Brassicaceae. In this family the tapetal proteins are transferred to the exine of the pollen grain and the stigmatic proteins are carried to the pellicle that covers the surface of the stigma. At pollination the exine-bound proteins diffuse out and interact with those of the pellicle. If the proteins are identical, a rejection response occurs in the papillae and pollen tubes do not penetrate the stigma (De Nettancourt, 1977). However, other mechanisms may well occur such as ovarian inhibition, a system where levels of ethylene and indole-3-acetic acid increase prior to pollen tube-ovule contact in incompatibly pollinated flowers. In fact, Negrón-Ortiz (1998) documented a mechanism of ovarian inhibition in the self-incompatible opuntioid cactus *Consolea corallicola*.

8.3. Materials and methods

Data for this study were compiled from personal information based on many years of observing, studying and collecting species of this genus. Extensive fieldwork was carried out during the course of 48 trips to different locations in Cuba, Haiti, the Dominican Republic, and Puerto Rico, between October 1975 and October 2000. Out of a total number of 20 taxa (17 species and 3 subspecies), 14 species and 2 subspecies were surveyed for possible pollinators. These surveys were made continuously throughout the night and also during daytime if flowers remained open after dawn. Three additional species, plus one subspecies, were studied, but during exclusively the daytime. Only three species and one subspecies of *Leptocereus* —20% of all taxa, as

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circumscribed in this work— could not be surveyed for visiting animal vectors. Important dates and locations for pollination observations are given in Table 25.

At each site I studied the floral biology of 2 to 16 plants and made pollination observations on 2 to 6 individuals, selecting those with more accessible flowers. Nocturnal observations were made using headlamps and flashlights, while daytime studies required small binoculars. Animal visitors were identified directly in the field (birds), or captured with various types of nets (insects, bats) for subsequent identification. All captured arthropods were identified by L. R. Hernández (former curator at the National Museum of Natural History, Havana, now at University of Mayagüez, Puerto Rico), while I determined the vertebrates. No relative frequency of vectors on flowers, or of stigma contacts, were recorded during visits, and no analysis of pollen loads on vectors were made. Therefore, the record of an animal in a flower does not necessarily mean it is a reliable pollinator of the species (Tables 34-40).

The onset of stigmatic receptivity was assessed by means of the peroxidase reaction (Baum, 1995): a drop of 5% hydrogen peroxide was placed on the stigma and observed with a hand-lens (magnification ×10). A positive reaction produced bubbles of oxygen (this test determines the onset of receptivity but cannot be used to detect the cessation of receptivity). After observations flowers were preserved either in FAA or 70% ethanol for subsequent morphological studies.

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TAXON	LOCALITY	DATES
L. albellus	Sierra de San Carlos, Cuba	26-29 Mar, 1992
L. arboreus	Yaguanabo, Cuba	7-9 Jul, 1993
L. assurgens	Viñales, Cuba	19-24 Feb, 1979
L. chrysotyrius	San Diego, Cuba	2-5 Nov, 1976
L. ekmanii	Sierra de Guane, Cuba	6-8 June, 1984
L. leonii (I)	Sierra de Anafe, Cuba	28-29 Oct, 1975
L. leonii (II)	Sierra de Anafe, Cuba	2-4 Nov, 1975
L. maxonii	Rio Tacre, Guantánamo, Cuba	19-21 Mar, 1990
L. paniculatus (I)	La Descubierta, Dominican Republic	7-8 Jan, 1995
L. paniculatus (II)	West to Azua, Dominican Republic	20 Dec, 1998
L. prostratus	Sumidero, Cuba	5-9 March, 1992
L. quadricostatus quadricostatus (I)	Salinas ca. Boquerón, Puerto Rico	13 Jun, 1995
L. quadricostatus quadricostatus (II)	Guayanilla, Puerto Rico	15 Dec, 1995
L. quadricostatus quadricostatus (III)	Cabo Rojo, Puerto Rico	10-11 Jan, 1996
L. quadricostatus parvispinus	Guánica, Puerto Rico	1-3 Feb, 1996
L. santamarinae	Santa Lucía, Cuba	13-14 Apr, 1990
L. sylvestris	Pilón, Cuba	3-5 May, 1993
L. weingartianus weingartianus (I)	Samaná, Dominican Republic	8 June 1991
L. weingartianus weingartianus (II)	Bayahibe, Dominican Republic	2 Jan, 1995
L. weingartianus weingartianus (III)	Cabo Engaño, Dominican Republic	3 Jan, 1995
L. weingartianus demissus (I)	Pedernales, Dominican Republic	5 Jun, 1995
L. weingartianus demissus (II)	Pedernales, Dominican Republic	22 Dec, 1998
L. weingartianus demissus (III)	Pedernales, Dominican Republic	27 Oct, 2000
L. wrightii wrightii	Bahía de Ortigosa, Cuba	12-13 Dec, 1993

Table 25. Dates and study sites for flower visitors. The order of taxa is alphabetical.

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Flowering dates of *Leptocereus* specimens used to study the duration of anthesis are given in Table 26. Because no *Leptocereus* species has ever been tested for SI, two simple experiments, pollen viability and self-pollination test, were carried out with cultivated specimens from two West Indian outdoor collections: Cojímar, Havana (Cuba), and Hacienda Paraíso, Ponce (Puerto Rico). These experiments were performed on adult plants during a seven-year period (1992 to 1998). Pollen viability and also self-pollination were tested on all but one species of *Leptocereus* (*L. arboreus*), the flowers of which were not available at the time. Plants were selfed many times in 3 to 8 cultivated individuals in at least two consecutive years. To test for pollen viability fresh mature anthers from tagged flowers of each species were stained for 24 to 36 hours with aniline blue in lactophenol following the Hauser and Morrison procedure (1964). After staining, pollen grains were observed and scored under a light microscope. Hand-pollinated flowers were tagged and fruit and seed set —if produced— observed on all flowering plants growing in Cuba and Puerto Rico under cultivated conditions. Extreme precautions were taken to prevent transference of *Leptocereus* pollen by animals or even wind from other species, by allowing only one *Leptocereus* plant to bear open flowers at any given time. Pollinators were excluded by covering the flower bud and upper portion of the branch with a paper bag before anthesis (Faegri and Van der Pijl, 1979). The bagged flowers remained isolated for at least 24 hours, until completely closed. Bags were only momentarily removed to check the anthesis process, to test for the onset of stigmatic receptivity, and to hand-pollinate the flowers with their own pollen. To measure seed set on tagged flowers, fruits were left to mature on the plants

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TAXON	FLOWERING DATES (M/D/Y)
L. assurgens	4/2/76; 2/8/77; 3/14/84; 3/10/99; 4/17/01; 4/20/01; 4/23/01
L. chrysotyrius	3/20/83; 3/22-23/83; 4/19/91; 8/15/91; 8/17/91; 8/19-26/91; 8/28/91; 9/2/91
L. ekmanii	2-3/7/80; 5-8/7/80; 4/4/91; 3/27-28/92; 3/30/92
L. prostratus	3/30-31/84; 4/1/84; 4/4/84; 7/9/91; 3/5/92; 3/7/92; 3/9/92; 3/11-12/92; 3/15/92; 3/17-18/92; 3/21/92; 3/23/92; 3/25/92; 3/30/92; 5/7/92; 2/14/93
L. albellus	2/8/92; 2/10/92; 2/14/92; 2/20/92; 2/28/92; 3/3/92; 3/6/92; 3/11/92; 3/18/92; 3/20/92; 1/31/93; 3/26/93
L. wrightii (*wr.*)	5/4/79; 5/10/79; 4/19/91; 3/31/92; 4/3-4/92; 4/6/92; 4/10/92; 4/15/92; 4/17/92; 4/19/92; 4/23/92; 4/26/92; 5/22/92; 5/29/92; 4/8/93; 8/24/93
L. scopul.	4/2-3/76; 6/4/91; 3/25/92; 4/20/01
L. leonii	5/8/79; 8/23/79; 6/11/89; 3/12/92; 3/18/92; 3/25/92; 3/30-31/92; 4/4/92; 4/8/92; 4/10/92; 4/18/92; 4/22/92; 4/28/92; 5/3/92; 5/6-7/92; 5/10/92; 5/14/92
L. arboreus	4/2/76; 4/4/76; 5/24/92
L. carinatus	5/9/79; 3/14/91; 6/18/91; 8-9/18/91; 5/25/92
L. sylvestris	4/26/79; 5/3/79; 4/24/83; 5/6/90; 8/18/91; 3/29/92
L. santamarinae	4/15/79; 4/17/79; 4/21-22/79; 4/27/79; 4/30/79; 5/1/79; 5/5/79; 5/8/79; 5/12/79; 5/6/90; 4/1/92
L. weingart. (*we.*)	6/8/91; 7/29/91; 8/15/91; 9/23/92; 11/2/92; 1/4/93; 6/13/93; 6/15/93; 8/11/93; 8/29/93; 9/8/93; 9/13/93; 9/21/93; 11/4/93
L. paniculatus	7/6-7/93; 7/11/93; 7/13/93
L. quadri. (*quad.*)	5/25/93; 6/3/93; 8/1/93; 8/10/93
L. quadri. (*parv.*)	5/22/92; 6/1-9/92; 11/9/92; 12/20/92; 4/12/93; 8/12/93; 9/9/93; 9/13/93
L. grantianus	1/29/01; 1/31/01; 4/12/01; 4/14/01

Table 26. Flowering dates used to study the duration of anthesis in *Leptocereus*.

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and then dissected to remove the seeds. A simple test for seed viability was performed by placing the seeds in petri dishes and keeping them moistened in wet filter paper until germination occurred.

8.4. Results

The reproductive biology of a cactus species depends largely on the shape, size, color and other morphological features of its flowers, and its phenological behavior. In *Leptocereus*, the flowers are tubular, campanulate or funnelform, and their length varies from 2 cm (*L. ekmanii*), to nearly 8 cm (*L. arboreus*). The diameter of a fully expanded bloom fluctuates from 1.1 or 1.5 cm (*L. ekmanii*), to 4.2 cm (*L. wrightii*), and the variation of the proximal (maximum) diameter of the receptacle tube is from 0.7 cm (*L. ekmanii*) to 2.7 cm (*L. arboreus* and *L. wrightii*). Stigma lobes, densely covered by minute papillae over the upper surface and along the edges, are usually enclosed, but in *L. ekmanii* these are manifestly exserted (Plate 21, E). Stamens may be enclosed (*e.g.*, in *L. arboreus* and *L. quadricostatus*), somewhat exserted (*e.g.*, in *L. carinatus*), or distinctly exserted from the receptacle tube, as in *L. chrysotyrius* (Plates 20, H and 21, G). The upper wall of the ovary and the ridge, to which the inner row of stamens is attached, demarcate a nectar chamber filled with a copious light honey-sweet secretion. In most species flowers are scentless or nearly so, but members of sections *Costanthus* and *Spinosissimus* of subgenus *Leptocereus* (*i.e.*, *L. arboreus*, *L. carinatus*, *L. sylvestris*, and *L. santamarinae*) may have a light, somewhat unpleasant smell.

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Although the most frequent color of inner perianth segments is white, or creamy, they can also be pink (*e.g.*, *L. leonii*), orange (*e.g.*, *L. wrightii*), or yellow (*e.g.*, *L. prostratus*). Scent and color —when present— act as long-distance signals for attraction, while nectar and pollen production serve adequately the purpose of rewarding visiting animal vectors. During anthesis, perianth segments expand and bend outwards to various degrees. The expansion may lead to a strongly reflexed limb, such as that of *L. paniculatus* (Plates 20, G, and 24, A). In *L. chrysotyrius*, however, expansion ceases when segments are about perpendicular to the floral axis, the inner whorl forming a nearly flat, daisylike arrangement around the stamens.

Initiation of anthesis, here defined as the opening of the flower bud from the earliest formation of a small, 1 mm diameter pinhole at its tip, takes place in the evening or late afternoon in all but the five species of section *Leptocereus* of subgenus *Leptocereus*. In this section blooms begin to open in the morning or around noon (exceptionally early afternoon, in *L. albellus*). *Leptocereus ekmanii* is unique among the species of this group because its flowers initiate anthesis between 9:00 and 10:00 a.m., and close the following day at dusk. The maximum duration of anthesis recorded for this taxon, which is both diurnal and nocturnal, is 23 hours (Tables 27 to 29). The shortest anthesis period (10 to 12 hours) corresponds to the strictly nyctigamous (vespertinal) *L. quadricostatus* subsp. *parvispinus*. The relatively short-lived flowers of this latter taxon, and of all other *Leptocereus* taxa, are commonly for one single night nyctigamous, but some vespertine-matutinal species of this group may close their

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Table 27. Duration of anthesis in *Leptocereus*. IA, initiation of anthesis (hereby defined by presence of a 1 mm diam. pinhole at tip of floral bud); MA, point of maximum anthesis; IC, initiation of closing period; FC, flower closed (defined by the time when limb extends parallel to the longitudinal axis of flower; some species close beyond this point while some others do not). *Leptocereus. maxonii, L. wrightii* subsp. *gracilis,* and *L. weingartianus* subsp. *demissus* were not included in this study.

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TAXON	IA	MA	IC	FC
L. assurgens	12 m-1 p.m.	6:30-8 p.m.	10-10:30 a.m.	1-2 p.m.
L. chrysotyrius	11 am-12 m	7-8 p.m.	5:30-10 a.m.	8 am-5 p.m.
L. ekmanii	9-10 a.m.	12:30-3 p.m.	4-5:30 p.m.	6:30-8 p.m.
L. prostratus	9 am-4 p.m.	5-8:30 p.m.	8:30 am-1 p.m.	10:30 am-6 p.m.
L. albellus	3-4 p.m.	8:30-10 p.m.	10-11:30 a.m.	12 m-1pm
L. wrightii (*wr.*)	5:30-6:30 p.m.	9:30-10 p.m.	8-9:30 a.m.	9:30-11:30 a.m.
L. scopul.	5:30-7 p.m.	9-10 p.m.	10:30 am-12 m	12:30-1:30 p.m.
L. leonii	6:30-7:30 p.m.	9-10:30 p.m.	12:30-5:30 p.m.	3-8 p.m.
L. arboreus	6-7 p.m.	8-10 p.m.	7-9:30 a.m.	8:30-11 a.m.
L. carinatus	5:30-6:30 p.m.	8:30-10 p.m.	6:30-8 a.m.	7:30-9 a.m.
L. sylvestris	6-7 p.m.	8:30-11 p.m.	6:30-8:30 a.m.	8-9:30 a.m.
L. santamarinae	5:30-7 p.m.	8:30-10 p.m.	6:30-8:30 a.m.	7:30-9:30 a.m.
L. weingart. (*we.*)	9-10 p.m.	10:30-11:30 p.m.	4-8:30 a.m.	9:30 am-12:30 p.m.
L. paniculatus	8-9:30 p.m.	10-11:30 p.m.	8-10 a.m.	11:30 am-1:30 p.m.
L. quadri. (*quad.*)	5-8:30 p.m.	11 pm-12:30 a.m.	6:30-9 a.m.	9-11 a.m.
L. quadri. (*parv.*)	7-9 p.m.	11 pm-12 m	5:30-7:30 a.m.	6:30-9 a.m.
L. grantianus	6:30-8 p.m.	11 pm-12:30 a.m.	5:30-8 a.m.	7-10 a.m.

Table 27.

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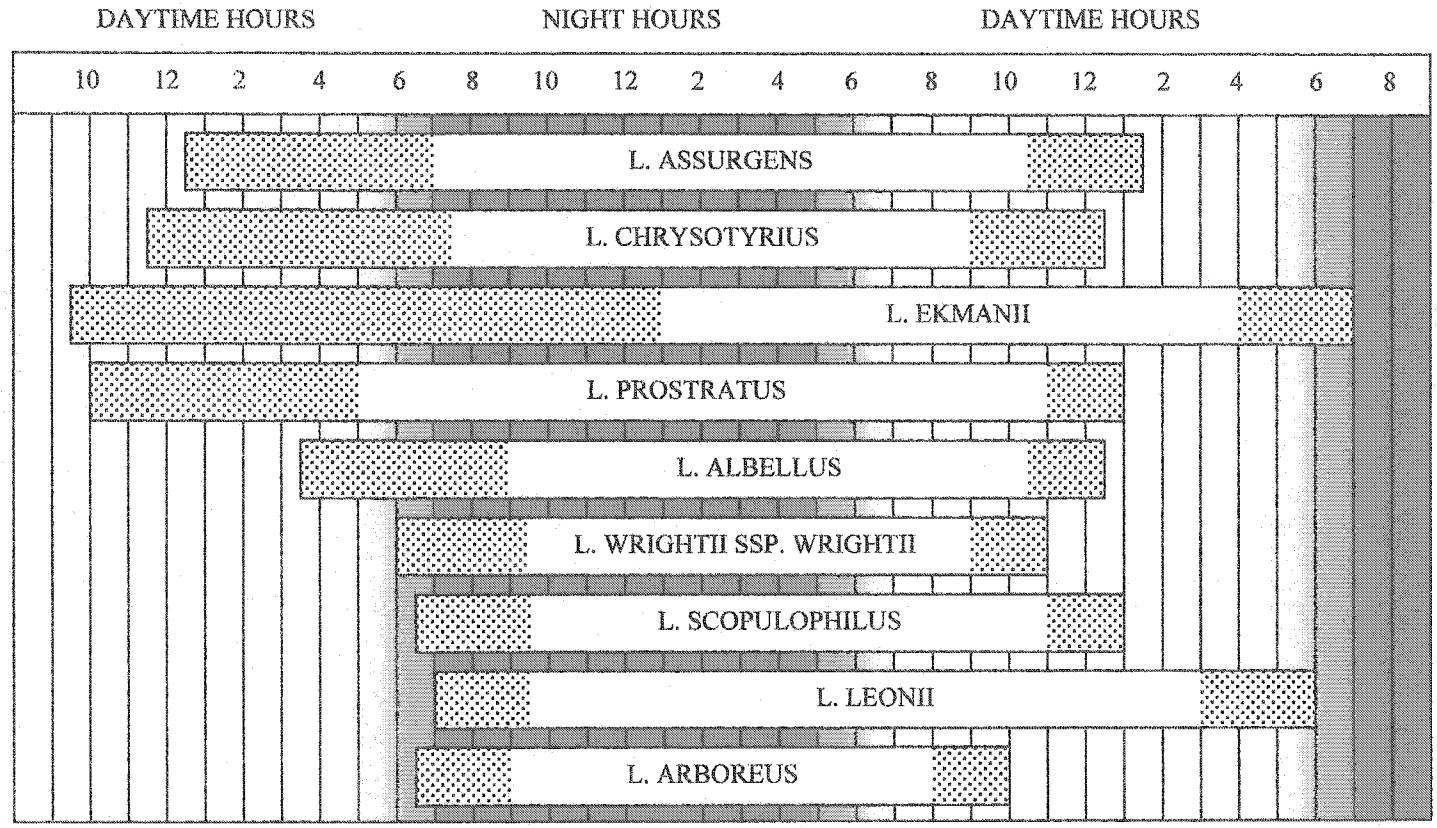

Table 28. Duration of anthesis in *Leptocereus*: graphical representation of Table 3. (I). Sections *Leptocereus, Roseiflori*, and *Costanthus* of subgenus *Leptocereus*. Shaded areas represent night hours; flower opening/closing periods are marked with small dots.

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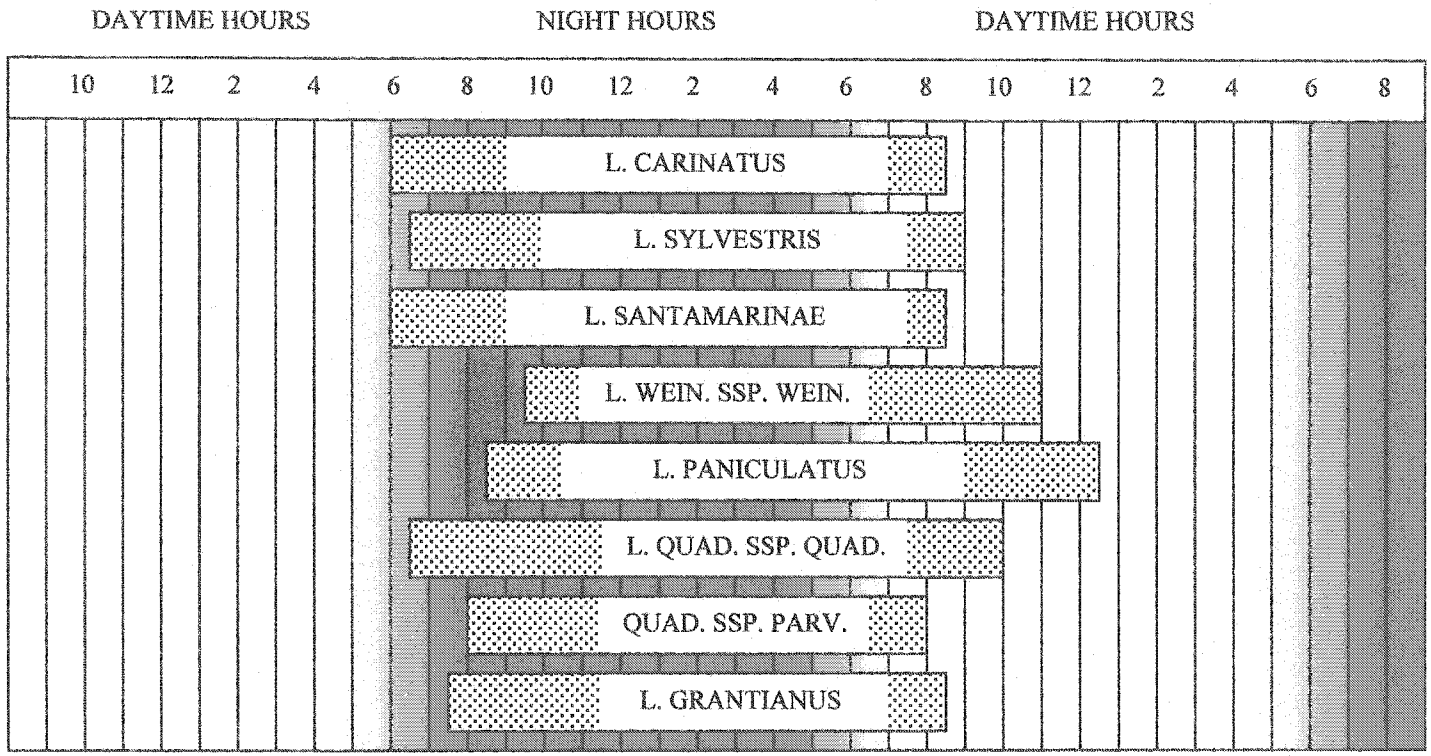

Table 29. Duration of anthesis in *Leptocereus*: graphical representation of Table 3. (II). Section *Spinosissimus* (subgen. *Leptocereus*), and sections *Tenuicaulis* and *Cephaliphora* (subgen. *Weingartianea*). Shaded areas represent night hours; flower opening/closing periods are marked with small dots.

flowers around noon. Under cloudy conditions, by exception, *L. leonii* can keep its bright-colored blooms open until the evening of next day (8:00 p.m.).

On the day of anthesis the rounded tip of the floral bud swells and outer perianth segments begin to separate slowly. About 2 to 4 hours after swelling a small hole appears at flower tip and usually the stigma becomes visible. At this point stigma lobes, which have already expanded, react positively with the peroxidase test indicating fully stigmatic receptivity. Having been infolded in bud, the lobes start to expand shortly before anthesis. In *Leptocereus*, expansion of stigma is very limited and lobes usually set at low angles (10 to 30°) with respect to the floral axis. However, lobe angles occasionally reach 45° in *L. ekmanii* (Plate 24, C, E), while in *L. scopulophilus* the stigma does not seem to distend at all (Plate 22, E). I presume that in this case pollen has to get trapped in the papillae of the edges of the lobes for its germination to take place. Like those of the adaxial surface, these papillae also exude a glutinous secretion that adheres pollen grains to the stigmatic surface. Anthers dehisce synchronously in all species studied, and pollen is released approximately 1 to 3 hours after initiation of anthesis. Duration of anthesis in *Leptocereus* is influenced by weather conditions, and most susceptible species seems to be *L. leonii*. Heavily overcast skies and eventual rain may delay closure of flowers of this taxon for up to five hours.

Coastal and subcoastal species of *Leptocereus* occurring in dry forests and drought-deciduous shrublands flower throughout the year, with peaks in the wet season

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(the timing of which varies across the Greater Antilles). For species occurring in semi-deciduous forests, namely *L. scopulophilus, L. leonii, L. carinatus*, and all members of section *Leptocereus* of subgenus *Leptocereus*, flower production increases during the dry months of December through March or April, probably due to an increment of solar radiation at ground level following defoliation of upper canopy. Whether coincidental with rainy periods or defoliation of upper canopy layer, flowering peaks seem to fit a steady-state pattern, extending over two to six weeks or more, with very few flowers produced per plant in a 24 hour period. The number of blooms yielded by each ultimate stem segment in a growing season varies from one to three (strictly apical or subapical, as in *L. arboreus*), to more than 30 including apical/subapical and lateral flowers, as in *L. ekmanii*. By contrast to the large flowers of *L. arboreus*, those of *L. ekmanii* are rather small and contain relatively little nectar —due to their small size— but because they open serially the flowering segment remains attractive to foragers for up to several weeks. *Leptocereus ekmanii*, which occurs in colonies at the summit of Sierra de Guane —an isolated haystack mountain range in western Cuba— is likely pollinated by small *Eurema* butterflies of local distribution (a native *Augochlora* bee was also recorded as a visitor). By occurring in relatively dense colonies and producing flowers that open serially is *L. ekmanii* capable to maintain a functional outcrossing system dependant on small local vectors. Hybridization with other Cuban haystack mountain dwellers such as *L. assurgens* and *L. prostratus* is practically impossible, inasmuch as pollinators of high energy expenditure cannot consistently feed from the little rewarding flowers of *L.*

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ekmanii while making long flights between haystack ranges (*e.g.*, those of Sierra de Guane, Sierra de San Carlos, and Sierra de Viñales).

As opposed to *Leptocereus* that blossoms sparingly almost throughout the year (with peaks coinciding with rainy epochs or partial defoliation of forest), blooming of *Cereus* (*Hamannia*) *fabiolae* is massive and synchronous. This strictly nyctaginous species has a short and very definite flowering period within the dry season, ranging from early December through January. Anytime during this two-month interval, but more often by late December, over 80% of all flowers produced yearly open synchronously in two to four consecutive nights. Such mass flowering is usually limited to plants growing in rather open situations and to the forest canopy —where they get plenty of solar radiation— probably because only such plants accumulate enough energy to divert to simultaneous bloom. These open or high situations allow pollinators with high energy requirements, such as bats, to locate the flowers without difficulty, and maneuver freely among them.

Leptocereus is not highly species-specific or even group-specific for pollinatiors, as in general more than one species of vector from different animal groups may be seen visiting various species of the genus. Tables 34 to 40 give the complete spectrum of visiting agents to the flowers of most species of *Leptocereus*, as I have observed. The lack of high specificity of the genus is not surprising, in view of the fact that no extreme floral syndrome is exhibited by any species in particular. Nonetheless, some

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preferences occur, founded on sets of morphological features that altogether usually favor one or two groups of pollinator agents over the others. The blooms of *L. arboreus*, for example, seem more close to a bat flower than to any other floral syndrome, while those of *L. ekmanii* are rather of the butterfly type. Although there are many indications that point to the hawkmoth syndrome as the dominant type in *Leptocereus*, evidences for bat, butterfly, bird, and bee pollination suggest that other animal groups may also play a role in the breeding system of this genus. In terms of species recorded, butterflies represent the largest group of visitors (42.1% of all records), but because many of them were presumably acting as commensals, it is uncertain if, as a group, they contribute significantly to pollination (Tables 30 and 31).

ANIMAL GROUP	N° OF SPECIES	%
Butterflies (Lepidoptera: Rhopalocera)	16	42.1 %
Moths (Lepidoptera: Heterocera)	13	34.2 %
Bees (Hymenoptera)	6	15.8 %
Bats (Chiroptera: Phyllostomatidae)	2	5.3 %
Hummingbirds (Apodiformes: Trochilidae)	1	2.6 %
TOTAL	38	100%

Table 30. Animal groups recorded as visitors to the flowers of *Leptocereus* spp.

Probably the most effective reproductive systems in *Leptocereus* are those involving wide-ranging pollinators such as hawkmoths, birds, and bats. In these "moth"

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TAXON	DISTRIBUTION
Butterflies (Lepidoptera: Rhopalocera):	
Agraulis vanillae Maynard	Greater Antilles to Dominica (Lesser Antilles)
Anartia jatrophae subsp. *guantanamo* Munroe	Native to Cuba, Bahamas and South Florida
Aphrissa orbis subsp. *orbis* Poey	West Cuba and the Cayman Islands
A. statira subsp. *cubana* D'Almeida	Greater Antilles (excl. Hispaniola); Cayman Isl.
A. statira subsp. *hispaniolae* Munroe	Endemic to Hispaniola
Appias drusilla subsp. *poeyi* Butler	Distributed in Cuba and the Bahamas
Ascia monuste subsp. *eubotea* Godart	Restricted to the Antilles
Danaus plexipus subsp. *plexipus* L.	Cuba; Bahamas; North and Central America
Dryas iulia subsp. *nudeola* Bates	Endemic to Cuba
Eurema daira subsp. *palmira* Poey	Restricted to the Antilles
E. lucina Poey	Endemic to western Cuba
Ganyra josephina subsp. *josephina* Godart	Endemic to Hispaniola
Heliconius charitonius subsp. *ramsdeni* C. & B.	Endemic to Cuba
Phoebis argante subsp. *formax* Butler	Endemic to Cuba
P. sennae subsp. *sennae* L.	Distributed in Florida and the Antilles
Rhabdodryas trite subsp. *watsonii* Brown	Hispaniola, Puerto Rico, and the Lesser Antilles

Table 31. Flower-visiting species to *Leptocereus* spp., and their approximate geographical distribution. (I). Butterflies. Distribution patterns from L. R. Hernández personal notes, National Museum of Natural History (unpubl.).

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and "bat" plants, few medium to large flowers are produced in each stem segment during a relatively long period of time. Each bloom provides a comparably great caloric reward, which allows their visitors to fly a regular path between them, even when the distances implied are considerable —*e.g.*, *Leptocereus santamarinae*, in the *Avicennia germinans* evergreen shrubland of northeastern Cuba, a community locally known as "playazo" that in Cayo Sabinal may extend continuously for tens of kilometers (Areces-Mallea *et al.*, 1999).

Moths (Lepidoptera: Heterocera) account for being the second largest group of vectors to be attracted by *Leptocereus* blooms: eleven species of nocturnal hawkmoths, in addition to two diurnal species, were seen on the flowers of this genus. They represent 34.2% of all visiting records (Tables 30 and 32). The hawkmoth syndrome is mainly exhibited by subgenus *Weingartianea*, and members of section *Costanthus* and *Spinosissimus* of subgenus *Leptocereus*. As to be expected, between 40 and 100% of all animal visitors to the flowers of these plants were moths (Tables 38 to 40). Section *spinosissimus*, which includes *L. sylvestris*, *L. maxonii*, and *L. santamarinae*, has comparatively more hawkmoth records (87.5 %) than any other section. None of these flowers, however, display the long slender tubes of typical moth-pollinated blooms, such as those of *Epiphyllum* and *Harrisia*, for example, and although pleasant, their scent is not particularly strong (in the Cactaceae, the hawkmoth syndrome is characterized by white or whitish, sweet-scented nyctigamous blooms, with long, slender floral tubes and abundant light nectar). Only the flowers of *L. weingartianus*

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subsp. *weingartianus*, which are conceivably more suited to pollination by hawkmoths than those of other species, have a somewhat narrow floral tube (Plates 20, B-E, and 21, B). Field observations have indicated, accordingly, that 80 % of the recorded visitors to this taxon are hawkmoths (Table 39).

TAXON	DISTRIBUTION
Moths (Lepidoptera: Heterocera):	
Aellopos tantalus L.	Antilles (except Jamaica); South America
Cautethia grotei subsp. *grotei* Edwards	Native to the Greater Antilles and Florida
Celerio lineata subsp. *lineata* Fabricius	Greater and Lesser Antilles
Cocytus antaeus subsp. *antaeus* Drury	Restricted to the Greater Antilles
Epistor lugubris subsp. *lugubris* L.	Widely distributed from Eastern U.S. to Argentina
Erinnys alope Drury	Dispersed from Florida to Argentina
Herse cingulata Fabricius	Widely distributed from Canada to South America
Phlegethontius sextus subsp. *jamaicensis* Butler	Restricted to the Greater Antilles
Pholus labruscae L.	Neotropical
Protambulyx strigilis L.	Dispersed from Mexico to Brazil
Pseudosphinx tetrio L.	Widely distributed from southern U.S. to Brazil
Uranidia boisduvalii Guérin	Endemic to Cuba
Xylophane pluto Fabricius	Southern U.S. to South America

Table 32. Flower-visiting species to *Leptocereus* spp., and their approximate geographical distribution. (II). Moths. Distribution patterns from L. R. Hernández personal notes, National Museum of Natural History, Havana, Cuba (unpubl.).

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Hawkmoths started their visits between 1.5 and 3 hours after dusk —if open flowers were available— and ended shortly before dawn. The peak visitation rate observed was 6 visits in one hour (*Herse cingulata*, in *L. santamarinae*). The insects hovered in front of the flowers for several seconds, inserting their long proboscides down to the base of the floral tube to reach the nectar chamber. Because small to medium-sized moths such as *Cautethia grotei* subsp. *grotei* were clearly seen coming into contact with anthers and stigma in the process of feeding (*e.g.*, in *L. assurgens*), I have no to doubt that these animals are efficient pollinators. It was not clear, however, if visits of larger moths resulted in pollination. Some of the very long-tongued species, particularly *Herse cingulata*, *Phlegethontius sextus* subsp. *jamaicensis*, and *Pholus labruscae*, seemed to never have been into contact with anthers and stigma, since their foraging maneuvers were too far off the flower's mouth. According to Nilsson (1988), hawkmoths do not approach blooms closer than it is necessary to forage nectar. Hence, those *Leptocereus* flowers that were significantly shorter than the moth's proboscis probably could not deposit pollen on the insects' body. It is questionable whether these large visitors are then acting as thieves, collecting nectar that would otherwise serve as an attractant for legitimate pollinators, or commensals that simply collect excess nectar. Inasmuch as the spectrum of animal visitors to the flowers of *L. arboreus* only included very log-tongued hawkmoths and bats, I presume that the winged insects are not the main agents of pollination of this species, but the phyllostomatid bats (Table 37).

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Bats seem to be part of the pollination syndrome of some *Leptocereus* species, particularly *L. arboreus*, whose flowers emit a sour odor reminiscent of cabbage (Table 33). The scent is not strong, but rather unpleasant. Such odors are characteristic of bat pollinated blooms (Faegri and Van der Pijl, 1979). Bat pollination is not uncommon in columnar cacti, having been reported in *Carnegia gigantea* (Alcorn *et al.*, 1959, 1961; McGregor *et al.*, 1962), *Stenocereus thurberi* (Alcorn *et al.*, 1962), *S. griseus* (Paulus, 1978), *Pachycereus schottii* (Grant and Grant, 1979), *Neobuxbaumia tetetzo* (Valiente-Banuet *et al.*, 1996), and *Pilosocereus catingicola* subsp. *salvadorensis* (Locatelli *et al.*, 1997).

The flowers of *L. arboreus*, *L. santamarinae*, and *L. wrightii* subsp. *wrightii* were visited by the glossophaginid (Phyllostomatidae) bat *Monophyllus redmani* subsp. *clinedaphus* (Tables 36, 37, and 38). This bat is characterized by its small size, weighting between 8 and 14 g (Silva-Taboada, 1979). Visits occurred sporadically throughout the night, but were more frequent between 8:30 p.m. and midnight. *Leptocereus wrightii* subsp. *wrightii* showed the lowest visitation rate (only 2 visits per flower in one night), while in *L. arboreus* the rate was up to 6 visits per flower in a 3-hour interval. Because the bat hovers in front of the flower and introduces its head in the upper receptacle-tube, pollen transfer seems inevitable. After a visit, portions of floral anthers and upper filaments can be seen either chewed, or missing. *Monophyllus redmanii* subsp. *clinedaphus* probably is, according to its body size and foraging behavior, an effective pollinator.

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TAXON	DISTRIBUTION
Bees (Hymenoptera):	
Apis mellifera L.	Cosmopolitan
Augochlora sp.	————
Ceratina cyaniventris Cresson	Endemic to Cuba
Exomalopsis pulchella Cresson	Native to Florida and the Greater Antilles
Megachile poeyi Guérin	Only in the Bahamas, Cuba and Jamaica
Xylocopa cubaecola Lucas	Endemic to Cuba
Hummingbirds (Apodiformes: Trochilidae):	
Chlorostilbon ricordii Astley	Only in Cuba and the Bahamas
Bats (Chiroptera: Phyllostomatidae):	
Monophyllus redmani subsp. *clinedaphus* Miller	Dispersed in the Bahamas, Cuba, and Hispaniola
Phyllonycteris poeyii Gundlach in Peters	Endemic to Cuba

Table 33. Flower-visiting species to *Leptocereus* spp., and their approximate geographical distribution. (III). Bees, birds, and bats. Distribution patterns of bees and hummingbird from L. R. Hernández and J. Genaro personal notes, National Museum of Natural History, Havana, Cuba (unpubl.). Bat distribution from Silva-Taboada, 1979.

Another bat species, *Phyllonycteris poeyii* (Phyllostomatidae: Phyllonycteridinae), was also caught visiting the flowers of *Leptocereus arboreus*, although less frequently (Table 33). While foraging, this medium-sized bat (15 to 29 g of body weight,

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Leptocereus assurgens:

LEPIDOPTERA		HYMENOPTERA
RHOPALOCERA (**Butterflies**)	HETEROCERA (**Moths**)	(**Bees**)
Phoebis sennae ssp. *sennae* L.	*Uranidia boisduvalii* Guér.	*Apis mellifera* L.
Dryas iulia ssp. *nudeola* Bates	*Cautethia grotei* ssp. *grotei* Edwards	*Xylocopa cubaecola* Lucas
Ascia monuste ssp. *eubotea* Godart		*Ceratina cyaniventris* Cresson
Aphrissa orbis ssp. *orbis* Poey		

Leptocereus chrysotyrius:

LEPIDOPTERA	HYMENOPTERA (**bees**)	AVES : APODIFORMES
RHOPALOCERA (**Butterflies**)		TROCHILIDAE (**Hummingbirds**)
Phoebis sennae ssp. *sennae* L	*Apis mellifera* L.	*Chlorostilbon ricordii* Astley
Phoebis argante ssp. *formax* Butler	*Megachile poeyi* Guérin-Méneville	
Dryas iulia ssp. *nudeola* Bates	*Exomalopsis pulchella* Cresson	
Heliconius charitonius ssp. *ramsdenii* C. & B.		
Anartia jatrophae ssp. *guantanamo* Munroe		

Table 34. Spectrum of animal visitors recorded in *Leptocereus assurgens* and *L. chrysotyrius*. *Uranidia boisduvalii* is a diurnal moth.

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Leptocereus ekmanii:

LEPIDOPTERA	HYMENOPTERA
RHOPALOCERA **(Butterflies)**	**(Bees)**
Eurema lucina Poey *Eurema daira* ssp. *palmira* Poey	*Augochlora* sp.

Leptocereus prostratus:

LEPIDOPTERA	HYMENOPTERA **(bees)**	AVES : APODIFORMES
RHOPALOCERA **(Butterflies)**		TROCHILIDAE **(Hummingbirds)**
Phoebis sennae ssp. *sennae* L. *Heliconius charitonius* ssp. *ramsdenii* C. & B. *Appias drusilla* ssp. *poeyi* Butler	*Apis mellifera* L.	*Chlorostilbon ricordii* Astley*

Table 35. Spectrum of animal visitors recorded in *Leptocereus ekmanii* and *L. prostratus*. No nocturnal observations were made on *L. prostratus*.

* Although no records were made in habitat, Cuban Emerald Hummingbirds were often seen visiting the flowers of a cultivated specimen of *L. prostratus* in Cojímar, Havana, about 180 km from the westernmost population of this species.

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Leptocereus albellus:

LEPIDOPTERA
RHOPALOCERA (**Butterflies**)
Ascia monuste ssp. *eubotea* Godart

Leptocereus wrightii subsp. *wrightii*:

LEPIDOPTERA		AVES : APODIFORMES	CHIROPTERA (**Bats**)
RHOPALOCERA (**Butterflies**)	HETEROCERA (**Moths**)	TROCHILIDAE (**Hummingbirds**)	PHYLLOSTOMATIDAE
Danaus plexipus ssp. *plexipus* L. *Agraulis vanillae* Maynard	*Pseudosphinx tetrio* L.	*Chlorostilbon ricordii* Astley	*Monophyllus redmani* subsp. *clinedaphus* Miller*

Table 36. Spectrum of animal visitors recorded in *Leptocereus albellus* and *L. wrightii* subsp. *wrightii*. No nocturnal observations were made on *L. albellus*.

* *Monophyllus redmani* subsp. *clinedaphus* is a glossophaginid (Phyllostomatidae: Glossophaginae) bat.

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Leptocereus leonii:

LEPIDOPTERA	HYMENOPTERA (bees)	AVES : APODIFORMES
RHOPALOCERA (**Butterflies**)		TROCHILIDAE (**Hummingbirds**)
Phoebis sennae ssp. *sennae* L.	*Apis mellifera* L.	*Chlorostilbon ricordii* Astley
Aphrissa statira ssp. *cubana* D' Almeida		
Dryas iulia ssp. *nudeola* Bates		

Leptocereus arboreus:

LEPIDOPTERA	CHIROPTERA (**Bats**)
HETEROCERA (**Moths**)	PHYLLOSTOMATIDAE
Herse cingulata Fabricius	*Phyllonycteris poeyii* Gundlach in Peters*
Phlegethontius sextus ssp. *jamaicensis* Butler	*Monophyllus redmani* ssp. *clinedaphus* Miller**

Table 37. Spectrum of animal visitors recorded in *Leptocereus leonii* and *L. arboreus*. No nocturnal observations were made on *L. leonii*.

* *Phyllonycteris poeyii* is a phyllonycterid (Phyllostomatidae: Phyllonycteridinae) bat.
** *Monophyllus redmani* ssp. *clinedaphus* Miller is a glossophaginid (Phyllostomatidae: Glossophaginae) bat.

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Leptocereus sylvestris:

LEPIDOPTERA
HETEROCERA (**Moths**)
Celerio lineata ssp. *lineata* Fabricius
Pseudosphinx tetrio L.
Cocytus antaeus ssp. *anthaeus* Drury

Leptocereus maxonii:

LEPIDOPTERA
HETEROCERA (**Moths**)
Erinnys alope Drury
Pholus labruscae L.

Leptocereus santamarinae:

LEPIDOPTERA	CHIROPTERA (**Bats**)
HETEROCERA (**Moths**)	PHYLLOSTOMATIDAE
Herse cingulata Fabricius	*Monophyllus redmani* ssp. *clinedaphus* Miller*
Phlegethontius sextus ssp. *jamaicensis* Butler	
Cocytus antaeus ssp. *anthaeus* Drury	
Pseudosphinx tetrio L.	

Table 38. Spectrum of animal visitors recorded in *Leptocereus sylvestris, L. maxonii* and *L. santamarinae*.

* *Monophyllus redmani* ssp. *clinedaphus* Miller is a glossophaginid (Phyllostomatidae: Glossophaginae) bat.

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Leptocereus paniculatus:

LEPIDOPTERA	
RHOPALOCERA (**Butterflies**)	HETEROCERA (**Moths**)
Aphrissa statira ssp. *hispaniolae* Munroe	*Aellopos tantalus* L.
Phoebis sennae ssp. *sennae* L.	*Xylophane pluto* Fabricius
	Pholus labruscae L.
	Protambulyx strigilis L.

Leptocereus weingartianus subsp. *weingartianus*:

LEPIDOPTERA	
RHOPALOCERA (**Butterflies**)	HETEROCERA (**Moths**)
Ganyra josephina ssp. *josephina* Godart	*Pseudosphinx tetrio* L.
	Epistor lugubris ssp. *lugubris* L.
	Herse cingulata Fabricius
	Protambulyx strigilis L.

Table 39. Spectrum of animal visitors recorded in *Leptocereus paniculatus* and *L. weingartianus* subsp. *weingartianus*. *Aellopos tantalus* is a diurnal moth.

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Leptocereus weingartianus subsp. *demissus*

LEPIDOPTERA
RHOPALOCERA (**Butterflies**)
Rhabdodryas trite ssp. *watsonii* Brown

Leptocereus quadricostatus subsp. *parvispinus*:

LEPIDOPTERA
HETEROCERA (**Moths**)
Erinnys alope Drury *Herse cingulata* Fabricius

Leptocereus quadricostatus subsp. *quadricostatus*:

LEPIDOPTERA	
RHOPALOCERA (**Butterflies**)	HETEROCERA (**Moths**)
Ascia monuste subsp. *eubotea* Godart *Rhabdodryas trite* subsp. *watsoni* Brown	*Erinnys alope* Drury *Protambulyx strigilis* L.

Table 40. Spectrum of animal visitors recorded in *Leptocereus weingartianus* subsp. *demissus*, *L. quadricostatus* subsp. *parvispinus* and *L. quadricostatus* subsp. *quadricostatus*. No nocturnal observations were made on *L. weingartianus* subsp. *demissus*.

according to Silva-Taboada, 1979) clings to the upper portion of the receptacle-tube, leaving distinct scratches and claw marks on it (perianth segments may be even torn apart by the animal). In view of the bat's conduct, I would also suspect that it is an effective agent of pollen transfer. To me, however, it is a mystery how this bat manages to avoid the pungent spines of the flowers' receptacle-tube when feeding.

Five species of *Leptocereus* were recorded to have bees as frequent visitors to their flowers: *L. assurgens, L. chrysotyrius, L. ekmanii, L. prostratus,* and *L. leonii* (Tables 33, 34, 35, and 37). The flowers of the first four species promote bee pollination because their visible color spectrum matches that preferred by bees: bright yellow. The fifth species, *L. leonii*, has reddish and pink flowers that are also attractive to hymenopteroid insects. Aside from their mostly bright color, a typical bee flower usually has a cup-shaped perianth with actinomorphic symmetry, and nectar and pollen —the pollinator rewards— are accessible to the insects. Since nectar in *Leptocereus* flowers is hidden in narrowly closed nectar chambers that are virtually inaccessible to bees, the abundant pollen may be the reward. The clustering of the stamens of *L. chrysotyrius* in a relatively compact fascicle that is exserted from the floral mouth, with all the anthers densely set on the flat top, seems to be an effective secondary adaptation for attracting pollen gathering bees (Plates 20, H; 21, G, and 25, D). Abundance of pollen as a compensating factor for the lack of nectar in the Cactus family has been documented in *Echinocereus engelmannii* (Cota, 1993). Also, the rather small amounts

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of nectar produced by the bee pollinated flowers of *E. viridiflorus* is certainly not the major reward to the insects, but pollen (Leuck and Miller, 1982; Cota, 1993).

The bee-visited species reported in this work all pertain to Cuban sections *Leptocereus* and *Roseiflori* of subgenus *Leptocereus*, and probably not by coincidence they have the longest period of anthesis (Table 28), and some of the widest spectra of animal visitors. Native bees were noted as frequent visitors in *L. assurgens, L. chrysotyrius,* and *L. ekmanii*, while only cosmopolitan *Apis mellifera* bees were seen in *L. prostratus* and *L. leonii* flowers. Because each of the five native bees were not recorded in more than one species of *Leptocereus* (Tables 34 and 35), it would be interesting to check if there is some kind of flower fidelity or specific preferences by these insects, or, if it is just that we need to spend more time on diurnal surveys to complete the pollination spectrum of these plants. I presume that the recorded bees do not exhibit selective behavior in choosing a particular bee flower in the species-rich communities of the haystack mountains of western Cuba, where staggering of synchronous blooming by different species throughout the year (allowing utilization of the same species of pollinators for many species of plants) seems to be the usual condition.

Floral attributes other than those that promote generalist bee pollination co-exist in the flowers of all members of sections *Leptocereus* and *Roseiflori*. Because they attract animal vectors from additional groups (*i.e.*, butterflies and birds), these attributes

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may eventually cause stochastic pollination. Butterflies (Lepidoptera: Rhopalocera) are very common visitors to the bright-colored blooms of western Cuban *Leptocereus*, perhaps an unusual behavior for a group of invertebrates that was thought not to show much interest in cactus flowers. Typical butterfly blooms are salverform (*i.e.*, hypocrateriform), that is, with a relatively long narrow tube abruptly expanded into a shorter, essentially flat spreading limb acting as a platform for the insects to land. According to Rowley (1980), from hawkmoth blooms the most patent distinctions are the colored perianth, lack of scent, and daytime opening. These three distinguishing characteristics are present in *L. assurgens*, *L. chrysotyrius*, *L. ekmanii*, and *L. prostratus*.

In reality, no cactus flower is adapted to butterfly pollination as are those of, for example, the Apocynaceae and Rubiaceae, but neither are the so-called "bee flowers" of the Cactaceae comparable in specialization to those of the Scrophulariaceae and Lamiaceae. Why then has the occurrence of the bee syndrome in cactus flowers been so well acknowledged and the butterfly syndrome has not? First, for the reason that bee pollination is the most common pollination system in the family. Second, due to the unfortunate fact that *Leptocereus* taxa are rare and particularly underrepresented —or not represented at all— in most live cactus collections, and herbaria (the unmistakable small salverform flowers of *L. ekmanii* would not have passed unnoticed since 1931). Third, because Faegri and Van der Pijl in their classic work (1979) stated that one of the most obvious features of butterfly flowers, apart from being salverform, is their

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large size. This may be true for all continental Paleo- and Neotropical floras, but certainly does not apply to the individual floras of the Caribbean Islands. As a matter of fact, one of the most striking features of Antillean plants, and particularly of those of Cuba, is "micranthia," *i.e.*, the abundance in small-flowered taxa (Borhidi, 1996). Many of these small flowers are associated with an abounding and extremely rich micro-lepidopteroid fauna of very local occurrence.

There is little doubt that the small, 2 cm long salverform flowers of *L. ekmanii* (Plate 24, C, E), and also those of *L. chrysotyrius*, with their bright yellow, flat dish-like landing stage (Plates 20, H; 21, G, and 25, D), are appealing to butterflies: about 56 % and nearly 67 % of all the recorded visitors to these species, respectively, belong to this insect group (Tables 34 and 35). With no exceptions, these minute visitors, one of which (*Eurema lucina*) is endemic to Western Cuba, have a restricted Caribbean distribution (Table 31.). The contribution of other butterflies to pollination is, however, more questionable. Some species such as *Ascia monuste* subsp. *eubotea*, and *Rabdodryas trite* subsp. *watsoni*, occasionally landed on the flowers of the nyctigamous species *L. quadricostatus* (subsp. *quadricostatus*) in the morningtime, well into the course of their closing period. Apparently, the butterflies were acting as minor nectar-thieves, but in the absence of information about the flower's ability to reabsorb excess nectar, it is unclear whether these insects have a net negative or indifferent effect on the cactus plant. Additional work is needed to assess the individual role of these and other butterfly species in the pollination biology of *Leptocereus*.

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The common Cuban Emerald hummingbird was observed visiting the blooms of three species of *Leptocereus* (subgen. *Leptocereus*) in the wild, in search of nectar: *L. wrightii* and *L. leonii* (section *Roseiflori*), and *L. chrysotyrius* (section *Leptocereus*). This hummingbird was also seen repeatedly inserting its beak in the open flowers of a cultivated specimen of *L. prostratus* (subgen. *Leptocereus*, section *Leptocereus*), in Havana (Tables 34, 35, and 36). During nectar foraging the birds approached the flowers directly and hovered for several seconds in front of them. Visits were more frequent in the early morning (6:00-7:30 a.m.) and lasted until mid morning (around 10 or 10:30 a.m.). As many as four visits per hour were observed in this period of time. Emerald hummingbirds also visited the flowers of *L. chrysotyrius* and *L. prostratus* during the opening period between mid morning and early afternoon, when expansion and bending of perianth segments were not yet completed (at this time, however, the stigma was receptive and anthers had already dehisced). Except for the yellow-flowered *L. prostratus*, all the mentioned *Leptocereus* species have reddish floral tubes. *Leptocereus leonii* and *L. wrightii*, in addition, have pink and orange perianth segments, respectively.

Most members of section *Roseiflori* of subgenus *Leptocereus* exhibit distinctive features of the hummingbird —or bird—floral syndrome, such as medium to small size, non-scented, diurnal (in part) flowers, with relatively short, reddish to orange perianth segments. Nectar is light and copious. Since *L. leonii* has the reddest blooms and the maximum duration of anthesis within this section, covering most of the daytime if

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conditions are favorable, I would suspect that in this taxon diurnal pollination is more likely to occur, than vespertinal (Table 28). Complete lack of scent in the flowers may support this supposition. Thorough night surveys should be made, however —including proof of stigma contacts and study of pollen loads on vectors— before discarding cross-pollination of this species by nocturnal animals.

Leptocereus is, essentially, a semi-incompatible genus: both spontaneous and hand self-pollinated flowers failed to form fruits in 10 out of 16 species tested (62.5 %). Only six species, *L. leonii*, *L. chrysotyrius*, *L. albellus*, *L. maxonii*, *L. quadricostatus* (both the typical form and the new subspecies), and *L. grantianus* produced fruits after the selfing treatment, and seed set occurred in all of them. These seeds were over 90 % viable, as indicated by their ability to germinate in wet filter paper at room temperature. Except for *L. arboreus* that was not scrutinized, viability of pollen of *Leptocereus* was also very high. Depending upon the taxon, between 83 and 94 % of pollen grains (300 grains examined in each taxon) was viable as assessed by aniline blue stainability.

8.5. Discussion

Looking at the genus *Leptocereus* as a whole, it is obvious that it manifests high diversity in its floral biology, much of which reflects interspecific differences in its pollination biology. Several elements may account for this diversity, but the most important and influential one seems to be a combination of strong selective pressures,

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acting on populations separated by highly efficient isolation mechanisms that existed during relatively long periods of time. In isolated populations, these selective pressures eventually led to phenological adaptations to new habitats and new pollinators, following various events of coastal migration. Isolation was due to, or favored by insularity (external isolation), and other geographical and topographical factors (internal isolation), while migration of costal habitat was caused by eustatic changes in sea level and active emergence/subsidence dynamics of Caribbean Islands since Late Eocene. Many open coastal habitats with strict nyctigamous *Leptocereus* populations were probably left behind after the great sea regression of Late Miocene. As a matter of fact, a number of ancient, elevated rocky shore lines that ended up inland, far away from the sea, can be observed today in western Cuba, where the highest species diversity of the genus occur. I presume that shortly after the sea began to retreat from the coastal cliffs, these *Leptocereus* populations initiated a gradual adaptation process for survival in the denser, more humid and shady inland habitats. Because under a dense canopy layer bats and large hawkmoths cannot not maneuver as well as in open coastal habitats, the isolated plants began their shift in pollination system, a process that seems to be actively continuing today (Figs. 11 and 12).

The short-lived flowers of *Leptocereus* age rapidly and start to turn black shortly after pollination, enabling the plant to put its energy into fruit production and probably also encouraging pollinators to visit other younger flowers of the same plant. It is remarkable how the species of *Leptocereus* have learned to juggle two apparently conflicting factors:

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Fig. 11. Possible trend towards pollination by diurnal animal vectors in *Leptocereus* based in the total number of visiting species (I).

A. *L. arboreus*. **B.** *L. santamarinae*. **C.** *L. sylvestris*. **D.** *L. weingartianus* subsp. *weingartianus*. *L. arboreus* is more often visited by bats, while *L. santamarinae* shows more affinity for hawkmoths. The flowers of *L. sylvestris* and *L. weingartianus* ssp. *weingartianus* seem taylor-made to fit a hawkmoth but because those of the latter species remain open until 9:00-11:00 a.m., they also receive butterfly visitors. Ordinate numbers of y-axis represent the number of animal species reported as visitors. NL: nocturnal Lepidoptera (moths); DL: diurnal Lepidoptera (butterflies and diurnal moths); BATS: bats (Chiroptera). Blocks representing strictly diurnal animal vectors, in light gray.

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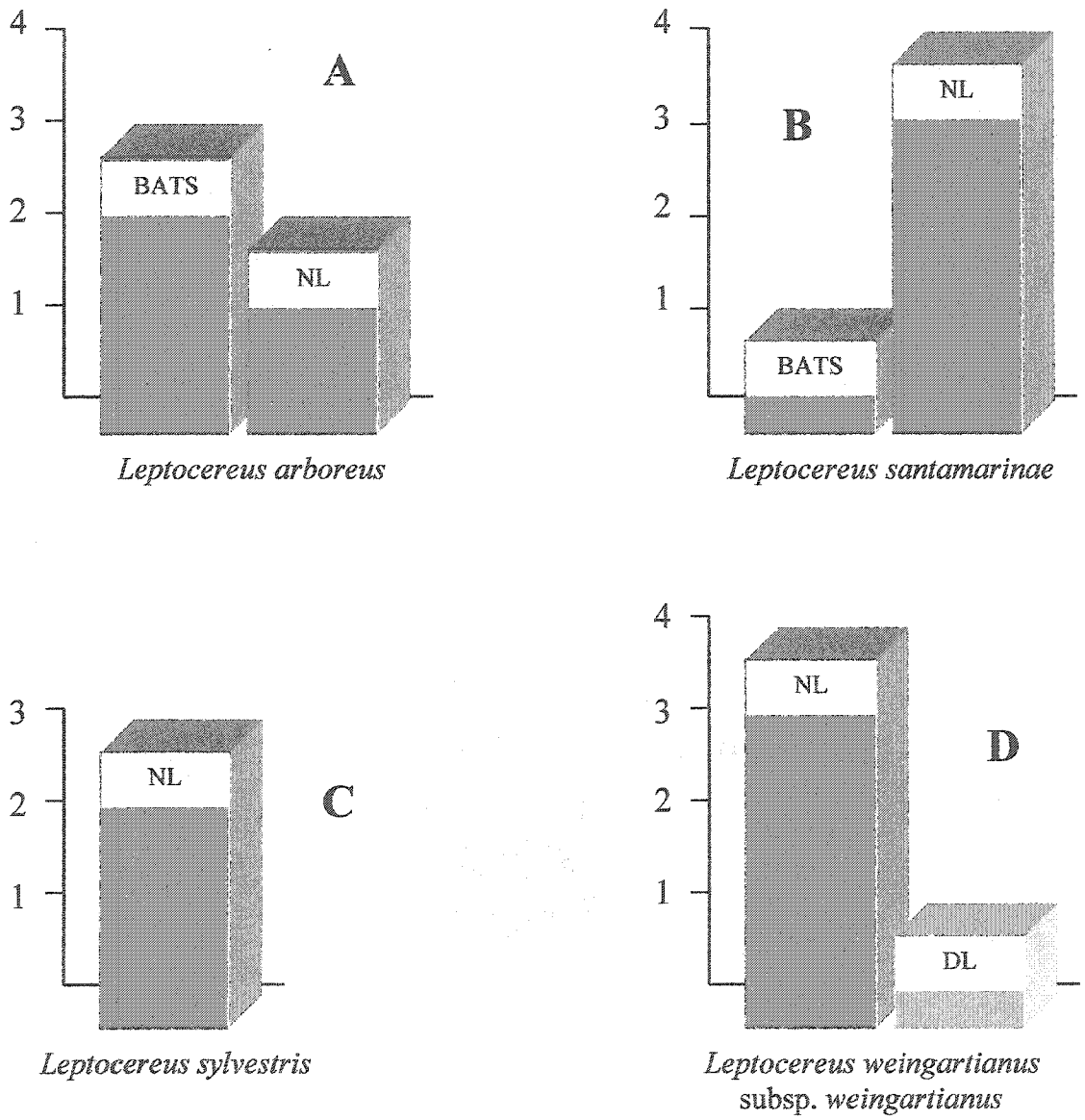

Fig. 11.

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Fig. 12. Possible trend towards pollination by diurnal animal vectors in *Leptocereus* based in the total number of visiting species (II).

A. *L. paniculatus*. **B**. *L. wrightii* subsp. *wrightii*. **C**. *L. assurgens*. **D**. *L. chrysotyrius*. *Leptocereus paniculatus* seems to indiscriminately exploit butterflies and moths as pollinators. However, the widest pollination spectrum is apparently exhibited by *L. wrightii* ssp. *wrightii*. *Leptocereus assurgens* and *L. chrysotyrius* also seem to adjust to different pollinator agents, mostly active during daytime. Ordinate numbers of y-axis represent the number of animal species reported as visitors. NL: nocturnal Lepidoptera (moths); DL: diurnal Lepidoptera (butterflies and diurnal moths); BATS: bats (Chiroptera); BEES: bees (Hymenoptera); BIRDS: hummingbirds (Apodiformes: Trochilidae). Blocks representing strictly diurnal animal vectors, in light gray.

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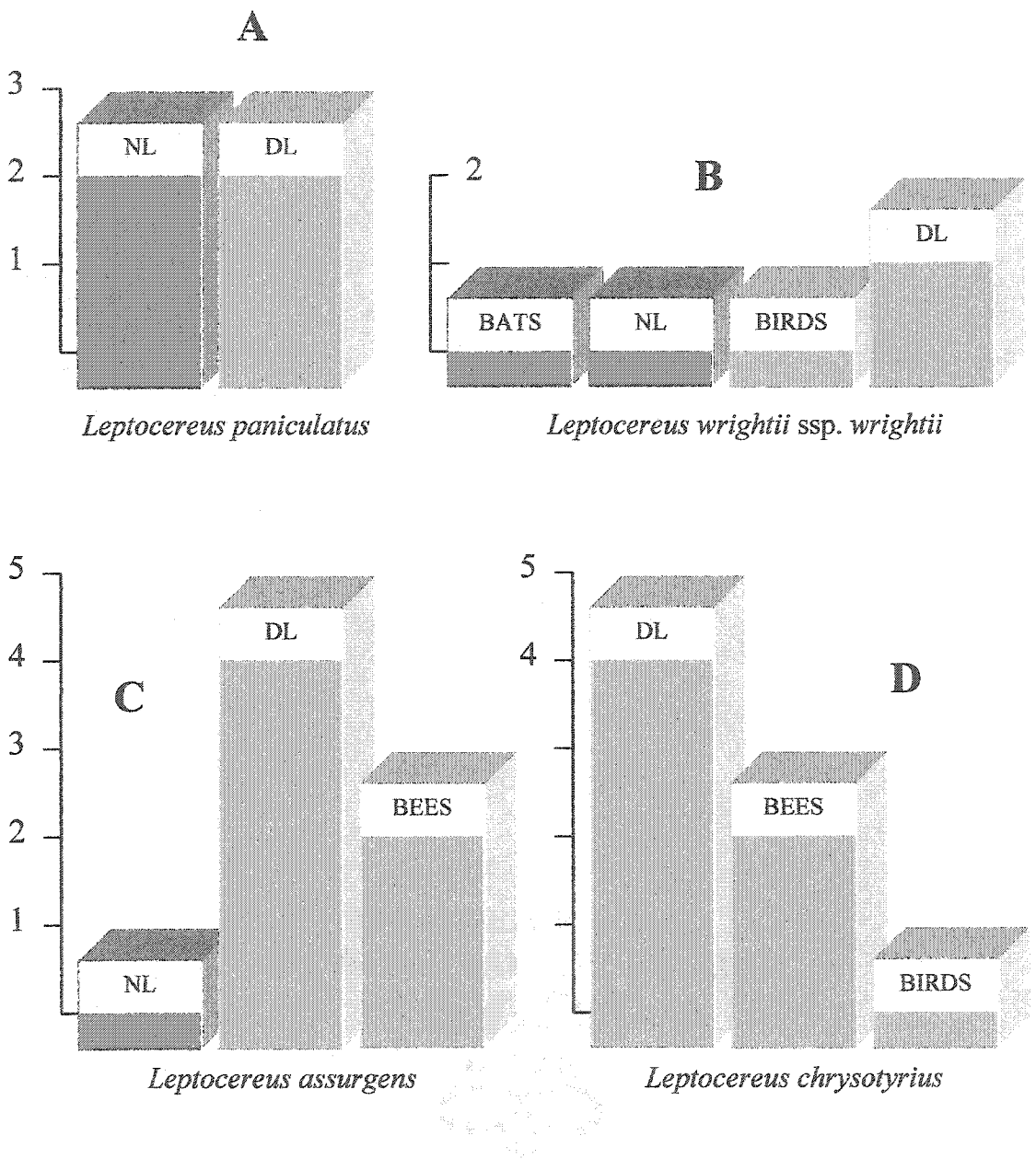

Fig. 12.

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the cost of producing a flower, with all its areoles, spines, perianth segments and functional structures, and the need to keep it open long enough to achieve pollination. I presume that producing a fleshy, spiny flower consumes a significant portion of the energy that a *Leptocereus* plant hardly garners with its reduced photosynthetically active surface. Keeping this flower open also drains energy from the cactus plant, and the soft, delicate inner perianth segments, stamens and stigma lose water rapidly to the dry air.

Most *Leptocereus* habitats but especially those in coastal areas are warm, windy and very sunny. In such places, where rates of solar radiation are about as high as they can possibly get in tropical areas (at sea level), and moisture is in particularly short supply, it seems cheaper for these plants to produce new flowers than to maintain existing ones. Strict nyctigamous species of *Leptocereus* (*e.g.*, *L. arboreus*, *L. sylvestris*, *L. santamarinae*) mitigate the loss of water during anthesis by opening their flowers at night. For those species that keep their blooms open some extra hours during daytime (*e.g.*, *L. wrightii, L. leonii, L. chrysotyrius*) the possibilities to be visited by pollinators increase so dramatically that for all one it seems worth the energy and water costs. The flowers of *L. ekmanii* are rather small and cannot rely upon bats and large hawkmoths for pollination. However, they seem to have developed highly efficient lock-and-key relationships with small *Eurema* butterflies (*E. lucina* and *E. daira*). Bats, hawkmoths, bees, butterflies and hummingbirds in *Leptocereus* habitats are so abundant and active that even short-lived flowers opening for 8 to 10 hours are likely to

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be visited by pollinators. Cooler climates, for example, often support fewer pollinating animal vectors, which sometimes must wait several hours in the morning before their muscles have warmed up sufficiently to permit flight. Cool weather, especially when it is cloudy or rainy, also reduces the rate of both photosynthesis and water loss, however, and it may be more economical under these conditions to keep existing flowers open than to produce new ones. As opposed to *Leptocereus*, for example, an individual flower of the lady-slipper orchid *Paphiopedilum hirsutissimum* may last for an entire month (Primack, 1999).

Except for *L. weingartianus* subsp. *weingartianus*, and *L. paniculatus*, which extend to Haiti and the Dominican Republic, all *Leptocereus* taxa occur in small, isolated populations. Beside the two aforementioned taxa, which seem to be self-incompatible, more than half of the species represented by a relatively small number of individuals maintain breeding systems that prevent self fertilization. Because self-incompatibility (SI) carries such weight within the genus, I am inclined to hypothesize that *Leptocereus* evolved from a primarily outcrossing ancestor with a functional SI system. Perhaps the maintenance of variability in the small populations is so highly selected that autogamy is not possible. It is surprising, however, that under the extreme ecological conditions prevailing in the nearly inaccessible karstic limestone ranges of western Cuba, no *Leptocereus* species tried autogamy as a mechanism to gain phenotypic uniformity. When a plant finally adapts to thrive on bare, cavernous rock on top of a vertical cliff, a high degree of phenotypic uniformity may be advantageous.

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Maybe it was the abundance of potential pollinators in these otherwise floristically rich and humid areas that prevented the shift to self-pollination (autogamy). In *Melocactus praerupticola*, for instance, a mountain species of Hispaniola occurring on very steep, nearly vertical cliffs, morphology of individuals is fairly uniform and corresponds well to habitat requirements (Areces-Mallea, 2000). This is to be expected because outcrossing rarely or never takes place, and seed sets largely —or maybe wholly— by self-pollination. Selfing, as an alternative system to outcrossing in the relatively cold environment of the upper Cordillera Central of Hispaniola, may well respond to a significant reduction of winged animal vectors at over 1000 m altitude.

Despite the numerous animal vectors reported as visitors to the flowers of subgenus *Leptocereus*, section *Leptocereus* of western Cuba, including *L. assurgens, L. chrysotyrius, L. ekmanii, L. prostratus*, and *L. albellus*, fruiting in this group constitutes a rare event. Except for one reference in *L. prostratus* (Britton and Rose, 1919-1923), there is no other information on literature on the subject, and no true fruit of any of these species from either wild or cultivated plants exists in any dry or liquid-preserved collection.

All but two species of section *Leptocereus* (*L. chrysotyrius* and *L. albellus*) failed the autogamy test, and only two and one fruit, respectively, was all that could be obtained after multiple trials. In wild populations, ovaries are prone to abort and fall off several days after anthesis. The reason why members of this section rarely set fruits

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may be related to population size: perhaps the total number of organisms of these species became so small that most individuals now share the self-incompatibility (SI) allele, the loss of S alleles being due to the genetic drift caused by reduction of populations. If so, most populations are actually clones of a single lineage. This hypothesis is supported by the finding that the pollen grains of all members of section *Leptocereus* are viable. Population reduction in the nearly inaccessible limestone ranges of West Cuba may have occurred, but certainly not caused by human activity.

An alternative explanation to population size is polyploidy. Different ploidy levels occur in the Cactus family, and it has been hinted that polyploidy is an event that has led to speciation in this group (Cota and Philbrick, 1994; Pinkava *et al.*, 1985). A series of relatively recent polyploidization events may have originated the "infertile" species of section *Leptocereus*. If this is true, low genetic diversity of populations is expected, and infertility could be explained by meiotic problems resulting from polyploidy, but this has to be proven with chromosomal studies. The pollen grains of the presumably infertile species *L. assurgens* and *L. ekmanii*, however, develop normally. Whatever the cause might be, if the section simply lacks the capacity to set fruits regularly, the development of an effective mechanism for asexual reproduction should have occurred. No such mechanism, however, has been recognized so far in the group: stem segments do not abscise, and aborted ovaries never proliferate or develop roots as in many Opuntioids. Agamospermy, which is not rare in the Cactaceae (Cota, 1993; Naumova, 1992), has not been checked, but this event is totally irrelevant in a group that seldom

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—or never— sets fruits. Much further work is needed, however, to elucidate these interesting problems.

After documenting both, the floral and pollination biology of the vast majority of the species of *Leptocereus* —as circumscribed in this work— the next challenge is to explain the evolutionary mechanisms that have led to this floral diversity. Fortunately, I produced a phylogenetic scheme of the genus based on combined morphological and molecular data, so a number of specific questions can be addressed and their possible answers examined. Which, for example, could have been the basic pollination type in the genus? To what extent has natural selection influenced individual characteristics so as to improve pollination efficiency by the current pollinating vectors? Which floral traits are ancestral and which are secondary adaptations?

As mentioned earlier, most cactus scholars consider bee pollination to be the primitive condition, while hawkmoth, bird, and bat pollination are regarded as derived. In *Leptocereus*, by contrast, the trend towards producing a flower that is appealing to bees seems to be a derived condition present in section *Leptocereus* of subgenus *Leptocereus*. Based on the strict consensus phylogram determined earlier in this work from parsimony analysis of combined morphological and molecular data (Fig. 9), I presume that the primitive, ancestral flower type of *Leptocereus* must have been a relatively large, nyctigamous bloom that was indistinctively visited by hawkmoth and bats. Seemingly, it was from this hawkmoth/bat pollinated ancestor whose flowers must

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have looked very much like those of *L. arboreus*, that floral types with secondary attributes or adaptations for attraction of bees, butterflies, and birds had evolved. This explains why the moth syndrome attributes occur in two subgenera, in relatively unrelated sections (sections *Weingartianea* and *Costanthus*, for example), in dissimilar life form and habitat preference. *Leptocereus weingartianus*, with smaller, narrowly tubular flowers, soon perfected the hawkmoth attracting syndrome and abandoned bats as potential pollinators. The extended phenology of other species, particularly those of sections *Leptocereus* and *Roseiflori* of subgenus *Leptocereus* is, accordingly, a consequence of secondary adaptations to additional pollinators. In some instances, *e.g.*, *L. assurgens, L. chrysotyrius,* and *L. leonii*, these additional pollinators seem to play a more important role than the supposedly primary ones. Most important secondary adaptations for attraction of additional pollinators in *Leptocereus* are: clustering of stamens in an exserted staminal fascicle with great production of pollen; flattening of the floral limb to produce a dish-like landing stage; presence of brightly colored betalain pigments in the perianth segments and floral tube; and extension of the anthesis period to allow diurnal pollinators to visit. Champion in the "art" of adjusting to the needs of different potential pollination vectors by means of secondary adaptations, is *L. wrightii* subsp. *wrightii*; its spectrum of animal visitors include butterflies, moths, birds, and bats (Table 36; Plate 22, A, B). By contrast to the primitive, unselective flowers of *Pereskia*, the flowers of *L. wrightii* subsp. *wrightii* became secondarily selective for a wide range of potential pollinators. It is, however, unclear, if these have a positive, negative, or neutral effect on the species' reproductive output.

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Because in *Leptocereus* a presumably hawkmoth/bat flower may be ancestral, relationships of this genus with groups of Central and South American columnar Cactoideae where these floral types are more common, should be investigated. With all its plesiomorphic traits, it is by no means impossible that *Leptocereus* is actually the basal genus —phylogenetically speaking— of tribe Pachycereeae.

During the long and tedious hours spent in the field recording possible pollinators, some animals were found to have non-anthecological relationships with *Leptocereus* (Plates 53 and 54). Whether these interactions are favorable or detrimental to the plants, we do not know. Based solely on my observations I assume that *Leptocereus* reproduces, at least for the most part, by seeds. Stem segments do not detach easily, so any vegetative dispersal mechanism comparable to that of many Opuntioids (*e.g.*, *Consolea*, *Cylindropuntia*, *Opuntia* series *Curassavicae*) is discarded. However, old, fallen trees of *L. santamarinae* were seen regenerating a year after a hurricane passed. In highly disturbed areas, many observations on rooting of branches severed by machetes were frequently made. No predator was seen foraging on fruits other than hermit crabs, but conceivably the reddish fruits of *L. leonii* are appealing for birds. Indeed, more fieldwork is needed to answer these interrogations. Perhaps we should have payed close attention to Rowley (1980) when he suggested to go to the field to pursue research on cactus-animal interactions. Many of us would have been better employed in these tasks than in the never-ending obsessive search for new species!

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Plate 53. Animal life related to *Leptocereus* spp. (I).

A. Larva of the cactus moth, *Cactoblastis cactorum*, on the West Indian prickly pear *Opuntia dillenii*. Very fortunately, the unpalatable stems of *Leptocereus* are not attractive to this devastating South American pest recently introduced to the Caribbean. **B**. Male Arctiidae moth, *Ecpantheria icasia*, resting under the spines of *Leptocereus quadricostatus* subsp. *quadricostatus* shortly after matting. **C**. Female moth of same species laying eggs on a stem segment of *Leptocereus quadricostatus* subsp. *quadricostatus*. **D**. Close-up of package of eggs after being laid. **E**. Largest of Cuban endemic rodents, *Capromys pilorides*, feeding on *Stenocereus hystrix*. *Capromys* teeth markings on the bark and cortex of *Leptocereus arboreus* have been recorded near Yaguanabo, South-central Cuba. Grazing on these columnar cacti may come into play most dramatically during drought cycles because these plants become the most important source of water for the rodents. **F**. On clear nights it is relatively common to see brown grasshoppers (Locustidae: *Schistocerca pallens*) resting among the spines of *Leptocereus quadricostatus* subsp. *quadricostatus* in coastal grasslands. This practice may well deter insectivorous bats from assaulting. **G**. Cuban tree frog concealed from sight among the ribs of a cultivated *Dendrocereus nudiflorus* cactus. Tree frogs also tend to hide during daytime in cultivated *Leptocereus santamarinae*, *L. arboreus* and *L. wrightii* specimens. (A, E, from from Guantánamo Naval Station, Guantánamo Bay, Cuba —9 Oct 1996; B-D, F, from Salinas de Cabo Rojo, Puerto Rico —10 Jan 1996; G, from my cactus collection at Cojímar, Cuba —12 Jun 1988).

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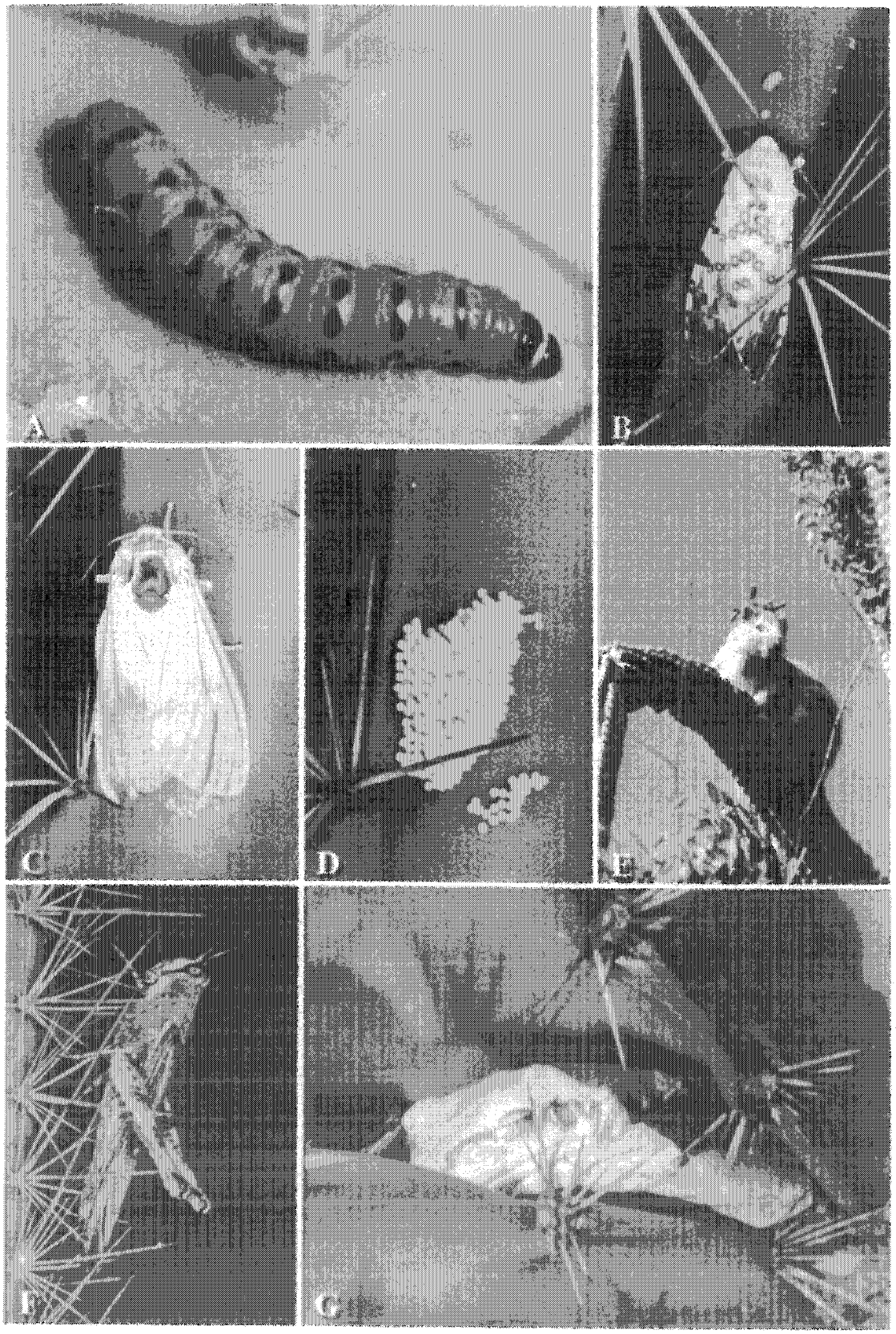

Plate 53.

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Plate 54. Animal life related to *Leptocereus* spp. (II).

A. The yellow-banded legs of the spider *Argaeopea* sp. mimic the shaded pattern exhibited by the spines of *Leptocereus carinatus* under strong sunlight. **B**. A large Caribbean hermit crab (*Coenobita clipeata*) feasting on the fallen fruit of the cactus *Harrisia taylorii*. This same crab species has been seen nourishing —during nighttime— on the semi-rotten fruits of *Leptocereus santamarinae*, in Cayo Sabinal, Cuba; it is the only animal known to benefit from a *Leptocereus* fruit. **C**, **D**. The small lizard *Anolis cristatellus* likes to sunbathe on *Leptocereus quadricostatus* subsp. *quadricostatus*. **E**. A young *Leptocereus sylvestris* plant is a secure place to nest. **F**. The grown chick of a presumably migratory warbler still returns to the nest pictured in E to spend the night. **G**. Common ground dove (*Columbina passerina*) perching on *Leptocereus quadricostatus* subsp. *parvispinus*. The ground dove is an abundant resident of coastal habitats in the West Indies. (A, from Sierra de Najasa, Cuba —12 Sep 1990; B, from Guantánamo Naval Station, Guantánamo Bay, Cuba —14 Oct 1996; C, D, from Salinas de Cabo Rojo, Puerto Rico —10 Jan 1996; E, F, from Cabo Cruz, Cuba —3 Jan 1987; G, from Guánica, Puerto Rico —2 Feb 1996).

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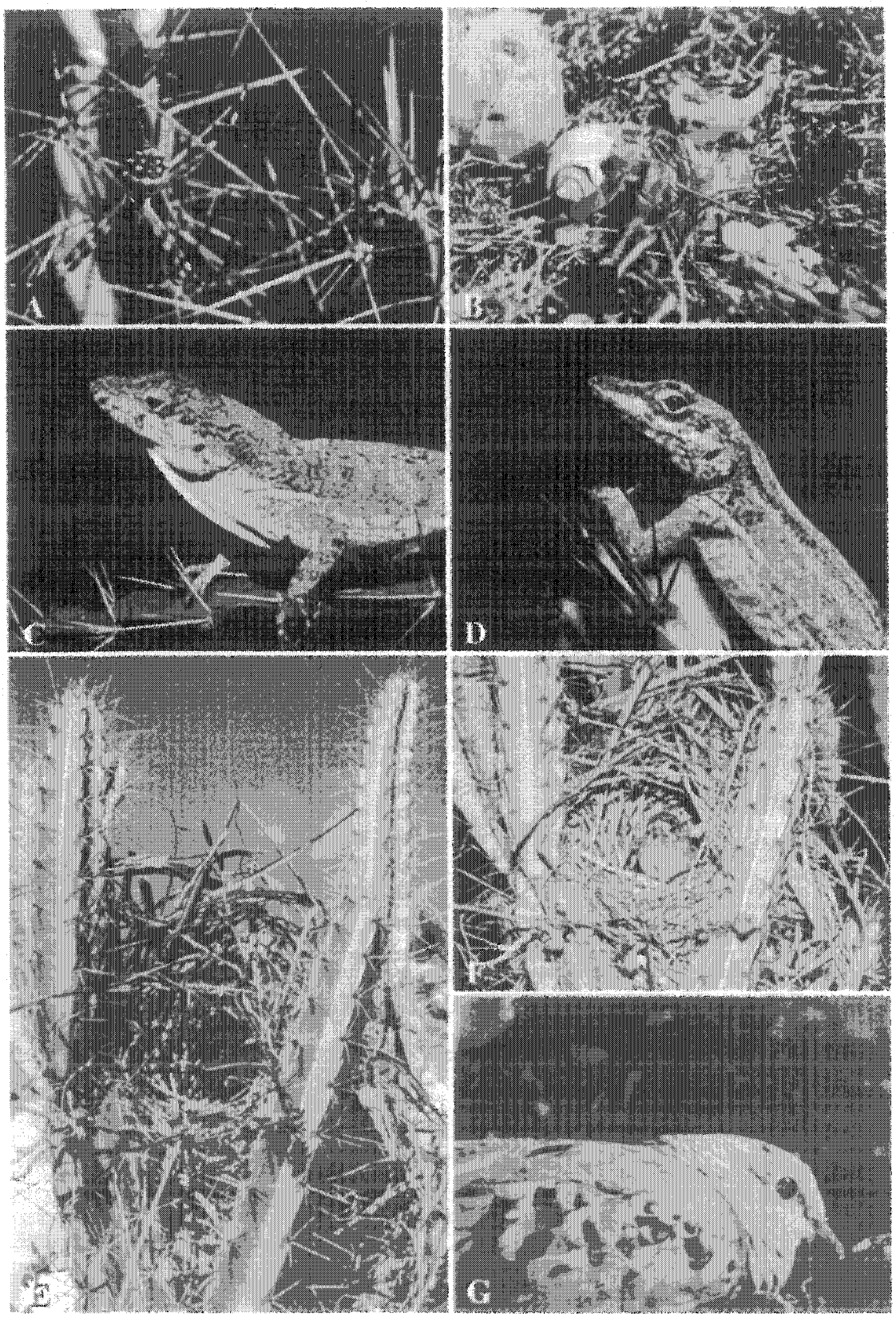

Plate 54.

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9. CONSERVATION

Leptocereus is a highly vulnerable genus. Some of the species and subspecies herein recognized are disappearing rapidly as a result of increasing human encroachment, particularly in coastal areas. This chapter starts by discussing briefly the meaning of the concept "biodiversity" —as applicable to *Leptocereus*— followed by discussion of the most significant threats to the genus and conservation status of its taxa. A number of action proposals oriented to reduce the strain on these plants is also provided.

9.1. Biodiversity concept

In its strict sense, biodiversity is defined as "variety and variability among living organisms and the ecological complexes in which they occur" (Office of Technology Assessment, 1987). This broad definition can be extended downward to cover the genetic variability of a taxon and upward to accommodate habitat and ecosystem diversity. I believe, however, that biodiversity can be more practically expressed as diversity of taxa (weighted for rarity, endemism, and taxonomic distinctiveness) per surface unit. This will be the definition of biodiversity used in this chapter.

In the last decade, efforts to link habitat protection with sustainable development in highly productive ecosystems have caused a notable expansion of the meaning of the concept "biodiversity conservation." Often, the expansion of this concept has led to the

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identification of biodiversity conservation with ecological services such as clean air and water. The World Resources Institute (WRI) has clearly stated in an international policy document: "Biodiversity conservation entails a shift from a defensive posture — protecting nature from the impacts of development— to an offensive effort seeking to meet peoples' needs from biological resources while ensuring the long-term sustainability of Earth's biotic wealth" (WRI *et. al.*, 1992). The result of this utilitarian tendency has significantly shifted away the notion of conservation of biodiversity from species protection towards sustainable use. The shift has been very effective in increasing the appeal of conservation efforts to a use-oriented audience; it may have even proven useful and operative in managing some large continental ecosystems, but in the fragile Caribbean Islands, where human population has risen to 40 million, it is likely to produce negative upshots. The adoption of an "expanded" biodiversity concept in this multi-national insular region is making a dramatic difference in conservation strategies. Unfortunately, the utilitarian perspective is favoring the implementation of conservation strategies where there is little or no need for strictly protected areas. In the West Indies, for example, there has been a reduced commitment to protected areas in the last years, which explains why most of the action proposals contained in the SSC/IUCN conservation plan for cacti and succulents have not been implemented yet in the region (Areces-Mallea, 1997).

Focused more on tropical rain forests, Kramer and van Schaik (in Kramer, *et al.*, 1997) pointed out that sustainable use rather than protection may be more likely to lead to local extinction of species. If this is true for a rain forest, what should we expect for

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those slow-growing xeric communities composed of plants with exceptionally low levels of metabolism and very limited production of biomass? In the Caribbean, the largest number and highest density of endemics occur in arid zones (*e.g.*, coastal areas), and in physiologically dry habitats (*i.e.*, limestone karsts, sandy soils, and serpentine-derived soils). Many xerophyllous relicts of drier climates, which have taken refuge in these areas, have placed in the Caribbean dry lands their last hope for survival. The potential impact of the new utilitarian conservation strategy in the arid or physiologically dry habitats, where *Leptocereus* thrives, is certainly going to be detrimental for their unique plant communities. In cases like this, adherence to an expanded biodiversity concept focusing on sustainability rather than protection, will inexorably (and ironically!) cause reduction of biodiversity. With regard to *Leptocereus*, if we are not more oriented towards a species perspective, where there is an emphasis on the scientific and ethical values of biological taxa, there will be little hope for conservation of this relict genus.

9.2. Threats

Leptocereus is mostly composed of small, ecologically restricted populations not capable of adapting to major environmental changes, nor resisting foreign competitors. These features are of common occurrence in island floras, particularly those with high endemism. The smallest semi-natural population of *Leptocereus*, for example, is that of *L. grantianus* of Culebra island (east of Puerto Rico), with only about 50 individuals in one site. The ability of these small populations to recuperate from external pressures is

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usually very limited, which explains why they are so vulnerable. There is, in fact, a genetic reason for the vulnerability of island communities: the reduced gene pool from which the ancestral populations that colonized the new insular biotopes were selected. This gene pool does not have the opportunity to diversify much, not even in a long period of time.

The "island effect" of the flora of the Greater Antilles has been additionally accentuated by the long paleogeographic history of these Islands. The largest of the Greater Antilles, particularly Cuba, originated from former archipelagos that merged into individual landmasses in relatively recent times. Hence, most of the larger island floras in the Greater Antilles actually consist of groups of ancient, isolated floras (Borhidi, 1996). The allopatric distribution of *Leptocereus* in Cuba, for example, with nearly all species occurring on individual tectonic blocks (former islands?) that have remained subaerial since Late Eocene, typically reflects an older insular origin within the main island of Cuba. As a consequence of isolation, the ecological tolerance and genetic flexibility of populations decrease, lowering the competitiveness of species. In other words, these plants cannot react satisfactorily to new environmental shifts, cannot take advantage of natural or man-induced successions, and cannot resist or force back new competitors. The vulnerability of *Leptocereus* and other succulent endemic taxa of the Caribbean is particularly pronounced because they have adapted to the extreme ecological conditions of oligotrophic or bare substrates (Areces-Mallea, 1997). Under severe conditions, metabolism rates drop substantially, lowering the capacity of plants for competition and their degree of sociability. Furthermore, it seems that most of the

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oligotrophic and rocky substrates to which *Leptocereus* has adapted represent relict habitats from drier epochs. It is quite likely that since Pleistocene times the formerly widespread xerophilous elements of the largest Caribbean Islands retreated to dry coastal and subcoastal areas, serpentines, and the slopes and cliffs of conical karsts. (Borhidi, 1996). This was probably due to changes from a drier to a more humid climate. The relict character of many Caribbean Cactaceae, another condition that increases vulnerability, is indicated by: (1) the presence of relatively primitive isolated taxa, most of them being narrow endemics (*e.g.*, *Leptocereus* spp., *Dendrocereus* spp., and the dioecious Antillean group of *Pereskia* spp), (2) the abundance of disjunct geographical distribution types (*e.g.*, *Dendrocereus nudiflorus, Cylindropuntia caribaea, Consolea* spp.), and (3) the large number of local endemics represented by small populations (*e.g.*, *Leptocereus* spp., *Opuntia* spp., *Cylindropuntia hystrix*.). Accordingly, it is not surprising that with so many attributes acting against it, *Leptocereus* has become one of the most endangered genera in the entire Caribbean region. As a matter of fact, 70% of all its taxa are threatened to some degree and thus qualify for the World Conservation Union (IUCN) Red List Categories. This overall 70% is further divided into a 10% of taxa that are hereby considered extinct in the wild; 15% critically endangered; 5% endangered, and 40% vulnerable. Only 30% is at low risk, but this category includes a 10% portion of conservation dependent taxa that survive in a well-managed protected area in Puerto Rico, namely the Bosque Seco de Guánica (Table 41 lists each taxon with the IUCN category that applies). Major threats to *Leptocereus* biodiversity have been: (1) urbanization and tourism, (2) clearing for agriculture, (3) grazing, (4) fire, (5) mining and quarrying, and (6) competition with

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introduced species. Other less important threats but nevertheless worth of mention are (7) local use, and (8) collecting for horticulture.

9.2.1. Urbanization and tourism

There are 16 cities in the Caribbean with over 100,000 inhabitants, most of which are located in coastal areas (Areces-Mallea, 1997). Urban centers, large or small, that have significantly impacted *Leptocereus* populations are: Havana, Viñales, Sumidero, San Diego de Los Baños, Cienfuegos, Trinidad, Pilón, Santiago de Cuba (Cuba); Montecristi, Azua, La Romana, Barahona, Pedernales, Oviedo (Dominican Republic); Port-au-Prince, Gonaives, Port-de-Paix, Jean Rabel (Haiti); Guánica, Boquerón, Ponce, Dewey (Puerto Rico, including Culebra Island). The two largest cities in Haiti, Port-au-Prince and Gonaives, were raised on *L. paniculatus* and *L. weingartianus* land. A more dramatic example follows: *L. wrightii* subsp. *wrightii*, former occupant of the rocky coastal areas of Habana harbor and its environs (Cuba), is now extinct in the wild. The last plant was discovered by the author in 1974 in Cojímar, where the "Villa Panamericana" and its sport facilities are now located. A second plant was seen about a decade ago, more towards Bahía Honda (Ortigosa), in a very precarious situation (a voucher, *Areces 6414*, NY). Unfortunately, *L. wrightii* subsp. *wrightii* is not the only victim of the relatively old and populous capital city of Cuba. Two interesting Euphorbiaceae, *Cnidoscolus quinquelobatus* and *C. fragrans*, both endemic to the Havana city area, seem to have been erased from the planet too; no one has seen them for more than half a century.

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The growth of tourism in the Greater Antilles over the past 50 years has resulted in hotel development along coastlines that have attractive sandy beaches. This has often meant a complete change to the landscape, involving removal of natural vegetation and planting exotic trees, shrubs, and cespitose grasses for lawns and golf courses. Playas del Este, Santa Lucia, and Varadero (Cuba), La Romana and Playa Las Terrenas (Dominican Republic), and Isla Verde (Puerto Rico), are clear examples of this landscaping abuse. Mosquito control and marina development have eliminated mangroves and littoral thickets in many places. New roads have often been constructed to give access to coastal areas, and to connect cays to the mainland. Movement of people from rural areas to towns and resorts, with the lure of employment opportunities in servicing the new tourism, has coincided with the decline of export-based plantation agriculture in Cuba and the Dominican Republic. Increased demand for fresh fruit and vegetables has often resulted in unacceptable levels of cultivation on unsuitable land, *e.g.*, in southeastern Cuba, where *Leptocereus maxonii* is native.

9.2.2. Clearing for agriculture

The human population of the Caribbean Islands, estimated to be 35 million in 1991, is projected to rise to nearly 60 million by 2025 (see FAO human population estimates in Areces-Mallea, 1997). Although all-island totals are increasing, in general, the incremental rates and proportions of populations economically active in agriculture have fallen over the past decade. These trends reflect increase in mechanization and

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efficiency on farms and in importation of foods replacing local produce, combined with migration to towns and coastal tourist resorts. Higher growth-rates are associated with larger rural populations and relatively smaller movements away from agricultural pursuits, as in Haiti and the Dominican Republic. During the past decade, the total number of people comprising agricultural communities actually rose in Haiti (by 7.5%), the country that probably had the largest coverage by *Leptocereus* proportionally to its size. This trend matches several of the poorer Central American republics where, however, numbers of those actually economically active on the land also fell (Areces-Mallea, 1997).

Except for Haiti, most agricultural development has been carried out on the seasonal evergreen forest life zone, and on lowlands formerly occupied by semi-deciduous forests, which are not *Leptocereus*-rich communities. Nevertheless, important coastal shrubwood areas in western Cuba, with *Pilosocereus robinii* and presumably *Dendrocereus nudiflorus* and *L. wrightii* subsp. *wrightii* as well, have been cleared for sisal (*Agave sisalana* and *A. furcroydes*) plantations. Traditional cassava, maize, and other small crop cultivation has also been attempted locally, with limited success, in many scrub areas with *L. paniculatus* and *L. weingartianus*, in Haiti and the Dominican Republic.

9.2.3. Grazing

The impact of drought-resistant cattle in the seasonally dry vegetation of the West

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Indies is well known. In the eastern lowlands of Cuba many stands of semi-deciduous and drought-deciduous xerophytic forests with *Pereskia zinniiflora* and *Harrisia* sp. have been cleared for grazing. Feral cattle have done considerable damage in the cays of north-central Cuba, where *Leptocereus santamarinae* thrives. Goats are grazed heavily in the succulent-rich shrublands of south-eastern Cuba, central and north-western Haiti, and western Dominican Republic, having a definite repercussion on *L. maxonii, L. sylvestris, L. weingartianus,* and *L. paniculatus* populations. Goats have been the main agents of anthropogenic desertification in many dry areas of the world, and their impact on some fragile island ecosystems (*e.g.*, in the Galápagos Islands and the Hawaiian archipelago) has often been documented as disastrous events.

In the succulent-rich Guantánamo basin of southeastern Cuba, overgrazing by irruptive, unbalanced populations of "hutías" (*Capromys pilorides*, a Cuban endemic herbivore rodent) and "white-tailed" deer (*Odocoileus virginianus*, an introduced North American ungulate) have posed severe threats to native plant communities. Dead standing or fallen skeletons of distinctly browsed columnar cacti can be seen, at present, in many natural vegetation types occurring in the area. Hutías and especially exotic ungulates such as goats and deer relentlessly damage the tender seedlings of cacti and interfere with the natural regeneration of many of these plants. This seems to explain why in grazed areas virtually no *Leptocereus* seedlings can be found. Grazing may come into play most dramatically during drought cycles; years of reduced rainfall place additional stress on cacti because these plants become the most important source of water for herbivores. *Cylindropuntia caribaea,* which is considered a pest in

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Hispaniola, is one of the few Caribbean native cacti that increases rapidly in grazed areas, benefiting largely from this detrimental activity (Areces-Mallea, 1997).

9.2.4. Fire

The natural vegetation of the Caribbean Islands has not evolved the fire-tolerant life forms that are found throughout much of tropical Africa or South America, so fire has been comparatively more destructive to plant biodiversity in this archipelago than it has been in continental Paleo- or Neotropical areas. *Harrisia portoricensis*, for example, a slender-stemmed cactus, became extinct in the main island of Puerto Rico mainly due to fire. Burning is a common practice used to clear land for agriculture and settlements, to "clean" undergrowth in forests, and to encourage new growth in savannas and shrublands in the dry season for pasturage. Some of the tree-like West Indian opuntioids (*e.g.*, *Consolea moniliformis*), with thick-barked trunks, are more fire-tolerant than the smaller or slender cacti, but in general burning is a major threat to the native succulent plant flora. Particularly susceptible to fire damage are the slender-stemmed, thin-ribbed *Leptocereus*. Half a century ago, *L. quadricostatus* was fairly common in the Cabo Rojo area, in southwestern Puerto Rico. This endemic species literally disappeared from the site, along with *Opuntia borinquensis*, due to severe burning. Cabo Rojo was also considered an important breeding ground for *Melocactus intortus* in Puerto Rico; today few adult individuals of this species remain in the area (Areces-Mallea, 1997).

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9.2.5. Mining and quarrying

Threats to the landscape in the West Indies arise mostly from mining activities. Whatever type of mining is carried out, vegetation is cleared and there is always some surface disturbance either from stripping operations or dumping of tailings. The exploitation of bauxite in south-western Dominican Republic has had a significant impact on the dry shrubwoods of the Pedernales area, where *Leptocereus weingartianus* subsp. *demissus* occur. Quarrying for limestone in the haystack karstic mountains of western Cuba, particularly those of Havana province, has produced significant changes in local landscapes and nearly fatal, or fatal, strain on various species, notably *L. leonii* and *L. scopulophilus*. The former species is critically endangered because quarrying operations have largely destroyed its habitat at Anafe, while *L. scopulophilus* ended extinct in the wild after complete destruction of its only site of occurrence.

Riverside and beaches in the Caribbean Islands are often exploited destructively for sand and gravel, and these removals may have primary detrimental consequences to the local cactus flora, and secondary effects in the form of erosion, flooding, pollution, and loss of visual aesthetic. *Leptocereus weingartianus, L. paniculatus,* and *L. maxonii* have suffered from sand and gravel mining to varying degrees. Likewise, salt extracting operations in open coastal salines such as Salinas de Cabo Rojo (Puerto Rico), and Saline Saint Michel (Haiti) have impacted local populations of *L. quadricostatus* and *L. weingartianus*, respectively.

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9.2.6. Competition with introduced species

The introduction of the extremely aggressive legume shrub *Dichrostachys cinerea* from the savannas of Africa into Cuba and Marie Galante (of the Lesser Antilles) has been an ecological disaster. The plant regenerates vigorously from the smallest root fragments, forming dense monodominant communities. In south-central Cuba this invader has had a detrimental impact on *Leptocereus arboreus* and the xerophytic indigenous vegetation with which this species is associated (Areces-Mallea, 1997).

9.2.7. Local use

None of the greenish, glutinous fruits of *Leptocereus* are used as sources of food in the Caribbean Islands; their hard, viscid funicular pulp being inedible. The unarmed, plum-colored, and relatively juicier fruits of *L. leonii* are perhaps the most palatable, but the rarity of this species and the lack of a pre-Hispanic "cactus culture" in the Caribbean (such as that of Mexico and Northern Chili, for example) never favored the use of this or any other species of cactus as a food source.

Leptocereus paniculatus, with its relatively large and compact woody trunk, has been for many years the source of timber for construction of furniture in the Lake Enriquillo area (Dominican Republic). The species has also been exploited for fuelwood and charcoal production for domestic consumption in both Haiti and the Dominican Republic. According to the U.S. Fish and Wildlife Service (1994), the

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spineless *L. grantianus* may have been cut in the past for use as livestock feed. *Leptocereus santamarinae* has been used locally as live fencing in northeastern Cuba.

9.2.8. Collecting for horticulture

Some Caribbean cacti are of considerable horticultural interest and have been exploited to the detriment of wild populations. *Mammillaria* and especially *Melocactus* are the most demanded genera. The demand for *Melocactus actinacanthus* in Cuba, for example, has led to the wholesale removal of nearly all the wild population. At present, only a handful of individuals of this beautiful cactus that is now on the verge of extinction, survive in its original location in very steep, nearly inaccessible serpentine cliffs (Areces-Mallea, 1997). *Leptocereus* species are not particularly attractive, which dininishes horticultural interest (except the spineless *L. grantianus* that has some potential for cultivation). *Leptocereus grantianus* is the only species that has been subject to collection (locally) for use as an ornamental.

9.3. Conservation status

It remains difficult to estimate population size and area of dispersal for rare plant species of the Caribbean Islands. Gaps in the flora coverage and the limited number of botanists with specialized knowledge have restricted the availability of data on the conservation status of West Indian plants, while taxonomic uncertainties have added much to the difficulties of applying conservation categories. Thus, very preliminary and

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incomplete assessments of the cacti and other succulents of the Caribbean were made before 1997, when the Species Survival Commission (SSC)/World Conservation Union (IUCN) Status Survey and Conservation Action Plan was shaped (Areces-Mallea, 1997). Before 1997, for example, the World Conservation Monitoring Center (WCMC) had records of over 100 Caribbean cacti in its Plant Database. Of these, only 40 were considered threatened on a world scale (Areces-Mallea, 1997).

Although in the SSC/IUCN Status Survey I attempted an assessment of the conservation status of *Leptocereus*, it is not until now that a more realistic evaluation can be made based primarily on the improvements of my field knowledge of the group since 1997. Table 41 lists all *Leptocereus* taxa with their corresponding IUCN category of threat (the IUCN Red List Categories and their acronyms are those approved by the 40th Meeting of the IUCN Council, Gland, Switzerland, 30 November 1994).

9.4. Priority sites for conservation

Leptocereus occurs naturally in three of the four islands that comprise the archipelago of the Greater Antilles, and involves four countries, namely, Cuba, Haiti, Dominican Republic, and Puerto Rico. Within each of these countries the genus has an essentially scattered distribution. Hence, rather than a few large protected areas, the coverage of such a disperse group in terms of conservation needs requires a number of

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Table 41. IUCN categories of threat given for *Leptocereus* as circumscribed in this work (the order of taxa is systematic).

TAXON	CATEGORY	CONSERVATION INFORMATION
L. assurgens	—LR (lc)—	Low Risk (Least Concern) at present, taking into account its total range and inaccessibility of habitat.
L. chrysotyrius	—LR (nt)—	Low Risk, but under the subcategory Near Threatened (nt) because part of its range, which is more accessible than that of its near relative *L. assurgens*, is currently being impacted by the tourist industry.
L. ekmanii	—VU—	Vulnerable. Range restricted to a small limestone range (Sierra de Guane) with a potential for future limestone quarrying.
L. prostratus	—LR (nt)—	Low Risk (Near Threatened) with great potential for becoming Vulnerable due to accelerated growth of urbanization and tourism in the area.
L. albellus	—VU—	Vulnerable in view of its rarity and local occurrence. Range restricted to a single limestone range (Sierra de San Carlos), with only one population of limited extent. Needs field surveys to check for the existence of other populations within the range.
L. wrightii subsp. *wrightii*	—EW—	Probably Extinct in the Wild due to urban expansion.

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		A decade ago there was a single, unprotected plant left in the Bahia Honda area (Pinar del Río province, West Cuba), in a very precarious situation.
subsp. *gracilis*	—CR—	Rare subspecies currently known from only a single collection in an area that continues to be developed for tourism. Considered Critically Endangered on present knowledge and urgently in need of further field studies to determine if its range is somewhat more extensive.
L. scopulophilus	—EW—	Extinct in the Wild after complete destruction of its habitat (Sierra de Somorrostro), due to quarrying of limestone. This species is on the verge of total extinction since it is scarcely in cultivation; only two botanical gardens and one private collector maintain living material from the type plant.
L. leonii	—CR—	Critically Endangered. Ongoing quarrying operations have largely destroyed its habitat at Sierra de Anafe.
L. arboreus	—EN—	Endangered. Affected by continuous clearance of coastal forests for urban expansion and agriculture since the 18th Century. Accelerated tourism development in the last decades is posing very serious threats to this species. Needs monitoring.
L. carinatus	—VU—	Low Risk at present, but found only on a limestone

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		range of limited extension and therefore potentially at risk from quarrying activities in the long term.
L. sylvestris	—VU—	Vulnerable. Known only from the coastal region between Cabo Cruz and Pilón (southeastern Cuba), where urban expansion and considerable development for tourism is taking place.
L. maxonii	—VU—	Vulnerable from habitat modification by the expanding tourist industry in coastal areas.
L. santamarinae	—VU—	Vulnerable. The species is known from a region where considerable development for tourism is currently taking place.
L. weingartianus		
subsp. *weingart.*	—LR (lc)—	Because of its abundance and wide distribution in the eastern sector of its range —western Dominican Republic and Haiti— this subspecies is considered at Low Risk (Least Concern). Perhaps should be treated as Near Threatened (nt) in the East of Hispaniola where tourist development is altering its habitat. Needs to be monitored.
subsp. *demissus*	—VU—	Vulnerable, due to its limited range and habitat affected by burning, charcoal production, and mining of bauxite.

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L. paniculatus	—VU—	Vulnerable. Relatively wide-ranging in western Hispaniola, but use of timber for construction of furniture, local collection of fuelwood, and charcoal production for domestic consumption is placing a strain on the species despite its range.
L. quadricostatus		
subsp. *quadricost.*	—LR (cd)—	Low Risk (Conservation Dependent) since included in a protected area. Remaining populations outside the "Bosque Seco de Guánica" are not likely to survive.
subsp. *parvispinus*	—LR (cd)—	Low Risk (Conservation Dependent). Totally dependent on the maintenance of its habitat in a well managed protected area.
L. grantianus	—CR—	Critically endangered. Presently known from a single population consisting of about 50 individuals threatened by agricultural, residential, and tourist development, as well as by damage from hurricane surges (the population is located along a rocky shoreline only 8 to 10 m from high tide). It may have been cut in the past for use as livestock feed (U.S. Fish and Wildlife Service, 1994).

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small-sized sites. Most important areas for *Leptocereus* conservation are:

CUBA:

1. ***Coast and lowlands of Baconao, sections El Indio-El Morrillo (Reserva de Santiago).*** Important part of the dry scrubwoods and cactus scrubs of southeastern Cuba. Includes the type locality of *L. maxonii*.
2. ***Coastal section between Pilón and Cabo Cruz.*** Also in southeastern Cuba, it includes the entire site of occurrence of *L. sylvestris*.
3. ***Coastal terrace between Gibara and Puerto Padre Bay.*** Perhaps the most important area in Cuba for the so-called northeastern xerophytic plant communities, with *L. santamarinae*.
4. ***Coco, Paredón Grande, Romano, and Sabinal cays.*** The largest islets of the Camagüey Archipelago, in north central Cuba. These cays support large populations of *L. santamarinae*.
5. ***Coast and lowlands from Playa Girón to Cienfuegos Bay, and from Cienfuegos to Trinidad.*** These sections include the entire range of *L. arboreus*.
6. ***Western haystack mountain complex of Sierra de Los Organos.*** The whole karstic mountain range of Los Organos, including Sierras de Guane, Viñales, Sumidero, San Carlos, La Güira and Guacamaya, with *L. ekmanii, L. assurgens, L. prostratus, L. chrysotyrius, L. albellus,* and *L. wrightii* subsp. *gracilis*.
7. ***Sierra de Anafe.*** Isolated limestone mountain range in Havana province, being the type locality for *L. leonii*.

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8. ***Sierra de Najasa.*** Another interesting limestone range, with the rare *L. carinatus* at its only site of occurrence.

HISPANIOLA:

1. ***Lake Enriquillo Valley, encircled by Jimaní, la Descubierta, and Neiba-Duvergé*** (Dominican Republic). Richest portion of the southwestern semi-desert cactus communities dominated by *L. paniculatus, Stenocereus hystrix*, and *Consolea moniliformis*. *L. weingartianus* subsp. *weingartianus* is also present. Isla Cabritos National Park, a small island within Lake Enriquillo, gives insufficient protected coverage to this cactus assemblage.
2. ***Lowlands and hills between Azua and Barahona*** (Dominican Republic). Dry shrublands with *L. paniculatus* and *L. weingartianus* subsp. *weingartianus*.
3. ***Coast and lowlands between Oviedo and Pedernales*** (Dominican Republic). Scarcely disturbed dry shrubwoods and semi-desert cactus scrubs with *L. weingartianus* subsp. *demissus*.
4. ***Limestone terraces north of Bayahibe*** (Dominican Republic). Important area for *L. weingartianus* subsp. *weingartianus*.
5. ***Eastern tips of Hispaniola (Cabo Engaño, Cabo Samaná, Cabo Cabrón)*** (Dominican Republic). Limestone capes with small but nevertheless important populations of *L. weingartianus* subsp. *weingartianus*.
6. ***Coast and lowlands between Môle Saint Nicolas and Port-de-Paix*** (Haiti). Another breeding ground for *L. weingartianus* subsp. *weingartianus*.

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7. ***Coast and lowlands around Bahie de Henne, and East to this bay*** (Haiti). Large population of *L. paniculatus*, particularly old trees.

PUERTO RICO:

1. ***Coast and hillsides from Bahia de Guayanilla to Boquerón.*** Highly disturbed but nevertheless important area covering the entire range of *L. quadricostatus* subsp. *quadricostatus,* and of *L. quadricostatus* subsp. *parvispinus*.
2. ***Southeastern Culebra Island*** (East of Puerto Rico). Includes the type locality and only site of occurrence of *L. grantianus.*

9.5. Existing conservation measures

Until very recently conservation of Caribbean biodiversity was not recognized as being of importance by international conservation agencies. There has been remarkably little attention paid to the conservation needs of the endemic cactus and succulent flora, in general. Undoubtedly, the historical preoccupations with tree forest, and especially our present-day concern for tropical rain forests, have diverted attention from other vegetations types of equally deserving botanical merit in the Caribbean (Adams, 1997). Recently attention has been concentrated on the establishment of marine protected areas. These may incidentally protect the succulent flora of coastal areas (*e.g.* Buck Island, in Saint Croix, U.S. Virgin Islands), but do not necessarily protect the habitats of endemic and/or threatened succulent species (Areces-Mallea, 1997).

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Sometimes areas of cactus scrub vegetation are protected within various sites set aside for conservation throughout the Caribbean. In the British Virgin Islands, for example, The Fallen Jerusalem and West Dog Island Forestry Parks support this type of vegetation. Some priority sites for the protection of specifically representative areas of cactus scrub in the Greater Antilles are: Cabo Corrientes and Baconao Reserves (Cuba); Isla Cabritos National Park (Dominican Republic); Guánica State Forest and Mona Island Reserve (Puerto Rico). Of all these, only Isla Cabritos and Guánica are important for *Leptocereus*.

9.6. Protected areas

Because, protected areas currently cover not more than 6.6% of the Caribbean Islands' land area (Areces-Mallea, 1997), West Indian biodiversity is not fully represented. This small percentage focuses mainly on areas of montane and submontane rainforests, seasonal evergreen, semi-deciduous and coniferous forests, where *Leptocereus* does not occur. Consequently, the situation does not favor *Leptocereus* conservation, not even in the reduced areas, where some species are supposed to be protected. In fact, most of the protected areas that do exist in the region are not adequately protected on the ground. In the Caribbean Islands only 33 % of the protected area coverage is considered under suitable regime of protection and management; 43% is partially protected, and the remaining 24% is practically unprotected (Areces-Mallea, 1997). The only areas important for *Leptocereus* conservation within the Greater Antilles are given in Table 42, with the IUCN category

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of protected area and surface coverage that corresponds. The truth is only six species of *Leptocereus*, out of 17 (35.3%), are "technically" covered.

PROTECTED AREA	SPECIES	AREA (Km^2)	CATEGORY
CUBA:			
Desembarco del Granma	*L. sylvestris*	258	National Park
Viñales	*L. assurgens*	134	National Park
Sabana-Camagüey	*L. santamarinae*	179	Protected Landscape
HISPANIOLA:			
Isla Cabritos	*L. paniculat., L weingartianus*	24	National Park
Jaragua	*L. weingartianus*	1,374	National Park
PUERTO RICO:			
Guánica State Forest	*L. quadricostatus*	?	National Park

Table 42. Protected areas covering *Leptocereus* in the Greater Antilles

9.7. National, regional, and global international legislations

Some Caribbean islands have national legislation protecting the environment (*e.g.*, Law no. 33 of 12 July 1981, in Cuba). Although rare and threatened plant species are considered in some of these legislations, in general legal protection for *Leptocereus* and

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other endangered cacti have not been fully elaborated. The Protocol on Specially Protected Areas and Wildlife (SPAW) was developed under the Cartagena Convention on the Protection of the Marine environment of the Wider Caribbean Region. Annex I of the Protocol lists 56 vascular plants that should be protected from all forms of destruction or disturbance, including picking, collection, or commercial trade. As far as possible, activities that adversely affect the habitats of these species will be subject to regulation. Only two species of *Leptocereus* are included in Annex I: *L. wrightii* and *L. grantianus*. Annex III of the Protocol lists "harvestable" species of flora and fauna, exploitation of which will be regulated according to management plans. No *Leptocereus* species is mentioned in this other Annex. It is obvious that, at least with respect to *Leptocereus* and other succulent taxa, these Annexes are far from complete and up to date (Table 43). Conservation of species on both Annexes will require not only protection but also measures to enable the recovery of wild populations.

In addition to the regionally protected species listed in Annexes I and III, parties are required to "identify endangered or threatened species of flora or fauna within areas over which it exercises sovereignty, or sovereign rights or jurisdiction, and accord protected status to such species." The SPAW Protocol also sets out a cooperative program for protected areas in the Caribbean region. This will support the selection, establishment, planning, management, and conservation of protected areas and buffer zones where necessary, and the creation of a protected area network. If effectively implemented, the SPAW Protocol may provide the impetus to update or develop new

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legislations where all endangered *Leptocereus* taxa could be specifically and effectively targeted (Areces-Mallea, 1997).

SUCCULENT PLANT FAMILY	SPECIFIC TAXA
ANNEX I	
Cactaceae	*Echinocereus reichenbachii* var. *albertii.*
	Harrisia fragrans.
	Harrisia portoricensis.
	Leptocereus grantianus.
	Leptocereus wrightii.
	Melocactus guitartii.
	Melocactus harlowii s.l.
	Pilosocereus deeringii.
	Pilosocereus robinii
ANNEX III	
Agavaceae	*Nolina brittoniana*
Asclepiadaceae	*Asclepias viridula*
Cactaceae	*Melocactus intortus*

Table 43. Succulent species listed in the Annexes of the SPAW Protocol of the Cartagena Convention

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Cactus plants are of major horticultural importance forming the basis for a multi-million dollar international industry. They are sold both as general houseplants and as botanical specimen plants for specialist collectors. Collection of plants from the wild for international trade has been one of the main threats to certain species, and despite the development of sophisticated propagation techniques, this threat remains a significant problem. The principal means by which international trade in cacti is controlled is the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). This convention first came into force in 1976 and has now grown to become one of the largest and best known of all conservation conventions, with over 130 member states. The general aim of CITES is to regulate trade in threatened wild species as listed in three appendices. Species listed on Appendix I of CITES are considered to be at serious risk from any commercial trade and thus all international trade in wild plants between countries who are members of the convention is banned under the terms of the Convention. Species listed on Appendix II of the Convention are those which may be threatened by excessive levels of trade without appropriate regulation. Species may also be included in Appendix II because of their similarity to more threatened species, as an aid to enforcement. International trade in wild specimens of Appendix II species is permitted under the convention, but is controlled and monitored through a licensing system. Appendix III is used by countries that may want to control trade in particular species of their own flora and fauna that are not listed on the other Appendices. As mentioned earlier in this chapter, *Leptocereus* species are not particularly attractive plants. Maybe the spineless *L. grantianus* has some potential for cultivation (this is the only species that has been subject to collection

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for use as ornamental), but in general the genus lacks horticultural interest. Because of this situation, no *Leptocereus* taxa have ever been listed in Appendices I, II, or III of CITES.

9.8. *Ex situ* conservation and reintroduction

Cultivation of plants in botanical gardens, arboreta, private collections, and nurseries is an *ex situ* conservation method that is used by plant biologists and conservationists to assure, at least, some protection of threatened species. Plant material in *ex situ* cultivation may be used for reinforcing existing wild populations, or in the re-establishment of wild populations following the IUCN *Guidelines for Re-Introduction* (IUCN, 1995). Although examples of small-scale reintroduction projects for cacti have taken place in Cuba, Puerto Rico, and Guana (British Virgin Islands), none of them have included *Leptocereus* (Areces-Mallea, 1997). For *L. scopulophilus* and *L. wrightii*, which are extinct in the wild, there is no other alternative at this point in time than to conserve and propagate them *ex situ*. Studies need to be carried out to find similar habitats for possible replanting after propagation.

To meet the demand for large supplies of threatened *Leptocereus* species for possible reinforcing of existing populations, or for establishing new ones, propagation techniques have to be improved. Tissue culture, which can provide rapid and mass propagation of virtually any plant, might be the right answer to this problem.

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9.9. *In vitro* propagation of *Leptocereus*

Cacti are traditionally propagated from either seed or cuttings, which may pose some difficulties. Cactus seeds are slow-growing and very susceptible to damping-off, while many sexually mature cacti are self-sterile and produce no fruits unless cross-pollinated with another individual of its kind, providing that this one is not a clone of the former. In addition, a large number of cactus species produce few or no offshoots to be potentially used as cuttings. The majority of *Leptocereus*, for example, are either self-sterile, or very rarely set fruit after self-pollination. Only *L. leonii, L. quadricostatus*, and *L. grantianus* have proven to produce fruits easily in cultivation, following self-pollination (*L. arboreus* was not tested). *Leptocereus chrysotyrius* and *L. albellus* may set fruit after selfing their flowers, but it takes a great number of trials and patience to succeed. Subgenus *Leptocereus* section *Leptocereus* of western Cuba, including *L. assurgens, L. chrysotyrius, L. ekmanii, L. prostratus*, and *L. albellus*, seem to have the capacity to produce fruits and reproduce sexually, but fruiting is a very rare event in this group. Although *L. ekmanii* blooms profusely throughout the year, for example, no mature fruit of this species has ever been collected, described, or documented in any way from either wild or cultivated plants. Moreover, the slow-growing seedlings of *Leptocereus,* if we are lucky enough to collect fruits, are easy prey of bacteria and fungi whenever the germination medium is not thoroughly sterilized.

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Because tissue culture techniques can overcome the limitations associated with conventional propagation of cacti, they have emerged as a powerful tool for the propagation of rare and endangered species. The establishment of callus cultures from several genera of cacti have been reported since 1957 (King, 1957; Minocha and Mehra, 1974; Havel and Kolar, 1983), while about 30 species of cactus from more than 15 genera have been micropropagated by rooting of shoots proliferated through axillary branching (Mauseth, 1979; Starling, 1985; Starling and Dodds, 1983; Rubluo *et al.*, 1986; Cayton *et al.*, 1990). Micropropagation of *Leptocereus* taxa has not been attempted previously to this work.

Although *Leptocereus* is an offshoot producer, tissue-culture methods were partially tested for potential large-scale propagation of threatened taxa (Areces-Mallea *et al.*, 1997). After a number of unsuccessfully attempts, a standard method was developed for *in vitro* rapid growth of *Leptocereus* tissues using Murashige and Skoog (1962) basic medium supplemented with 15 mg of 2, 4-D and 1 mg-liter of kinetin/liter (PH adjusted to 5.5). Primary explants of five species of *Leptocereus* (*L. assurgens, L. prostratus, L. scopulophilus, L. quadricostatus*, and *L. grantianus*) were placed in culture tubes, which were capped, sealed with Parafilm M, and cultured at 24° C for up to 10 weeks. The explants consisted of 5 to 8 mm thick transverse sections of young stems obtained from 3 to 5 cm long cutting samples that were held in the flame of an ethanol lamp to burn off the spines (if the spines failed to catch fire, the tip of the cutting was dipped in 95 % ethanol and then lit). These pieces were placed in a jar containing 15 % hypochlorite solution for 20 minutes, and then washed thoroughly with

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sterile distilled water prior to sectioning. Primary explants exhibited callus growth at the cut surface after 4 to 6 weeks (Plate 24, G). This method of initiation and growth of callus, which seems to work better with members of *Leptocereus* subgenus *Weingartianea* than with those of subgenus *Leptocereus*, will be completed for shoot and root differentiation, using different combinations of growth regulators, and the successful establishment of the new plants in container culture under greenhouse conditions. The aim of this research is to study the morphogenetic responses of *in vitro* cultured stem sections of *Leptocereus*, as influenced by growth regulators, as a part of a plan intended to serve as a basis for a rapid an effective recovery program. Whether to adopt this expensive technique for propagation of endangered *Leptocereus* taxa in the foreseeable future, or to use the traditional methods, probably will depend upon each individual situation and the availability of funds. Because the situation is so critical for *Leptocereus*, a rapid *in vitro*-based method of propagation is always preferred, but in the eventuality of a lack of funds for implementing a rapid recovery plan, conventional propagation methods should otherwise be used. Although slow and very limited in terms of plant production, the conventional system of propagation by stem cuttings, which works with *Leptocereus*, is practical, easy to implement, and the most economic to use (Areces-Mallea *et al.*, 1997).

9.10. Action Proposals

The actions required to conserve *Leptocereus* biodiversity can be divided into various categories. Some are straightforward and relatively inexpensive, for example,

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provision of information to conservation decision-makers. Others are more complex and demand more time, efforts and financial resources; for example, development of protected area systems. A number of actions for *Leptocereus* conservation will be listed and discussed, as follows:

1. ***Provision of information.*** This monographic work brings together certain data for the first time. Information given here on the conservation status of all *Leptocereus* taxa using the new World Conservation Union (IUCN) categories will be incorporated into the Plants Database maintained at the World Conservation Monitoring Center (WCMC, Cambridge, UK). Provision needs to be made in Cuba, Haiti, the Dominican Republic, and Puerto Rico, for the regular updating of species data by the Cactus and Succulent Specialist Group of Species Survival commission (SSC) of IUCN, in association with WCMC. It is particularly important that information on the conservation status of species coupled with data on priority habitats for *Leptocereus* species conservation should be maintained and made available to national protected area agencies for use in designing new protected area systems, or reviewing existing ones.

2. ***Creation of a SSC Specialist Group for the flora of the Caribbean Islands.*** There is an urgent need for conservation activities relating to the plants of the Caribbean Islands; not only are species of *Leptocereus* facing extinction, but also many taxa within the Arecaceae, Myrtaceae, Rubiaceae, Melastomataceae, Magnoliaceae, Eriocaulaceae, Xyridaceae, and other families. In a multinational region such as the

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Caribbean, the best way to make conservation activities effective is by coordinating them through the creation of an international Specialist Group.

3. ***Analysis of the distribution of Leptocereus taxa in relation to the current protected areas.*** After comparison between *Leptocereus* distribution and the protected area network, recommendations are to be made for the expansion of protected area coverage, to include all taxa. Site selection for the expansion of protected area coverage should be based on representative examples of the vegetation defined by structure, species richness, and the presence of threatened *Leptocereus* taxa. Priorities sites may include:

   3.1. Coast and lowlands from Guantánamo to Maisí (Cuba).

   3.2. Coastal terrace between Gibara and Puerto Padre (Cuba).

   3.3. Lake Enriquillo valley (Dominican Republic) extended to the Cul-de-Sac plain (Haiti).

   3.4. Shrublands between Baní and Azua (Dominican Republic).

   3.5. Coast and lowlands from Môle Saint Nicolas to Port-de-Paix (Haiti).

4. ***Creation of new protected areas.*** Protection of all the priorities sites for *Leptocereus* identified in the SSC/IUCN Action Plan (Areces-Mallea, 1997) is urgently required. A feasibility study should be carried out to determine the best form of protection, site boundaries, management requirements, requirements of local people, and the costs involved. Most of the sites proposed are small in terms

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of area coverage. Thus, their selection follows the general strategy conceived under "Priority sites for conservation." Funding proposals should be developed for the creation of reserves, where the agreement in principle of all interested parties has been reached. Proposed sites are:

4.1. Sierra de Anafe (Cuba).

4.2. Lomas de Camoa, near Somorrostro (Cuba).

4.3. Sierra de Najasa (Cuba).

4.4. Coast and lowlands around Bahie de Henne, and dry hills East to this bay (Haiti).

4.5. Bayahibe coast and lowlands (Dominican Republic).

4.6. Eastern tips of Hispaniola (Cabo Engaño, Cabo Samaná and Cabo Cabrón, in the Dominican Republic).

4.7. Salinas de Cabo Rojo area, South to Boquerón (Puerto Rico).

5. ***Assessment of strict nature reserves.*** Many if not most protected areas in the Greater Antilles are not adequately protected on the ground. Assessment of the condition and realistic prospects for long-term protection of *Leptocereus* in the existing protected areas of Cuba, Haiti, the Dominican Republic, and Puerto Rico is to be done. Recommendations to secure the protected status of the plants involved should be given to government agencies, non-governmental organizations, and international conservation agencies.

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6. ***Development of plant conservation legislation.*** All countries included within the domain of the Greater Antilles should develop plant conservation legislations to give special protection to the endangered species of *Leptocereus*, and/or to other rare and threatened plants as well.

7. ***Development of CITES Scientific Authorities.*** Development of Caribbean Scientific Authorities for plants, for the Convention on International Trade in Endangered species of Wild Fauna and Flora (CITES) with a mechanism for regional coordination, is absolutely necessary.

8. ***Completion to the SPAW Protocol Annexes.*** Completion and amendments to the succulent taxa of the Caribbean's SPAW Protocol Annexes is required, to include all threatened *Leptocereus* taxa in Annex I.

9. ***Improvements in nursery monitoring.*** Closer monitoring of cactus collections and production for export in the commercial West Indian nurseries is important, to make sure no *L. grantianus* or any other species coming from the wild is used for profit. Details of stock plants and their origin, and levels of production and trade by species should be maintained. Procedures for the monitoring of nurseries by regular inspection and review of documentation should be established. Training within the CITES Management Authority for a member of staff with responsibility for control of plant exports should be arranged.

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10. ***Collection of stem cuttings and/or seeds of all threatened or rare Leptocereus taxa, if available, to be sent to botanical institutions throughout the world for ex situ conservation.*** Creation of well-documented and well-maintained *Leptocereus* collections that include all extant taxa is urgently needed. Due to the potential for adverse natural environmental factors in the Caribbean Islands, such as hurricanes, it is desirable to have several collections in this region. A coordinated approach should be made with botanical gardens throughout the world to ask for their willingness to participate in an *ex situ* conservation effort for threatened *Leptocereus* taxa. All botanical gardens and large privately owned collections with *Leptocereus* plants shall be registered as holders of an International Organization for Succulent Plant Studies (IOS) Reserve Collection. Rescue operations for threatened taxa from areas intended for development shall be coordinated with local agencies and gardens. These rescued plants will be grown in cultivation with the intention to reintroduce them to another suitable and safe site according to IUCN guidelines (IUCN, 1995).

11. ***Implementation of educational programs.*** There is a need to develop educational programs for Caribbean islanders to make them acquainted with the richness and value of the dry vegetation types, where *Leptocereus* occur. Preparation of a popular guide to the threatened succulent plant species of the Greater Antilles for regional use would be very useful. These programs should aim to dispel the general misconception that Caribbean thorn scrubs and dry shrublands are useless, and to

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move people to the forefront of the battle to conserve the rare and unique plants that are only found in these communities.

Caribbean countries, like other countries of the world, will only protect effectively their natural heritage when compelled to do so by a majority of citizens, but this majority may well not make its voice heard until other *Leptocereus* species follow *L. wrightii* and *L. scopulophilus* in their route to extinction. Perhaps only then will people say: "if only we had..." Let us hope that Caribbean islanders will change forever this unfortunate course of events.

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10. SYSTEMATIC TREATMENT

10.1. Generic description

Leptocereus (A. Berger) Britton & Rose, Contr. U. S. Natl. Herb. 12(10): 433. 1909.

Type: *Leptocereus assurgens* (C. Wright) Britton & Rose, Contr. U. S. Natl. Herb. 12(10): 433. 1909. (= *Cereus assurgens* C. Wright in Grisebach, Cat. Pl. Cub. 116. 1866, non *sensu* Britton & Rose (1920).

Syn.: *Cereus* subgen. *Leptocereus* A. Berger, Annual Rep. Missouri Bot. Gard. 16: 79. 1905.

Neoabbottia Britton & Rose, Smithsonian Misc. Collect. 72(9): 1-6, pl. 1-4, figs. 1, 2. 1921.

Lit.: Britton & Rose, Cactaceae 2: 77-82, pl. 13(1), figs. 112-121. 1920; Moscoso, Cactáceas Fl. Sto. Domingo, An. Univ. Sto. Dom. 5 (1-2): 23. 1941; Marshall & Bock, Cactaceae 79, fig. 26. 1941; León & Alain, Fl. Cuba 3: 372-374, Contr. Ocas. Mus. Hist. Nat. La Salle 13, fig. 168. 1953; Backeberg, Cactaceae 4: 1958-1964, figs. 1886-1890. 1960; Backeberg, Kakteenlexikon 200-201. 1966; Buxbaum, Orig. tribe Browningieae, Cact. Succ. J. (US) 38(1): 43-46. 1966;

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Haustein, Kakteenführer 70. 1986; Pilbeam, Cacti Conn. 71. 1987; Cullmann, Götz & Gröner, Encycl. Cacti 190. 1987; Barthlott & Hunt, Cactaceae, in Fam. Gen. Vascular Pl. (K. Kubitzki, ed.) 2: 177. 1993; Anderson, Cactus Fam. 391-395, 8 figs. 2001.

Eponymy: From the greek λεπτοσ, meaning thin-cereus, with reference to the thin ribs of *L. wrightii* (Figs. 2, J1-J4, and 3, A), a plant erroneously taken by A. Berger (1905) and Britton & Rose (1909) for the type species *L. assurgens*.

Medium-sized trees 8-10 m tall, small trees, or miniature arborescent with a well-developed trunk, or sometimes scandent, prostrate, procumbent-arched, or dangling plants, but most often large, medium-sized, or small shrubs ramified near ground level or above, with or without a short, thick trunk, rarely with fleshy, tuberous root thickenings. *Trunk*, when present, to 40 cm in diam., woody, terete or nearly so, covered with a 1-1.5 cm thick grayish-brown or brown bark, smooth or longitudinally fissured, usually becoming spineless in age, the wood medium- to fine-grained, creamy to tawny or light yellow. *Main branches* (in trees and large shrubs) often decurrent, not candelabriform but forming an umbrella-like crown by diffuse ramification; periderm forming continuously or in rounded patches. *Stems* segmented, ribbed, thin to moderately thick, ascending, arched, climbing (by leaning on neighboring vegetation for support), trailing along the ground or hanging loosely, not producing aerial roots, usually with an extensive network of cortical bundles; epidermis bright, bright green, dark green or dull, waxy, bluish- or grayish-green; cortex extremely mucilaginous,

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generally showing a darkening reaction upon injury; vascular cylinder often strongly woody; pith narrow, 1-6 mm in diam.; sinuses of ultimate segments acute and usually demarcated by a sharp line, or less commonly rounded to broadly rounded. *Ribs* 3-10, usually thin and prominent, their margin commonly crenate, sometimes straight or nearly so, rarely undulate or with a small notch halfway between the areoles. *Areoles* usually not differentiated into vegetative and fertile, or sometimes highly modified to produce terminal, cephalioid structures, commonly circular, broadly elliptical, or elliptic-oblong, most often located at the deepest part of the crenatures, sometimes leveled with the rib margin, rarely elevated or positioned between the crest of an undulation and the adjacent depression, 0.8-4 cm apart, indeterminate but often with a dormancy period, rarely unarmed, most often bearing spines and small, curly, ribbon-like, multicellular-uniseriate trichomes. *Trichomes* 0.2-0.5 mm long, 35-50 μm wide, creamy or tawny to brown or dark reddish-brown in youth, weathering to grayish with age. *Spines* usually 5-24 in each areole, rarely none, 0.1-7 cm long, long-lasting and generally increasing in number on old stems, pinkish, yellow or brownish-yellow to dark brown, dark reddish-brown or nearly black in youth, becoming grayish with age, pale green or dilute yellow at the growing base when young, the tip usually yellow, on occasions brownish, most often slender, straight, acicular, sharp-pointed, elliptic in cross-section and therefore slightly twisted, or terete, with notably broadened, bulbose or conical base, rarely subulate, spreading and nearly equal in length, width and color, to paired and rather unequal, the centrals often slightly longer to markedly longer and stouter than the radials; radial spines to 15, rarely none; central spines mostly 1-18, commonly porrect, rarely deflexed. *Cephalia* seldom present at the stem apex with

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Cephaliphora at the stem apex with densely clustered areoles arranged in spirostichies; wooly hair and short cephalium bristles creamy or tawny to dark brown, tending to wear off with age, leaving a stubby, cylindrical or angular, terminal stem that cannot revert to vegetative growth. *Flower buds* cylindrical to cylindric-obconical, rounded at apex. *Flowers* actinomorphic, small, 2-8 cm long, 1-4 cm wide, produced from apical, subapical, or lateral areoles (sometimes borne on cephalia), solitary in each areole and stem segment to more than 20 grouped in the upper portion of a stem, narrowly tubular, cylindrical, obconical, or campanulate, scentless or sometimes with a faint sour odor reminiscent of cabbage, for one night nyctigamous, sometimes also vespertinal, matutinal, or diurnal; pericarpel green or greenish, smooth or seldom with rib-like pleats following ortostichy lines (only in the pedicellar zone), its areoles spiny or unarmed; receptacle-tube short, tubular, obconical, or cylindrical, rarely ribbed, green, greenish-red (githagineous), wine-colored, yellow, or tawny to yellowish-olive, with rather prominent podaria bearing areoles with clusters of stiff, pungent spines, sometimes bristles, or less frequently bearing unarmed, woolly areoles rarely subtended by minute scales. *Perianth segments* short, oblong or ligulate to spathulate or narrowly obovate, usually rounded, obtuse or truncate at apex, rarely emarginate, often spreading, occasionally rotate, flat or somewhat curved to slightly double-folded, perpendicular to the floral axis to strongly reflexed, usually greenish-white, white, or creamy, sometimes yellow, pink, or orange, the inner ones thin and delicate, the outermost somewhat fleshy, with their abaxial surface occasionally tinged at middle with a green, brown, blackish, or vinaceous color. *Stamens* numerous, borne on the inner wall of the receptacle tube and the upper nectar chamber ridge, usually inserted or

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very little exserted, less frequently to 5-6 mm exserted, loosely set or grouped in compact column; filaments white to greenish-white; anthers creamy, oblong, with complete longitudinal dehiscence. *Nectar chamber* markedly striated, elongated, straight or sometimes a little swollen, not demarcated to slightly demarcated by external tube constrictions, with copious light honey-sweet secretion. *Style* terete, white. *Stigma* lobes 5-15, creamy, erect, linear, their tips usually inserted with respect to the perianth and stamens, or slightly exserted, seldom completely exserted. *Ovary locule* oblong or narrowly oblong to narrowly elliptical or obconical in outline, filled with numerous ovules; funicles white. *Fruits* fleshy, indehiscent, globose, obovate, ellipsoid, or fusiform, 1.5-10 cm long, with erect, black, often spiny receptacle-tube remnants persisting at apex, usually covered by areoles that are often persistent or less frequently shed at maturity, bearing woolly trichomes and clusters of stiff, acicular spines to 2 cm long, occasionally with bristly spines —numerous or scattered— or unarmed; pericarp commonly smooth, sometimes with slightly elevated ortostichy lines or longitudinal ribs originated by coalescence of decurrent podaria, green or greenish-yellow with or without streaks of pink or wine-red color, yellowish, pink, or pinkish-green to brownish, greenish-red (githagineous), or entirely wine-colored; funicular pulp firm, greenish or greenish-gray, translucent and extremely mucilaginous. *Seeds* 10-12 in each fruit to more than 100, mussel-shaped (cochleariform) or less commonly tear-shaped to nearly hemispherical, laterally flattened, rostrate, dark brown to nearly black, verrucose; exotesta cells convex, their outline round, oblong, or elliptic-oblong, sometimes forming a dorsal keel-like ridge on the seed, cuticular folds fine to very coarse; hilum oblong or narrowly oblong to narrowly oblong-lanceolate or triangular,

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non-strophiolated. *Seedlings* fleshy, elongate, cotyledons conical-depressed, the first areoles elevated on minute podaria.

A West Indian genus of 17 species, whose combined distribution extends in an arc from western Cuba through Hispaniola to Puerto Rico and the small island of Culebra.

10.1.1. Notes on keys, terms, and abbreviations

In order to facilitate the rapid identification of both sterile and fertile material, two separate keys for sterile, and flowering or fruiting specimens are provided. These keys are artificial and do not intend to reflect the natural order of categories expressed in Tables 3 and 4, or in the sequence of subgenera, sections, species, and subspecies given in the systematic treatment.

Leptocereus is poorly represented in herbaria, and many, if not most, specimens available are incomplete or fragmentary, and lack fertile organs; their spines are frequently broken, flowers and fruits have often become detached and lost, and shrinkage and changes in color are significant. Therefore, the number of useful characters to be found in an average herbarium specimen of *Leptocereus* is very small (for more information on the limits imposed by the study of cacti exsiccata see chapter 1, epigraph 1.2 The genus *Leptocereus*). Because of this hard fact (*nuda veritas*!), most measurements and diagnostic observations on which the keys and specific descriptions are based were taken on living plants, or on recently made collections (prior to the

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pressing and drying process). For characters other than color, FPA-preserved material was eventually used (FPA is a formaldehyde-propionic acid-ethanol solution). When special treatments are involved (e.g., those required for SEM studies), these are specifically stated. Measurements of some organs are given as length × width (e.g., the areoles); measurements of dried material with no obvious shrinkage, such as areoles, trichomes, spines, and seeds, apply both to live material and herbarium specimens. Inmature organs (stem segments, areoles, fruits, etc.,) were not included in this study. Morphological terms used in the keys and taxa descriptions were those discussed in chapters 2 (general morphology), 3 (seed morphology), and 5 (anatomy), and in part illustrated in Figures 1 and 2 (stems), Figure 3 (stems, flowers, and fruits), Figure 4 (ribs), and Figure 5 (seeds and seedlings). Herbarium acronyms follow Holmgren *et al.* (1990).

10.2. Keys to species and subspecies of *Leptocereus*

10.2.1. Key for sterile specimens

1. Prostrate plants with dorsal spines slightly longer than the ventrals; rib margin dentate, its areoles elevated; vascular cylinder of old stems slightly excentrical .... 4. *L. prostratus*

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1'. Trees and shrubs (rarely dangling plants), with radially symmetrical stems and no differentiation between dorsal and ventral spines; rib margin crenate, its areoles sunken in the crenatures; vascular cylinder centrical

2. Stem grooves of ultimate segments broadly rounded, its deepest part not sharply defined

3. Roots thickened, tuberous; stem segments dull, clear to grayish-green, not showing an abrupt change in cortical color (from green to black) when sectioned; rib margin continuous between areoles; epidermis with 15-25 % non-functional stomata lacking guard cells (SEM)

4. Tree or large shrub with stem segments 2-3.5 cm in diam.; ribs deeply crenate, 6-10 mm thick at base ... 14a. *L. weingartianus* subsp. *weingartianus*

4'. Small scandent shrub with stem segments 1.3-2 cm in diam.; ribs straight or nearly so, 3-5 mm thick at base ..... 14b. *L. weingartianus* subsp. *demissus*

3'. Roots not thickened; stem segments bright, vivid green, showing an abrupt change in cortical color (from green to black) when sectioned; rib margin often with small notch between areoles; epidermis with nearly 100% perfect, functional stomata (SEM)

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5. Small tree with arching branches; *Ultimate stem segments* 3.8-6 cm in diam.; ribs 1.3-2.4 cm high; epidermal cells with convex periclinal walls and straight anticlinal boundaries (SEM)

6. Spines of *Ultimate stem segments* spreading, the central ones longer, to 2.5-4.5 cm long; radial spines 6-10 ..... 6a. *L. wrightii* subsp. *wrightii*

6'. Spines of *Ultimate stem segments* erect and nearly of the same length, to 1-1.5 mm long; radial spines none ..... 6b. *L. wrightii* subsp. *gracilis*

5'. Shrub with erect branches; *Ultimate stem segments* 2.5-4.2 cm in diam.; ribs 0.8-1.2 cm high; epidermal cells with flattened periclinal walls and undulated anticlinal boundaries (SEM) ..... 7. *L. scopulophilus*

2'. Stem grooves of ultimate segments acute or obtuse, its deepest part often defined by a clear line

7. Suffruticose plants less than 1.5 m high; tomentum of young areoles whitish-yellow; cortex radius (distance between the crest of a rib projection and the vascular cylinder) 5-6 mm ..... 3. *L. ekmanii*

7'. Trees or shrubs more than 1.5 m high; tomentum of young areoles tawny or brown; cortex radius 7-26 mm

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8. Tomentum of young areoles tawny

9. *Ultimate stem segments* 2.5-3 cm in diam.; spines very unequal in areole, the upper-central ones to 4-5.3 cm long ..... 2. *L. chrysotyrius*

9'. *Ultimate stem segments* 3.5-6 cm in diam.; spines nearly of the same length in areole, the upper-central ones to 3.5 cm long

10. Tip of spines brown; stem segments dull bluish- or grayish-green; epidermis irregularly multistratose, its cells with flattened periclinal walls (SEM) ..... 15. *L. paniculatus*

10'. Tip of spines yellow; stem segments bright green; epidermis uniformly unistratose, its cells with convex periclinal walls (SEM)

11. Stem ribs 4-5; areoles 1.6-4 cm apart; cortex radius (distance between the highest margin of rib and the vascular cylinder) 2.3-2.5 cm .... 9. *L. arboreus*

11' Stem ribs 5-6; areoles 1.2-1.8 cm apart; cortex radius 1.4-2.2 cm .... 13. *L. santamarinae*

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8'. Tomentum of young areoles brownish to dark reddish-brown

12. Rib margin sinuate (wavy), the areole not positioned at the deepest part of the sinus ..... 10. *L. carinatus*

12'. Rib margin crenate, the areole positioned at the deepest part of the crenature

13. Stems deep dark green; ribs 3 or 4 (very rarely up to 5 in *L. grantianus*)

14. Spines slightly compressed and twisted, acicular, spreading, the longest ones 2-4 cm long .16a. *L. quadricostatus* subsp. *quadricostatus*

14'. Spines (if present) terete, subulate, adaxially or radially oriented, the longest ones 0.5-1.3 cm long

15. Areoles with a fascicle of 10-15 adaxially oriented spines 3-13 mm long; tomentum of young areoles tan to light brown .....
.....16b.*L. quadricostatus* subsp. *parvispinus*

15'. Areoles unarmed or with up to 4 reduced, mostly radial spines 0.5-2 mm long; tomentum of young areoles dark brown .....
..... 17. *L. grantianus*

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13'. Stems clear, bright green to somewhat verdigris-green; ribs 5-10

16. Central spines 1-4 in each areole

17. Plants procumbent or dangling; *Ultimate stem segments* 3-4 cm in diam. ..... 5. *L. albellus*

17'. Plants tree-like or shrubby; *Ultimate stem segments* 1.5-2.5 cm in diam.

18. Stem ribs 2-6 mm high; cortex radius (distance between the crest of a rib projection and the vascular cylinder) 7-8 mm; stomatal apparatus often in sunken zones (SEM) ..... 1. *L. assurgens*

18'. Stem ribs 9-11 mm high; cortex radius 10-11 mm; stomatal apparatus superficial (SEM) ..... 8. *L. leonii*

16'. Central spines 6-10 in each areole

19. Tree-like to 5 m tall; central spines not markedly longer than the radials, to 2.5-3.5 cm long, lemon-colored to light yellowish-brown when young ..... 11. *L. sylvestris*

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19'. Shrubby, to 1.5 m tall; central spines markedly longer than the radials, to 4.5-7 cm long, brown or dark brown when young .... 12. *L. maxonii*

10.2.2. Key for flowering and fruiting specimens

1. Mature stem segments lacking terminal cephalia

2. Flower buds blackish at tip; flowers with winglike projections, the tube bearing black spines; fruits markedly ribbed .....10. *L. carinatus*

2'. Flower buds not blackish at tip; flowers without projections, the tube bearing yellow or brownish bristles/spines; fruits smooth or with slightly elevated ortostichy lines

3. Inner perianth segments yellow

4. Flower tube purplish-red (often with a mixture of green); stamens tightly grouped in a compact column; perianth limb flat, perpendicular to floral axis ..... 2. *L. chrysotyrius*

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4'. Flower tube pure green, greenish-yellow, or yellow; stamens loosely set; perianth limb slightly inflexed, or reflexed

5. Flowers up to 30 grouped in upper portion of stem segment, 1.1-1.5 cm wide; tube yellow, 0.5-0.7 cm in diam. ..... 3. *L. ekmanii*

5'. Flowers solitary or up to 10 grouped in upper portion of stem segment, 2.2-3.1 cm wide; tube green or greenish-yellow, 1-1.8 cm in diam.

6. Flowers tubular, the tube 1.1-1.3 cm in diam. above; perianth limb often slightly inflexed; staminal ring 0.9-1.3 cm in diam. ..... 4. *L. prostratus*

6'. Flowers tubular-obconical or obconical, the tube 1.4-1.8 cm in diam. above; perianth limb distinctly reflexed; staminal ring 1.4-1.8 cm in diam. ..... 1. *L. assurgens*

3'. Inner perianth segments white, creamy, pinkish or orange

7. Inner perianth segments pale pink, pinkish-orange, or orange

8. Flowers campanulate; pericarpel 1.8-2.1 cm in diam.; inner perianth segments pinkish-orange to orange

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9. Longest spines of flower tube 8-13 mm long, spreading .....
.....6a. *L. wrightii* subsp. *wrightii*

9'. Longest spines of flower tube 5-7 mm long, adaxially oriented .....
.....6b. *L. wrightii* subsp. *gracilis*

8'. Flowers obconical; pericarpel 0.8-1.4 cm in diam.; inner perianth segments pale pink

10. Flowers 4.5-6.5 cm long, with numerous acicular spines; tube bright green; fruit ellipsoid or ellipsoid-globose > 5 cm in diam., spiny .....
.....7. *L. scopulophilus*

10'. Flowers 3.2-4.3 cm long, spineless or with scattered bristle-like spines; tube purplish-red; fruit globose, 2-3 cm in diam., naked or with a few scattered bristles .....8. *L. leonii*

7'. Inner perianth segments pure white or creamy

11. Pericarpel showing a rapid change in cortical color (from green to black) when cut open; seeds not narrowed at the hilum-cup insertion level; hilum-micropilar region surrounded by an angular rim (SEM)

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12. Flowers obconical; floral areoles with up to 10-12 spines; fruits 1.8-2.5 cm long ....5. *L. albellus*

12'. Flowers cylindrical, cylindrical-campanulate, or campanulate; floral areoles with up to 20-35 spines; fruits 4-10 cm long

13. Tomentum of floral areoles dark brown; abaxial surface of outermost perianth segments brownish; seeds without a dorsal keel-like ridge; dorsal exotesta cells about as large as the lateral ones, or slightly larger (SEM)

14. Proximal (maximum) diam. of floral tube 1.8-2.5 cm; areoles of fruits separated by wide spaces, often dropping off at maturity; fruit not covered by a continuous lattice of overlapping spines .... 11. *L. sylvestris*

14'. Proximal (maximum) diam. of floral tube 1.4-1.8 cm; areoles of fruits densely set, persistent at maturity; fruit covered by a continuous lattice of overlapping spines ..... 12. *L. maxonii*

13'. Tomentum of floral areoles tawny; abaxial surface of outermost perianth segments greenish-white or reddish; seeds with a dorsal keel-

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like ridge; dorsal exotesta cells 4-7-times larger than the lateral ones (SEM)

15. Flowers cylindrical-campanulate or campanulate; perianth segments almost enclosed in the spine lattice of tube; abaxial surface of outermost perianth segments greenish-white; fruits with elevated ortostichy lines .....9. *L. arboreus*

15'. Flowers cylindrical; perianth segments spreading freely; abaxial surface of outermost perianth segments reddish; fruits smooth, even ..... 13. *L. santamarinae*

11'. Pericarpel not showing a rapid change in cortical color when cut open; seeds narrowed at the hilum-cup insertion level; hilum-micropilar region surrounded by a curved rim (SEM)

16. Flowers narrowly tubular, spineless or with small, bristle-like spines 1-3 mm long; areoles of floral tube 0.25-0.75 mm in diam. ....14a. *L. weingartianus* subsp. *weingartianus*

16'. Flowers obconical, armed with stiff spines up to 9-11 mm long; areoles of floral tube 2-2.75 mm in diam. ....14b. *L. weingartianus* subsp. *demissus*

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1'. Mature stem segments with terminal cephalia

17. Cephalium simple, 10-25 mm wide, creamy or tawny; floral areoles subtended by small scales; seed hilum linear, < 90 μm broad (SEM) .....15. *L. paniculatus*

17'. Cephalium occasionally ramified, 4-9 mm wide, dark brown to nearly black; floral areoles not subtended by scales; seed hilum oblong to narrowly oblong-lanceolate, > 100 μm broad (SEM)

18. Flowers tubular, spiny; tube to 1.4-1.7 cm in diam., constricted above nectar-chamber; seeds > 1.4 mm long (SEM)

19. Areoles of upper flower tube with 5-9 spines 4-9 mm long; fruit areoles with 11-18 spines to 10 mm long, easily detaching at maturity .....
.....16a. *L. quadricostatus* subsp. *quadricostatus*

19'. Areoles of upper flower tube with 2-6 (7) spines 1-2 (3) mm long; fruit areoles with 4-12 spines to 3.5 mm long, not easily detaching at maturity .....
.....16b. *L. quadricostatus* subsp. *parvispinus*

18'. Flowers tubular-obconical to nearly obconical, spineless or nearly so; tube to 1.8-2.1 cm in diam., non-constricted above nectar-chamber; seeds < 1.4 mm long (SEM) .....17. *L. grantianus*

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10.3. Description of species and subspecies of *Leptocereus*

Leptocereus (A. Berger) Britton & Rose, Contr. U. S. Natl. Herb. 12(10): 433. 1909.

Subgenus ***Leptocereus*** A. Berger, Annual Rep. Missouri Bot. Gard. 16: 79. 1905, *emend.* Areces.

Type: **Leptocereus assurgens** (C. Wright) Britton & Rose, Contr. U. S. Natl. Herb. 12(10): 433. 1909.

Frutices prostrati vel erecti aut arbores usque 8-10 m alti, non nisi cubensis; cortex mox nigrescentes et manifeste fibroso-reticulatus; reticulum fibris totam caudicis longitudinem percurrens; flores plerumque vespertino- vel nocturno-matutini aliquando diurni et nocturni itaque vivide colorati, interdum tantum nocturni; tubo nullo modo constricto; loculus nectariferus subcylindraceous; semina inaequilatero-obovata, breviter rostellata, annulo angulato vel scalprato hilo-micropyle cavitati cingenta; testa cellulis valde inaequilongis, majoribus ultra 100 μm diam., cuticula subtiliter ruguloso-plicata obtecta.

Prostrate or erect shrubs, to trees to 8-10 m tall; stem cortex showing a rapid darkening reaction upon injury, manifestly fibrose-reticulated; reticulum fibers of cortex extending longitudinally the whole length of the stems and trunk; flowers often vespertine- or nocturnal-matutinal, sometimes diurnal and nocturnal, and in those cases

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brightly colored, occasionally strictly nocturnal; receptacle-tube not constricted (above and below nectar chamber); nectar chamber subcylindric in outline; seeds unequally obovate (mussel-shaped), slightly rostellate (somewhat beaked); hilum-micropilar cavity surrounded by an angular rim often having a sharp edge; testa cells very unequal, the largest (dorsal) ones more than 100 μm in diameter, their periclinal (outer) surface finely wrinkled (i.e., covered with thin cuticular folds). Thirteen species, all of Cuba.

Section ***Leptocereus*** Areces, sect. nov.

Type: **Leptocereus assurgens** (C. Wright) Britton & Rose, Contr. U. S. Natl. Herb. 12(10): 433. 1909.

Section readily distinguished from other sections of genus *Leptocereus* by its low, shrubby, prostrate or dangling habit, its mostly yellow, rarely white, vespertine-nocturnal-matutinal or diurnal-nocturnal flowers, often grouped in clusters, and its small fruits barely 1.5 to 2 cm in diameter. This section includes five species from western Cuba, two of them herein described as new (*Leptocereus chrysotyrius* Areces and *L. albellus* Areces).

1. **Leptocereus assurgens** (C. Wright) Britton & Rose, Contr. U. S. Natl. Herb. 12(10): 433. 1909 (as to name, excluding the illustration citation).

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Bas.: *Cereus assurgens* C. Wright, in Griseb. Cat. Pl. Cub. 116. 1866. — Type: Cuba. Prov. Pinar del Río (western Cuba), in 1862 (fl), C. *Wright 2622* (holotype: GH; isotypes: HAC, US).

Lit.: Sauvalle, Fl. Cubana, 1: 58. 1868; Schumann, Gesamtb. Kakteen 140, fig. 33. 1903; Urban, Fl. Dom., in Symbol. Ant. 8: 461. 1903-11 (name erroneously applied to *L. weingartianus* subsp. *weingartianus*); Berger, Syst. Rev. *Cereus*, Rep. Mo. Bot. Gard. 16: 79. 1905; Britton & Rose, Cactaceae 2: 79, 1920 (name erroneously applied, description and fig. 114 corresponding to *L. wrightii* León); Werdermann, Ekman Westind. Gesam. Cactaceae, Fedde Rep. 29: 234. 1931; Moscoso, Cactáceas Fl. Sto. Dom., Anal. Univ. Sto. Dom. 5(1-2): 23. 1941 (erroneously taken as a synonym of *L. weingartianus* s. lat.); Moscoso, Cat. Fl. Dom. 1: 404. 1943; Marshall & Bock, Cactaceae 79. 1941; León & Alain, Fl. Cuba 3: 372-373, Contr. Ocas. Mus. Hist. Nat. La Salle 13. 1953; Backeberg, Die Cactaceae 4: 1961-1962. 1960; Backeberg, Kakteenlexikon 201. 1966; Anderson, Cactus Fam. 391-392. 2001.

Figs. 2 A1, A2; 4 N. Plates 5 A, B; 8 A; 12 E, F; 23 H: 24 F, H; 41 C-E; 46 A; 55.

Shrub ramified near ground level or above it, to 1-1.5 m tall, with a very short trunk to 4-6 cm in diameter, diffusely branched. *Ultimate stem segments* usually sloping with a downward inclination, 0.3-2 m long, 1.5-2.2 cm in diameter (to 2.5 cm in diameter under cultivation); stem sinuses acute, usually demarcated by a line, 3-5 mm

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Plate 55. Flower of *Leptocereus assurgens* photographed in the haystack mountain ranges of Viñales, Pinar del Río province, western Cuba. The species was first collected by C. Wright between 1860 and 1864 and described in Grisebach's *Catalogus* of 1866. There was a great confusion with the application of the name of this taxon because no precise locality was mentioned in the original publication, and the type specimen actually consisted of material belonging to two different species collected at two different sites.

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Plate 56. The color of the fruits of *Leptocereus chrysotyrius* —a new species from western Cuba– may be defined as *githagineous* (i.e., greenish-red). The name is derived from *Githago*, and it refers to red or purple ribs on a green calyx, such as occurs in some species of *Silene* (Lindley, 1832).

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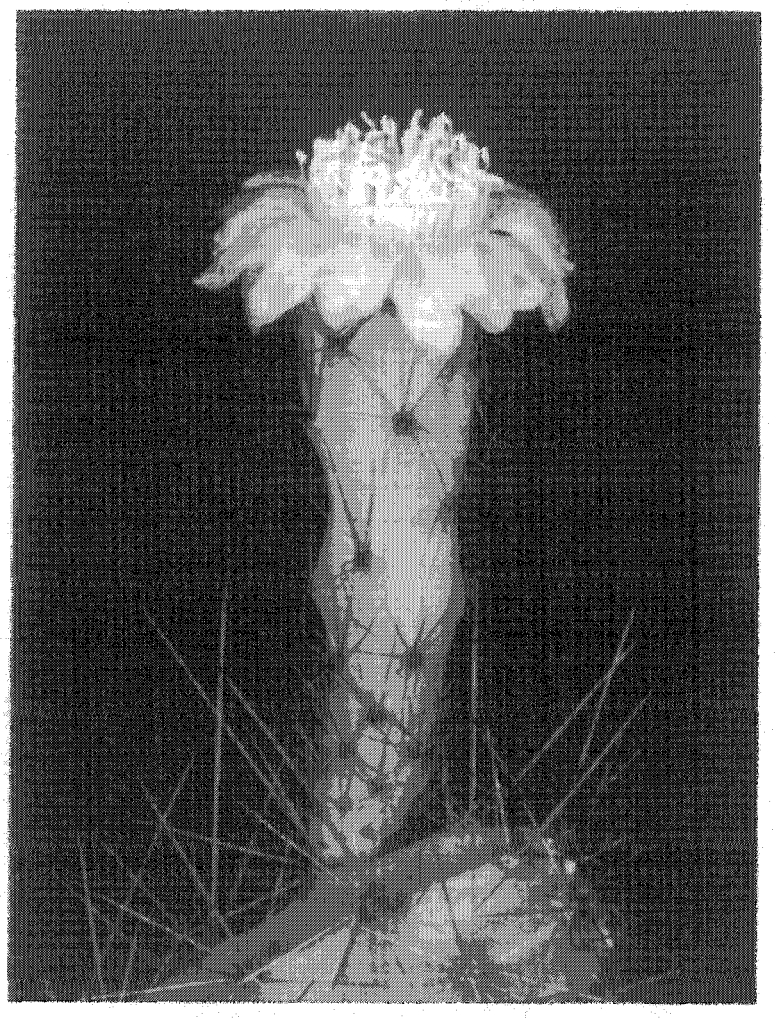

Plate 57. Tubular flower of *Leptocereus prostratus*, endemic to the limestone ranges of Sumidero, Pinar del Rio province, western Cuba. The species is unique in having procumbent stems with a slight differentiation between the dorsal and ventral sides, the vascular cylinder often being a little excentrical. Unlike other members of the genus, the stem areoles of this species are not sunken but elevated.

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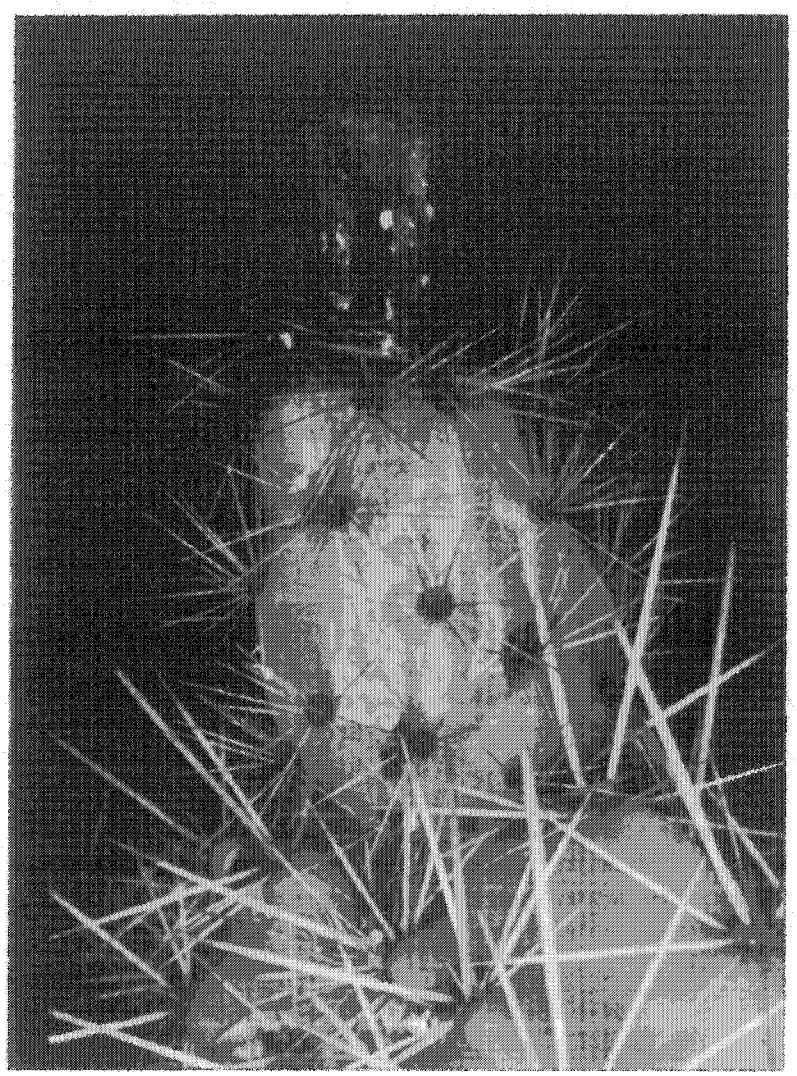

Plate 58. As in all members of section *Leptocereus* of subgenus *Leptocereus*, the fruits of the cliff dweller *L. albellus* spec. nov. are rather small. They are produced at the apex of dangling stems that may reach four meters long.

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deep; cortex fibrous, 3-4 mm wide at the grooves, 7-8 mm wide at the crest of a rib projection (podarium); vascular cylinder 4-5 mm in diameter; pith 2.5-3.5 mm in diameter. *Ribs* (6) 7 or 8 (10), 2-6 mm high, 2-4 mm wide at base, their edges separated 0.5-1 cm from each other, distinctly crenate, subcrenate, to barely crenate, the crenatures commonly 1-1.5 mm deep bearing the areoles at the bottom of the depressions. *Areoles* mostly rounded, 2-3 × 2-2.5 mm, 0.9-1.5 cm apart (to 1.8 cm apart *fide* León, 1940), those of a young stem tufted with short, chesnut-brown (badius) tomentum becoming tawny and finally grayish or grayish-white with age (tomentum white *fide* León, *op. cit.*), armed with (10) 12-16 slightly unequal spines. *Spines* straight, rigid, acicular, in youth brownish-yellow, brownish-yellow tinged with pink, or pale pure yellow, their growing bases whitish-yellow, becoming ash-gray, 0.5-2 cm long, 0.1-0.3 mm in diameter; radial spines 7 or 8 (12), 0.5-1.5 cm long, 0.1-0.2 mm in diameter; central spines (3) 4, (0.9) 1.3-2 cm long, 0.2-0.3 mm in diameter. *Flowers* vespertine-nocturnal-matutinal, borne on apical and lateral areoles towards the apex of the stem, frequently in clusters of 3-15, 2-6 of them opening simultaneously, 3.8-4.5 cm long (3-5 cm long in cultivated specimens), 2.5-3 cm wide, cylindrical to cylindro-obconical, spinose; pericarpel clear bright green, spinose, 8-11 mm in diameter; receptacle-tube bright green at base, turning gradually into clear yellow at apex, to 1.4-1.8 cm wide above; perianth segments reflexed, pale bright yellow; stamens forming a lax staminal ring 1.4-1.8 cm in diameter (to 2 cm in cultivated specimens), exserted 2-5 mm beyond the floral throat during anthesis; stigma 4-6 mm long, extending ca. 3 mm beyond the upper stamen level. *Fruit* unknown.

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Distribution: limestone cliffs in the vicinity of Viñales, Pinar del Río Province, western Cuba.

Although Charles Wright distinguished this taxon from another species of western Cuba, also collected and informally described by him in 1862, only *Leptocereus assurgens* was validly published (in Grisebach, Cat. Pl. Cub., 116. 1866). His manuscript description of the second species —*L. wrightii*, a plant that was named after him by León 82 years later— remained untouched on the isotype specimen of *L. assurgens* deposited in the Sauvalle Herbarium in Cuba (*Wright 2622*, HAC). This isotype exsiccatus (not the holotype at GH) contained mixed material of the two *Leptocereus* species discovered by Wright, one from Pinar del Río province (*L. assurgens*), and the other from coastal areas near Havana. Probably because Britton never saw the isotype with Wright's description and the mixed plant material, he took the coastal *Leptocereus* taxon for *L. assurgens*. This is surprising, considering that the original description of the species, that Britton and Rose obviously overlooked, clearly states that the plant has 6 to 8 ribs and green-yellow flowers (Wright, in Grisebach, 1866). By contrast, the other *Leptocereus* species that Britton and Rose took for *L. assurgens*, has only 4 to 5 ribs, and reddish flowers. Thus, the description and figure 114 given by these authors in 1920 (Cactaceae 2: 79), along with plate 8, fig. 4, correspond to *L. wrightii*, not *L. assurgens*. León (1940) unraveled this interesting problem by naming and describing the neglected species as a tribute to Charles Wright, its first discoverer.

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2. **Leptocereus chrysotyrius** Areces, spec. nov.

Type: Cuba. Prov. Pinar del Río: vicinity of San Diego de Los Baños, steep limestone hillsides near the Río San Diego, ca. 1 km north of the town, 3 Nov 1976 (fl, fr in cult.), *Areces 4547* (holotype: HAC, to be deposited; isotype: NY, to be deposited).

Figs. 3 F1, F2; 4 I. Plates 2 E, F; 9 D; 14 A; 20 H; 21 G; 25 D; 37 E-H; 41 H, I; 46 A; 56.

Shrub diffusely and densely branched, lacking a definite trunk, with numerous arched stems, to 0.8-1.2 m tall, the older branches becoming woody at base, to 4 cm in diameter at ground level. *Ultimate stem segments* commonly sloping downward, 0.15-1 m long, 2.5-3 cm in diameter; stem sinuses acute, usually demarcated by a line, 5-10 mm deep; cortex fibrous, 4-5 mm wide at the grooves, 11-13 mm wide at the crest of a rib projection (podarium); vascular cylinder 5-6 mm in diameter; pith 3.6-4 mm in diameter. *Ribs* almost invariably 6 or 7, 8-13 mm high, 4-8 mm wide at base, their edges separated 1.2-1.5 cm from each other, scantily crenate when young, in age usually not crenate, the crenatures of young stems to 1-2 mm deep bearing the areoles at the bottom of the depressions. *Areoles* rounded or nearly so, 4-5 × 3.5-5 mm, 1.5-2 cm apart, those of a young stem tufted with short, tawny (fulvus) tomentum, becoming grayish and finally grayish-white with age, armed with (9) 11-12 (13) unequal spines, those of the upper half of the areole longer and thicker. *Spines* straight, rigid, acicular,

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in youth light rusty-brown (ferrugineus), yellow at tip, their growing bases pale green, becoming ash-grey, 0.9-5.3 cm long, 0.2-0.7 mm in diameter; radial spines (6) 8 (9), 0.9-2.4 cm long, 0.2-0.5 mm in diameter; central spines (3) 4 (5), 2.2-5.3 cm long, 0.4-0.7 mm in diameter, the upper one longest, porrect or more often ascending. *Flowers* vespertine-nocturnal-matutinal, borne on apical and lateral areoles towards the apex of the stem, frequently in clusters of 5-25, 3-5 of them opening simultaneously, 3.7-4.1 cm long, 2.1-2.5 cm wide, cylindrical, spinose, the spines thin, brownish-pink to reddish-brown; pericarpel greenish-red (githagineous) to wine-colored (vinaceous), spinose, 9-11 mm in diameter; receptacle-tube greenish-red with the podarium tips wine-colored to entirely wine-colored, to 1.3-1.5 cm wide above; perianth limb flat, perpendicular to floral axis; inner perianth segments pale bright yellow; stamens tightly grouped in a compact column 0.9-1.3 cm in diameter, exserted 4-6 mm beyond the floral throat during anthesis; stigma 4-5 mm long, extending 1-3 mm beyond the upper stamen level. *Fruits* pear-shaped, greenish-red, with very fine spines, small, 1.7-2.2 cm in diameter; seeds few.

Distribution: haystack mountains near San Diego, and Sierra de la Güira, Pinar del Río Province, western Cuba.

Leptocereus chrysotyrius seems more closely related to *L. assurgens* than to any other species of section *Leptocereus*. It differs from the latter, however, in having thicker stem segments with larger ribs and areoles; in the spination pattern, the spines being unequal, longer and more stout, particularly the upper central ones; in the

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peculiar flowers that have a shorter and more cylindrical receptacle-tube that is greenish-red or vinaceous; the daisy-like arrangement of the limb, with perianth segments that spread flat, not reflexed, and in the grouping of the relatively long-exserted stamens, which form a compact column, not a lax staminal ring.

3. **Leptocereus ekmanii** (Werdermann) F. M. Knuth, in Backeb. & Knuth, *Kaktus-ABC* 302. 1935.

Bas.: *Cereus ekmanii* Werderm. Repert. Spec. Nov. Regni. Veg. 29: 235. 1931. — Type: Cuba. Prov. Pinar del Río: Guane, Sierra de Guane, on the highest top of the Sierra, in very exposed localities, 14 May 1924 (fl), *E. L. Ekman 18724* (holotype: B, destroyed; lectotype: S, here designated).

Lit.: Marshall & Bock, Cactaceae 79. 1941; León & Alain, Fl. Cuba 3: 372, Contr. Ocas. Mus. Hist. Nat. La Salle 13. 1953; Backeberg, Die Cactaceae 4: 1961. 1960; Backeberg, Kakteenlexikon 201. 1966; Anderson, Cactus Fam. 392. 2001.

Figs. 2 H1, H2; 4 D. Plates 5 C; 6 A, B; 9 E; 11 A; 13 A; 15 A; 17 B; 21 E, F; 22 F, G; 24 C, E; 40 C; 41 A, B; 46 A.

Suffruticose plant, or small *shrub* to 1 m tall, much branched, its main stems diffusely ramified near ground level or above it, with a secondarily grown shoot stele at the base but manifesting very retarded periderm formation (stems may undergo aging

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remaining as green and photosynthetic as they were when their apical growth ceased). *Ultimate stem segments* numerous straight, ascending, inclined at a wide range of angles, or extended in a horizontal direction, relatively short and slender, 0.1-0.5 m long, 1-1.7 cm in diameter; stem sinuses acute, usually demarcated by a line, 2-3 mm deep; cortex fibrous, 3-6 mm wide at the grooves, 5-6 mm wide at the crest of a rib projection (podarium); vascular cylinder 2-3 mm in diameter; pith 1-1.9 mm in diameter. *Ribs* 6 or 7, low, 3-5 mm high, 2-3 mm wide at base, their edges acute (or nearly so) and rather sharp, separated by 4-6 mm, finely crenate, the crenatures 0.5-1 mm deep bearing the areoles at the bottom of the depressions. *Areoles* transversely oblong to subrounded, 1.5-2.5 × 1.5-2.5 mm, 0.8-1.5 mm apart, those of a young stem tufted with short, creamy to light brown tomentum becoming grayish-brown and finally grayish with age, armed with 9-13 unequal spines. *Spines* straight, rigid, acicular, in youth bright yellow to brownish, their growing bases whitish-yellow, becoming sooty gray, 0.3-4.3 cm long, 0.1-0.3 mm in diameter; radial spines 6-9 (10), 0.3-3 cm long (to 4 cm long *fide* Werdermann, 1931), 0.1-0.2 mm in diameter; central spines (1) 3 or 4, 0.9-4.3 cm long, 0.2-0.3 mm in diameter, one porrect and the others ascending. *Flowers* both diurnal and nocturnal, borne on apical and lateral areoles towards the apex or on the half distal part of the stem, grouped in clusters of 8-30 or more, 2-15 of them opening simultaneously, 1.9-2.8 cm long including the exserted stigma, 1.1-1.5 cm wide, cylindric-salverform, with elevated podaria and bristle-like spines; pericarpel greenish-yellow or yellow, bristly, 5-6 mm in diameter; receptacle-tube yellow, to 0.6-0.7 mm wide above; perianth segments bright yellow, 3-5 mm long; stamens forming a staminal ring 0.3-0.5 mm in diameter, the anthers at the floral throat level or nearly so

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during anthesis, or slightly inserted; stigma 2-3 mm long, extending 1-5 mm beyond the upper stamen level. *Fruit* unknown.

Distribution: restricted to the eroded top of Sierra de Guane, the westernmost limestone range of Cuba, in Pinar del Río province.

4. **Leptocereus prostratus** Britton & Rose, Cact. 2: 79. 1920. — Type: Cuba. Prov. Pinar del Río: La Güira, north of Sumidero, on high, dry, exposed rocks, 17 Aug 1912 (fl), *Shafer 13754* (holotype: NY; isotypes: A, US).

Lit.: León, in Giménez-Lanier, León & Marshall, Cuban Cacti, Cact. & Succ. J. (US) 9(1): 11. 1937; León & Alain, Fl. Cuba 3: 373, Contr. Ocas. Mus. Hist. Nat. La Salle 13. 1953; Backeberg, Die Cactaceae 4: 1961. 1960; Backeberg, Kakteenlexikon 201. 1966; Anderson, Cactus Fam. 393, 1 fig. 2001.

Figs. 1D; 2 E1, E2; 4 K1, K2. Plates 10 A; 11 E; 14 G; 15 E, F; 16 H; 17 K; 22 C, D; 39 C-E; 41 F, G; 44 D; 46 A; 57.

Procumbent *shrub* ramified near ground level, to 0.7 m tall, with slightly bilaterally symmetrical, crawling branches arising from a common, woody base; branches rather slender, at first arching, soon becoming prostrate, with a perceptible differentiation between dorsal and ventral sides that also involves the internal anatomy (dorsal cortex and stele a little thicker). *Ultimate stem segments* at first arching, soon

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lying flat on the ground, 0.3-1.5 m long, 1.5-2 (3) cm in diameter; stem sinuses broadly rounded, not demarcated by a line, 3-5 mm deep; cortex fibrous, 5-8 mm wide at the grooves, 9-11 (13) mm wide at the crest of a rib projection (podarium); vascular cylinder 6-8 mm in diameter; pith 3.7-4.3 mm in diameter. *Ribs* 7 (8), 5-8 mm high, 7-9 mm wide at base, their outline conical in transverse section, their edges acute, separated 0.9-1.3 cm from each other, usually dentate, sometimes straight, commonly bearing the areoles at the tip of raised podaria. *Areoles* to 1.5 mm elevated, rounded, 2-4 × 2-4 mm, 1-1.9 cm apart, those of a young stem tufted with short, brownish to tawny tomentum becoming grayish-white with age, armed with (15) 17-20 very unequal spines; areoles of the dorsal side of mature stems often a little larger and with somewhat longer spines. *Spines* straight, rigid, acicular, in youth brownish-yellow with some admixture of pink, their growing bases whitish-yellow, soon becoming yellowish and finally ash grey, 0.6-5.2 cm long, 0.1-0.5 mm in diameter; radial spines (9) 10-12, nearly of the same length in each areole, 0.6-1.5 cm long, 0.1-0.2 mm in diameter; central spines (6) 7 or 8 (10), the upper central one often notably long, 1.3-5.2 cm long, 0.2-0.5 mm in diameter. *Flowers* both diurnal and nocturnal, borne on apical and lateral areoles towards the apex of the stem, frequently in clusters of 3-12, 2-5 opening simultaneously, 3.7-4 cm long (to 5.8 cm long in a cultivated specimen), 2.2-2.7 cm wide, cylindrical, spinose; pericarpel clear, bright green, spinose, 8-10 mm in diameter; receptacle-tube bright green at base, gradually turning into clear yellow at apex, to 1.1-1.3 cm wide above; perianth limb often cup-shaped (cupulate), sometimes reflexed, the segments inflexed or reflexed, pale, bright yellow; stamens forming a staminal ring 0.9-1.3 cm in diameter, exserted 0-4 mm beyond the floral throat during anthesis; stigma 4-

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5 cm long, extending 0-2.5 mm beyond the upper stamen level. *Fruits* ca. 1.5 cm in diameter (*fide* Britton & Rose, 1920).

Distribution: occurring only on top of the haystack mountains near Sumidero, Pinar del Río Province, western Cuba.

5. **Leptocereus albellus** Areces, spec. nov.

Type: Cuba. Prov. Pinar del Río: vicinity of San Carlos, in Sierra de San Carlos, on vertical cliffs surrounding the sinkhole Hoyo de los Helechos, within the Majagua-Cantera cavernous system, 28 Mar 1992 (fl; fr in cult.), *Areces 6343* (holotype: HAC, to be deposited; isotype: NY, to be deposited).

Figs. 3 C1, C2; 4 A. Plates 3 E; 23 B; 38 A-D; 46 A; 58.

Dangling shrub ramified at ground level (or nearly so), to 0.3 m tall, with long, moderately thick, 4-5 cm in diameter, radially symmetric hanging branches arising from a common, woody base to 6-10 cm in diameter. *Ultimate stem segments* produced horizontally or nearly so, soon becoming pendent, 0.38-1.90 m long, 3-4 cm in diameter; stem sinuses acute, usually demarcated by a line, 5-8 mm deep; cortex fibrous, 4-6 mm wide at the grooves, 13-15 mm wide at the crest of a rib projection (podarium); vascular cylinder 6-8 mm in diameter; pith 3.5-5 mm in diameter. *Ribs* 6 or 7, 9-13 mm high, 7-10 mm wide at base, compressed (as seen in transverse-section),

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their edges rounded, separated 1.5-2 cm from each other, crenate, the crenatures 1-2 mm deep bearing the areoles at the bottom of the depressions. *Areoles* subrounded to transversely oblong, 3-4 × 3-4 mm, 0.9-1.5 cm apart (to 1.8-2 cm apart in cultivated specimens), those of a young stem tufted with short, dull, dark brown tomentum becoming dark gray with age, armed with (10) 12-15 slightly unequal spines. *Spines* straight, rigid, acicular, in youth brownish-yellow, their growing bases whitish-yellow, becoming sooty gray, 0.6-2.5 cm long, 0.1-0.5 mm in diameter; radial spines (6) 7 or 8 (11), the upper ones a little larger, 0.6-1.8 cm long, 0.1-0.4 mm in diameter; central spines 4, 1.5-2.5 cm long, 0.4-0.5 mm in diameter, often increasing their number to 6-9 on the lower half of the stems by indeterminate growth of the areoles. *Flowers* vespertine-nocturnal-matutinal, most often borne on apical and subapical areoles, frequently in clusters of 3-10, 2-4 opening simultaneously, 4.6-5.4 cm long, 3.2-3.6 cm wide, cylindric-obconical to obconical, spinose; pericarpel clear, bright green, spinose, 10-17 mm in diameter; receptacle-tube from top to bottom clear, bright green, to 2-2.3 cm wide above; perianth segments reflexed, white; stamens forming a lax staminal ring 2.1-2.5 cm in diameter, exserted (2) 5-9 mm beyond the floral throat during anthesis; stigma ca. 5 mm long, extending 4-6 mm beyond the upper stamen level. *Fruits* obovate, somewhat compressed, green, with bristly spines, small, 1.9-2.3 cm long, ca. 1.7 cm wide, ca. 1.4 cm thick; seeds 14-17 in each fruit.

Distribution: a typical cliff dweller confined to the Sierra de San Carlos mountain range, southwest to San Carlos, Pinar del Río Province, western Cuba, only thrives on partially shaded, vertical or nearly vertical escarpments.

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Section ***Roseiflori*** Areces, sect. nov.

Type: **Leptocereus wrightii** León, Mem. Soc. Cub. Hist. Nat. 14: 133. 1940.

Section characterized by its erect, small arborescent or shrubby habit (2-5 m tall) with definite, cylindrical trunk to 20-30 cm in diameter, its campanulate or obconical, nocturnal-matutinal flowers often with upper receptacle-tubes deep purplish-red, and its striking pink, purple-red, or orange perianth limbs. Three species from western Cuba, one of them, and one subspecies, described as new (*Leptocereus scopulophilus* Areces, and *L. wrightii* subsp. *gracilis* Areces).

6. **Leptocereus wrightii** León, Mem. Soc. Cub. Hist. Nat. 14: 133, pls. 2, 2a, 19, 20. 1940.

Small *tree* or *shrub* 2-3 m tall, ramified above, with a cylindrical trunk 0.7-1.5 m long, to 20 cm in diameter, the bark creamy, rather smooth, bearing scattered areoles with grayish spines 1-8 (9) cm long. *Ultimate stem segments* 0.15-1.65 m long, 4-6 cm in diameter; stem sinuses rounded, not demarcated by a line; cortex fibrous. *Ribs* 4 (5), distinctly crenate, often with a subtle indentation halfway between the areoles, the crenatures bearing the areoles at the bottom of the depressions. *Areoles* rounded to broadly oblong, rarely oblong, those of a young stem tufted with short, dark brown tomentum that soon turns tan (or grayish, in areoles with determinate growth), spinose.

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Spines straight, rigid, slightly unequal or nearly of the same length, in youth brownish-yellow with some admixture of pink, yellow at tip, their growing bases whitish-yellow (pale green in spines of old stem areoles with indeterminate growth), becoming yellowish and finally ash grey. *Flowers* nocturnal-matutinal, borne on apical and subapical areoles, solitary or in groups of 2 or 3 (4) on the stem apex, campanulate, spinose; pericarpel clear, bright green, usually spinose; receptacle-tube usually bright green at base, turning gradually into deep purplish-red at apex, the transition zone greenish-red, spinose; perianth segments oblong-ligulate, 5-10 mm long, the outer ones reflexed or extended, wine-colored to bright purplish-red, the inner ones extended, sometimes with the distal half a little inflexed, pink, pinkish-orange or pale orange; stamens forming a lax staminal ring, exserted 3-7 mm beyond the floral throat during anthesis; stigma 4-5 mm long, extending 1-6 mm beyond the upper stamen level.

6a. **Leptocereus wrightii** León, subsp. **wrightii**.

Leptocereus wrightii León, Contr. Estudio Cact. Cuba, Mem. Soc. Cub. Hist. Nat., 14: 2, 133-137, pls. 19, 2, 2a, 20. 1940. — Type: Cuba. Prov. Ciudad de La Habana: west of Cojímar, on coralline coastal terraces, Jun 1939 (fl, fr), *León 16556* (holotype: HAC).

Cereus assurgens sensu descript. Britton & Rose, Cactac. 2: 79, pl. 8(4), fig. 114. 1920, non *Cereus assurgens* C. Wright, in Grisebach, Cat. Pl. Cub., 116. 1866.

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Lit.: León, in Giménez-Lanier, León & Marshall, Cuban Cacti, Cact. & Succ. J. (US) 9(1): 10-11, 1 fig. 1937 (referred to as *L. assurgens*); León & Alain, Fl. Cuba 3: 373, Contr. Ocas. Mus. Hist. Nat. La Salle 13. 1953; Backeberg, Die Cactaceae 4: 1962-1963, figs. 1887-1889. 1960; Backeberg, Kakteenlexikon 201. 1966; Areces, Cact. Succ. Pl. 140, 1 fig. 1997; Areces, W. Indies, in I.U.C.N./S.S.C. Cact. Succ. Pl., 140, 1 fig. 1997; Anderson, Cactus Fam. 395, 1 fig. 2001.

Figs. 2 J1-J4; 4 C1-C3. Plates 3I; 4F, G; 8 B; 8 D, E; 12 C, D; 15 C; 16 G; 17 D; 18 A; 22 A, B; 25 H; 33 I-L; 42 A, B; 44 E; 46 A, B.

Small *tree* or *shrub* densely ramified above. *Ultimate stem segments* 0.15-1.65 m long, 4-5 (6) mm in diameter; stem sinuses 10-16 mm deep; cortex 2-4 mm wide at the grooves, 18-26 mm wide at the crest of a rib projection (podarium); vascular cylinder 5-7 mm in diameter; pith 3-5.2 mm in diameter. *Ribs* 14-24 mm high, 6-9 mm wide at base, their edges separated 2.3-4.2 cm from each other, the crenatures 2.5-5 mm deep. *Areoles* 4-5 (6) × 3-5 (6) mm, 1-3 (4) cm apart, armed with 9-15 (20) spreading spines. *Spines* acicular, 0.6-4.5 cm long, 0.1-0.7 mm in diameter; radial spines (6) 8 (10), 0.6-2.4 cm long, 0.1-0.5 mm in diameter; central spines (3) 6-8 (10), somewhat longer than the radials, (1.2) 2-3.5 (4.5) cm long, 0.3-0.7 mm in diameter, usually spreading, the longest one porrect or slightly ascending. *Flowers* 5.9-7.1 cm long, 3.3-4.1 cm wide (5-6.5 × 3.3 *fide* León, 1940), long-spinose; pericarpel long-spinose, 18-21 mm in diameter; receptacle-tube to 2.4-2.7 cm wide above, long-spinose, its spines to 13 mm

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long; staminal ring 2-2.2 cm in diameter. *Fruits* obovate to nearly rounded, green to yellowish-green, 6.5-10 × 6-8 cm, with spines 0.8-1.8 cm long; seed numerous.

Distribution: coralline terraces of northern Ciudad de La Havana and Pinar del Río provinces, from Cojímar to Bahía Honda, in coastal thickets.

6b. **Leptocereus wrightii** León, subsp. **gracilis** Areces, subsp. nov.

Type: Cuba. Prov. Pinar del Río: vicinity of San Diego, rocky riverbanks and low hillsides along Río San Diego, ca. 2 km north of town, in semi-deciduous forests, 27 Nov 1985 (fl in cult.), *Areces 5777* (holotype: HAC, to be deposited; isotype: NY, to be deposited).

Figs. 3 A; 4 C4. Plates 8 F; 11 D; 12 B; 17 E; 18 B, C; 18 F; 42 C, D; 46 A.

Small *tree* or *shrub* with a rather loose, open top. *Ultimate stem segments* 0.25-1.90 m long, 3.8-4.5 (5.5) mm in diameter; stem sinuses 6-12 mm deep; cortex 3-4 mm wide at the grooves, 18-23 mm wide at the crest of a rib projection (podarium); vascular cylinder 5-7 mm in diameter; pith 2.8-4.8 mm in diameter. *Ribs* 13-22 mm high, 6-10 mm wide at base, their edges separated 2.2-3.8 cm from each other, the crenatures 3-4.5 mm deep. *Areoles* 4-5 × 3-4.5 mm, 1.5-2.7 cm apart, armed with 6-18 adaxially oriented spines. *Spines* subulate, more or less grouped in a loose fascicle that ascends at 30-45° angles, 0.1-1.5 cm long, 0.1-0.4 mm in diameter; radial spines none.

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Flowers 5.7-7 cm long, 3.4-4.2 cm wide, short-spinose; pericarpel short-spinose, 18-20 mm in diameter; receptacle-tube to 2.5-2.7 cm wide above, short-spinose, its spines to 5-7 mm long; staminal ring 1.8-2.1 cm in diameter. *Fruits* unknown.

Subspecies *gracilis* is similar in many respects to subsp. *wrightii* from which, however, it is geographically and ecologically well separated. It also differs in its much less ramified habit, longer (to 1.9 m) stem segments that are also somewhat narrower, more closely set stem areoles (to 2.7 cm apart) bearing no radial spines, and central spines that are not acicular but subulate, less stout (to 0.4 mm diam.), shorter (1-1.5 cm long), and adaxially oriented, not spreading. Floral spines in subsp. *gracilis* are also less numerous and shorter (to 7 mm long at most).

Distribution: only known from the type locality.

7. **Leptocereus scopulophilus** Areces, Brittonia 45(3): 226, figs. 1 C, D, 2 A, B. 1993. — Type: Cuba. Prov. Ciudad Habana: vicinity of Jamaica, 25 km SE of La Habana, on the limestone summit of Somorrostro Hill, ca. 23°02' N, 82°10' W, 4 Jun 1975 (fl, in cult., 17 Apr 1976), *Areces 4601* (holotype: MNHN; isotypes: HAC, HAJB, NY).

Lit.: León, in Giménez-Lanier, León & Marshall, Cuban Cacti, Cact. & Succ. J. (US) 9(1): 11. 1937 (referred to as *L. leonii*); Anderson, Cactus Fam. 393, 1 fig. 2001.

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Figs. 3 D1-D3; 3 I1, I2, J; 4 J. Plates 3 G; 10 H; 13 C; 17 F; 22 E; 33 E-H; 41 L, M; 46 B; 59.

Erect *shrub* to 2-3 m tall, with a simple, nearly cylindrical trunk to 10-20 cm in diameter, the older branches bearing long spines to 8-10 cm long. *Ultimate stem segments* ascending or diverging at 30° to 45° angles, 0.25-1.50 m long, (2.5) 3-4.2 cm in diameter (to 4.8 cm in diameter under cultivation); stem sinuses rounded, not demarcated by a line, 4-8 mm deep; cortex fibrous, 2-3 mm wide at the grooves, 11-13 mm wide at the crest of a rib projection (podarium); vascular cylinder 5-7 mm in diameter; pith 3-3.8 mm in diameter. *Ribs* 4 or 5 (6), 8-12 mm high, 3-9 mm wide at base, their edges separated 1.4-1.8 cm from each other, crenate although not markedly so (older stems and branches subcrenate), often with a subtle indentation halfway between the areoles, the crenatures 0.5-2 mm deep, bearing the areoles at the bottom of the depressions. *Areoles* mostly rounded or subrounded, sometimes transversely elliptic, suboblong, or oblong, 3-4.5 × 2-4 mm, (1.5) 1.9-2.8 (3.3) cm apart, those of the tip of a growing stem tufted with a brown tomentum that soon becomes tawny or tawny-yellowish, armed with (7) 11-16 (19) very unequal spines, with precocious indeterminate growth (shortly after the areoles are formed, they begin to produce long, supplementary spines on most stem segments; this new growth is often more active at one side of the stem, or one rib). *Spines* straight, rigid, acicular, brownish-yellow to dark brown in youth, their growing bases pale yellowish-green, in age becoming gray, 0.8-6.5 cm long, 0.2-0.7 mm in diameter; radial spines (5) 8 (13), the lower pair smaller, 0.8-2.5 cm long, 0.2-0.3 mm in diameter; central spines (2) 3-6, (1.9) 2.8-5.5

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(6.5) cm long, 0.3-0.7 mm in diameter (older stem segments with an upper, central spine to 7-9 cm long and ca. 1 mm in diameter), porrect or slightly ascending. *Flowers* nocturnal-matutinal, most often borne on apical and subapical areoles, solitary or 2-5 grouped towards the stem apex, 4.5-6.5 cm long, 3-3.8 cm wide, obconical, spinose; pericarpel clear, bright green, spinose, 8-14 mm in diameter; receptacle-tube from top to bottom clear, bright green, to 1.8-2.2 cm wide above; outer perianth segments ligulate or oblong-ligulate, rounded at apex, pale wine-colored, the inner ones pale pink to nearly white; stamens forming a lax staminal ring 1.5-2.8 cm in diameter, exserted 5-6 mm beyond the floral throat during anthesis; stigma 6-8 mm long, extending 4-7 mm beyond the upper stamen level. *Fruits* ellipsoid to ellipsoid-globose, 6.5 × 5.5 cm, bearing areoles with persistent spines.

Since 1922 when Ekman collected *Leptocereus scopulophilus* for the first time at Lomas de Camoa (*Ekman 13713,* S), followed by León, in 1923 in Somorrostro Hill (*León 11446* GH, HAC), this species has been considered conspecific either with *L. assurgens* (Werdermann, 1931) or *L. leonii* (León, in Giménez-Lanier *et al.*, 1937; León & Alain, 1953). Doubting the likehood of correct identification of a plant lacking its flowers, I collected several adult, living specimens on the summit of Somorrostro Hill. Nine months later one individual flowered in cultivation, providing the type specimen for the new species. Undoubtedly, *L. scopulophilus* is more closely related to *L. leonii* than to any other known species of the genus. The latter differs, however, from the new taxon in being a small tree to 5 m tall with branches horizontally diverging and even arching; in the narrower stem segments that are usually 6- to 8-ribbed and have

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smaller spines; in the less prominent ribs that are crenate and bear closely set areoles at the bottom of the crenatures, tufted with a dark brown tomentum when young, and in the somewhat smaller, nearly unarmed flowers with inserted stigma lobes and purplish-red receptacle-tubes. The fruits of *L. leonii* also differ from those of *L. scopulophilus* in being smaller and practically naked.

Distribution: only known from the type locality at Somorrostro Hill, and from the neighboring range Lomas de Camoa (Prov. Habana), western Cuba.

8. **Leptocereus leonii** Britton & Rose, Torreya 12(1): 15. 1912. — Type: Cuba. Prov. Habana (formerly, in the extreme eastern part of the province of Pinar del Río): Sierra de Anafe, also known as Sierra del Esperón, near Guayabal, 9 Nov 1911 (fr), *León 2819* (holotype: NY; isotype: HAC).

Syn.: *Cereus leonii* (Britton & Rose) Vaupel, Sieb. Neue Kakt. Kuba, Monatsschr. Kakteenk. 22(5): 66. 1912. — Type: Cuba. Prov. Habana: Sierra de Anafe, near Guayabal, 9 Nov 1911 (fr), *León 2819* (holotype: NY; isotype: HAC).

Lit.: Britton & Rose, Cactaceae 2: 78, fig. 113. 1920; Werdermann, Ekman Westind. Gesam. Cactaceae, Fedde Rep. 29: 234-235. 1931; León, in Giménez-Lanier, León & Marshall, Cuban Cacti, Cact. & Succ. J. (US) 9(1): 11. 1937; Marshall & Bock, Cactaceae 79. 1941; León & Alain, Fl. Cuba 3: 372, fig. 168, Contr. Ocas. Mus. Hist. Nat. La Salle 13. 1953; Backeberg, Die Cactaceae 4: 1960-1961, fig.

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1886. 1960; Backeberg, Kakteenlexikon 201. 1966; Areces, L. scopul., new sp. west. Cuba, Brittonia 45(3): 226-230, figs. 1 A, B. 1993; Anderson, Cactus Fam. 392. 2001.

Figs. 3 E; 3 K1, K2, L; 4 H. Plates 9 G; 13 E; 16 F; 23 A; 25 E; 27 D; 28 I; 33 A-D; 37 A-D; 41 J, K; 44 C; 46 A, B; 60.

Tall *shrub* or small *tree* to 5 m tall; trunk cylindrical, to 30 cm in diameter, with a scaly-roughened bark, the old areoles 1-1.5 cm apart in vertical rows, profusely ramified above. *Ultimate stem segments* slender, most often 0.1-0.9 m long, 1.5 (2.3) cm in diameter; stem sinuses acute, usually demarcated by a line, 3-8 mm deep; cortex fibrous, 3-4 mm wide at the grooves, 10-11 mm wide at the crest of a rib projection (podarium); vascular cylinder 3-5 mm in diameter; pith 1.8-2 mm in diameter. *Ribs* (5) 6-8, 9-11 mm high, 4-7 mm wide at base, their edges separated 1-1.3 cm from each other, distinctly crenate, the crenatures 1.5-3.5 mm deep bearing the areoles at the bottom of the depressions. *Areoles* oblong-rounded to oblong, 2.4 × 1.5-3 mm, 1-1.8 (2.2) cm apart, those of a young stem tufted with short, dark brown tomentum fading to dilute brown and finally turning to sooty brownish-gray with age, armed with 6-12 (13) unequal spines, with retarded indeterminate growth (the areoles usually do not produce suplementary spines during the first 2 or 3 years after being formed). *Spines* straight, rigid, acicular, diluted reddish-brown when very young, their growing bases and tip pale yellow, soon turning to brownish-yellow, in age becoming ash gray, 0.8-2.7 cm long (2-9 cm long *fide* Britton & Rose, 1912), 0.2-0.4 mm in diameter; radial spines (5)

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6-8 (9), 0.8-1.5 cm long, 0.2-0.35 mm in diameter; central spines (1) 2-4, (1.5) 1.8–2.5 (2.7) cm long, 0.3-0.4 mm in diameter, porrect or to a 45° angle ascending. *Flowers* nocturnal-matutinal, rarely nocturnal and diurnal, most often borne on apical and subapical areoles, frequently in clusters of 2-9, 2 or 3 opening simultaneously, 3.2-4.3 cm long, 2.5-3 cm wide, obconical, spineless or more frequently bearing 1-4 thin, bristle-like spines in each areole; pericarpel greenish-red, commonly unarmed, 8-9 mm in diameter; receptacle tube from top to bottom deep purplish-red, somewhat expanded towards the throat, to 1.7-2.1 cm above; perianth segments oblong to broadly oblong, reflexed or more or less extended, pink; stamens forming a lax staminal ring 1.7-2 cm in diameter, exserted 3-6 mm beyond the floral throat during anthesis; stigma often at or a little below the upper stamen level. *Fruits* usually globose, sometimes ellipsoid-globose, wine-colored, 2.3-3.2 × 2-2.8 cm, naked or with few bristly spines; seeds numerous.

Distribution: only known from the type locality.

Section ***Costanthus*** Areces, sect. nov.

Type: **Leptocereus arboreus** Britton & Rose, Torreya 12: 15. 1912.

This section distinguishes a small group of species characterized by having large flowers with distinct vertical ribs formed by the coalescence of decurrent podaria in the pericarpel, or by the confluence of the podaria of the pericarpel and receptacle-tube. The fruits are also unique in having vertical ribs and/or raised orthostichy lines

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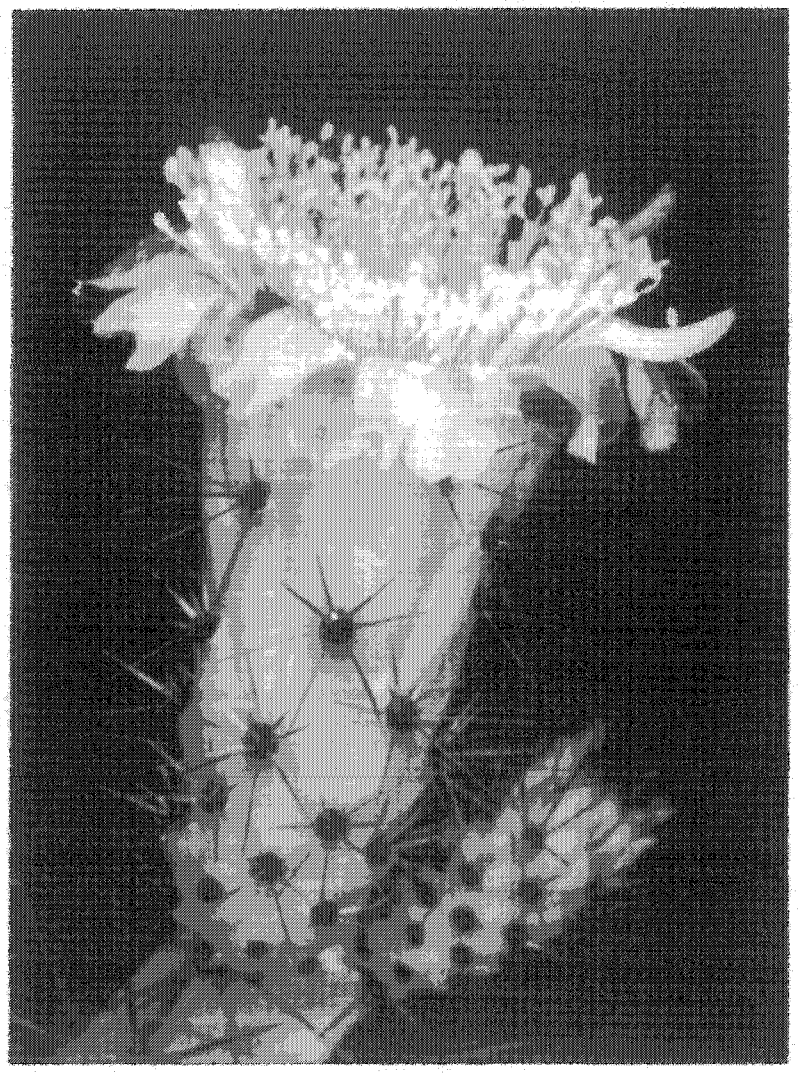

Plate 59. Flower of the type specimen of *Leptocereus scopulophilus* during maximum anthesis. This species was described by the author in 1993 as endemic to the almost inaccessible limestone summit of Somorrostro Hill, 25 km southeast of Havana, Cuba (Brittonia 45: 226-230).

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Plate 60. With occasional thin, bristle-like scattered spines, the fruits of *Leptocereus leonii* are practically unarmed. At maturity, they are entirely colored with a wine-red betalain pigment, a very diagnostic character for this *Leptocereus* species. This interesting cactus was described in 1912 by Britton and Rose (Torreya, 12: 15) from the steep rocky slopes of Sierra de Anafe, an isolated limestone range of western Cuba.

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connecting the areoles. Two species from central and eastern Cuba, one of them described as new (*Leptocereus carinatus* Areces).

9. **Leptocereus arboreus** Britton & Rose, Torreya 12(1): 15. 1912. — Type: Cuba. Prov. Cienfuegos (formerly, in province Santa Clara): Cienfuegos, in Punta Sabanilla, mouth of Cienfuegos Bay, 24 Feb 1910 (fl, fr; fr in liquid), *Britton, Earle & Wilson 4573* (holotype: NY; isotype: US).

Syn.: *Cereus arboreus* (Britton & Rose) Vaupel, Monatsschr. Kakteenk., 22(5): 65. 1912. — Type: Cuba. Prov. Cienfuegos: Cienfuegos, in Punta Sabanilla, mouth of Cienfuegos Bay, 24 Feb 1910 (fl, fr, fr in liquid), *Britton, Earle & Wilson 4573* (holotype: NY; isotype: US).

Lit.: Britton & Rose, Cactaceae 2: 80, pl. 13(1), fig. 116. 1920; León, in Giménez-Lanier, León & Marshall, Cuban Cacti, Cact. & Succ. J. (US) 9(1): 11-12. 1937; León & Alain, Fl. Cuba 3: 373-374, Contr. Ocas. Mus. Hist. Nat. La Salle 13. 1953; Backeberg, Die Cactaceae 4: 1962. 1960; Backeberg, Kakteenlexikon 200-201. 1966; Anderson, Cactus Fam. 391, 1 fig. 2001.

Figs. 1 A, B; 3 H; 4 G. Plates 3 F; 4 H; 9 A, B; 13 G; 16 A; 20 A; 25 A; 27 A; 34 A-D; 42 E, F; 44 A; 46 B.

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Tree up to 6-8 m tall, profusely ramified above, with a simple, cylindrical trunk to 25-30 cm in diameter, armed with large spiny areoles in 4-6 vertical rows, these with indeterminate growth, 1-1.5 cm wide or more, often bearing 25-40 long spines to 8-10 cm long. *Ultimate stem segments* 0.15-1 (2) m long, 4.2-6 cm in diameter, abruptly narrowed at base, gradually narrowing towards the apex, ascending and later arching; stem sinuses acute, usually demarcated by a line, 11-16 mm deep; cortex fibrous, 3-5 mm wide at the grooves, 23-25 mm wide at the crest of a rib projection (podarium); vascular cylinder 7-8 mm in diameter; pith 5.2-5.4 mm in diameter. *Ribs* 4-6, 15-25 mm high, 5-10 mm wide at base, their edges separated 2.3-4.4 cm from each other, crenate, often with a little notch or depression halfway between the areoles, the crenatures 2-4 mm deep bearing the areoles at the bottom of the depressions. *Areoles* commonly rounded or subrounded, sometimes rounded-oblong, 3-4 × 2.5-3.5 mm, (1.6) 2.5-4 cm apart, those of the tip of a growing stem tufted with a tawny tomentum that becomes sooty gray or whitish-gray with age, armed with (8) 10-12 (17) spreading spines about the same length and width, or with little difference in size, with a short dormancy period, soon producing supplementary spines on the proximal half of the stem. *Spines* straight, rigid, acicular, in youth yellow or brownish-yellow, their growing bases pale green, becoming ash-gray with age, poorly differentiated into radials and centrals, usually 0.5-3.5 cm long (older stems with increasingly longer spines), 0.2-0.4 mm in diameter; radial spines (6) 8-10, 0.5-1.4 cm long, 0.2-0.3 mm in diameter; central spines 2-6 (7), 1.3-3.5 cm long, 0.3-0.4 mm in diameter. *Flowers* nocturnal-matutinal, for the most part borne on apical areoles, usually solitary, sometimes in groups of 2 or 3 on the stem apex, rather large, 5.8-7.7 cm long, 2.9-3.8 cm wide (2-3

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cm long *fide* Britton & Rose, 1920), cylindrical, rarely cylindrical-campanulate or campanulate, very spiny; pericarpel clear, bright green, ribbed at base, spinose, 19-21 mm in diameter; receptacle-tube from top to bottom green, densely covered with yellow spines, to 2.2-2.7 cm wide above; perianth segments 1.2-2 cm long, creamy to whitish, almost enclosed in the lattice of spines of the upper receptacle-tube; stamens forming a lax staminal ring 1.8-2.1 cm in diameter, at the floral throat level or very little exserted during anthesis; stigma most often at the upper stamen level. *Fruit* spiny, obovoid to ellipsoid, green, with raised orthostichy lines connecting the areoles, (7) 8.5-9.5 (10.5) × (5.5) 6-6.8 (7.3) cm; seeds numerous.

Distribution: endemic to the dry coastal plains and slopes of south-central Cuba, between Cienfuegos (Prov. Cienfuegos) and Trinidad (Prov. Sancti Spiritus), in dry forests.

10. **Leptocereus carinatus** Areces, Moscosoa 7: 243, figs. 1-4. 1993. — Type: Cuba. Prov. Camagüey: Najasa, Sierra de Najasa, ca. Belén, on karstic hills, 200-250 m, 21° 01' N, 72° 42' W, 12 Sep 1990 (fl, fr), *Areces 5489* (holotype: MNHN: isotypes: HAC, HAJB, NY, to be deposited).

Lit.: Anderson, Cactus Fam. 392, 1 fig. 2001.

Figs. 2 I1-I3; 4 L. Plates 9 C; 11 G; 13 D; 16 B; 17 G; 22 H; 23 C; 25 G; 28 A; 36 A-D; 41 N, O; 44 B; 47 A; 54 A.

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Erect *shrub* ramified near or above ground level, to 2-2.5 m tall, with a main stem 4-8 cm in diameter, not much ramified. *Ultimate stem segments* ascending, 0.3-2 m long, (2.5) 3-3.5 (4) cm in diameter; stem sinuses acute, usually demarcated by a line, 6-14 mm deep; cortex fibrous, 3-4 mm wide at the grooves, 13-15 mm wide at the crest of a rib projection (podarium); vascular cylinder 5-6 mm in diameter; pith 3-3.5 mm in diameter. *Ribs* 4-6, 8-17 mm high, 3-7 mm wide at base, sometimes coiling around the stem, their edges separated 1.7-2.5 cm from each other, distinctly sinuate (wavy), the sinuses 3.5-5 mm deep, not bearing the areoles at the bottom of the depressions but a little above it. *Areoles* transversely oblong to widely transversely oblong, commonly 4-6 × 3-4.5 mm, 1.4-3.5 cm apart, those of the tip of a growing stem tufted with brownish to tawny tomentum that soon becomes creamy, and finally white with age, armed with (5) 8 or 9 (11) very unequal spines, with retarded indeterminate growth. *Spines* straight, rigid, acicular, in youth brownish or brownish-yellow, often black at tip, their growing bases pale yellow, from tip to bottom becoming white with age, 0.7-6.1 cm long, 0.2-1 mm in diameter; radial spines (4) 6, 0.7-3 cm long, 0.2-0.5 mm in diameter, the upper ones longer; central spines (1) 2 or 3 (5), 2.6-6.1 cm long, 0.2-1 mm in diameter. *Flowers* nocturnal, for the most part borne on apical areoles, usually solitary, 5-6.7 cm long, 2.5-3.7 cm wide, cylindrical, with vertical ribs, spinose; pericarpel clear, bright green, ribbed, usually unarmed, 12-14 mm in diameter; receptacle-tube from top to bottom clear, bright green, to 1.5-2 cm wide above, with ribs that are 2-5 mm high and bear spiny areoles at their margins, each of these with (1) 3-6 (10) short black spines, 0.1-10 mm long; perianth segments oblong, the outer ones

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3.5-7 mm long, greenish-white, the inner ones white, 4-10 mm long; stamens at the floral throat level or very little exserted during anthesis; stigma rather inserted, usually 1-4 mm below the upper stamen level. *Fruit* markedly 5 or 6-ribbed, obovoid to fusiform in outline, green, (5) 6-7 (8.2) × (3) 3.5-4 (4.7) cm; seeds numerous.

Distribution: only known from the type locality.

Section ***Spinosissimus*** Areces, sect. nov.

Type: **Leptocereus sylvestris** Britton & Rose, Cact. 2: 81. 1920.

Section of plants often with arborescent habit and large, rather spiny flowers and fruits, the flowers strictly nocturnal (nyctigamous), cylindrical, with white or creamy perianth limbs, and receptacle-tubes that are tawny, brownish-green or yellowish-olive. Fruits large, globose or nearly so, spiny to very spiny. The seeds are characterized by a recurved rostrum tip, the dorsal wall of the hilum cup abruptly bending backwards. Three species from eastern Cuba, one of them described as new (*Leptocereus santamarinae* Areces).

11. **Leptocereus sylvestris** Britton & Rose, Cactaceae 2: 81, figs. 117, 118. 1920. — Type: Cuba. Prov. Granma (formerly, in province Oriente): vicinity of Pilón, Ensenada de la Mora, in coastal woods, 20-29 Mar 1912 (fr), *N. L. Britton, Cowell & Shafer 13060* (holotype: NY; isotype: US).

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Lit.: Carabia, Distr. Cacti Cuba, Cact. & Succ. J. (US) 8: 203. 1936; León, in Giménez-Lanier, León & Marshall, Cuban Cacti, Cact. & Succ. J. (US) 9(1): 12. 1937; León & Alain, Fl. Cuba 3: 374, Contr. Ocas. Mus. Hist. Nat. La Salle 13. 1953; Backeberg, Die Cactaceae 4: 1963. 1960; Backeberg, Kakteenlexikon 201. 1966; Anderson, Cactus Fam. 394. 2001.

Figs. 2 C1, C2; 4 M1, M2; 5 A-H. Plates 3 H; 6 G; 10 G; 13 F; 20 F; 21 A; 22 I; 23 E; 25 C; 29 A; 32 I-L; 36 E-H; 42 I, J; 47 B; 54 E, F.

Small *tree* up to 4-5 m tall, profusely ramified above, with a definite trunk to 15-20 cm in diameter, rarely a diffusely branched shrub (when growing on bare, sterile rock). *Ultimate stem segments* bright green, 0.23-1.10 m long, 2-3.2 cm in diameter; stem sinuses acute, usually demarcated by a line, 6-12 mm deep; cortex fibrous, 3-5 mm wide at the grooves, 14-16 mm wide at the crest of a rib projection (podarium); vascular cylinder 4-8 mm in diameter; pith 2.6-5 mm in diameter. *Ribs* 5-7, 9-16 mm high, 5-7 mm wide at base, their edges separated 1.4-2.1 cm from each other, distinctly crenate, the crenatures 3-6 mm deep bearing the areoles at the bottom of the depressions. *Areoles* rounded or subrounded, 3-4 × 2.5-3 mm, 1-2.3 cm apart, tufted with a dark brown tomentum that is very resistant to decoloration, those of older stem segments (2nd and 3rd order, not ultimate) eventually fading to light brown, and finally becoming ash-gray with age, armed with (15) 18 or 19 (20) slightly unequal spines, with retarded indeterminate growth. *Spines* straight, rigid, acicular, from tip to base yellow or brownish-yellow in youth, their growing bases whitish-yellow, becoming

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whitish with age, 0.5-3.4 cm long, 0.1-0.5 mm in diameter; radial spines (9) 10-12, 0.5-1.4 cm long, 0.1-0.25 mm in diameter; central spines (6) 7 (8), 1.2-3.5 cm long, 0.3-0.5 mm in diameter. *Flowers* nocturnal, borne on apical areoles, solitary or in groups of 2-7, but not more than 2 flowers opening simultaneously, large, 5.4-7 cm long, 2.8-4.2 cm wide, cylindrical, very spiny; pericarpel clear, bright green or more often green with the bases of the upper podaria tinged with a tawny-green color, spiny, 13-16 mm in diameter; receptacle-tube green or tawny-green at base with the podaria apices green, turning gradually into brownish-green above, to 1.8-2.5 cm wide above, bearing areoles with dark brown tomentum and spines that often overlap by their tips those from areoles on adjacent podaria; perianth segments white, the abaxial surface of the outermost ones clear brown; stamens forming a compact staminal ring 1.4-2 cm in diameter, a little inserted, at the floral throat level or 1-2 mm exserted during anthesis; stigma extended 3-5 mm beyond the upper stamen level. *Fruits* most often globose or subglobose, sometimes globose-obovate, usually 7-8 cm in diameter, green, bearing deciduous areoles that drop off at maturity, these with numerous spines that do not not overlap those from areoles on adjacent areoles; seeds numerous.

Distribution: lower coastal terraces between Pilón and Cabo Cruz, in Province Granma, southeastern Cuba.

12. **Leptocereus maxonii** Britton & Rose, Cactaceae 2: 80, fig. 115. 1920. — Type: Cuba. Prov. Santiago de Cuba (formerly, in Province Oriente): Verraco, 8 miles east of Daiquirí, Mar 1912 (fl), *Britton & Cowell 12657* (holotype: NY; isotypes:

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US, GH, BM, S), non *Cereus maxonii* (Rose) Vaupel, Monatsschr. Kakteenk., 23: 23. 1913. = *Cephalocereus maxonii* Rose, Contr. U.S. Natl. Herb.12: 417. 1909.

Lit.: Carabia, Distr. Cacti Cuba, Cact. & Succ. J. (US) 8: 203. 1936; León, in Giménez-Lanier, León & Marshall, Cuban Cacti, Cact. & Succ. J. (US) 9(1): 11. 1937; León & Alain, Fl. Cuba 3: 374, Contr. Ocas. Mus. Hist. Nat. La Salle 13. 1953; Backeberg, Die Cactaceae 4: 1962. 1960; Backeberg, Kakteenlexikon 201. 1966; Anderson, Cactus Fam. 392. 2001.

Figs. 3 G1, G2; 4 B1, B2. Plates 6 D; 7 A, B; 9 H; 14 D; 17 C; 18 D, E; 21 H; 27 B, C; 32 A-D; 35 A-D; 42 K, L; 47 B.

Shrub, densely ramified near or above ground level, lacking a definite trunk, with numerous, rather spiny erect stems that curve outwards with age, becoming woody at base, 1-1.7 m tall. *Ultimate stem segments* pale dull green, ascending, 0.2-0.95 m long, 2.1-3.5 cm in diameter; stem sinuses usually acute and demarcated by a line, or sometimes obtuse, 2-6 mm deep; cortex fibrous, 6-7 mm wide at the grooves, 12-14 mm wide at the crest of a rib projection (podarium); vascular cylinder 5-7 mm in diameter; pith 3.9-4.7 mm in diameter. *Ribs* (5) 6 (7), 5-15 mm high, 6-9 mm wide at base, their edges separated 0.9-1.3 cm from each other, distinctly crenate, the crenatures 2-4 mm deep bearing the areoles at the bottom of the depressions. *Areoles* most often rounded, sometimes elliptic-rounded, 3.5-4.5 × 3-4.5 mm, 1.2-2.3 cm apart, those of

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the tip of a growing stem tufted with dark brown tomentum that soon fades to light brown, and finally grayish-white with age, armed with (17) 19-21 (24) very unequal spines. *Spines* straight, rigid, acicular, in youth yellow (radials) and yellowish-brown (centrals), their growing bases whitish-yellow, becoming ash-gray with age, strongly differentiated into radials and centrals, 0.5-7 cm long, 0.1-0.6 mm in diameter; radial spines thin and nearly bristle-like, usually not persisting in old areoles, (10) 12-14, 0.5-1.7 cm long, 0.1-0.15 mm in diameter; central spines stout, 7-10, 1.2-7 cm long, 0.3-0.6 mm in diameter, the longest ones porrect or slightly ascending. *Flowers* nocturnal, borne on apical areoles, solitary or in groups of 2-5, but rarely 2 flowers opening simultaneously, 5-6.2 cm long, 2.7-3.5 cm wide, cylindrical, very spiny; pericarpel clear, bright green with the bases of the upper podaria tinged with a tawny-green color, rather spiny, 10-15 mm in diameter; receptacle-tube tawny-green at base with the podaria apices green, turning gradually into yellowish-olive above, to 1.4-1.8 cm wide above, bearing areoles with creamy tomentum and numerous spines that largely overlap those from areoles on adjacent podaria; perianth segments creamy, the abaxial surface of the outermost ones clear brown; stamens forming a compact staminal ring 1.4-1.6 cm in diameter, a little inserted, at the floral throat level, or 1-2 mm exserted during anthesis; stigma most often at the upper stamen level or slightly inserted. *Fruits* globose, (3.5) 4-5.3 (6) cm in diameter, green, bearing persistent, closely set areoles with numerous spines that largely overlap those from adjacent areoles; seeds numerous.

Distribution: coastal thickets from Punta Verraco (Province Santiago de Cuba), eastwards to Maisí (Province Guantánamo), southeastern Cuba.

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13. **Leptocereus santamarinae** Areces, Brittonia 44(1): 45, figs. 1-3. 1992. — Type: Cuba. Prov. Camagüey: vicinity of Santa Lucía Beach, 2 km east of Nuevitas Bay, in a dry evergreen littoral forest rich in *Acacia* species, 15 April 1990 (fl, fr), *Areces 5341* (holotype: HAC; isotypes HAJB, MNHN).

Lit.: Anderson, Cactus Fam. 394, 1 fig. 2001.

Figs. 2 B1, B2; 4 F1, F2. Plates 3 A-D; 6 F; 10 F; 13 H; 21 D; 23 D; 27 H; 32 E-H; 40 H; 42 G, H; 47 A, B.

Tree up to 6-8 m tall, or sometimes on very rocky or saline substrate a 2-3 m tall shrub; trunk cylindrical, to 30 cm in diameter, with a rusty-brown scaly bark. *Ultimate stem segments* bright green a little verging to yellowish-green, 0.25-1.10 m long, 3.5-5.5 cm in diameter; stem sinuses acute, usually demarcated by a line, 6-14 mm deep; cortex fibrous, 4-5 mm wide at the grooves, 14-22 mm wide at the crest of a rib projection (podarium); vascular cylinder 6-9 mm in diameter; pith 4.6-5.6 mm in diameter. *Ribs* 5 or 6, 10-21 mm high, 3-9 mm wide at base, their edges separated 1.7-2.5 cm from each other, distinctly crenate, the crenatures 1.5-3 mm deep bearing the areoles at the bottom of the depressions. *Areoles* most often rounded, rarely oblong-rounded or oblong, 3-4.5 × 3-4 mm, 1.2-1.8 cm apart, those of the tip of a growing stem tufted with creamy tomentum that usually becomes tawny with age, and finally sooty gray, armed with (8) 13-19 (25) spreading spines about the same length, with

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retarded indeterminate growth. *Spines* straight, rigid, acicular, in youth yellowish or brownish-yellow, their growing bases whitish-yellow, becoming translucent, and finally ash-gray with age, 0.5-2.4 cm long, 0.1-0.4 mm in diameter; radial spines hardly differentiated from the centrals, (6) 8-10 (12), 0.5-1.3 cm long, 0.1-0.2 mm in diameter; central spines (2) 6-9 (13), 0.9-2.4 cm long, 0.25-0.4 mm in diameter. *Flowers* nocturnal, borne on apical areoles, solitary or in groups of 2-5, but rarely 2 flowers opening simultaneously, large, 5.7-7.2 cm long, 3.1-3.6 cm wide, cylindrical, very spiny; pericarpel mostly clear, bright green with the bases of the upper podaria tinged with a tawny-green color, spiny, 11-19 mm in diameter; receptacle-tube tawny-green at base with the podaria apices green, turning gradually into yellowish-olive above, to 2-2.3 cm wide above, bearing areoles with creamy tomentum and spines that often overlap by their tips those from areoles on adjacent podaria; perianth segments white, the abaxial surface of the outermost ones reddish at tip; stamens forming a compact staminal ring 1.5-1.7 cm in diameter, a little inserted, at the floral throat level, or 1-2 mm exserted during anthesis; stigma extended 3-5 mm beyond the upper stamen level. *Fruits* globose, ellipsoid-globose, or widely obovate, often 6-8 × 5-7 cm, green, bearing persistent areoles with numerous spines that slightly or not overlap those from adjacent areoles; seeds numerous.

Distribution: occurring in Cuba, from the larger keys of the north coast of Camagüey Province, eastward to the northern mainland coast of Las Tunas and Holguín provinces, in coastal forests.

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Subgenus ***Weingartianea*** Areces, subgen. nov.

Type: **Leptocereus weingartianus** (E. Hartmann) Britton & Rose, Cactaceae 2: 77. 1920.

Frutices ramis arcuatis vel scandentibus seu arbores usque 10 m alti, hispaniolicis aut portricensis; cortex non vel vix tarde paulo atrantes, non fibroso-reticulatis; flores admodum nocturni, albi, tubo interdum binatim leviter constricto; loculus nectariferus doliiformis, plerumque ad basim contractus, a basi ad medium expansi et a medio ad apicem denuo contractus; semina dacryoidea, longe rostellata; annulo crasso rotundato hilo-micropyle cavitati cingenta; testa cellulis non vel paulo inaequilongis, majoribus minus quam 100 µm diam., cuticula valde grosse ruguloso-plicata obtecta

Shrubs with arching or scandent branches, to trees up to 10 m tall; stem cortex not showing a darkening reaction upon injury, or if so the reaction is very weak and retarded, not fibrose-reticulated; flowers essentially nocturnal, white; receptacle-tube sometimes with two discrete, perceptible constrictions; nectar chamber barrel-shaped in outline, usually constricted above and below, slightly expanded at middle; seeds with a broad rounded end tapering to a pointed end (tear-shaped), largely rostellate (strongly beaked); hilum-micropilar cavity encircled by a rounded, thickened rim; testa cells nearly isodiametric, the dorsal ones slightly or not differentiated in size and shape from the laterals, less than 100 µm in diameter, with their periclinal (outer) surface coarsely pleated, the thick cuticular folds often running between cell boundaries. Four species

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from Hispaniola, Puerto Rico, and a small island (Culebra) off the northeast coast of Puerto Rico.

Section ***Tenuicaulis*** Areces, sect. nov.

Type: **Leptocereus weingartianus** (E. Hartmann) Britton & Rose, Cactaceae 2: 77. 1920.

Section characterized by having tuberous roots and very variable habits, from trees to shrubs with long, scandent to trailing branches, narrowly tubular (rarely obconical) flowers with very reduced perianth limb, and seeds with a small constriction at the hilum-cup insertion level, coupled with an abrupt flattening of the exotesta cells on the cup side. One species widely distributed in Hispaniola, with one new suspecies herein described (*Leptocereus weingartianus* subsp. *demissus* Areces).

14. **Leptocereus weingartianus** (E. Hartmann) Britton & Rose, Cactaceae 2: 77, fig. 112. 1920.

Low, fruticose or trailing shrub, large, divaricate shrub often with scandent branches that climb among shrubs and trees, to *tree-like* up to 6-8 m tall, with a definite trunk. Roots thickened, fleshy, tuberous. *Ultimate stem segments* stiff and self-supportive, or elongated and leaning on rocks or neighboring vegetation for support; stem sinuses rounded, not demarcated by a line; cortex not fibrous. *Ribs* 5-7, straight or

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crenate, the crenatures bearing the areoles at the bottom of the depressions. *Areoles* of the tip of a growing stem tufted with a light brown to tawny tomentum that becomes ash-gray with age, armed with spreading spines that are slightly unequal, with retarded indeterminate growth. *Spines* straight, rigid, acicular, in youth yellowish or brownish-yellow, their growing bases whitish-yellow, becoming ash-gray with age, the centralmost one somewhat larger, porrect or slightly ascending. *Flowers* nocturnal, borne on apical or subapical areoles, solitary or in small groups, usually spiny, rarely unarmed; pericarpel most often clear, bright green; receptacle tube green; perianth segments strongly reflexed during anthesis, the inner ones white; stamens forming a staminal ring, most often at the floral throat level during anthesis; stigma usually not extended beyond the anthers. *Fruits* obovate narrowly obovate, fusiform, or ellipsoid, green or pinkish, commonly spiny; seeds numerous.

Curiously, the person in whose honor this species was named, did not recognized it; instead he published a short paper expressing that the taxon was conspecific with *Cereus assurgens* (Weingart, 1905).

14a. **Leptocereus weingartianus** (E. Hartmann) Britton & Rose subsp **weingartianus**.

Bas.: *Cereus weingartianus* E. Hartmann in Dams, Monatsschr. Kakteenk. 14(1): 152, 1 fig. 1904. — Type: Haiti, no specimen cited. Neotype (designated here): Haiti. Département du Nord Ouest: Presqu'île du Nord Ouest, coastal limestone terrace

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2 km NE to Môle Saint Nicolas, on the road to Jean-Rabel, in cactus woodlands, 19 Jan 1995 (fl, fr), *Areces 6815* (NY, to be deposited).

Lit.: Urban, Fl. Dom., in Symbol. Ant., 8: 461. 1903-11 (erroneously referred to *L. assurgens*); Weingart, Cereus weingartianus, Monatsschr. Kakteenk., 15(1): 6-9. 1905; Berger, Syst. Rev. *Cereus*, Rep. Mo. Bot. Gard., 16: 79. 1905; Werdermann, Ekman Westind. Gesam. Cactaceae, Fedde Rep. 29: 234. 1931; Marshall, in Giménez-Lanier, León & Marshall, Cuban Cacti, Cact. & Succ. J. (US) 9(1): 13. 1937; Moscoso, Cactáceas Fl. Sto. Dom., Anal. Univ. Sto. Dom. 5 (1-2): 23. 1941; Moscoso, Cat. Fl. Dom. 1: 404. 1943; Backeberg, Die Cactaceae 4: 1960. 1960; Backeberg, Kakteenlexikon 201. 1966; Fleming, Notes Cact. Sp. Dom. Rep., Cact. & Succ. J. (U.S.), 56(3): 126, figs. 6, 7. 1984; Haustein, Kakteenführer, 70. 1986; Anderson, Cactus Fam. 395. 2001.

Figs. 1 F; 2 K1-K4; 4 E1-E3. Plates 4 A, B; 5 G-I; 10 D; 14 E; 20 B-E; 21 B; 24 B; 25 F; 28 F; 29 B-F; 31 E-H; 40 A, B; 40 E-G; 43 A-C; 48 A, B; 50 F.

Low or tall, divaricate *shrub*, often with scandent branches that climb, sometimes to 8-10 m high, to *tree-like* up to 8 m tall with a trunk to 15-20 cm in diameter. *Ultimate stem segments* straight or more often elongated, 0.15-1.5 m long, 2-3.5 cm in diameter; stem sinuses 3-8 mm deep; cortex 3-5 mm wide at the grooves, 8-14 mm wide at the crest of a rib projection (podarium); vascular cylinder 4-6 mm in diameter; pith 2.6-5 mm in diameter. *Ribs* most often 5 or 6, 6-12 mm high, 6-10 mm wide at

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base, their edges separated 1-1.9 cm from each other, usually crenate, sometimes subcrenate to nearly straight, the crenatures 1.5-4 mm deep. *Areoles* oblong to elliptic-oblong, 3-4 × 2-3 mm, 1.1-1.6 cm apart, armed with (13) 16-18 (20) spines. *Spines* 0.7-3 (3.5) cm long, 0.1-0.5 mm in diameter; radial spines 8-14, 0.7-1.5 cm long, 0.1-0.3 mm in diameter, the two lower ones a little smaller; central spines 4-7, 1-3.5 cm long, 0.2-0.5 mm in diameter. *Flowers* solitary or in groups of 2-4, no more than 2 flowers opening simultaneously, 4.7-7.4 cm long, 1.9-2.9 cm wide, narrowly tubular, unarmed or more frequently with small spines; pericarpel usually unarmed, 7-12 mm in diameter; receptacle tube green, the podaria sometimes tinged with pale brownish or pinkish at apex, to 1.2-2 cm wide above, distinctly constricted above and below nectar chamber, with minute areoles 0.25-0.75 mm in diameter usually bearing 1-7 bristle-like spines 1-3 mm long, rarely spineless; abaxial surface of some of the outermost perianth segments sometimes pinkish; stamens forming a staminal ring 1.2-1.8 cm in diameter, most often at the floral throat level or to 1 mm exserted during anthesis, rarely inserted; stigma to 3 mm inserted, at the upper stamen level, or to 2 mm extended beyond the anthers. *Fruits* usually obovate to somewhat narrowly obovate, rarely fusiform, green or pinkish, 6-10 × 4-5 cm, bearing areoles to 2.5 cm apart, with short spines that are markedly separated from those of other areoles.

Distribution: widely distributed in the dry areas of Haiti and the Dominican Republic, except in Pedernales province (D.R.) and southern Haiti (Département du Sud Ouest).

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14b. **Leptocereus weingartianus** (E. Hartmann) Britton & Rose subsp **demissus** Areces, subsp. nov.

Type: Dominican Republic. Prov. Pedernales: on limestone terraces of maritime origin along both sides of the road to Pedernales, 10 km southeast of Cabo Rojo, in dry forests with *Dendrocereus undulosus*, 22 Dec 1998 (flowered in cultivation), *Areces 6812* (holotype: JBSD, to be deposited; isotypes: HAC and NY, to be deposited).

Figs. 2 L1, L2; 4 E4. Plates 4 C-E; 10 E; 11 B; 14 F; 17 J; 28 G; 31 I-L; 42 M-O; 48 A; 61; 62.

Low, *shrubby plants* with relatively few, long, slender, scandent or trailing branches that may climb with the aid of supporting points. *Ultimate stem segments* elongated, 0.3-3 m long, 1.3-2 cm in diameter; stem sinuses 1-2 mm deep; cortex 3-5 mm wide at the grooves, 5-7 mm wide at the crest of a rib projection (podarium); vascular cylinder 3-4 mm in diameter; pith 2.2-2.6 mm in diameter. *Ribs* 6 or 7, 2.5-6 mm high, 3-5 mm wide at base, their edges separated 0.7-1 cm from each other, straight. *Areoles* rounded, 2-4 × 2-4 mm, 0.8-1.6 cm apart, armed with 15-22 spines. *Spines* 0.5-2.5 cm long, 0.1-0.5 mm in diameter; radial spines 10-14, 0.5-1.3 cm long, 0.1-0.3 mm in diameter, the two lower ones as long as the others; central spines 4-8, 0.7-2.5 cm long, 0.2-0.5 mm in diameter. *Flowers* usually solitary, 5-6 cm long, 2.8-3.2 cm wide, obconical, strongly armed with spines; pericarpel spiny, 15-21 mm in

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diameter; receptacle tube green, to 2-2.5 cm wide above, not constricted, with areoles 2-2.75 mm in diameter bearing 6-15 stiff spines to 9-11 mm long; abaxial surface of outermost perianth segments green, with their tips brownish; stamens forming a staminal ring 1.6-2 cm in diameter, at the floral throat level; stigma not extended beyond the anthers. *Fruits* ellipsoid, green, 5-6.5 × 3.5-4.5 cm, bearing areoles to 1.7 cm apart, with long spines that often overlap by their tips those from adjacent areoles.

This novelty is closely related to subsp. *weingartianus*, from which it differs by its trailing habit, the longer (to 3 m) and more slender stem segments, with low, straight ribs that have rounded areoles, the obconical, non-constricted flowers, with thicker, rather spiny pericarpels, beset with larger areoles and numerous long, stiff spines, and the ellipsoid fruits bearing areoles more closely set (to 1.7 cm apart), with much longer spines that often overlap by their tips the spines of adjacent areoles.

Distribution: subspecies *demissus* is apparently restricted to southwestern Dominican Republic (Pedernales Province) and southern Haiti.

Section ***Cephaliphora*** Areces, sect. nov.

Type: **Leptocereus quadricostatus** (Bello) Britton & Rose, Contr. U.S. Natl. Herb. 12(10): 433. 1909.

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Section *Cephaliphora* can be readily distinguished from other sections of genus *Leptocereus* by the low number of stem ribs, usually 3 to 5; the peculiar type of periderm formation characterized by small, confluent patches, the presence of a specialized, non-assimilatory flowering organ at the tip of the stems (cephalium), where most but not all flowers and fruits are produced, and the tendency towards a reduction of the number and length of spines on flowers and fruits. Three species, one of them occurring on Hispaniola, and the two others, with one new subspecies (*L. quadricostatus* subsp. *parvispinus* Areces), from Puerto Rico and neighboring islands.

15. **Leptocereus paniculatus** (Lam.) D. R. Hunt in D. R. Hunt & Taylor, Bradleya 9: 89. 1991.

Bas.: *Cactus paniculatus* Lam., Encycl. Méth. 1: 540. 1785. — Type: Haiti, based on Burman's plate 192 of Pl. Amer, 186, 1755, a published print of Plumier's original drawings 20 and 21.

Syn.: *Cereus paniculatus* (Lam.) DC., Prodr. 3: 466. 1828. — Type: Haiti, Plumier ed. Burman 186, pl. 192. 1755.

Neoabbottia paniculata (Lam.) Britton & Rose, Smithsonian Misc. Collect. 72(9): 3, pl. 1-4, figs. 1, 2. 1921. — Type: Haiti. Vicinity of Port-au-Prince, on the Cul-de Sac area, Apr 1920 (fl, fr), *Abbott & Leonard 3500* (holotype: US).

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Lit.: Urban, Fl. Dom., in Symbol. Ant., 8: 462. 1903-11; Britton & Rose, Cactaceae, 2: 82. 1920; Britton & Rose, Cactaceae, 4: 280-281, figs. 256-260, 1923; Werdermann, Ekman Westind. Gesam. Cactaceae, Fedde Rep. 29: 236-237. 1931; Moscoso, Cactáceas Fl. Sto. Dom., Anal. Univ. Sto. Dom. 5 (1-2): 24-25. 1941; Moscoso, Cat. Fl. Dom. 1: 405. 1943; Backeberg, Die Cactaceae 4: 1950-1958, figs. 1874-1885. 1960; Fleming, Notes Cact. Sp. Dom. Rep., Cact. & Succ. J. (U.S.), 56(3): 127, figs. 1, 15. 1984; Hunt, Cact. Plum. Bot. Amer., Bradl., 2: 39-64, 2 figs. 1984; Haustein, Kakteenführer, 72. 1986; Pilbeam, Cacti Conn., 100. 1987; Cullmann, Götz & Gröner. Encycl. Cacti, 239. 1987; García, & Castillo, Ecol., Stat. Usos Neoabbottia paniculata (Cact.) End. Is. Española. Moscosoa, 8: 53-64, figs. 1-3. 1994; Areces, W. Indies, in I.U.C.N./S.S.C. Cact. Succ. Pl., 102, 107, 1 fig. 1997; Anderson, Cactus Fam. 393, 1 fig. 2001.

Figs. 2 D; 4 Q. Plates 2 C, D; 7 C, D; 8 C; 9 I; 11 F; 13 B; 16 E; 17 A; 17 I; 18 G; 19 A; 20 G; 24 A; 28 H; 31 A-D; 38 E-H; 40 D; 43 D, E; 44 H; 48 A, B; 49 D; 50 F.

Tree up to 8-10 m high, profusely branched on top, with a simple, cylindrical trunk to 30-40 cm in diameter, unarmed or nearly so in age, the bark brown, smooth. *Ultimate stem segments* dull grayish-green, straight, attenuated at base and towards the apex, 0.15-0.5 (0.8) m long, 4.2-6 cm in diameter; stem sinuses usually acute and demarcated by a line, 7-15 mm deep; cortex not fibrous, 5-6 mm wide at the grooves, 21-25 mm wide at the crest of a rib projection (podarium); vascular cylinder 9-10 mm in diameter; pith 6-6.2 mm in diameter. *Ribs* (4) 5 (6), 13-26 mm high, 8-15 mm wide at base, their

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edges separated 2-3.6 cm from each other, crenate, the crenatures 1.5-3.5 mm deep bearing the areoles at the bottom of the depressions. *Areoles* rounded or subrounded, 3-4 × 2.5-4 mm, 1.5-2 (2.5) cm apart, those of the tip of a growing stem tufted with a creamy to tawny tomentum that becomes whitish with age, armed with 12-21 spreading spines about the same length and width, with retarded indeterminate growth. *Spines* straight, rigid, acicular, in youth yellow or brownish-yellow with their tip dark brown, their growing bases whitish-yellow, becoming ash-gray with age, poorly differentiated into radials and centrals, 0.4-2 cm long, 0.2-0.4 mm in diameter; radial spines 8-5, 0.4-1.3 cm long, 0.2-0.4 mm in diameter; central spines 4-6, 0.9-2 cm long, 0.3-0.4 mm in diameter. *Cephalium* simple, cylindrical, to 7-8 cm long, 1-2.5 cm wide, with persistent, creamy or tawny wool (while active). *Flowers* nocturnal-matutinal, usually borne on apical cephalia in groups of 2-6, rarely solitary on lateral areoles, 5-5.4 cm long, 2.5-3.2 cm wide, subcylindrical, unarmed or most often so; pericarpel clear, bright green, 13-16 mm in diameter; receptacle-tube to 2-2.2 cm wide above, green, the podaria usually tinged with greenish-red towards the apex, these provided with a small, depressed areole subtended by a minute, greenish-red to reddish scale, the areoles bearing brownish tomentum but commonly no spines; perianth segments whitish, reflexed during anthesis; stamens forming a staminal ring 1.2-1.4 cm in diameter, at the floral throat level or barely to 1 mm exserted; stigma inserted, or at the upper stamen level. *Fruits* most often ellipsoid, unarmed, 6-7 × 4-5.5 cm; seeds numerous.

Distribution: the species is endemic to south-central Hispaniola, from near Azua (Dominican Republic), westwards to the Cul-de-Sac area in Haiti. There is also a small

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population in the Département du Nord Ouest (Presqu'île du Nord Ouest), in northern Haiti.

16. **Leptocereus quadricostatus** (Bello) Britton & Rose, Contr. U.S. Natl. Herb. 16: 242. 1913.

Shrub densely branched at the base and above, to 2-4 m tall, often with a short trunk to 15-20 cm in diameter formed by decurrent branches, these usually erect, ascending, with patchy periderm formation, their areoles with indeterminate growth, those near the base enlarging and producing new spines, the bark grayish. *Ultimate stem segments* ascending or arching, dark bright green; stem sinuses acute, usually demarcated by a line; cortex not fibrous; vascular cylinder 5-6 mm in diameter. *Ribs* (3) 4, crenate, bearing the areoles at the bottom of the depressions, or nearly so. *Areoles* rounded or subrounded, with retarded indeterminate growth, tufted when young with a short tawny to light brown tomentum that becomes ash-gray with age, armed with spines that have nearly the same length except for the two short lowermost ones. *Spines* straight, rigid, dark brown to brownish-yellow in youth, their growing bases whitish-yellow, becoming ash-gray or white with age, poorly differentiated into radials and centrals; lower pair of radial spines smaller. *Cephalium* small and slender, 1-3 cm long, 0.4-0.9 cm wide, dark brown to nearly black, with short hairs that tend to wear off with age leaving a stubby, cylindrical joint. *Flowers* nocturnal, borne on cephalia or on apical and subapical areoles, solitary, or 2-6 grouped towards the stem apex but not more than 3 opening simultaneously, tubular, spinose; pericarpel clear, bright green,

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more or less spiny; receptacle-tube clear, bright green, often constricted above and below nectar chamber, the areoles bearing tan or brown tomentum, and spines; outer perianth segments green to greenish-white, sometimes with a small touch of brown at middle, the inner ones whitish; stamens forming a lax staminal ring, at the floral throat level or to 1.5 mm exserted during anthesis; stigma usually at the floral throat level, rarely to 2 mm exserted. *Fruits* ellipsoid, ovate or obovate, spiny, green 3-5 × 2.5-3.6 cm; seeds numerous.

16a. **Leptocereus quadricostatus** (Bello) Britton & Rose subsp. **quadricostatus**.

Bas.: *Cereus quadricostatus* Bello, Anales. Soc. Esp. Hist. Nat. 10: 276. 1881. — Type: Puerto Rico. Playas de Guánica, no specimen cited. Neotype (designated here): Puerto Rico. Municipio Yauco, Guánica, in Guánica State Forest, West to Bahía de la Ballena, rocky coastal terrace alongside of Route 333, just in front of the cays of Caña Gorda, 2 Feb 1996 (fl, fr), *Areces 6415* (NY, to be deposited).

Lit.: Stahl, Fl. P. Rico, 186. 1883; Schumann, Gesamtb. Kakteen, 88. 1903; Urban, Fl. Portoric., in Symbol. Ant., 4: 429. 1903-11; Berger, Syst. Rev. *Cereus*, Rep. Mo. Bot. Gard., 16: 79. 1905; Britton & Rose, Gen. *Cereus* and Allies in N. Am., Contrib. U. S. Natl. Herb. Misc. Papers, 12(10): 433. 1909; Britton & Rose, Cactaceae 2: 81-82, figs. 119-121. 1920; Britton, Native Cact. P. Rico & Virgin Is. Cact. & Succ. J. (U.S.), 1(12): 226-231. 1930; Britton, Undescr. Cact. Culebra Is., P. Rico. Cact. & Succ.

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Plate 61. The receptacle-tube of the flower of *Leptocereus weingartianus* subsp. *weingartianus* is tubular and very short-spined. By contrast, the receptacle-tube of subspecies *demissus*, as seen in this picture, is distinctly obconical and long-spined. This subspecies is restricted to southwestern Dominican Republic (Pedernales province) and southern Haiti.

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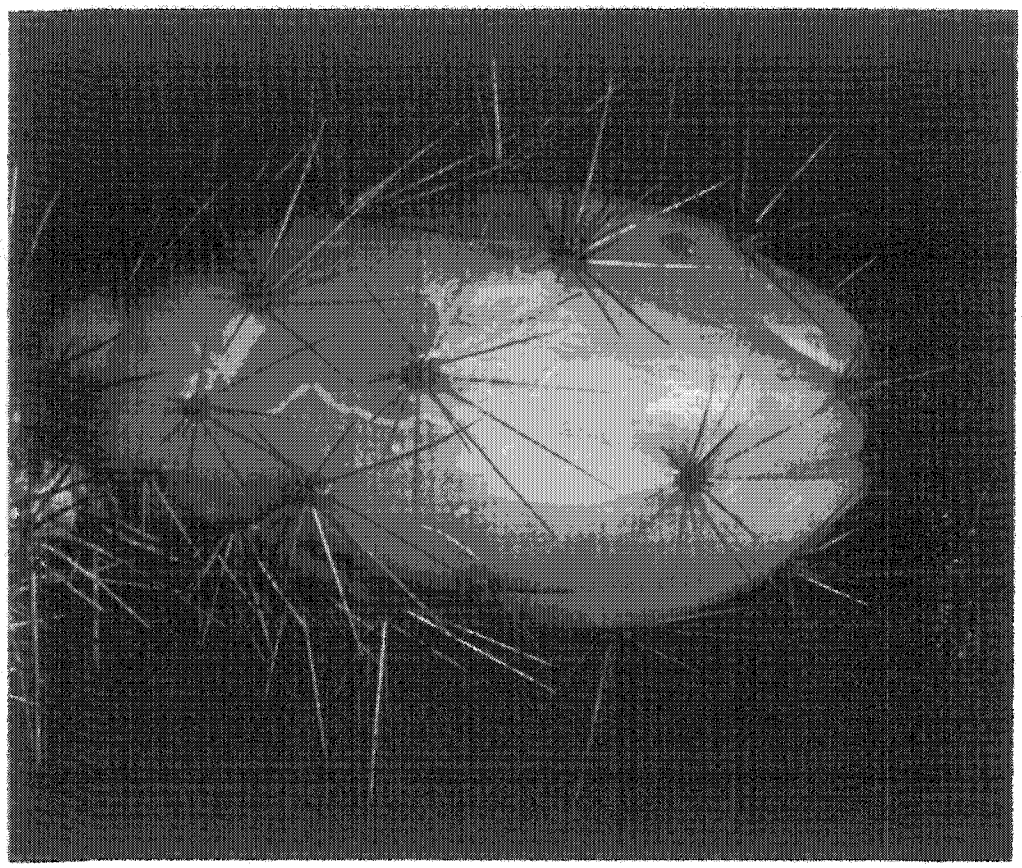

Plate 62. Long-spined fruit of *Leptocereus weingartianus* subsp. *demissus*, photographed at Côte-de Fer, southern Haiti. This new subspecies can be readily distinguished from subsp. *weingartianus* by its long, slender, scandent or trailing stem segments, obconical (not tubular) flowers, and strongly armed fruits.

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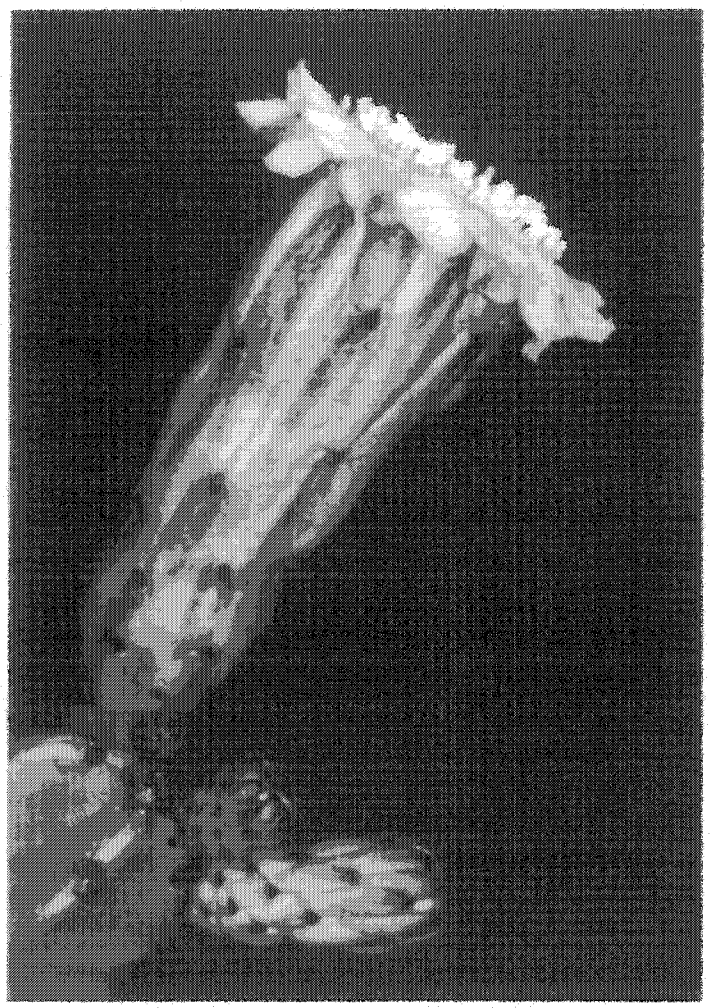

Plate 63. Spineless flower of a *Leptocereus grantianus* specimen occurring on the rocky shoreline of southwestern Culebra, an island off the northeast coast of Puerto Rico. This critically endangered species, nowadays reduced to a single population of about 50 individuals, is threatened by agricultural, residential, and tourist development. Because the surviving population is located only 8 to 10 meters from high tide, it is also threatened by eventual exposure to heavy storm and hurricane surges.

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J. (U.S.), 5(5): 469, 1 fig. 1933; Marshall, in Giménez-Lanier, León & Marshall, Cuban Cacti, Cact. & Succ. J. (US) 9(1): 12. 1937; Marshall & Bock, Cactaceae 79. 1941; Backeberg, Die Cactaceae 4: 1963. 1960; Backeberg, Kakteenlexikon 201. 1966; Liogier, Descrip. Fl. P. Rico 3: 315-316, fig 95-4. 1994; Anderson, Cactus Fam. 394, 1 fig. 2001.

Figs. 1 E; 2 F1, F2; 4 O1. Plates 5 E, F; 6 E; 10 B; 12 A; 14 B; 15 B; 15 D; 16 I; 19 B-D; 21 C; 24 D; 25 B; 27 F, G; 28 B-E; 30 A-D; 39 F-H; 43 F, G; 44 G; 48 C; 53 B-D; 53 F; 54 C, D.

Shrub to 3-4 m tall. Trunk and main branches bearing areoles enlarged up to 1-1.4 cm in diameter, producing to 25-40 spines, to 4.5-7 cm long. *Ultimate stem segments* (0.15) 0.5-1.20 m long, (2.5) 3-4 (6.2) cm in diameter; stem sinuses 6-14 mm deep; cortex 3-5 mm wide at the grooves, 19-22 mm wide at the crest of a rib projection (podarium); pith 2.8-3.4 mm in diameter. *Ribs* 9-23 mm high, 5-9 mm wide at base, their edges separated 2.2-3.2 cm from each other, the crenatures 3-5.5 mm deep. *Areoles* 2-6 × 2-5 mm, (2) 2.3-2.7 (3) cm apart, armed with 8-11 spreading spines. *Spines* acicular, somewhat compressed and twisted, 0.4-4 cm long, 0.2-0.6 mm in diameter; radial spines 6-8, the lower pair crossed, 0.4-2 cm long, 0.2-0.6 mm in diameter; central spines 2 or 3, 1.3-4 cm long, 0.4-0.6 mm in diameter. *Cephalium* occasionally ramified. *Flowers* 4-4.7 cm long, 2.6-3.5 cm wide; pericarpel 9-12 mm in diameter; receptacle-tube to 1.5-1.6 cm wide above, the areoles bearing 4-9 spines (3)

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4-9 mm long; staminal ring 1-1.9 cm in diameter, *Fruits* bearing areoles to 2 mm in diameter, usually with 11-18 spines to 1 cm long, easily detaching at maturity.

Distribution: southwestern Puerto Rico, on rocky coastal terraces, dry hillsides, and low, sandy or saline coastal and subcoastal plains.

16b. **Leptocereus quadricostatus** (Bello) Britton & Rose subsp. **parvispinus** Areces, subsp. nov.

Type: Puerto Rico. Guánica: Municipio Yauco, Guánica, in Guánica State Forest, about 4 km WSW to the State Forest headquarters, alongside the road to Playa Jaboncillo, 66°54'40'' N, 17°58'25'' W, in dry forests, 2 Oct 2002 (fl, fr), *Areces 6848* (holotype: UPR; isotype NY, to be deposited).

Figs. 2 G1-G3; 4 O2. Plates 5 D; 10 C; 14 C; 16 C, D; 23 F, G; 27 E; 30 E-H; 43 H, I; 44 F; 48 C; 54 G.

Shrub to 2-3 m tall. *Ultimate stem segments* (0.15) 0.5-1.30 m long, (3.5) 3-4 (6.3) cm in diameter; stem sinuses 6-15 mm deep; cortex 4-5 mm wide at the grooves, 20-21 mm wide at the crest of a rib projection (podarium); pith 2.9-3.1 mm in diameter. *Ribs* 10-25 mm high, 6-9 mm wide at base, their edges separated 2.3-4.4 cm from each other, the crenatures 2-4.5 mm deep. *Areoles* 3.5-6 × 2.5-5 mm, (2) 2.3-2.7 (2.9) cm apart, armed with 10-15 adaxially oriented spines. *Spines* subulate, terete 0.3-1.3 cm

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long, 0.1-0.5 mm in diameter; radial spines 8-10, the lower pair diverging, 0.3-1 cm long, 0.1-0.5 mm in diameter; central spines 2-4, 0.7-1.3 cm long, 0.3-0.5 mm in diameter. *Cephalium* not ramified. *Flowers* 4.6-5.3 cm long, 2.2-3 cm wide; pericarpel 9-11 mm in diameter; receptacle-tube to 1.4-1.7 cm wide above, the areoles bearing 1-6 (7) very short spines 1-2 (3) mm long; staminal ring 1.1-1.3 cm in diameter. *Fruits* bearing areoles to 2.5-2.6 mm in diameter, with 4-12 spines to 3.5 mm long, not easily detaching at maturity.

Subspecies *parvispinus* differs from subspecies *quadricostatus* mainly by having more spines (10 to 15) in the stem areoles, the spines being adaxially oriented (not spreading), subulate (not acicular), terete in cross-section (not compressed and twisted), and much shorter in length. Also, in the novelty here described the two lower radial spines of the stem areoles do not cross over each other —a good, simple diagnostic character— and the flowers are somewhat longer, although have a slightly narrower perianth. Likewise, fruit areoles, which bear much smaller spines than those of subspecies *quadricostatus*, do not detach and fall off easily at maturity.

Distribution: subspecies *parvispinus* is apparently restricted to the coastal and subcoastal areas between Guayanilla and Guánica Bay, southwestern Puerto Rico.

17. **Leptocereus grantianus** Britton, Cact. Succ. J. (US) 5(5): 469, 1933. — Type: Puerto Rico. Culebra Island, 1932, *Britton 9725* (NY, not located).

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Syn.: *Neoabbottia grantiana* (Britton) Buxbaum, Cact. Succ. J. (US) 38(1): 45. 1966. — Type: Puerto Rico. Culebra Island, 1932, *N. L. Britton 9725* (NY, apparently not deposited).

Lit.: Marshall, in Giménez-Lanier, León & Marshall, Cuban Cacti, Cact. & Succ. J. (US) 9(1): 13. 1937; Marshall & Bock, Cactaceae 79, fig. 26. 1941; Backeberg, Die Cactaceae 4: 1963-1964, fig. 1890. 1960; Backeberg, Kakteenlexikon 201. 1966; Liogier, Descrip. Fl. P. Rico 3: 315. 1994; Anderson, Cactus Fam. 392, 1 fig. 2001.

Figs. 3 B; 4 P. Plates 6 C; 9 F; 11 C; 12 G; 24 G; 43 J, K; 48 C; 63.

Shrub, loosely branched at the base and above, to 1.5-2 m tall, lacking a definite trunk; main branches thickening to 7-8 cm in diameter at base, with patchy periderm formation, soon arching, if touching the ground their apices often giving rise to new arching stems, their areoles usually with no indeterminate growth, or if so, then producing trichomes, not spines. *Ultimate stem segments* arching, (0.15) 0.5-1.50 m long, 3-4 (6) cm in diameter, dark bright green; stem sinuses acute, usually demarcated by a line, 6-15 mm deep; cortex not fibrous, 3-4 mm wide at the grooves, 20-23 mm wide at the crest of a rib projection (podarium); vascular cylinder 5-6 mm in diameter; pith 2.8-3.5 mm in diameter. *Ribs* (3) 4 (5), 10-20 (24) mm high, 5-9 mm wide at base, their edges separated 2.1-3.1 cm from each other, crenate, the crenatures 2.5-5 mm deep, bearing the areoles at the bottom of the depressions. *Areoles* rounded or

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subrounded, 2-4 × 2-3 mm, (2) 2.2-2.5 (2.8) cm apart, tufted when young with a short, deep dark brown tomentum that becomes sooty or grayish with age, unarmed, or with 1-4 short, inconspicuous spines (immature seedlings with up to 6 spines in each areole). *Spines* (if present) subulate, whitish-yellow when growing, dark brown to nearly black in youth, in age becoming brownish-yellow and later grayish, frequently falling off as the stem segments grow older, 0.5-2 mm long, 0.08-0.1 mm in diameter. *Cephalium* rarely produced, very small, usually 0.5-8 cm long 0.4-0.6 cm wide, dark brown to nearly black. *Flowers* nocturnal, terminal or subterminal, most often produced singly at apical areoles, or 2-12 grouped at the stem apex, not more than 3 opening simultaneously, rarely on cephalia, (3) 4.5-5.5 (6) cm long, 2.8-3.6 cm wide, tubular-obconical to nearly obconical, unarmed or nearly so; pericarpel for the most part greenish-red, 9-11 mm in diameter; receptacle-tube non-constricted, to 1.8-2.1 cm wide above, green, the podaria with a distinct dorsal purplish-red band, the areoles bearing deep dark brown tomentum but no spines, rarely with a few short bristles to 1mm long; outermost perianth segments often green with a touch of purplish-red at middle, the inner ones whitish; stamens forming a lax staminal ring 1.6-2.3 cm in diameter, at the floral throat level or to 2 mm exserted during anthesis; stigma usually at the floral throat level. *Fruits* ellipsoid or subglobose, unarmed, 3-4 × 2.3-3.8 cm; seeds numerous

Distribution: the only known population occurs along a rocky shoreline on the southwestern part of Culebra Island off the northeast coast of Puerto Rico.

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10.4 The "leptocereoid" cactus from Haiti is not a *Leptocereus*

In the course of one of many *Leptocereus*-hunting explorations, I collected in northwestern Haiti what I believed was, at first glance, a new leptocereoid taxon; the puzzling plant had slender stem segments and unusual, elongated yellow fruits. I was far away, however, from being its first discoverer. Although the plant was never named and described according to the modern rules, it was actually one of the earliest known cacti, having been depicted in the late seventeenth century by the French missionary Charles Plumier during one of his visits to the West Indies. Plumier referred to the species with the polynomial *"Melocactus arborescens folio striato spinosissimo fructu luteo suboblongo"* in his *Botanicon americanum seu historia plantarum in Americanis insulis nascentium*, a monumental, 8-volume manuscript containing 1219 plates that was never published. Fortunately, half a century after Plumier's death in 1704, Johannes Burman edited 262 of his relevant plates and descriptions, including a presumed drawing of the Haitian puzzling cactus (plate 195). Burman's *Plantarum americanarum fasciculus*, published in ten parts between 1755 and 1760, made available to botanists only a fraction of Plumier's *magnum opus*. The original drawings of Plumier, about 6000, are still deposited at the Muséum d'Histoire Naturelle at Paris; all his plant collections, however, seem to have been lost at sea (Urban, 1920).

The identification of Burman's plates of Plumier has engaged numerous renowned botanists, including Linnaeus, Lamarck, De Candolle, Haworth, Britton and Rose,

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Urban, and Hunt. Plate 195, however, remained a mystery until now when the enigmatic plant seems to have been finally traced to a Haitian coastal terrace.

Trying to explain the presence of elongated fruits on Burman's plate 195, Hunt (1984) erroneously thought that Plumier may have mistaken the elongated flower buds of *Harrisia nashii* —a relatively common Hispaniolan cactus— for a fruit, drawing the stamens and anthers as if they were ovules and funicles. Only the tiny bract-scales on the elongated fruits and flowers of the Haitian plant that I collected, which otherwise resemble Burman's plate 195, are much smaller (2 mm long) than those depicted by Plumier; the rest is about the same. Likewise, the flowers in Burman's plate 193 (currently associated with *Harrisia nashii*), with their long, exserted style, look like those of the novelty here described, but the fruits are definitively those of *Harrisia*. In this case Plumier may have truly mistaken the flowers of the puzzling Haitian cactus for those of *Harrisia nashii*, because of the resemblance of the stems and habit of both plants (Plate 1). This is very plausible, considering that Plumier did not get to see the flowers of the plant he depicted and described with nearly round, tuberculate fruits (Lamarck, 1783). So what is shown in his plate (Burman's plate 193) may be a chimera; an attempt to reconstruct the flowers, not from the floral remains on immature fruits as Hunt (1984) states, but from the flowers of a plant belonging to a different genus and species. Perhaps Britton and Rose (Cactaceae 2: 151) were right when they said that such a fabricated drawing, upon which *Cereus divaricatus* DC. was based, "cannot be certainly associated with any known cactus."

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More than two centuries later, in 1925, the intrepid Swedish explorer E. L. Ekman collected the Haitian plant at two different sites (*Ekman 4446* and *5377*, both S). Werdermann (1931), who studied these plants, considered them to be conspecific with *Cereus repandus* (L) Miller, a columnar cereoid with stems 10 to 20 cm in diameter and dark red fruits. This point of view was literally followed by Moscoso (1943), with no critical analysis of Werdermann's arguments. *Cereus repandus* is currently placed in a subgenus of *Cereus* (subgenus *Oblongicarpi*), restricted to the western Caribbean and northern South America (Hunt and Taylor 1992).

The last scholars to collect the Haitian novelty were E. C. and G. M. Leonard; it was in 1929 when they saw fertile specimens of this taxon in northwestern Haiti that were determined as *Cephalocereus nobilis* (Haworth) Britton & Rose. Their identification was reaffirmed in 1969, as *Pilosocereus nobilis* (Haworth) Byles & Rowley, by D.H. Nicolson and R. A. Defilipps, but not by N. P. Taylor, who thought (in 1992) that Leonard's collection could instead relate to *Leptocereus* (hand-written statement on labels of *Leonard & Leonard 13311, 13682*, US).

Standing well apart from *Leptocereus, Pilosocereus,* and from all known members of genus *Cereus* to which the rare Haitian cactus certainly belongs, both in morphology and distribution, it seems expedient to name and describe this neglected cactus without further delay. The species that inspired Plumier's original polynomial and drawings finally became *Cereus* (*Hamannia*) *fabiolae* Areces, more than 300 years after its first collection.

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Cereus (subgen. nov. *Hamannia*) *fabiolae*

Cereus fabiolae (subgen. nov. *Hamannia*) is herein described as a new subgenus and species, from the dry coastal terraces of northwestern Haiti. It differs from subgenera *Cereus*, *Oblongicarpi*, *Ebneria*, and *Mirabella* of genus *Cereus* by a unique combination of slender, fluted, mucilaginous stems with numerous low, thin, crenate ribs; relatively small, subrecurved tubular flowers bearing small bract-scales with axillary wool, and nearly undifferentiated, acuminate and strongly reflexed perianth segments. The stamens and style are very long and markedly exserted, the anthers oblong-linear to linear in profile, and the fruits cylindrical or cylindric-obovate, pendulous at maturity, crowned by the dry, persistent floral tube. A morphological description is provided, in addition to accounts of seed morphology, palynology and epidermal morphology, given earlier in chapters 3, 4, and 5.

Cereus Miller, Gard. dict. abr. ed. 4. 1754.

Hamannia Areces, *subgen. nov.*

TYPE: ***Cereus*** (subgen. ***Hamannia***) ***fabiolae*** Areces

Rami teretes graciles, costis numerosis haud altis, crenatis; flores curvi tubulosi parvi, perianthii segmentis reflexis tandem acuminatis, interioribus idem atque exterioribus; stamina stylusque perianthium longe superantes; antheris oblongo-

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linearibus vel linearibus; fructus maturi penduli, cylindracei, indehiscentes, nudi denique perianthio marcescenti coronati.

Cereus (Hamannia) fabiolae Areces, *spec. nov.* TYPE: HAITI. Département du Nord Ouest, Presqu'île du Nord Ouest, coastal limestone terrace 2 km NE to Môle Saint Nicolas, on the road to Jean-Rabel, in extremely xeromorphic cactus woodlands, 28 December 1998 (fl, young fr), *A. E. Areces* 6795 (holotype: EHH!; isotype: NY!).

Cereus repandus sensu Werdermann, Fedde Rep. 29: 236 (1931) non *Cereus repandus* (L.) Mill., (1768).

Figs. 1 C; 2 M1-M3. Plates 6 H; 7 E-G; 10 I; 11 H; 14 H; 17 H; 17 L, M; 18 H, I; 26 A-E; 29 G; 34 E-H; 35 E-H; 43 L-O; 48 A, B.

Arbor parva valde ramosa ad 3-4 m alta, trunco 15-20 cm usque diam. Rami teretes gracile (3-) 3.5-4.5 (-5) cm diam. Costae (10-) 12-15 (-16) humiles (6-) 7-9 mm altae, (4-) 5-9 mm latae, profunde crenatae. Areolae rotundatae vel elliptico-rotundatae (1.1-) 1.3-1.6 (-1.8) cm inter se distantes, spinae divergentes aciculares, juniores flavidae, utriusque areolae (11-) 13-18 (-19), 6-20 (-25) mm longae. Flores nocturni per unam noctem solam expansi (mens. Dec.-Jan.), curvi, tubulosi, parvi, pericarpello cum tubo (6.4-) 6.7-7.1 (-7.3) cm tantum longo, squamis minutissimis viridibus apice saepe vinaceis et lanula albido-eburnea valde sparsa obtectis; perianthii segmenta (26-) 28-31 (-34) lax *disposita, anguste triangularia apice paulum*

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acuminata, 2-3 (-3.3) cm x 4-5 (-6) mm, margine minute et irregulariter serrulata, valde reflexa ultra medium vinacea interiora exterioribus similia; staminibus tubo supra medium inserta, perianthium 1-1.5 (-1.7) cm superantibus, (1.3-) 1.8-3 cm longa, antherae oblongo-lineares vel lineares 3-5 mm longae, dilute flavo-salmoneae, stylus albidus longissimus perianthio 2.5-4 (-4.2) cm longior, stigmate incluso ad (6.4-) 6.9-7.3 (-7.5) cm longus, radiis (11-) 14, linearibus, 7-9 mm longis. Fructus maturus pendulus, cylindraceus apice sinuato-plicatus (9-) 9.5-12 (-13) x 4-5 (-5.3) cm, indehiscens, nudus, denique perianthio marcescenti coronatus.

Small *tree* up to 3-4 m, very ramose. *Trunk* distinct branched above base, short, cylindrical, up to 15-20 cm in diam., terete in cross section, the vascular cylinder moderately woody, densely armed with long, deflexed, brownish-yellow spines up to 12-14 cm long often banded with transverse brown stripes. Main *branches* diverging at 30-45° angles, spinose, 0.25-1 (-1.5) m long, 5-10 cm diam. *Stem segments* curving upwards, fluted, slender, (3-) 3.5-4.5 (-5) cm diam., up to 1.5 m in young plants, those of older individuals more often composed of several shorter joints (7-) 10-70 (-90) cm long, mucilaginous. *Ribs* (10-) 12-15 (-16), low, (6-) 7-9 mm high, 4-7 (-9) mm wide at base, the edge narrowly rounded and deeply crenate, bearing the areoles in the depressions, sinuses straight, acute. *Areoles* mostly orbicular or transversely elliptic-orbicular, to 3-4 (-4.6) mm in diameter, 1.3-1.7 (-1.9) cm apart, tufted when young with a pale yellow felt later becoming tawny, and provided with (12-) 15-20 (-22) spines. *Spines* diverging, slender, acicular, (0.1-) 0.2-0.3 (-0.5) mm in diameter at base, translucent pale yellow in youth, yellowish-brown later, with their growing bases of a

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whitish-yellow color; central spines usually (2-) 4-8, 1.8-3 (-4.5) cm long, those of old joints longer, more numerous and frequently banded with transverse brown stripes; radial spines somewhat smaller, 0.6-1.8 (-2) cm long. *Flower buds* apiculate at early stages of development, in age becoming acute, the stigma often protruding from within the appressed perianth segments and becoming visible 2 or 3 days before anthesis. *Flowers* on most areoles of the stems (within the upper 2-3 m of the plant), small, tubular, (6.4-) 6.7-7.1 (-7.3) cm from throat to base, (4.6-) 5-6.5 (-7.2) cm broad when fully expanded, for a single night nyctigamous; pericarpel 2.6-3.4 x 1.2-1.4 cm, cylindrical, terete, green, lustrose, with few triangular bract-scales (0.5-) 1-2 mm long bearing a small tuft of ivory-whitish wool in their axillae; tube 3.3-4.1 x 1.2-1.4 cm at base, flared to 2.5-3 cm at apex, constricted beneath and above nectar-chamber, curved, green, slightly grooved, with few, disperse, narrowly triangular, purplish-red-tipped bract-scales 1.5-4 mm long subtending small, nearly inconspicuous axillary tufts of ivory-whitish wool; perianth segments (26-) 28-31 (-34), narrowly triangular, slightly acuminate at apex, finely and irregularly serrulate at margin, 2-3 (-3.3) cm x 4-5 (-6) mm, greenish below, wine-colored above the middle, widely separated and strongly reflexed during anthesis, the inner segments not differentiated from the outer ones; nectar-chamber cup-shaped, striate, 1.1-1.7 cm long, 3-7 mm at base, widening to 9-12 cm above; stamens (1.3-) 1.8-3 cm long., numerous, exserted, the upper ones extended 1-1.5 (-1.7) cm beyond the flower throat during anthesis, filaments capillary, whitish, anthers of a diluted yellowish-salmon pink color, oblong-linear to linear, 3-5 mm long; style long-exserted, including the stigma (6.4-) 6.9-7.3 (-7.5) cm long, 1.5-2 mm thick, extended 2.5-4 (-4.2) cm beyond the flower throat and 1.5-2.6 cm beyond the upper

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stamens, whitish, not tapering upwards; stigma lobes (11-) 14, linear, erect or nearly so, yellowish, 7-9 mm long; ovary locule narrowly obconic in longitudinal section, 1.5-2.4 cm long, 2.2-3 mm at base, 4-7 mm above. *Fruits* (9-) 9.5-12 (-13) x 4-5 (-5.3) cm, indehiscent, unarmed, elongated, at first green, erect and subangular, the 10-12 longitudinal keels separated by rounded sinuses, later smooth and terete or nearly so in cross section, cylindrical or less commonly cylindric-obovate, usually sinuate-folded at apex, yellow and pendulous at maturity, with very sparse, tiny bract-scales to 2 mm long often bearing small tufts of white wool in their axillae, crowned by the persistent, black floral remnant which withers straight inserting 2-4 mm into the pericarp; pericarp 6-8 mm thick, smooth, yellowish-green; funicular pulp greenish-gray to grayish, very mucilaginous.

The novelty described here not only extends the range of genus *Cereus* into the Greater Antilles, but poses an interesting biogeographical question about its origin. Although *Cereus fabiolae* is morphologically distinct to merit recognition as a separate subgenus, it shares with other subgenera of *Cereus* a number of important characters, particularly with subgenus *Oblongicarpi* (Croizat) Hunt and Taylor of Colombia, Venezuela, the Dutch Antilles to Grenada. In fact, they both have elongated fruits and relatively small flowers, with a short tube more or less constricted above the pericarpel (where the style-base and tube are fused). Unlike subgen. *Oblogicarpi*, however, the Haitian novelty has slender, mucilaginous stems, numerous ribs that are not cross-furrowed, areoles lacking long trichomes at youth, flowers subrecurved with wider perianth-limb, markedly exserted stamens and style, and wooly bract-scales in

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pericarpel and tube. Also, the fruits, which have a persistent floral remnant at the apex, are not greenish but yellow, and the funicular pulp is grayish or grayish-green, not white (Plates 1 and 26).

While most West Indian cacti of coastal distribution produce flowers and fruits sparingly almost throughout the year —with peaks coinciding with rainy epochs— *Cereus* (*Hamannia*) *fabiolae* has a very definite flowering period in the dry season, ranging from early December through January. Anytime during this two-month interval a rather massive and synchronous blooming occurs, and 60 to 70% of all yearly produced flowers opening in one single night, and over 80% of the flowers open in two to four consecutive nights. Fruits are apparently ripe and fully formed also in the dry winter season, between late December and February (exceptionally earlier, cf. the cited material), a time when few botanists are travelling in Haiti. This explains why the taxon has remained unknown for so long. Flowering is apparently limited to plants growing in rather open situations where they get plenty of solar radiation. Tall plants emerging above the dry forest canopy also bloom profusely. Only such plants seem to accumulate enough energy to divert to simultaneous bloom. These open or elevated situations allow pollinators with high energy requirements, such as bats, to locate the flowers without difficulty, and maneuver freely among them. The night-blooming flowers of *Cereus fabiolae* exhibit various features associated both with bat- and hawkmoth pollination and may well be visited by these two animal groups. Widely opening greenish-white to wine-colored floral throat, unpleasant odor, and strongly reflexed perianth segments are floral features exhibited by most "bat flowers. The relatively slender tube, the long-

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exserted stamens and style, and the copious and continuous production of nectar in a rather narrow nectar-chamber are more typical of the hawkmoth floral syndrome. This combination of features seems to confirm that in the Cactaceae, it is most likely that no flower is visited exclusively by one species of pollinator alone.

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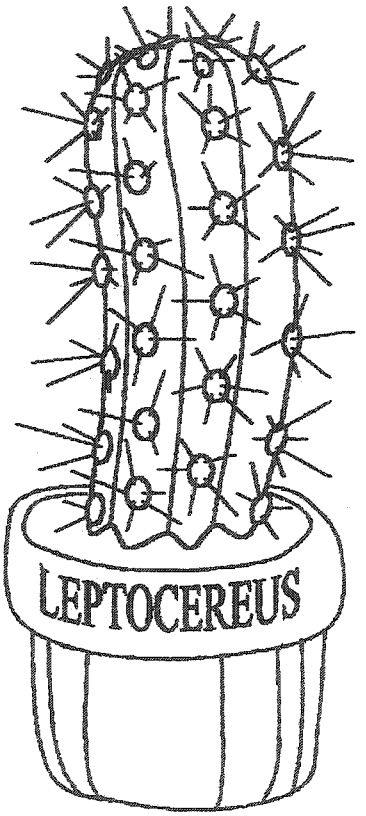

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