University of Reading

A taxonomic revision of the genus Leptocereus (Cactaceae) in Haiti and the Dominican Republic

Article

Published Version

Hoxey, P., Gdaniec, A., Hernandez, J. D., Guzmán, M., Corniel, W. and Culham, A. ORCID: https://orcid.org/0000-0002-7440-0133 (2023) A taxonomic revision of the genus Leptocereus (Cactaceae) in Haiti and the Dominican Republic. Bradleya, 2023 (41). pp. 4-80. ISSN 0265-086X doi: 10.25223/brad.n41.2023.a3 Available at https://centaur.reading.ac.uk/114747/

It is advisable to refer to the publisher's version if you intend to cite from the work. See Guidance on citing.

Identification Number/DOI: 10.25223/brad.n41.2023.a3
<https://doi.org/10.25223/brad.n41.2023.a3>

Publisher: BioOne

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the End User Agreement.

University of Reading

www.reading.ac.uk/centaur

CentAUR

Central Archive at the University of Reading

Reading's research outputs online

Bradleya 41/2023
pages 4–80

A taxonomic revision of the genus *Leptocereus* (Cactaceae) in Haiti and the Dominican Republic

Paul Hoxey[1], *Andrew Gdaniec*[2,3], *Jose Dolores Hernandez*[4], *Mario Guzmán*[4], *Wilmer Corniel*[4] *and Alastair Culham*[4]

1. Gibraltar Botanic Gardens, Red Sands Road, GX11 1AA, Gibraltar (paul@hoxey.com).
2. Gibraltar Botanic Gardens, Red Sands Road, GX11 1AA, Gibraltar (agdaniec@gibraltargardens.gi).
3. School of Biological Sciences, University of Reading, RG6 6AS, UK (a.gdaniec@pgr.reading.ac.uk).
4. Jardín Botánico de Santiago Profesor Eugenio de Jesús Marcano Fondeur, Avenida del Botánico Dr. José de Jesús Jiménez Almonte, No. 1, Santiago De Los Caballeros, Dominican Republic (direccionbotanico@correosol.com).

Photographs: Paul Hoxey and Andrew Gdaniec

Summary: Until recently the genus *Leptocereus* (Cactaceae) had been little studied on Hispaniola, an island in the Caribbean shared between Haiti and the Dominican Republic. For many years only three endemic species were accepted as being present: *Leptocereus paniculatus* (≡*Neoabbottia paniculata*), *L. undulosus* (≡*Dendrocereus undulosus*) and *L. weingartianus*. The identity of *L. weingartianus* is obscure and the type material is a seedling plant, originating from seed collected in Haiti, showing juvenile characters and lacking flowers or fruits. For many years this name was applied to all *Leptocereus* on the island of Hispaniola excluding *L. paniculatus* and *L. undulosus,* although two recently published species (*L. demissus* and *L. velozianus*) have been segregated from it. We propose that the likely identity of the type material of *L. weingartianus* is a seedling of *L. paniculatus* but due to the designation of an epitype we retain the name for a thin stemmed species found in south-central Hispaniola. Based on fieldwork in Haiti and the Dominican Republic supplemented with analyses of seed and seedling morphology at Gibraltar Botanic Gardens, we recognise nine species, all endemic to Hispaniola, including four which are described here for the first time (*L. rosei* sp. nov., *L. bayahibensis* sp. nov., *L. cremnophilus* sp. nov., and *L. septentrionalis* sp. nov.). We provide a key to the species and, for all taxa, we supply a description, distribution map, iconography, list of specimens studied and photographic plates.

Received 14 September 2022

We also propose three subgenera for *Leptocereus* (subgenus *Leptocereus*, subgenus *Dendrocereus*, and subgenus *Neoabbottia*), the latter two based on genera of the same names. All species from Hispaniola belong to *Leptocereus* subgenus *Neoabbottia* except for *L. undulosus,* which is a member of *Leptocereus* subgenus *Dendrocereus*.

Zusammenfassung: Bis vor kurzem war die Gattung *Leptocereus* (Cactaceae) auf Hispaniola, einer Insel in der Karibik, die von Haiti und der Dominikanischen Republik geteilt wird, kaum untersucht. Viele Jahre lang wurden nur drei endemische Arten als dort vorkommend akzeptiert: *Leptocereus paniculatus* (≡*Neoabbottia paniculata*), *L. undulosus* (≡*Dendrocereus undulosus*) und *L. weingartianus*. Die Identität von *L. weingartianus* ist unklar und das Typusmaterial ist eine Sämlingspflanze, die aus in Haiti gesammelten Samen stammt, juvenile Merkmale zeigt und keine Blüten oder Früchte hat. Viele Jahre lang wurde dieser Name auf alle Leptocereen Hispaniolas angewendet, mit Ausnahme von *L. paniculatus* und *L. undulosus*, obwohl zwei kürzlich veröffentlichte Arten (*L. demissus* und *L. velozianus*) davon abgetrennt wurden. Wir meinen, dass die wahrscheinliche Identität des Typusmaterials von L. weingartianus auf einem Sämling von *L. paniculatus* beruht, aber aufgrund der Festlegung eines Epitypus behalten wir den Namen für eine dünntriebige Art bei, die im südlich-zentralen Teil von Hispaniola zu finden ist. Basierend auf Feldforschungen in Haiti und der Dominikanischen Republik,

die durch Untersuchungen der Samen- und Sämlingsmorphologie im Botanischen Garten von Gibraltar ergänzt wurden, erkennen wir neun Arten an, die alle auf Hispaniola endemisch sind. Davon werden vier hier zum ersten Mal beschrieben (*L. rosei* sp. nov., *L. bayahibensis* sp. nov., *L. cremnophilus* sp. nov. und *L. septentrionalis* sp. nov.). Wir legen einen Schlüssel für die Arten sowie für alle Taxa eine Beschreibung, eine Verbreitungskarte, eine Ikonographie, eine Liste der untersuchten Exemplare und Fototafeln vor. Wir schlagen auch drei Untergattungen für *Leptocereus* vor (Untergattung *Leptocereus*, Untergattung *Dendrocereus* und Untergattung *Neoabbottia*), die beiden letzteren auf gleichnamigen Gattungen basierend. Alle Arten von Hispaniola gehören zur *Leptocereus*-Untergattung *Neoabbottia*, mit Ausnahme von *L. undulosus*, der zu *Leptocereus* subg. *Dendrocereus* gehört.

Keywords: Greater Antilles, Hispaniola, *Dendrocereus*, *Neoabbottia*, seedling morphology, seed morphology

Introduction

The name *Leptocereus* was first proposed at the rank of subgenus, *Cereus* subgenus *Leptocereus* by Berger (1905: 79), and he included three species: *Cereus assurgens* C.Wright ex Griseb., *Cereus gonzalezii* F.A.C.Weber and *Cereus tonduzii* F.A.C.Weber, with *Cereus assurgens* designated as the type. Britton & Rose (1909: 433) elevated the subgenus to generic rank, only including the type species, but speculated that another species, *Cereus quadricostatus* Bello from Puerto Rico also belonged there. They excluded from the genus both *Cereus gonzalezii* and *Cereus tonduzii,* which they correctly concluded are not closely related to the type species. By 1920, Britton & Rose (1920: 77–82) had expanded the genus *Leptocereus* (A.Berger) Britton & Rose to include eight species. Six originated from Cuba, one from Hispaniola: *L. weingartianus* (E.Hartmann) Britton & Rose (≡*Cereus weingartianus* E.Hartmann) and one from Puerto Rico: *L. quadricostatus* (Bello) Britton & Rose (≡*Cereus quadricostatus*).

The French missionary and naturalist Charles Plumier visited the Caribbean region at the end of the seventeenth century. He described and illustrated a large number of plants which he encountered, including cacti (Plumier, 1689–1697). These exist in an unpublished manuscript held at the Muséum d'Histoire Naturelle in Paris but some of the illustrations were copied and reproduced by Burman (1755–1760). Only recently have the original illustrations of all the cactus species drawn by Plumier been published (Mottram, 2002).

Two cacti that Plumier found in Haiti represent species later named *Cactus paniculatus* Lam. and *Cereus undulosus* DC. These two names are based exclusively on the illustrations and descriptions made by Plumier. Remarkably, both species, which grow to tree-sized proportions, remained unknown to botanists for over 200 years until the 1920s when Britton & Rose obtained material for study. They erected the monotypic genus *Neoabbottia* Britton & Rose (1921) for *Cactus paniculatus. Cereus undulosus* was included in the genus *Dendrocereus* (Britton & Rose, 1925), which they had created for the Cuban endemic *Cereus nudiflorus* Engelm. ex C.Wright (≡*Dendrocereus nudiflorus* (Engelm. ex C.Wright) Britton & Rose). Other authors such as Barker & Dardeau (1930), Moscoso (1941), Backeberg (1958–1962) and Hunt (1979) followed Britton & Rose and accepted the genera *Leptocereus*, *Neoabbottia* and *Dendrocereus* until Hunt & Taylor (1986: 69) suggested that *Neoabbottia* was congeneric with *Leptocereus*. Later, the name *Leptocereus paniculatus* (Lam.) D.Hunt was published and, since then, the genus *Neoabbottia* has almost universally been considered a synonym of *Leptocereus*.

The genus *Dendrocereus* continued to be accepted as a good genus, although its position in the phylogeny of the Cactaceae has been questioned. The flower of *Dendrocereus* is adapted for hawk-moth pollination, which led to speculation (Hunt & Taylor, 1986: 69) that it is related to the genus *Acanthocereus* (Engelm. ex A.Berger) Britton & Rose because both share the same pollination syndrome. Hunt & Taylor (1990: 89) considered *Dendrocereus* to be a synonym of *Acanthocereus,* but most authors, including Hunt et al. (2006a: 74), preferred to accept it as a good genus irrespective of its affinities. Backeberg (1955) was the first to mention the genera *Neoabbottia* and *Dendrocereus* are 'somewhat allied' but only recently has molecular data (Hernández–Hernández et al., 2011) suggested that *Dendrocereus* is closely related to *Leptocereus*. Another more recent study (Barrios et al., 2020) has confirmed that both species of *Dendrocereus* should be included within *Leptocereus* for it to remain a monophyletic genus, and they published the required combinations in *Leptocereus* including *L. undulosus* (DC.) D.Barrios & Majure. This study also shows that *Leptocereus* consists of the following well-supported clades:

1. A clade including the type species and all other Cuban species excluding *L. nudiflorus*;

2. A clade including all species from Hispaniola and Puerto Rico, including *Neoabbottia* but excluding *L. undulosus*;
3. A clade containing the two *Dendrocereus* species (*L. nudiflorus* and *L. undulosus*).

Guiggi (2020, 2021) interprets the data of the molecular study in Barrios et al. (2020) differently from the authors and considers the three clades to be three distinct genera. *Leptocereus* is restricted to the Cuban clade, *Neoabbottia* expanded to include all the species from Hispaniola plus Puerto Rico and *Dendrocereus* is retained as a genus with one species, *D. undulosus*, and one subspecies, *D. undulosus* subsp. *nudiflorus* (Engelm. ex C.Wright) Guiggi.

Areces-Mallea (2003: 22–23), using morphology as well as molecular data, proposed that the Cuba and Hispaniola (plus Puerto Rico) species should be separated into two groups and proposed a classification of two subgenera (subgenus *Leptocereus* for the Cuba species and subgenus *Weingartianea* for the Hispaniola/Puerto Rico species). This classification is not effectively published, because it appeared in a thesis (ICN Article 30.9), but we support this view and extend it to accept a third subgenus to accommodate the two species of *Dendrocereus*. Berger (1929: vi–vii) had already proposed that the genera *Dendrocereus* and *Neoabbottia* should be considered subgenera of *Cereus,* but in a classification with an enlarged concept of *Cereus* with no fewer than fifty-one subgenera in total. Within the taxonomic treatment section, we take these two well-known generic names and make the necessary combinations at subgeneric rank in *Leptocereus*. The third subgenus containing the type of *Leptocereus* is automatically created with the publication of the other two subgenera (Article 22.3) and does not require an author citation (Article 22.1).

If we consider the species of *Leptocereus* of Hispaniola within the circumscription of the enlarged genus, including *Neoabbottia* and *Dendrocereus*, from the time of Britton & Rose until recently, just three species have been accepted as being present on the island: *L. paniculatus, L. undulosus,* and *L. weingartianus,* although some authors (Urban, 1920–1921: 461 and Werdermann, 1931: 240) did not accept *L. weingartianus* as distinct from *L. assurgens* and preferred to use that name. The only historical disagreement from this view was held by Werdermann (1931: 240) who considered a collection by Ekman from north-west Haiti to be *Cereus maxonii* (Rose) Vaupel (≡*Cephalocereus maxonii* Rose), a name misapplied because it is not a *Leptocereus*. He intended to use the name *Leptocereus maxonii* Britton & Rose, a completely different species from eastern Cuba.

Recently, two additional *Leptocereus* species from Hispaniola have been described: *Leptocereus demissus* Areces and *Leptocereus velozianus* Clase, Y.Encarn., Peguero & Majure.

Material and methods

A total of nearly nine weeks of fieldwork in Haiti and the Dominican Republic was dedicated to the investigation of cacti. The genus *Pilosocereus* Byles & G.D.Rowley was our principal target, but we found *Leptocereus* at approximately seventy different localities. For some of these localities we obtained precise coordinates from herbarium specimens, for others we were aided by imprecise data from specimens or published information. The remainder we discovered as part of our field work. Except for *L. paniculatus,* which is found in large populations with a high density of individuals, all the other species are of more restricted distribution and grow in much smaller and usually scattered populations. They often dwell in forests or woodland and can be rather difficult to find.

We supplemented our fieldwork with the examination of herbarium material at JBSD and K, and through online digital images of herbarium specimens at DES, F, FLAS, MO, NY, U, and US. Herbarium material of *Leptocereus* is of variable quality. Fertile structures are frequently missing, and many specimens are little more than sterile stem fragments. The two species, *L. paniculatus* and *L. undulosus*, are usually easy to identify from stem material, but all the other species are difficult to distinguish from each other as dried specimens. Significant morphological features are often lost when the material is preserved, and this is probably why so many distinct taxa have remained unnamed until recently.

The seed images were taken using a Digital SLR camera with a macro lens and extension tubes given a reproduction ratio of two to one (double life-size). Focus stacking was employed which captures a series of photographs taken with different focus points, which are then combined into a single image using computer software. This avoids depth of field limitations at high magnification and ensures the complete seed is in focus. Additional post-processing was employed to remove the background and arrange the seeds for consistent scale, origination, and spacing for publication.

To study seedling morphology under standardised conditions, seeds were thoroughly cleaned using water to remove any residue pulp which could inhibit germination. Seeds were sown at Gibraltar Botanic Gardens under artificial lights on the surface of a crushed lava substrate with a particle size of 3–6mm. The seeds were left uncovered and temperatures were maintained around 18–20°C during the night and 25–30°C during the day, by the use of heating mats. *Leptocereus* seeds typically germinated between two to three weeks. Water was applied through capillary action by placing the pots in a tray of water to avoid the disturbance of seeds and small seedlings on the surface. After approximately four to six weeks the seedlings were pricked out into trays and introduced into greenhouse conditions under natural light without artificial heat. An inorganic, balanced fertiliser was applied to the developing seedlings, during every second watering, to supply nutrients.

Leptocereus seedlings grow rapidly and after six months reach approximately 10–20mm tall depending on the species. At this time, for each seed collection, seedlings were selected for study. Photographs were taken and measurements were made before preserving the material in alcohol for depositing in the herbarium GIB.

We used a chi-square test for associations to test whether the distribution of all *Leptocereus* species is associated with that of the iguana *Cyclura cornuta,* the most likely candidate for a seed dispersal vector following Barrios & Mancina (2017) who propose *Cyclura nubila* undertakes this functional for *Leptocereus* species in Cuba. To do so, we divided the map of Hispaniola into forty-five separate 0.5° latitude × 0.5° longitude quadrats and noted whether the following have been recorded in each quadrat, 1–no species (17 quadrats), 2–*Leptocereus* alone (4 quadrats), 3–*Cyclura cornuta* alone (6 quadrats) or 4–*Leptocereus* and *Cyclura cornuta* together (18 quadrats). For the distribution of *Leptocereus* species we used locality data from herbarium specimens and our field observations supported by photographic records. The distribution of *Cyclura cornuta* was taken from Alberts (1999).

The Articles of the *International Code of Nomenclature for algae, fungi, and plants* (ICN) cited throughout the text follow the *Shenzhen Code* (Turland et al., 2018).

Plant illustrations in this paper are annotated with observation numbers of the form *Hoxey* 0000.00. These are used to tie together all plants of a particular species at a single locality to a database maintained by the authors.

Results and discussion

At the time our fieldwork commenced in Hispaniola, *Leptocereus velozianus* was not yet described, and so we started from a position of there being four species native to Hispaniola. We initially accepted the consensus that the name *L. weingartianus* should be applied to any *Leptocereus* on Hispaniola not included in the other three species. This view became untenable after we encountered various populations with different morphological characters, which we could not consider to belong to a single species. This led us to investigate which plants should be assigned to the name *L. weingartianus*. The protologue is based on an immature plant, yet to flower, grown in Germany from seed collected in Haiti (Hartmann, 1904). We believe the description and lectotype illustration most closely resemble a seedling of *L. paniculatus*. Nevertheless, due to the designation of an epitype, we retain the name for a different species rather than considering it a synonym of *L. paniculatus*. This is explained in detail in the entry for *L. weingartianus* in the taxonomic treatment section.

Based on our observations in habitat and studies of seed and seedling morphology at Gibraltar Botanic Gardens we can identify nine distinct taxa of *Leptocereus* in Hispaniola. Five are previously described species: *L. demissus, L. paniculatus*, *L. undulosus, L. velozianus* and *L. weingartianus,* and four are described here for the first time: *L. bayahibensis* sp. nov., *L. cremnophilus* sp. nov., *L. rosei* sp. nov., and *L. septentrionalis* sp. nov.

One of the nine species, *L. undulosus* belongs to *Leptocereus* subgenus *Dendrocereus;* the other eight all belong to *Leptocereus* subgenus *Neoabbottia*. The taxonomic treatment section includes an entry for each species which consists of descriptions, distribution and habitat data, synonyms, herbarium specimens and published illustrations. Where appropriate, we comment on the typification of names, but otherwise follow Barrios & Majure (2022). The descriptions are compiled from our observations made in habitat except for flowers of the species *L. demissus* and *L. velozianus* which we have not observed first-hand so are transcribed from their respective protologue descriptions. This section concludes with a taxonomic key and a table summarising key morphological information for all species.

The distribution data which are repre-sented in the distribution maps (Figure 1) are based on herbarium specimens and illustrations cited in this paper. Additionally, we include our field observations supported by photographic figures reproduced here.

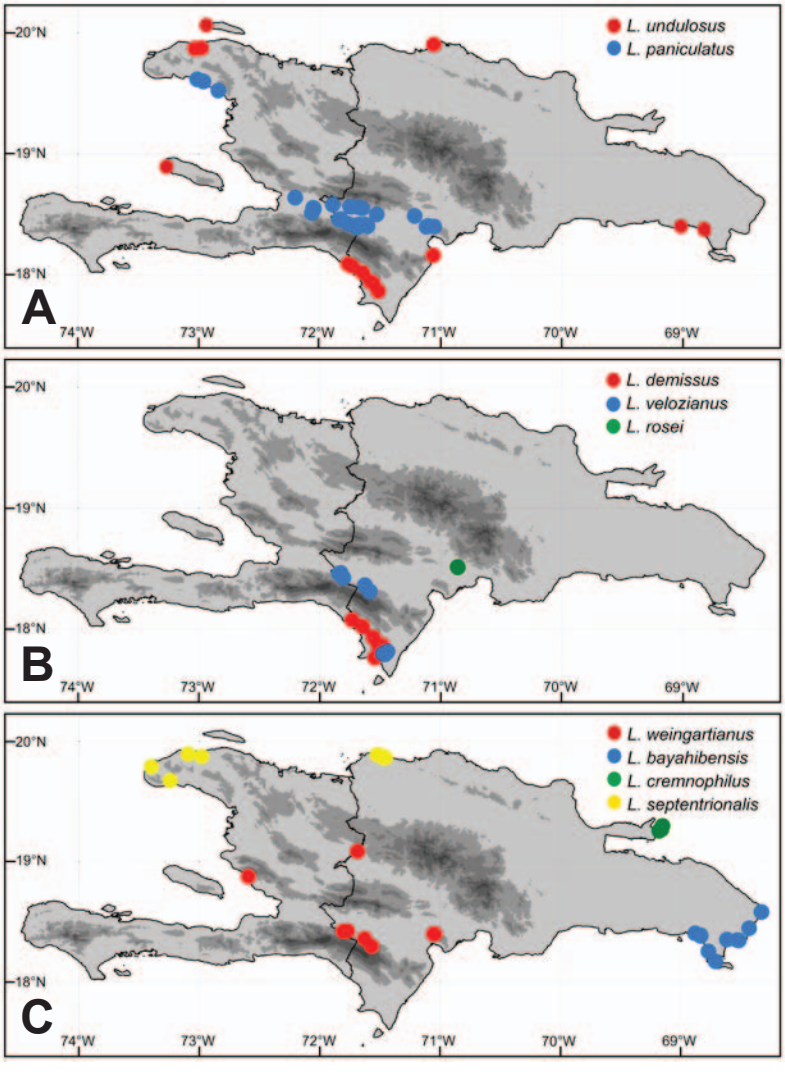


Figure 1. The distribution of the nine species of *Leptocereus* found in Hispaniola. Data points are based on herbarium specimens, habitat observations by the authors supported by photographic plates or published illustrations.

Sympatric species

Areces-Mallea (2001: 294) reports that *Leptocereus* species are rarely found growing together and he only states *L. paniculatus* and *L. weingartianus* grow sympatrically. However, by excluding *Dendrocereus* from *Leptocereus,* he ignores cases where *L. undulosus* grows together with other species of *Leptocereus*, which is a fairly common occurrence. We found *L. undulosus* growing with species in *Leptocereus* subgenus *Neoabbottia* in several places on Hispaniola. For example, *L. demissus* occurs with *L. undulosus* in the Parque Nacional Jaragua which is also reported by Majure et al. (2021: 22). Fleming (1984) reports *L. undulosus* growing with *L. weingartianus* at Bayahíbe although we do not consider this species to be *L. weingartianus* and publish the name *L. bayahibensis* for this taxon. Although we found *L. bayahibensis* is common in the area we could not locate any specimens of *L. undulosus.* We also encountered another distinct *Leptocereus* species (described in this paper as *L. septentrionalis*) growing with *L. undulosus* near Port-de-Paix in northern Haiti. Species of *Leptocereus* subgenus *Dendrocereus* and subgenus *Neoabbottia* have different flowers and are unlikely to share pollinators, so sympatric species are unlikely to be cross-pollinated even if compatible.

Majure et al. (2021: 22) report a case of *L. weingartianus* and *L. velozianus* growing together in the Sierra de Bahoruco, Dominican Republic, which is of significant interest because both species belong to *Leptocereus* subgenus *Neoabbottia.* We can confirm this association (Figure 2A) from our field observations. We also found *L. paniculatus* growing sympatrically with both *L. velozianus*

Figure 2. Examples of *Leptocereus* species growing sympatrically. **A–** *L. weingartianus* and *L. velozianus*. DOMINICAN REPUBLIC. Province Independencia. West of El Limón, 90m (*Hoxey* 1943). **B**–*L. weingartianus* and *L. paniculatus.* DOMINICAN REPUBLIC. Province Independencia. East of El Limón, 40m (*Hoxey* 1944).

Figure 3. *Leptocereus* encountered on the walk from Trudillé to Los Tres Charcos arranged from south (left) to north (right). The four stems on the left are *L. demissus* and the two on the right are *L. velozianus*.

Locality	Observed by	UN	PA	DE	VE	RO	WE	BA	CR	SE	UA
Port-de-Paix, HT	Hoxey and Gdaniec	●								●	
Bayahíbe, DR	Fleming (1984)	●						●			
Pedernales, DR	Hoxey and Gdaniec	●		●							
Jimaní, DR	Hoxey and Gdaniec		●		●						
Sierra Martín García, DR	Hoxey and Gdaniec		●				●				
Sierra de Bahoruco, DR	Majure et al. (2021)				●		●				
Sierra de Bahoruco, DR	Hoxey and Gdaniec				●		●				
Sierra de Bahoruco, DR	Hoxey and Gdaniec		●				●				
Sierra de Bahoruco, DR	Hoxey and Gdaniec				●		●				●
Sierra de Bahoruco, DR	Hoxey and Gdaniec			●	●						

Table 1. Summary of sympatric *Leptocereus* species. Localities in the Dominican Republic (DR) or Haiti (HT). Species epithets abbreviated to two letters: UN = *L. undulosus*, PA = *L. paniculatus*, DE = *L. demissus*, VE = *L. velozianus*, RO = *L. rosei*, WE = *L. weingartianus*, BA = *L. bayahibensis*, CR = *L. cremnophilus*, SE = *L. septentrionalis*, UA = unassigned taxon.

Figure 4. Seedlings of *L. demissus* (left) and *L. velozianus*,(right) both from south-west of Los Tres Charcos clearly show there are two species present south of the Sierra de Bahoruco, west of Oviedo. These two seedlings are from localities separated by only four kilometres.

and *L. weingartianus* (Figure 2B) although not all three together. However, we did find three species of *Leptocereus* subgenus *Neoabbottia* growing within twenty metres of each other in the Sierra de Bahoruco at a single locality. Two of the species are *L. velozianus* and *L. weingartianus* but the third species is of uncertain affinity. Neither flowers nor fruits were observed but the stem morphology is closest to *L. septentrionalis*. These plants are geographically distant from that species so we prefer not to attribute any published name to them pending further study. We observed *L. demissus* and *L. velozianus* growing in close proximity south of the Sierra de Bahoruco on the trail from Los Tres Charcos (near Oviedo) to Trudillé on the coast. Stem morphology (Figure 3) alone separates the two species but seed and seedling morphology (Figure 4) is distinct and confirms there are two species here. Near Los Tres Charcos the vegetation is relatively moist and only *L. velozianus* is found but when environmental conditions become drier towards the coast *L. velozianus* is replaced by *L. demissus*. The gap between the two species is about 500m. It is very likely these two species will also be found growing sympatrically if more extensive fieldwork is undertaken in the area. Table 1 summarises the examples of sympatric *Leptocereus* species that are known to us or have been recorded in the literature. Only two species (*L. rosei* and *L. cremnophilus*) are not found with any other *Leptocereus* species.

The Sierra de Bahoruco is a hotspot for *Leptocereus* diversity, with four or possibly five species growing in close proximity. The four positively identifiable species can be distinguished from each other by stem morphology alone (Figure 5).

The confirmation of multiple sympatric species does raise the question of whether species can cross-pollinate and if hybrid individuals exist today or if ancient hybridisation events contributed to speciation in the genus. We saw no evidence of hybridisation. This is a topic that requires further investigation. Chromosome counts for Hispaniola *Leptocereus* species are not recorded so incompatibility due to different ploidy levels is unknown. Only the chromosomes of *Leptocereus quadricostatus* from Puerto Rico have been counted (Spencer 1955) with 2n=22.

Vectors for seed dispersal

All *Leptocereus* on Hispaniola produce fruits of a similar size and structure with a thick pericarp. With one exception (*L. cremnophilus*) the seeds are contained in a very mucilaginous pulp. Variation is generally limited to the number, length, persistence of spines and relatively small differences in fruit shape and size. The fruits fall to the ground whole at maturity and, on a few occasions, we have found rotting examples (Figures 6A–B) underneath the mother plants and older fully decomposed fruits (Figure 6C) with just the spines and seeds left on the surface of the ground. Only once have we observed a fruit where the seeds had been removed through a hole in the pericarp and successfully dispersed (*L. demissus* at the coast near Trudillé, Figure 6D). A dispersal vector is required for two principal reasons, firstly, to distribute the seeds so offspring do not compete directly with the mother plant, and secondly to release the seeds from the thick pericarp and mucilaginous pulp. The most likely candidates to do this are large lizards of the genus *Cyclura* (family Iguanidae) as proposed by Barrios & Mancina (2017) through eating the fruits and distributing the seeds in their dung. Taylor (2021: 95) also suggests that other cactus species (*Pereskia* species) with mucilaginous fruits on Hispaniola are dispersed by passing through the gut of ground-dwelling animals. In the Barrios & Mancina study, undertaken in Cuba, the species involved

Group	1	2		3			4		
Species	**UN**	**PA**	**DE**	**VE**	**RO**	**WE**	**BA**	**CR**	**SE**
Length (mm)	2.8–3.2	2.2–2.4	2.2–2.6	3.2–3.4	3.4	3.0	2.4–2.7	2.6–2.7	2.3–2.6
Breadth (mm)	2.0.2–5	1.2	1.3	1.8–2.0	2.0–2.2	2.0–2.2	1.4–1.6	1.6	1.4
Depth (mm)	1.2–1.5	0.8	1.0	1.2–1.4	1.4	1.3	0.8	0.6	0.6
L+B+W sum	6.6	4.3	4.7	6.5	6.9	6.4	4.8	4.8	4.4
L / B ratio	1.3	1.9	1.8	1.7	1.6	1.4	1.7	1.7	1.8
L / D ratio	2.2	2.9	2.4	2.5	2.4	2.3	3.2	4.4	4.0
Hilum									
Length (mm)	1.5	1.0	1.0	1.3	1.8	1.4	0.8	1.0	1.0
Breadth (mm)	1.0	0.3	0.3	0.7	0.7	0.6	0.3	0.4	0.5
L / B ratio	1.5	3.3	3.3	1.9	2.5	2.3	2.6	2.5	2.0
Peripheral cells									
Size (μm)	20	10	10	15	10–15	15–20	15	20	15
Shape	High domed	High domed	High domed	Medium domed	Low domed	Medium domed	Medium domed	High domed	High domed
Apex	Round	Pointed	Partially pointed	Round	Round	Round	Round	Round	Pointed

Table 2. Seed morphology comparison of *Leptocereus* species. Species epithets abbreviated to two letters: UN = *L. undulosus*, PA = *L. paniculatus*, DE = *L. demissus*, VE = *L. velozianus*, RO = *L. rosei,* WE = *L. weingartianus,* BA = *L. bayahibensis*, CR = *L. cremnophilus,* SE = *L. septentrionalis.* The average value for length, breadth and width measurements has been used to calculate ratios.

is *Cyclura nubila* but the equivalent species on Hispaniola is *Cyclura cornuta* (Figure 7). This is an adaptable species and is found in a variety of environments but favours rocky limestone habitats including dry forests, thorn-scrub woodland, and semi-deciduous to subtropical moist forests (Alberts, 1999: 23–24). The distribution of *Cyclura cornuta* on Hispaniola is strongly associated with that of *Leptocereus* species (chi-square test for associations: $x^2_3 = 13.96$, $P = 0.003$; Figure 8). There is also a second species *Cyclura ricordii,* which is probably involved with *Leptocereus* seed dispersal. It is likely that other, now extinct, animals also consumed *Leptocereus* fruits such as giant tortoises (*Chelonoidis* species, family Testudinidae) or ground sloths (*Parocnus serus*, Family Megalonychidae). It has been noted that juvenile plants of *L. undulosus* are rarely found in the wild. This species has larger fruits than any other *Leptocereus* in Hispaniola so perhaps its principal dispersal vector is now extinct and regeneration from seed has been severely impacted due to this.

We do not know of any confirmed cases of *Cyclura cornuta* consuming *Leptocereus* fruits but Pasachnik & Martin-Velez (2017) report that a principal component of their diet is the fruit of *Consolea* species (Cactaceae) based on a study undertaken in the south-western Dominican Republic within the Jaragua National Park. C*onsolea* fruits are broadly similar in structure to *Leptocereus* fruits with a thick pericarp and seeds contained in a mucilaginous pulp. It is reasonable to assume *Leptocereus* fruits are also part of their diet. *Leptocereus* are not mentioned in this study but specimens are much scarcer in the study area than *Consolea* so would probably only account for a relatively small part of the diet of *Cyclura cornuta*

If *Cyclura cornuta* is the primary dispersal vector for *Leptocereus* seeds then recent trends of declining populations (Alberts, 1999: 23) and extirpation from their historical range will have a serious impact on the long-term viability of *Leptocereus* species irrespective of habitat destruction which would impact the plants as well as the animals. The principal issues affecting *Cyclura cornuta* are illegal hunting for food, medicinal use, and non-native species predation such as by dogs, cats, mongooses and pigs. During

Figure 5. The four species of *Leptocereus* can be found growing sympatrically in the Sierra de Bahoruco and adjacent areas in south-west Dominican Republic. From left to right: *L. paniculatus, L. velozianus, L. demissus* and *L. weingartianus.*

our fieldwork on Hispaniola, we failed to observe *Cyclura cornuta* except on Isla Beata. Any *in-situ* conservation activity involving *Leptocereus* also needs to consider its seed dispersal vector or vectors.

Seed morphology analysis and comparison

Photographs of seeds of all species are illustrated in Figure 9 and seed descriptions are included for each species within the Taxonomic treatment. Further analysis of seed dimensions and characters is summarised in Table 2. We consider the seeds belong to four informal groups. Group 1 contains the single species *L. undulosus,* which belongs to *Leptocereus* subgenus *Dendrocereus,* and Groups 2–4 contain species of *Leptocereus* subgenus *Neoabbottia*. We do not assign any taxonomic value to these groups, but they perhaps highlight possible relationships between the species.

Group 1 (*L. undulosus*): These seeds are easily identified as distinct from all other species which is unsurprising because they belong to a different subgenus. They are large, with the lowest length/breadth ratio (1.3 compared with 1.4–1.9) and lowest length/depth ratio (2.2 compared with 2.3–3.2) compared with the other eight species. The hilum-micropylar region is also much wider than all other species resulting in the lowest length/breadth ratio (1.5 compared with 1.9–3.3). The testa cells are large and high-domed giving the seed a distinctive tuberculate appearance.

Group 2 (*L. paniculatus* and *L. demissus*): These two species have the smallest seeds in the genus, slightly smaller than Group 4 and significantly smaller than Groups 1 and 3. The hilum-micropylar region is narrower than in any other group resulting in a higher length/breadth ratio (3.3 compared with 1.5–2.6). Both species have high domed cells on the testa with a pointed or partially pointed apex, a character shared with only one other species (*L. septentrionalis*). It is somewhat surprising that these two species have similar seeds because the plants are geographically isolated from each other and morphologically dissimilar, including growth form (large trees compared with low growing scandent stems), stems (thick compared with thin), flowers (narrow and nearly spineless compared with funnel form

Figure 6. Fallen fruits of *Leptocereus* in various states of decay. **A–***Leptocereus undulosus.* **B–***Leptocereus demissus.* **C–***Leptocereus* sp. **D–***Leptocereus demissus* with seeds removed by an unknown vector.

and spiny). The similarity could therefore be due to a common secondary dispersal vector, such as ants, and not indicative of a close relationship.

Group 3 (*L. velozianus*, *L. rosei,* and *L. weingartianus*): These three species have similar-sized seeds which are the largest (in all three dimensions) of the three groups in subgenus *Neoabbottia*. The sum of the three dimensions is 6.4–6.9 compared with 4.3–4.8. They also share a similar relatively smooth testa which consists of cells with a low to medium domed relief and rounded apex. Two of the three species (*L. velozianus* and *L. weingartianus*) grow sympatrically.

Group 4 (*L. bayahibensis*, *L. cremnophilus,* and *L. septentrionalis*): These species have seeds intermediate in length between Groups 2 and 3, although only marginally larger than Group 2. However, they have a lower depth than either resulting in a higher length/depth ratio (3.2–4.4 compared with 2.2–2.9). The testa cells are medium to high-domed and easily distinguished from the lower domed cells of Group 3. The three species in this group are widely separated from each other in discrete populations in northern and eastern Hispaniola but share many morphological characters. The seed of *L. septentrionalis* is a little anomalous due to the pointed apex on the testa cells which are only otherwise seen in Group 2.

Seedling morphology

Seedling morphology is a little used and underappreciated area of study in the Cactaceae yet it has a long history (De Fraine, 1910).

Figure 7. *Cyclura nubila* (family Iguanidae) on Isla Beata. A possible dispersal vector for *Leptocereus* seeds.

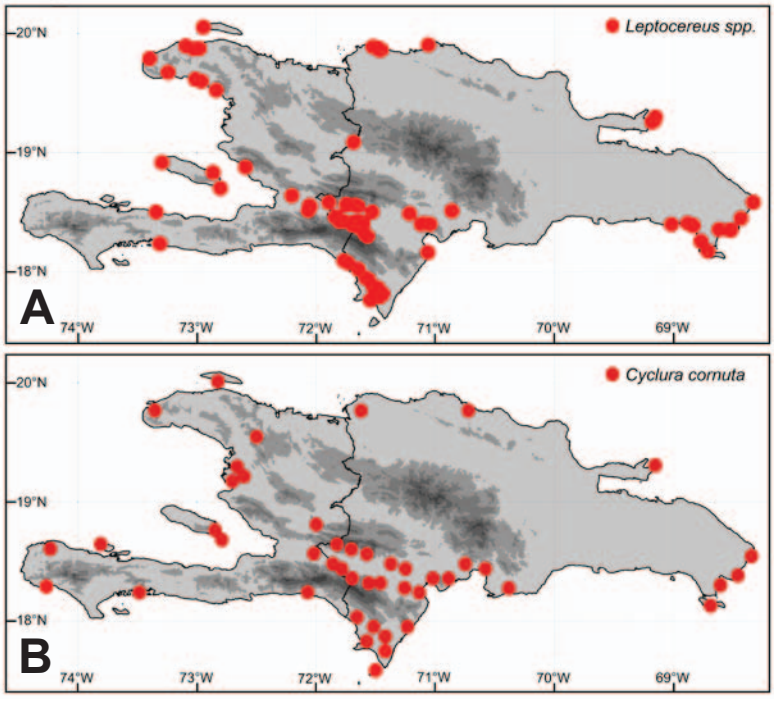


Figure 8. The distribution of *Leptocereus* (Map A) and *Cyclura cornuta* (Map B) is well correlated. The *Leptocereus* distribution is based on our observations and herbarium specimens data. The *Cyclura cornuta* distribution is derived from Alberts (1999: 26, Figure 3).

When grown under standardised conditions in cultivation we observed that *Leptocereus* seedling morphology has minimal variation within a population or between different populations of a species but it can be markedly different between species. This makes it a useful tool to distinguish between species even where adult plant morphology is similar. The eight species of *Leptocereus* subgenus *Neoabbottia* were examined and photographed (Figure 10). The seedlings fit into two informal groups:

Group 1 (*L. paniculatus, L. demissus* and *L. septentrionalis*): These three species all produce seedlings with a thin (to 4mm wide) but elongated stem (to 20mm long). The epidermis is greyish-green and has a reddish hue. The spination is very short (1–1.5mm long) without a longer central spine. Some differences can also be noted between the species. *L. demissus* is the most distinct with a high rib count (six compared with four for the other two) with an almost circular cross-section. Both *L. paniculatus* and *L. septentrionalis* have

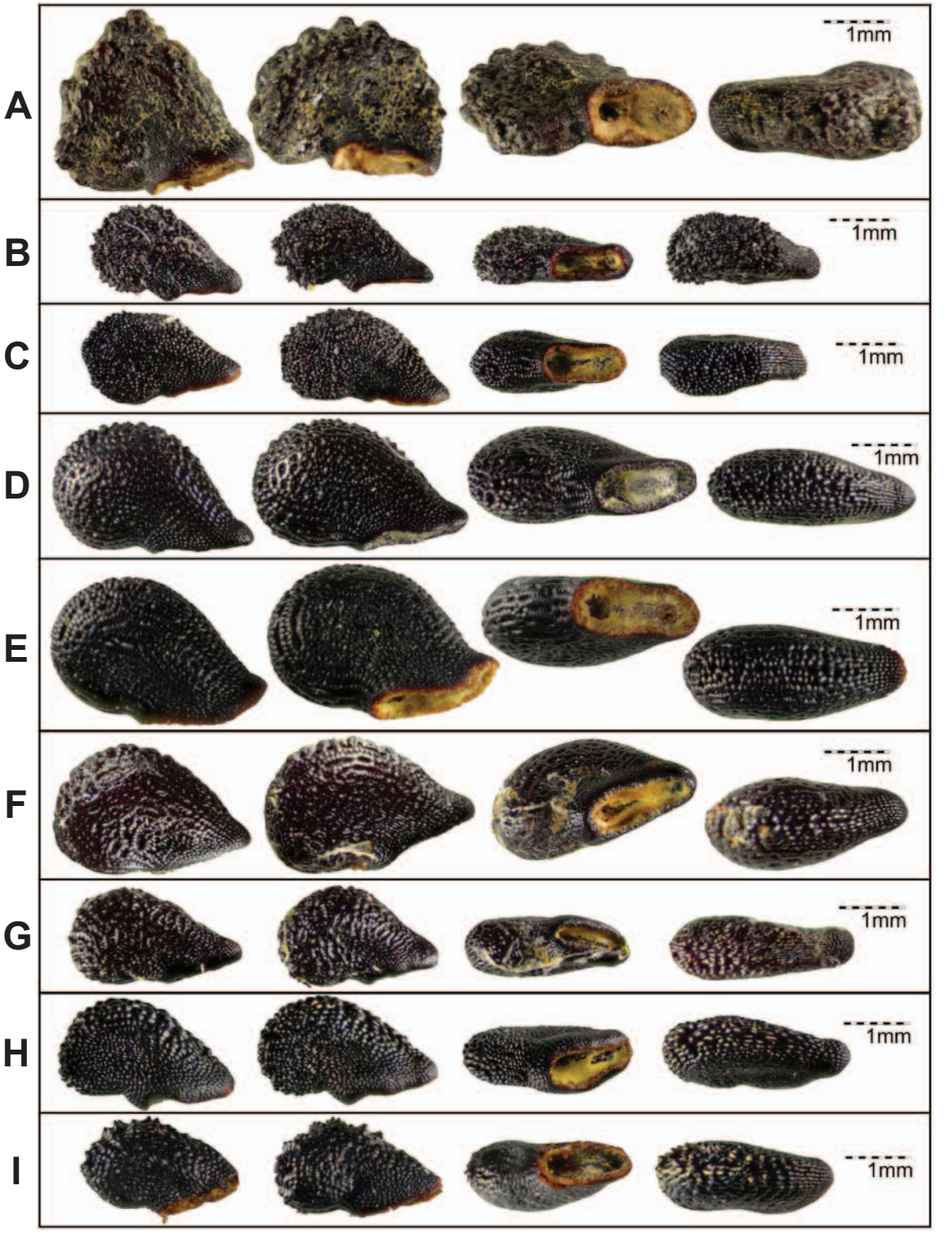


Figure 9. The seeds of *Leptocereus.* **A–***L. undulosus* (*Hoxey* 1312.06). **B–***L. paniculatus* (*Hoxey* 1858.05) **C–***L. demissus* (*Hoxey* 1866.01). **D–***L. velozianus* (*Hoxey* 1867.01). **E–***L. rosei* (*Hoxey* 1950.01). **F–***L. weingartianus* (*Hoxey* 1958.01). **G–***L. bayahibensis* (*Hoxey* 1850.01). **H–***L. cremnophilus* (*Hoxey* 1842.01). **I–***L. septentrionalis* (*Hoxey* 1970.01).

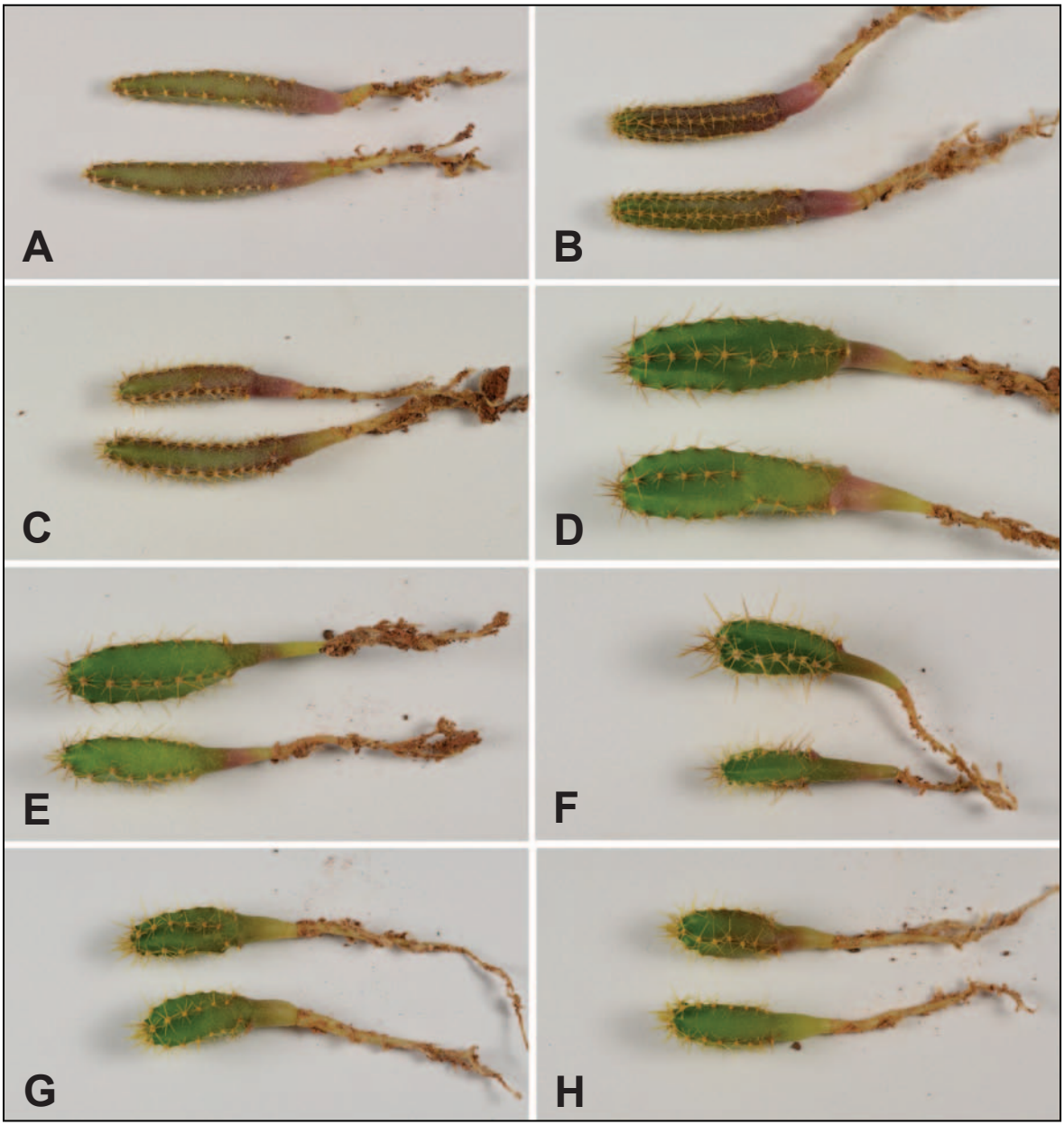


Figure 10. Seedlings of *Leptocereus* subgenus *Neoabbottia*, 6 months of age, reproduced approximately life-size. **A–** *L. paniculatus* (*Hoxey* 1959.01). **B–***L. demissus* (*Hoxey* 1956.01). **C–***L. septentrionalis* (*Hoxey* 1970.01). **D–***L. velozianus* (*Hoxey* 1943.01). **E–***L. weingartianus* (*Hoxey* 1944.01). **F–***L. rosei* (*Hoxey* 1952.01). **G–***L. bayahibensis* (*Hoxey* 1850.02). **H–***L. cremnophilus* (*Hoxey* 1842.01).

four ribs and the stems have a square cross-section. They can be separated by the spination which is noticeably less robust in *L. paniculatus*. Interestingly, these three species have similar seedling morphology yet are very different at maturity and easy to distinguish from each other. It is particularity surprising that *L. demissus* with thin stems and a scandent growth form groups with the two arboreal species. Nevertheless, *L. paniculatus* and *L. demissus* both appear in the same seed group and, although *L. septentrionalis* was not placed with them there, all three species have testa cells with a pointed apex. These three species never grow sympatrically.

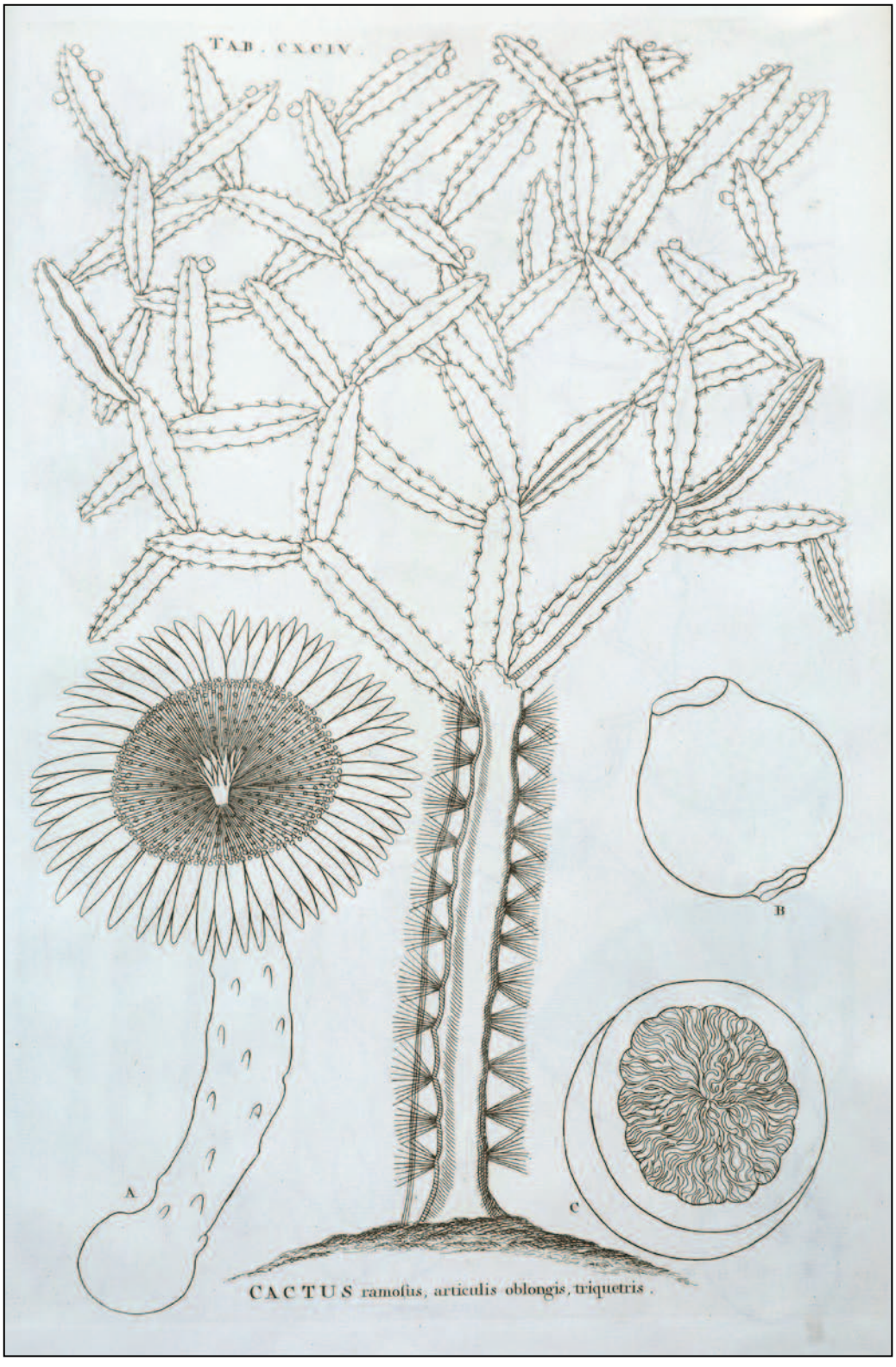


Figure 11. The lectotype of *Leptocereus undulosus* (≡*Cereus undulosus*) from Burman (1755–1760: fasc. 8. 187. t. 194.). Image scan Graham Charles.

Figure 12. *Leptocereus undulosus* HAITI. Department Nord-Ouest. West of Port-de-Paix, south of Baie des Moustiques, 30m (*Hoxey* 1295.01, close to the type locality). **A–**Plants of small stature in cleared woodland. **B–**Weakly spined 3-angled stem segments. **C–**Flower.

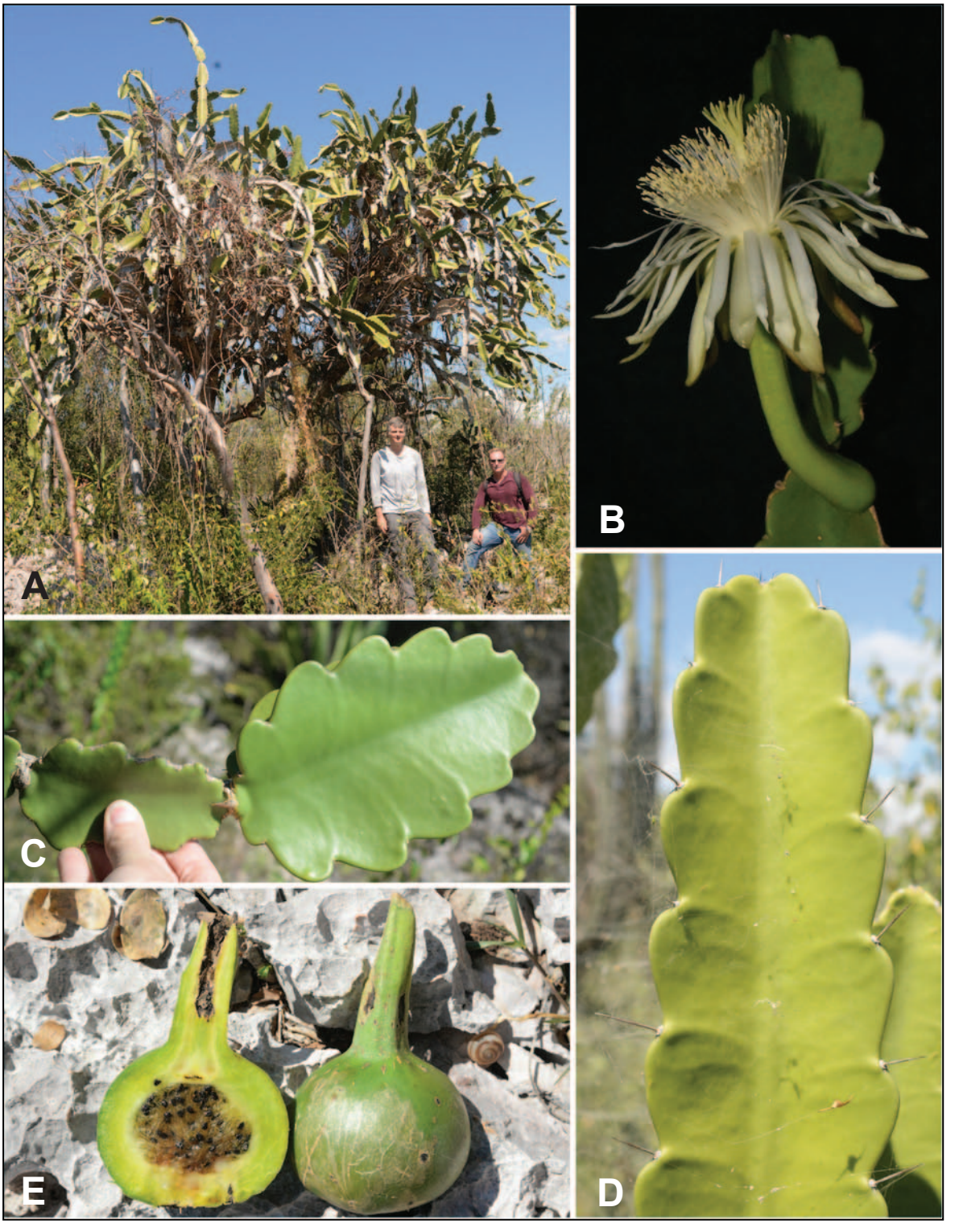


Figure 13. *Leptocereus undulosus* HAITI. Department Sud-Est. North of Anse-à-Pitre, 300m (*Hoxey* 1312.06). **A–** Mature specimen in partially cleared forest with the authors. **B–**Flower. **C–D.** Stem segments showing crenate rib margins. **E–**Fruit.

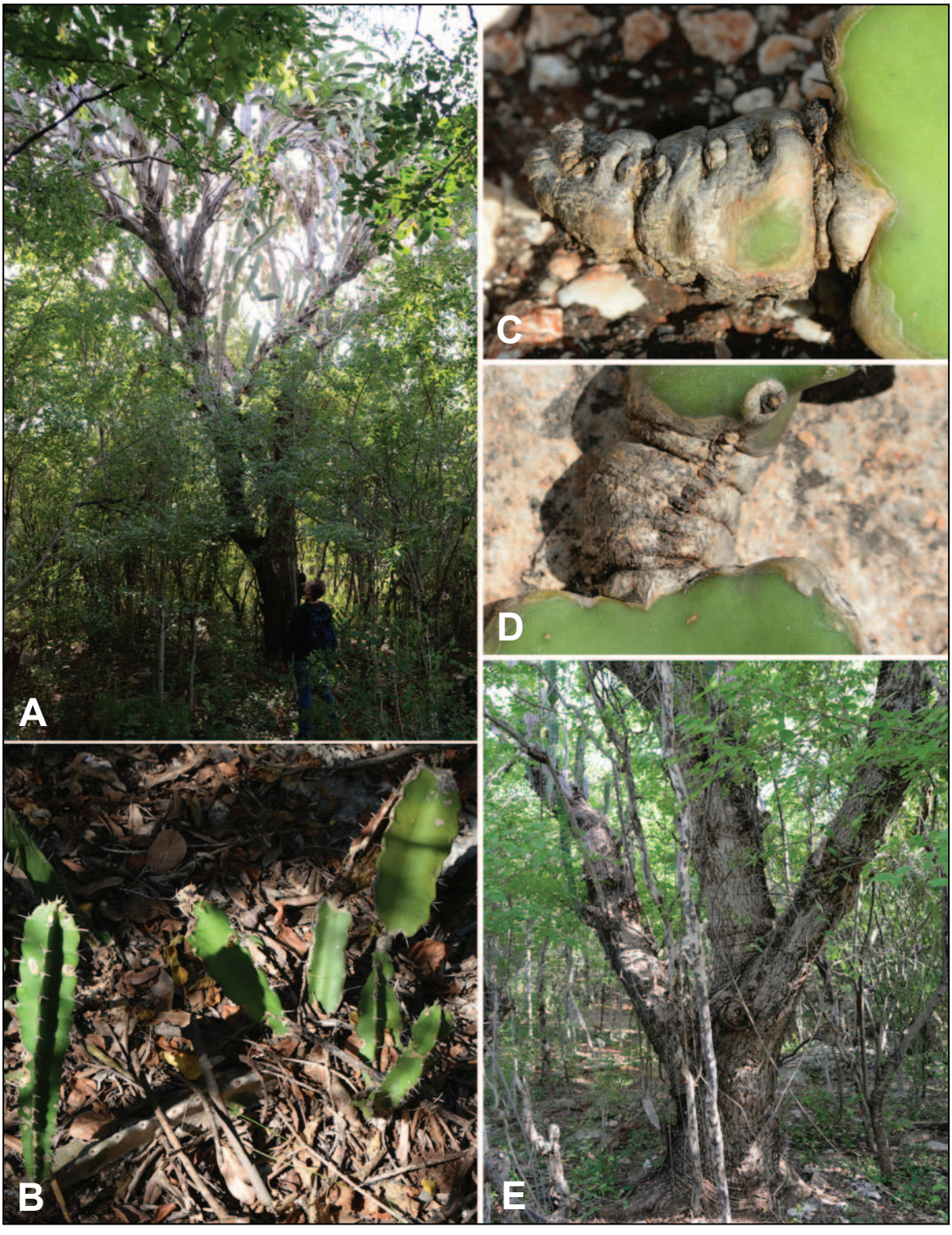


Figure 14. *Leptocereus undulosus* DOMINICAN REPUBLIC. Province Pedernales. West of Pedernales. 110m (*Hoxey* 1435.02). **A–**Mature specimen (*c.*8m tall) in intact forest. **B–**A fallen stem that has rooted and is producing new stems. **C–**Terminal brachyblast with closely spaced areoles. **D–**A terminal brachyblast that has reverted to normal stem growth. **E–**Trunk (*c.*50cm in diameter) of a mature specimen.

Group 2 (*L. velozianus*, *L. rosei, L. weingartianus, L. bayahibensis* and *L. cremnophilus*): These five species all have a green epidermis with very little if any red hue. Unlike the species in Group 1 they produce shorter (typically 10–15mm compared with 20mm) but thicker stems (5–6mm compared with 4mm). There are 4 or 5 well-developed ribs. The cross-section of the stems is winged rather than square. The spination is also more robust than Group 1 species, typically 2–3mm long (1–1.5mm long in Group 1). Usually, there is a noticeably longer central spine, erect from the centre of the areole, approximately 1mm longer than the radial spines. Differences between the species are not significant at this stage of growth but *L. velozianus* reaches larger dimensions than the other species and *L. rosei* has more robust spination. Two species in this group, *L. velozianus* and *L. weingartianus*, grow sympatrically.

Taxonomic treatment

Leptocereus (A. Berger) Britton & Rose, Contr. U.S. Natl. Herb. 12(10): 433 (1909) ≡*Cereus* subgenus *Leptocereus* A.Berger, Rep. (Annual) Missouri Bot. Gard. 16: 79 (1905).
Type: *Cereus assurgens* C.Wright ex Griseb., Cat. Pl. Cub. [Grisebach] 116 (1866).

A. *Leptocereus* subgenus *Leptocereus* ≡*Cereus* subgenus *Leptocereus* A.Berger, Rep. (Annual) Missouri Bot. Gard. 16: 79 (1905).
Type: *Cereus assurgens* C.Wright ex Griseb., Cat. Pl. Cub. [Grisebach] 116 (1866).

This subgenus is restricted to Cuba and contains about twelve species. It is not dealt with further in this paper.

B. *Leptocereus* subgenus *Dendrocereus* (Britton & Rose) Hoxey & Gdaniec **comb. nov.** ≡*Dendrocereus* Britton & Rose, Cactaceae (Britton & Rose) 2: 113 (1920) ≡*Cereus* subgenus *Dendrocereus* (Britton & Rose) A.Berger, Kakteen (Berger) vi, 125 (1929).
Type: *Cereus nudiflorus* Engelm. ex C.Wright, Anales Acad. Ci. Med. Habana 6: 98 (1869).

This subgenus contains two closely related taxa which are usually considered to be distinct species (Taylor et al., 2021; Majure et al., 2021). One species, *L. nudiflorus*, is endemic to Cuba and the second, *L. undulosus*, is endemic to Hispaniola and some offshore islands. Both species grow to tree-sized proportions and have large white nocturnal flowers adapted for hawk-moth pollination with a long and narrow hypanthium. The fruits are large, smooth and devoid of spines or hairs.

C. *Leptocereus* subgenus *Neoabbottia* (Britton & Rose) Hoxey & Gdaniec **comb. nov.** ≡*Neoabbottia* Britton & Rose, Smithsonian Misc. Collect. 72, no. 9: 2 (1921) ≡*Cereus* subgenus *Neoabbottia* (Britton & Rose) A.Berger, Kakteen (Berger) vi, 125 (1929).
Type: *Cactus paniculatus* Lam., Encycl. [J. Lamarck et al.] 1(2): 540 (1785).

This subgenus is restricted to Haiti and the Dominican Republic, Puerto Rico and the British Virgin Islands. Only the species from Hispaniola are considered further in this paper. It is characterised by species with variable growth forms, from shrubs with arching and scandent stems to tree-sized plants to 10m tall with well-developed woody trunks. All species, however, have specialised short terminal stems which distinguish them from *Leptocereus* subgenus *Leptocereus*. These terminal stems are usually thinner than typical branches and have a large number of closely spaced felted areoles and usually lack spines. We refer to this structure as a flowering brachyblast in this paper because it can be compared with the cephalium found in other genera of cacti which are specialised flowering stems. However, unlike genera which flower exclusively from cephalia, flowering in *Leptocereus* subgenus *Neoabbottia* is not restricted to the brachyblast structures and can also occur from areoles on typical growth near the stem apex. The flowers are nocturnal, opening after dusk and remaining open until the early morning. They are funnel-form or tubular-shaped to 60mm long and pollinated by moths and butterflies (Areces-Mallea, 2003).

1. *Leptocereus undulosus* (DC.) D.Barrios & Majure, Pl. Syst. Evol. 306(3, 63): 12 (2020) ≡*Cereus undulosus* DC., Prodr. [A. P. de Candolle] 3: 467 (1828) ≡*Cactus undulosus* (DC.) Kostel., Allg. Med.-Pharm. Fl. 4: 1393 (1835) ≡*Dendrocereus undulosus* (DC.) Britton & Rose, J. New York Bot. Gard. 26: 220 (1925) ≡*Acanthocereus undulosus* (DC.) Croizat, Caldasia 2(7): 137 (1943).
Lectotype (designated by Barrios et al. 2020: 12): HAITI. Near Port-de-Paix, abundant at the place that is called Le Moustique [Baie des Moustiques]. Illustration in Burman (1755–1760: fasc. 8. 187. t. 194.), reproduced here as Figure 11.
Epitype (designated by Barrios et al. 2020): HAITI. Department Nord-Ouest: Jean Rabel Road, vicinity of Cabaret, Baie des Moustiques, plain west of Cabaret, 12–18 January 1929, *Leonard & Leonard* 12085 (NY 03305544).

Plant tree-like to 10m tall with a well-developed woody trunk to 2–6m tall and 0.5m in diameter with occasional spine clusters. Branches are also woody with age and similar to the trunk, but a

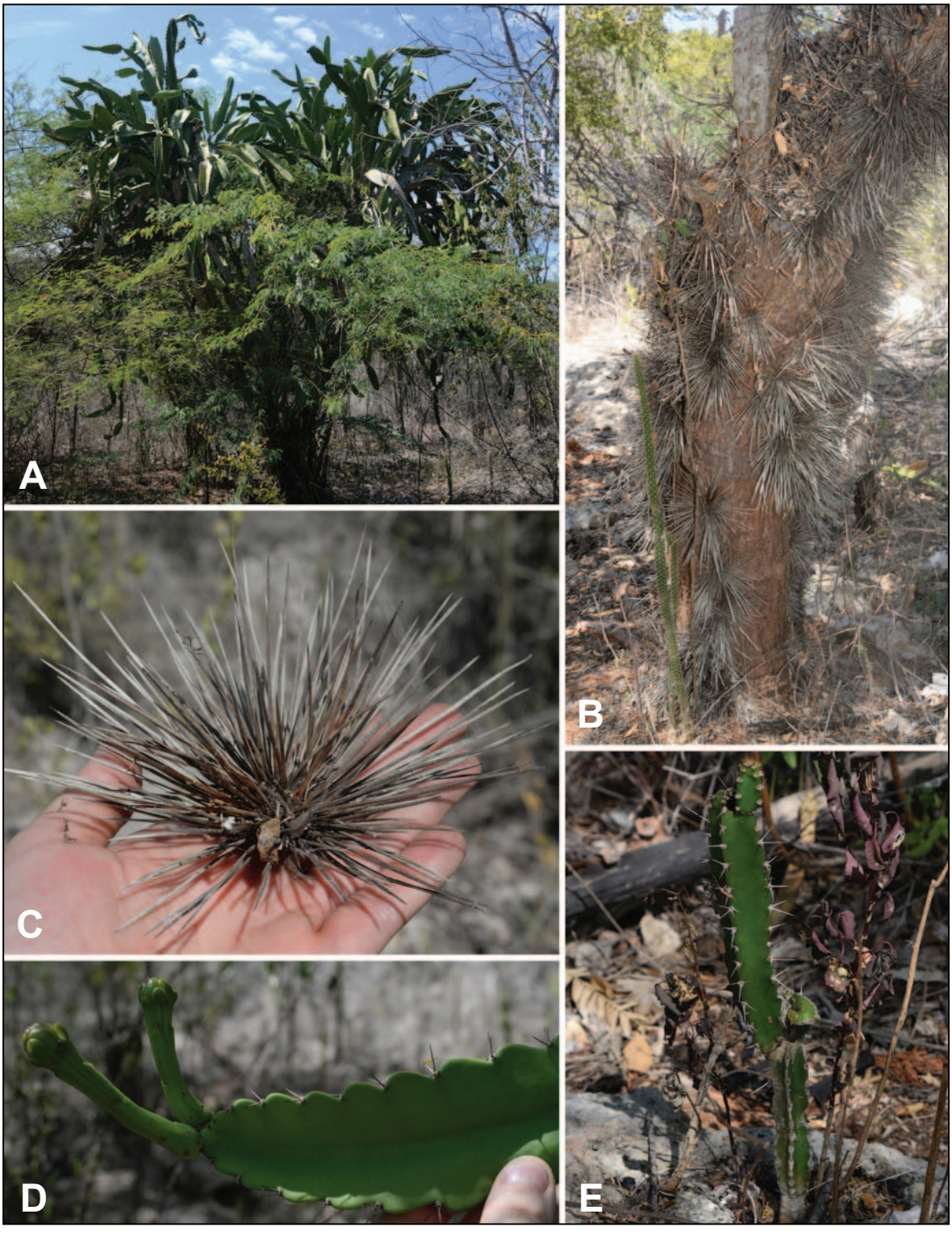


Figure 15. *Leptocereus undulosus* DOMINICAN REPUBLIC. Prov. Puerto Plata. Cabo Isabella, west of Luperón, 50m (*Hoxey* 1840.01). **A–**Mature specimen. **B** to **C–**Densely spined trunk and spine cluster. **D–**Stem segment with flower buds. **E–**Young seedling.

little less thick, with a profusely branched crown of many stem-segments. **Ultimate stem-segments** large, bright green with a shiny lustre, to 1m long and 150mm in diameter; *ribs* 3(–4), thin, to 5–8mm thick, 40–80mm tall, heavily crenate margins with 5–10mm difference due to undulations; *areoles* ovoid 2–3mm long and 4–6mm wide, white felt, situated within the lower part of the rib undulations, spacing 30–40mm; *spines* 0–3, variable length, to 20mm long but usually much shorter, pale grey with a darker tip, straight, acicular. **Terminal brachyblasts** occasionally form at the apex of the stem but are often absent, 15mm in diameter at the base, to 30mm long, tapering at the apex, with several closely spaced areoles, spineless. Epidermis initially green, later woody and brown. Often further stems can grow from the apex of the brachyblast giving a segmented appearance. **Flower** nocturnal, narrowly tubular, 150–200mm long. Cut surfaces of flowers start to discolour a few minutes after exposure to air and turn black within two hours; *pericarpel* 15mm long and wide, green, smooth, with a few tiny scales and felted areoles; *hypanthium* 120–150mm long and 15mm wide, 4mm thick, green, slightly ribbed with a few tiny scales and areoles towards the base; *nectar chamber* 30mm long and 8mm wide; *style* 150mm long and 4mm in diameter, cream-coloured; *stigma lobes*, 10–12, to 10mm long; *stamens* numerous, 40mm long white; *anthers* 1mm, cream; *outer perianth segments*, recurved at anthesis, numbering about 16, 30–50mm long and 10mm wide, slightly fleshy, reddish-green; *inner perianth segments* white, numbering about 20, 50mm long and 10mm wide, pointed apex. **Fruit** approximately globular to 80mm in diameter, sometimes with a well-developed appendage to 40–50mm long derived from the hypanthium surrounding the nectar chamber; *pericarp* smooth, very firm flesh 12–15mm thick, with very few scattered areoles without spines, green but eventually turning yellow in advanced maturity. Seeds contained within a very mucilaginous pulp with strong strands of fibrous funicles. **Seed** broadly oval, flattened, 2.8–3.2 × 2.0–2.5 × 1.2–1.5mm, matt black-brown; *testa* with large (20µm wide) high-domed cells. Cells on the hilum-micropylar border are smaller (5µm wide) and flat; *hilum* 1.5 × 1.0mm, oblique, edge brown.

Distribution and habitat: *Leptocereus undulosus* is widely distributed in Hispaniola and is found in both Haiti and the Dominican Republic. However, it is not endemic to the island and is recorded from the Haitian islands of Île de la Tortue (Ekman, 1928: 43) and Île de la Gonâve (Ekman, 1930: 49 and Majure et al., 2021: 32). Populations are noted to be widely scattered and usually small with a low number of individuals. The species favours seasonally dry forests and will reach large dimensions in undisturbed habitats with mature trees. It is also found where the forest has been degraded due to human activities and without tree cover. In such habitats, specimens are often much smaller in size. In Haiti we found plants to the west of Port-de-Paix (Figure 12), the type locality and in the far south-west of the country inland from Anse-à-Pitre (Figure 13), a locality first reported by Ekman (Werdermann, 1931: 236). In the Dominican Republic, the species is found relatively frequently in the dry forest between Pedernales and Oviedo in the south-west of the country. We know of several localities in this area and it appears to be the most important stronghold of this species and, where the largest specimens are encountered (Figure 14). We also know of a small population from just south of Barahona and a very interesting locality on the north coast of the Dominican Republic near Luperón (Figure 15). This is isolated from all other known localities by about 200 kilometres. *L. undulosus* has been reported from the south-east of the Dominican Republic in the area around Bayahíbe (Fleming, 1984) and La Romana (Werdermann, 1931: 236). We failed to find specimens in this region although Fleming illustrates plants on the road to Bayahíbe. They are not there today and, regrettably, are lost to land clearance and development, but we suspect plants will be found in more inaccessible localities in the area.

Discussion: *Leptocereus undulosus* has a fragmentary distribution with populations containing small numbers of individuals. Juvenile plants are rarely encountered and it appears that seedling recruitment is poor. An identical situation is also found in Cuba with *L. nudiflorus*. We have found fruits on *L. undulosus* at several localities so pollination and production of seed is not an issue. The fruit of *L. undulosus* is large with a very thick pericarp (Figure 13E). We have found examples rotting underneath mature plants (Figure 6A). It seems likely that, for successful germination, the fruit needs to be eaten and seeds passed through the gut of an animal. This process releases the seeds from the thick pericarp, disperses them from direct competition with the mother plant and perhaps removes germination inhibitors. As already discussed, *Cyclura cornuta* is likely to be the only dispersal vector now present, mirroring the situation in Cuba with *Cyclura nubila* (Barrios & Mancina, 2017) but perhaps other animals were historically involved which are now extinct (for example Giant Tortoises, *Chelonoidis* species).

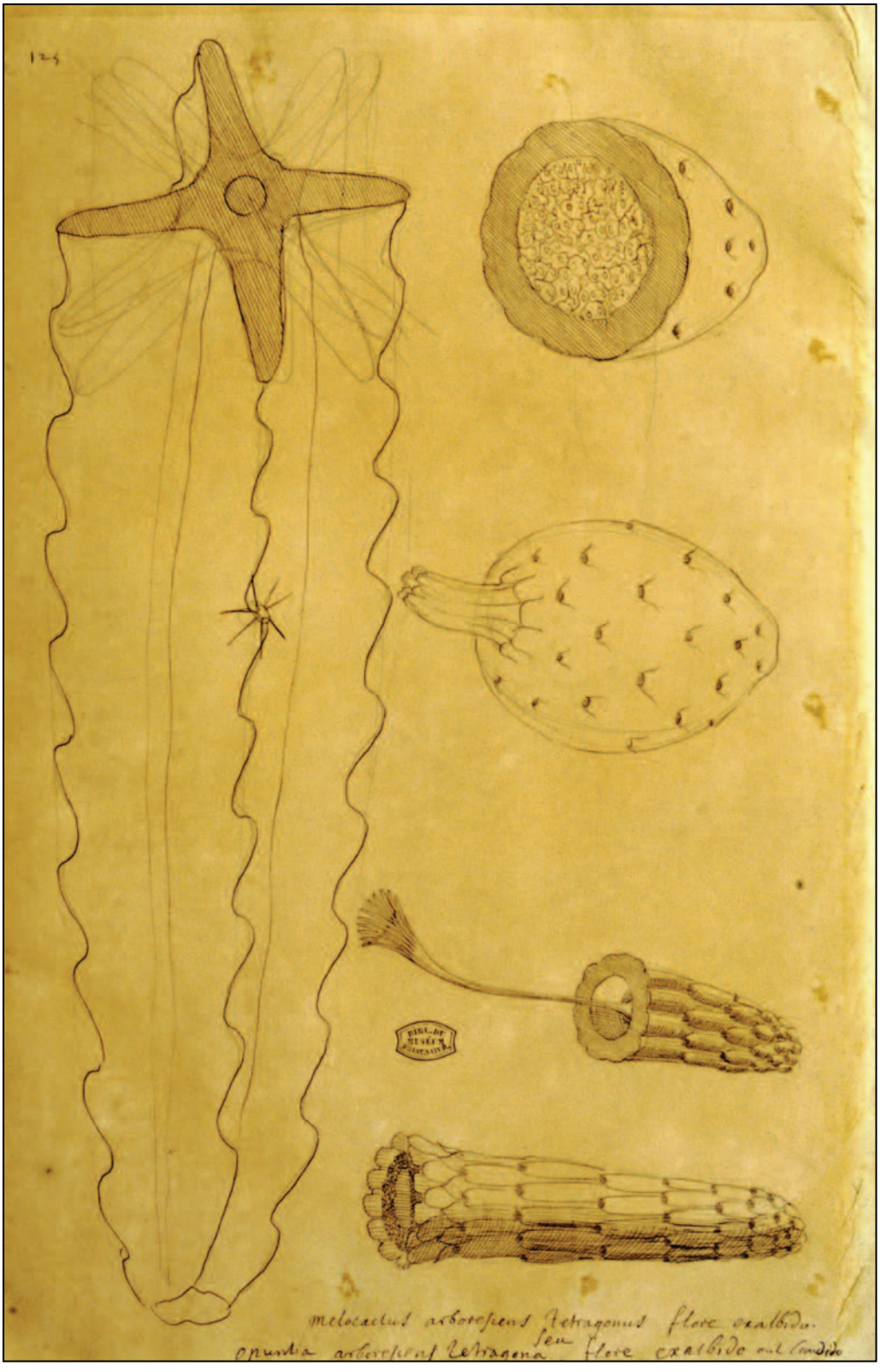


Figure 16. The lectotype of *Leptocereus paniculatus* (≡*Cactus paniculatus*) from Plumier (1689–1697: Volume 3. t.21). Image scan Roy Mottram.

Perhaps *L. undulosus* is more dependent on these extinct animals than other *Leptocereus* species which all appear to be successfully reproducing today. Very occasionally we have observed fallen stems rooting (Figure 14B) and possibly asexual reproduction is the principal method of propagation occurring today.

Leptocereus undulosus is known from two offshore islands (Île de la Gonâve and Île de la Tortue) which is interesting considering the fruits have not evolved to be attractive to birds so long-distance dispersal is unlikely. Plants may have reached the islands during the Last Glacial Maximum, 20,000–26,500 years ago, when sea levels were about 125m below those of the present day and both islands were attached to Hispaniola. Another possibility is *L. undulosus* reached the islands through lizards or other animals carrying seeds in their digestive system. It has been reported that lizards can be carried on mats of vegetation between islands after hurricanes (Censky 1998).

Iconography: Britton & Rose (1925: 218, unnumbered photograph) as *Dendrocereus undulosus*. Fleming (1984: Figures 8–9) as *Dendrocereus undulosus*. Mauseth et al. (1998: Figure 2) as *Dendrocereus arboreus*. Lodé (2015: 484, three unnumbered photographs) as *Dendrocereus undulosus*. Mottram & Hoxey (2020: Figure 37) as *Dendrocereus undulosus*. Majure et al. (2021: Figure 7), Taylor et al. (2021: Figures 4–8 and 14).

Additional specimens examined: DOMINICAN REPUBLIC. Province Barahona: Sierra de Bahoruco, *c*.0.8 kilometres north of Playa Azul, Barahona, 10m, 13 May 2019, *Majure* 7812 (FLAS 272922). **Province La Altagracia:** Between Bayahíbe and Presa Chavón, 20m, 30 March 1981, *Zanoni* et al. 12076 (JBSD 22412). **Province Pedernales:** Between Pedernales and Oviedo, 150m, 24–27 June 1975, *Liogier & Liogier* 23339 (JBSD 05794). Oviedo, Paraje Tres Charcos, Parque Nacional Jaragua, 138m, 3 February 2016, *Majure* 5974 (DES 00080347, DES 00080348, FLAS 272921, JBSD 127057). Parque Nacional Jaragua, south-west of Manuel Goya and Carretera 44, about 14.6 kilometres west of Oviedo, 245m, 16 November 2016, *Majure* 6586 (JBSD 128253). On the road to Las Mercedes, from Pedernales, 2.5 kilometres from the junction, 1 May 1998, *Villardebó* s.n. (JBSD 92114, BSD 92109). North of Cabo Rojo, 100m, 12 January 2022, *Hoxey & Gdaniec* 100 (GIB). **HAITI.** *Buch* s.n. (NY 03305542) **Department de l'Ouest:** Massif de la Selle, group Morne des Commissaires, Anse-à-Pitre, limestone cliff at Río Pedernales, on the road to Banane, 25 October 1926, *Ekman* H6730 (NY 03305545). **Department de Nord-Ouest:** Coastal terrace between Môle Saint Nicholas and Jean Rabel, 19 January 1995, *Areces* 6790 (NY 00948348). Between Port-de-Paix and Moustique, 1924, *Buch* s.n. (NY 01495730, NY 03305543).

2. *Leptocereus paniculatus* (Lam.) D.R.Hunt, Bradleya 9: 89 (1991): (1991) ≡*Cactus paniculatus* Lam., Encycl. [J. Lamarck & al.] 1(2): 540 (1785) ≡*Cereus paniculatus* (Lam.) DC., Prodr. [A. P. de Candolle] 3: 466 (1828) ≡*Neoabbottia paniculata* (Lam.) Britton & Rose, Smithsonian Misc. Collect. 72(9): 3 (1921).

Lectotype (designated by Mottram 2002: 90): HAITI. Le Cul de Sac. Illustration in Plumier (1689–1697): Vol. 3. t.21, reproduced here in Figure 16.

Epitype (designated by Barrios & Majure 2022: 223): HAITI. Department de l'Ouest: Vicinity of Étang Saumâtre, 4–12 April 1920, *Leonard* 3500 ([on two sheets] NY 01495801 and NY 01495802; isoepitypes: US 00176830 and *US* 00176831).

=*Neoabbottia paniculata* var. *humbertii* Backeb., Cact. Succ. J. (Los Angeles) 27: 53 (1955).

Lectotype (designated here): DOMINICAN REPUBLIC. The precise locality is unknown but reported to be 'Villa'. Photograph Backeberg (1955: 50, Figure 27P) of a stem with a flower. The lectotype illustration is also reproduced at a larger size in Backeberg (1958–1962: Figure 1885).

Plant tree-like 6–10m tall with a well-developed woody trunk 2–4m tall and 300–400mm in diameter, woody with brown bark, sometimes without spines but, when present, they appear as large spine clusters with robust spines to 50–10mm long which emerge from large areoles 12mm in diameter. Branches also woody with age and similar to the trunk but a little less thick. **Ultimate stem segments** grey-green, 0.3–0.5m long and 60–100mm in diameter; *ribs* 4–6, 20–30mm tall, 10–15mm wide at the base, tapering to rounded apex 5mm across; *crenate margins*, about 2–3mm difference, top to bottom; *areoles* ovoid 3mm tall and 4mm wide, white felt, situated within the lower part of the rib undulations, spacing 20–25mm; *spines* 15–25(–30), variable length, 5–20(–30)mm long, brownish-yellow when young, ash grey with age, straight, acicular, spreading, radials and centrals weakly differentiated. **Terminal brachyblast** cylindrical, up to 70–80mm long and 20mm in diameter, with many closely spaced areoles, with creamy white felt and spineless, with age becoming woody with the felt only retained on the newest areoles. **Flower** nocturnal, 50mm long and 15mm wide and usually borne singularly

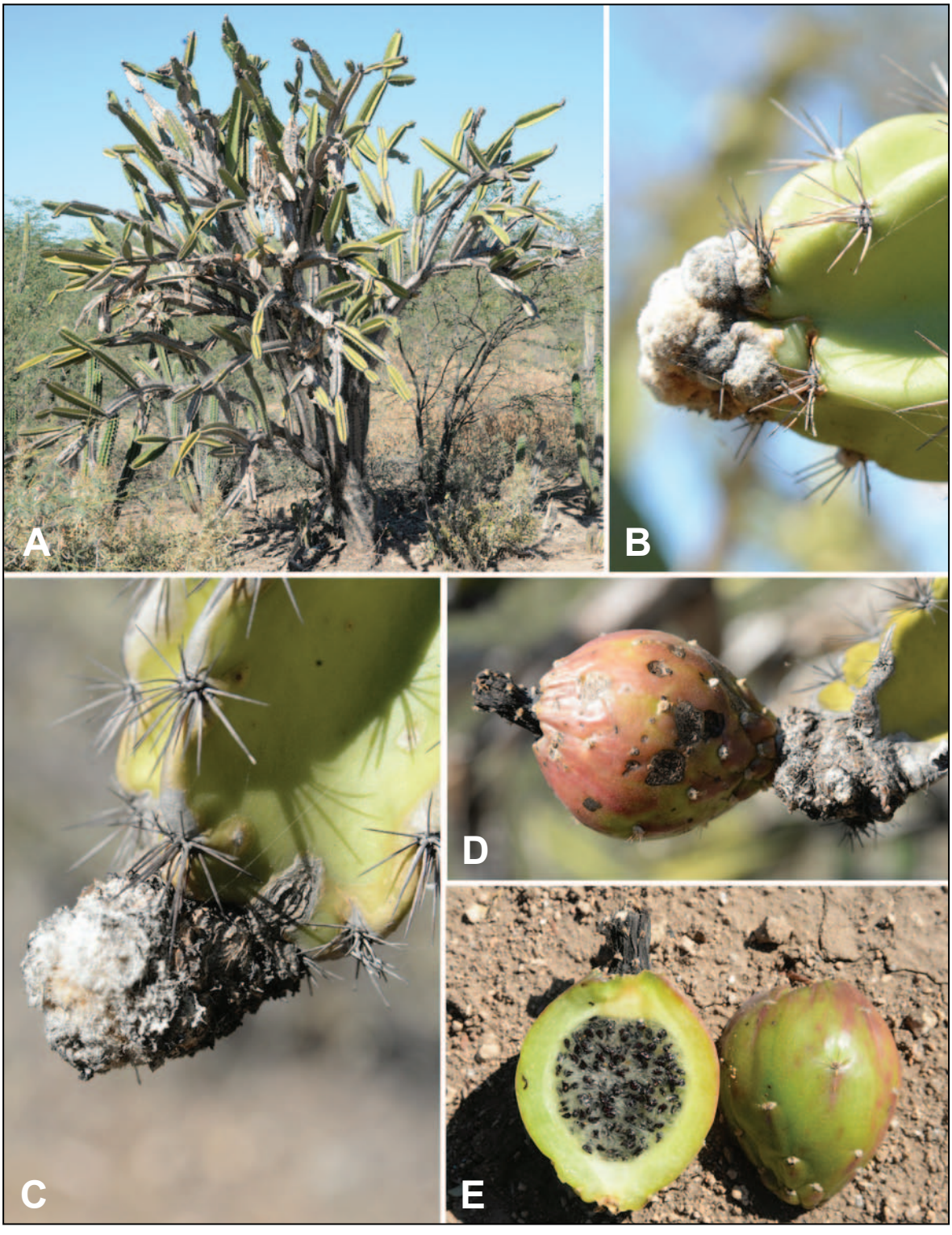


Figure 17. *Leptocereus paniculatus* HAITI. Department Ouest. West side of Étang Saumâtre, north of Ganthier, 40m (*Hoxey* 1308.01). **A–**Mature specimen in partially cleared woodland. **B** to **C–**Well-developed terminal brachyblasts. **D–**Mature weakly spineless fruit emerging from a terminal brachyblast. **E–**Sectioned fruit.

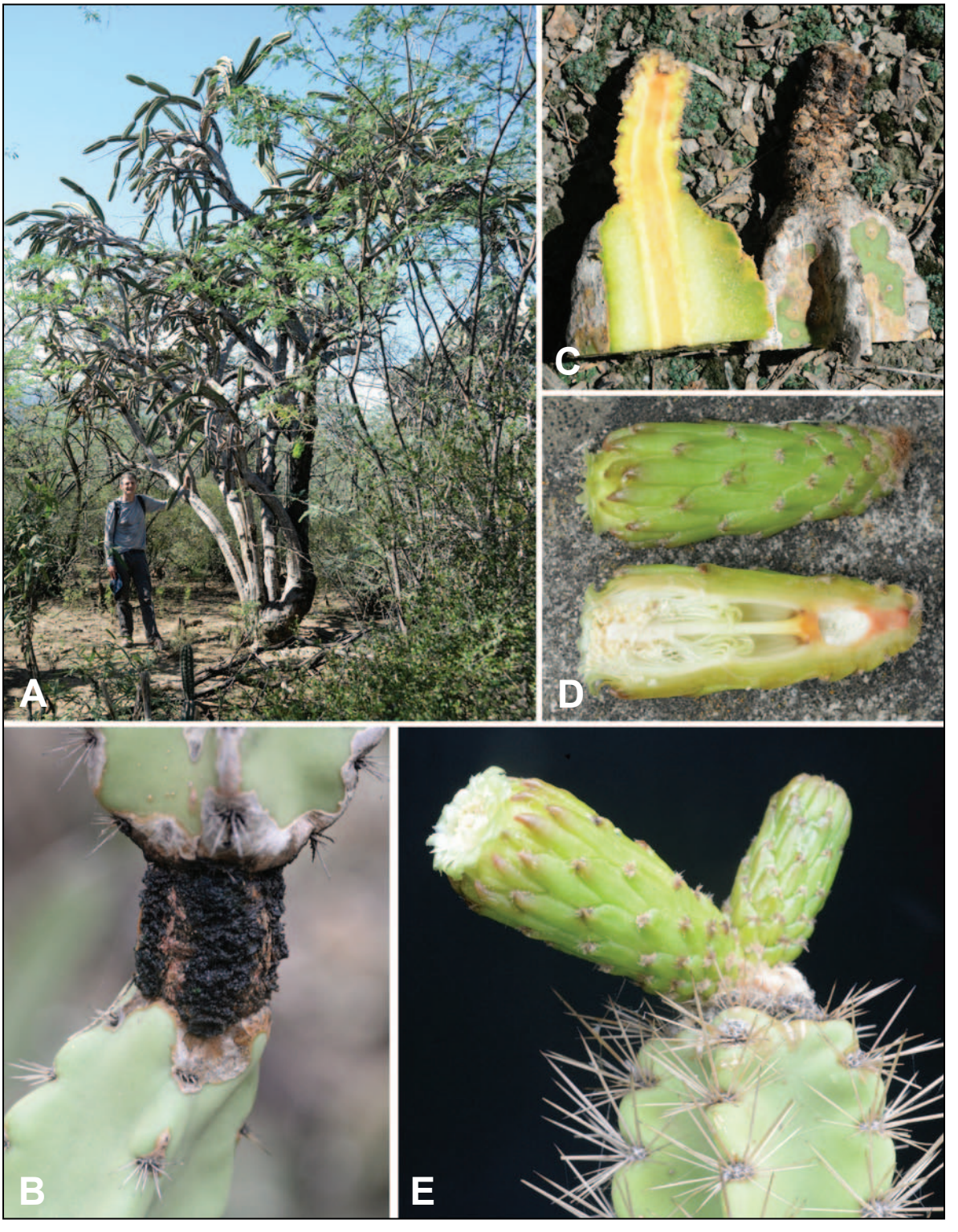


Figure 18. *Leptocereus paniculatus* DOMINICAN REPUBLIC. Vicinity of Lago Enriquillo. 20–220m, **A–**Mature specimen in xerophytic woodland (*Hoxey* 1423.02). **B–**A terminal brachyblast that has reverted to normal stem growth (*Hoxey* 1421.03). **C–**A very long terminal brachyblast, 50mm long (*Hoxey* 1424.02). **D** to **E–**Flower (50mm long) with very short petals and an almost spineless tube (*Hoxey* 1447.01).

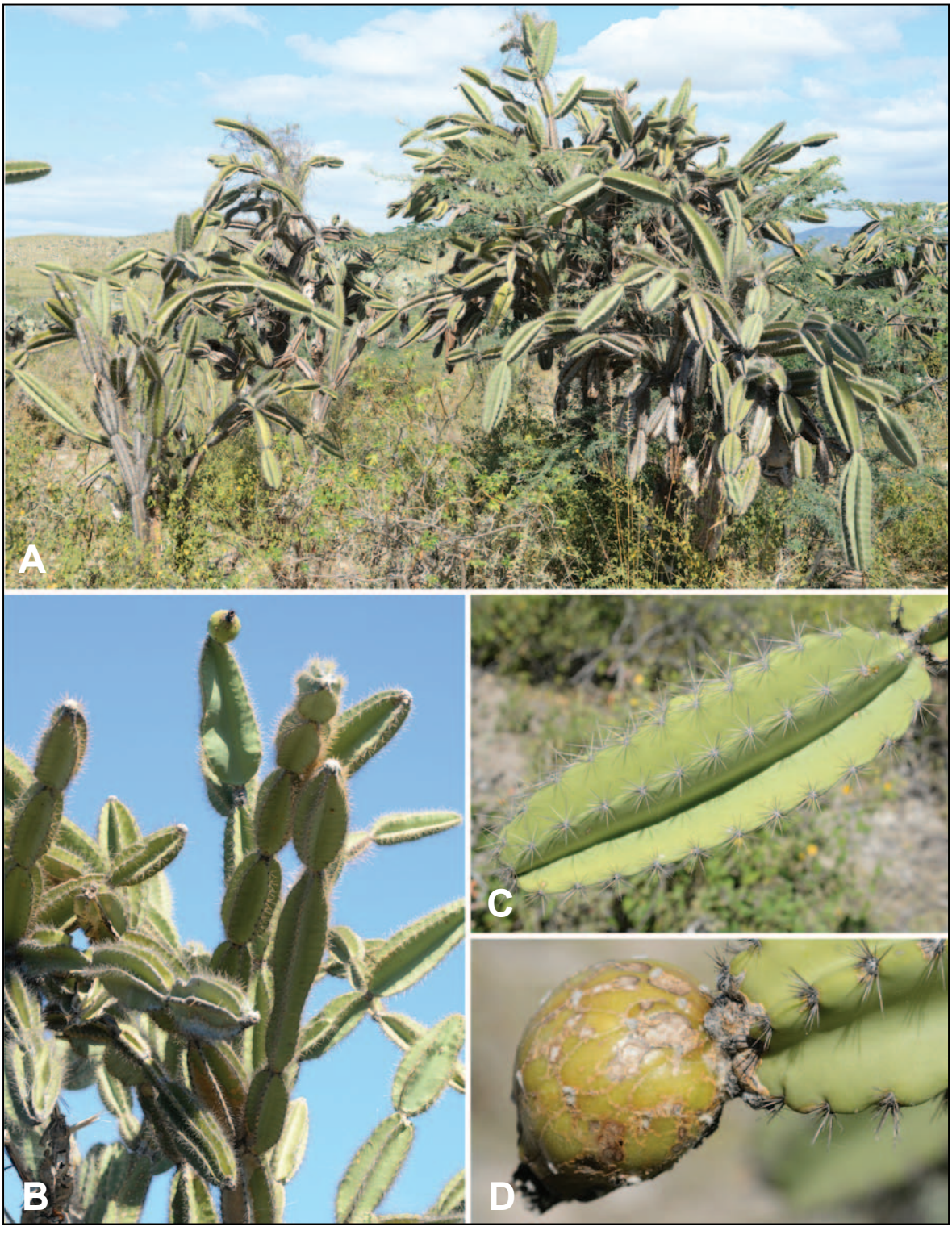


Figure 19. *Leptocereus paniculatus* HAITI. Department L'Artibonite. Petit Port-a-Piment, west of Gonaïves, 20m (*Hoxey* 1289.01). **A** to **B–**Mature specimens in cleared woodland. **C–**Stem segment. **D–**Mature spineless fruit emerging from a terminal brachyblast.

or in small groups (2–4) from the terminal brachyblast; *pericarpel* 18mm long and 12mm wide, green; *hypanthium* 30mm long and 15mm wide at the rim, walls 4mm thick, green, and slightly ribbed; *flower tube* with podaria topped with a very small reddish-green scale and small areole with light brown felt; *areoles* sometimes with 2–3 short, to 2mm long hair-like spines; *nectar chamber* 10mm long and 8mm wide; *style* 22mm long and 1.5mm diameter, white; *stigma lobes* 10–12, to 6mm long; *stamens* numerous, white, 12mm long within the tube, to 4mm long at the rim; *anthers* 1mm, cream; *perianth segments*, recurved at anthesis, whitish-cream, numbering about 20, 6–8mm long and 2–3mm wide. **Fruit** ovoid-globular, 60–70mm long, 50–55mm wide; *pericarp* mostly smooth, but a little tuberculate at both ends, green or reddish-green, very firm flesh to 10mm thick, with a few scattered areoles; *areoles* 2mm in diameter, spacing to 20mm, with white or light brown felt; *spines* up to 8, thin small to 4mm long but sometimes absent; *dried flower remains* stay attached at maturity, black, 15mm long 12mm wide. Seeds contained within a very mucilaginous pulp. **Seed** oval, flattened, 2.2–2.4 × 1.2 × 0.8mm, matt black. Testa with large (10µm wide) high-domed cells with pointed apex (10µm tall); *cells on the hilum-micropylar* border small (5µm wide) and flat; *hilum* 1.0 × 0.3mm, oblique, edge brown.

Distribution and habitat: *Leptocereus paniculatus* is endemic to the island of Hispaniola and is found in Haiti and the Dominican Republic. It is the only species in the genus to grow in a large population with a high density of individuals. The principal area of distribution extends from Port-au-Prince in the west through the Plaine de Cul-de-Sac and continues into the Dominican Republic through the Valle de Neiba to about twenty kilometres west of Azua. This area is characterised by a low elevation, xerophytic, thorny forest of small trees and bushes which almost can be considered a semi-desert. Cacti, of various species, are a conspicuous feature of the habitat. In Haiti, we observed *L. paniculatus* at several localities on the Plaine de Cul-de-Sac (Figure 17) between Port-au-Prince and the Dominican Republic border. Remnants of the thorny woodland exist but most of the woodland has been destroyed for charcoal production. Fortunately, specimens of *L. paniculatus* are often spared because they are unsuitable to make charcoal and plants can still be found in areas where the thorny forest has gone. This does not appear to be detrimental to the adult plants although the lack of nurse plants may limit seedling recruitment. Similar habitats in the Dominican Republic are in much better condition and large areas of the dry forest remain intact. *L. paniculatus* is very plentiful around Lago Enriquillo (Figure 18) and we noted plants from below sea level on the shores of the lake to an elevation of 220m, A single plant we observed at 620m in the Sierra Martín García is anomalous for this species which is otherwise restricted to low elevation. There is a second discrete and much smaller population reported from north-west Haiti (Areces-Mallea, 2003: 474) which we encountered on the coastal road west of Gonaïves, growing in remnants of the dry thorny forest or in open situations (Figure 19). Some charcoal production occurs in the region but there are still areas of natural vegetation remaining.

Discussion: At first sight, *L. paniculatus* appears similar to *L. undulosus* as noted by Britton & Rose (1921: 4). Both reach tree-sized proportions with a crown of numerous branching stems. However, this is due to convergence as the two species are not closely related and belong to different subgenera. The two also have distinct habitat preferences with *L. paniculatus* growing in a much more xerophytic environment within an open thorny forest. *L. paniculatus* is the most easily observed *Leptocereus* species in Hispaniola and exists in larger numbers than any other member of the genus. Britton & Rose (1921) were the first to note that this species produces terminal brachyblasts which they referred to 'as a kind of cephalium'. They are specialised flowering structures that are initially felted and look like a large areole but later can grow to over 50mm long and become woody, lacking felt, by which point they must be of some considerable age (Figure 18C). Britton & Rose (1921) suggest brachyblasts of 50mm long are twenty years old. Old, woody brachyblasts can appear to be dead but are very much alive and still capable of flowering and fruiting. Sometimes normal growth can resume from the tip of the brachyblast (Figure 18B) which gives the branches the appearance of segmented growth. Flowers appear predominately, but not exclusively, from the brachyblasts. Occasional flowers form on areoles near the apex of branches close to the base of the brachyblast.

Typification of *Neoabbottia paniculata* var. *humbertii*: Backeberg did not designate a type for this name. He states that plants were growing in the Marnier collection but appears to have based his description on plants collected in habitat by Professor Humbert. The locality given by Humbert is 'Villa' and the plant is said to grow in dry places near the coast of Hispaniola. Later, Backeberg (1958–1962: 1956) states that the plant is from

the Dominican Republic. No preserved material is known to exist but all the illustrations included within the protologue, which are annotated with this name, are considered to be original material (Article 9.4) and therefore available for lectotypification. We designate one of these illustrations; a photograph of a stem with a flower, as the lectotype.

Iconography: Britton & Rose (1921: Figures 1–2 and Plates 2–4) as *Neoabbottia paniculata*. Marshall et al. (1941: Figure 50) as *Neoabbottia paniculata*. Backeberg (1955: Figures 27K–L, 27R and 28S–V) as *Neoabbottia paniculata*. Backeberg (1955: 50–52, Figures 27J and 27M–Q) as *Neoabbottia paniculata* var. *humbertii*. Backeberg (1958–1962: Figures 1874–1881 and Tafel 165A) as *Neoabbottia paniculata*. Backeberg (1958–1962: Figures 1882–1885 and Tafel 165B–166) as *Neoabbottia paniculata* var. *humbertii*. Reppenhagen (1979: 19, unnumbered photograph) as *Neoabbottia paniculata*. Leuenberger (1984: 104–105, four unnumbered photographs) as *Neoabbottia paniculata*. Fleming (1984: Figures 1 and 15) as *Neoabbottia paniculata*. García & Castillo (1994: Figures 1–2) as *Neoabbottia paniculata*. Mauseth et al. (1998: Figures 13–14) as *Neoabbottia paniculata*. Barthlott & Hunt (2000: Plates 8.3 and 8.4), seed SEM. Anderson (2001: 393, unnumbered photograph). Hunt et al. (2006b: Figures 17.3 and 17.4). Lodé (2015: 638, two unnumbered photographs). Mottram & Hoxey (2020: Figure 40). Majure et al. (2021: Figure 6). Taylor et al. (2021: Figure 1).

Additional specimens examined: DOMINICAN REPUBLIC. **Province Barahona.** Barahona, 1913, *Fuertes 13.19* (NY 01495819, NY 01496028, NY 01496033). Sierra Martín García, approx 1.5 kilometres south of Higuito, 120m, 16 December 1995, *García* et al. 6119 (F 2052519, MO 5156653). Sierra Martín García, *c.*0.6 kilometres al north-east of the Cruce Vicente Noble, 108m, 13 November 2016, *Majure* 6581 (DES 00082208, DES 00082209, JBSD 128192). Lower slopes of the Sierra Martín García, 150m, 14 January 2022, *Hoxey & Gdaniec* 116 (GIB). **Province Independencia.** Sierra de Neiba, Ángel Félix, 400m, 24–26 March 1975, *Liogier* et al. 22786 (JBSD 005312). El Limón, 8 January 1995, *Areces-Malla* s.n. (NY 00948307, NY 00948335, NY 00948357). Sierra de Bahoruco, south of Lago Enriquillo, to the west *c.*15 kilometres de Duvergé, 5 February 2016, *Majure* 6003 (DES 00080346, FLAS 272917, JBSD 127091). Just south of Laguna del Rincón, 104m, 13 May 2019, *Majure* 7817 (FLAS 272918). Sierra de Bahoruco, *c.*1.5 kilometres to the east of El Limón, 13 May 2019, *Majure* 7840 (FLAS 272919). 2 kilometres west of Postrer Río, 20m, 9 January 2022, *Hoxey & Gdaniec* 97 (GIB). **HAITI. Department de l'Ouest.** Vicinity of Étang Saumâtre, 4–12 April 1920, *Leonard* 3500 (NY 01495796, NY 01495801, NY 01495802, US). Vicinity of Étang Saumâtre, 4–12 April 1920, *Leonard* 3500a-b (NY 01495798). Vicinity of Étang Saumâtre, 4–12 April 1920, *Leonard* 5344 (NY 01495800). Vicinity of Petionville, 350m, 15–28 June 1920, *Leonard 5326* (NY 01495816). Vicinity of Port-au-Prince, December 1920, *Pilkington* s.n. (NY 01495803, U 0244824).

3. *Leptocereus demissus* Areces, Cact. Succ. J. (Los Angeles) 89(3): 118 (2017) ≡*Neoabbottia demissa* (Areces) Guiggi, Cactology 5 (Suppl. 12): 2 (2021).
Type: DOMINICAN REPUBLIC. Province Pedernales: 10 kilometres south-east of Cabo Rojo on limestone terraces of maritime origin in dry forest, 22 December 1998, *Areces* 6812 (Holotype: JBSD; Isotypes: NY, HAJB, HNT).
Lectotype (designated by Guiggi 2020: 3): Photograph in Areces-Mallea (2017: 118, Figure 6) captioned 'Blooming stem-tip of the type collection of *Leptocereus demissus*'.
Epitype (designated by Barrios & Majure 2022: 221): DOMINICAN REPUBLIC. Province Pedernales. 5 kilometres west of Oviedo, 50m, 20 June 1977, *Liogier & Liogier* 26729 (JBSD 010283; isoepitype: NY 01495815).

Plant usually a sprawling shrub with arching and trailing stems reaching 1–2m tall, above that often requires the support of the surrounding vegetation but the largest plants to 3–4m tall with a woody, often spineless trunk to 50mm in diameter. **Ultimate stem segments** grey-green, 0.3–3m long and 15–20mm in diameter. Branch tips that touch the ground can root and form new branches; *ribs* (5–)6(–7), 3–6mm tall, 3–5mm wide at the base, tapering to rounded apex 2mm across; *rib margins* usually straight or sometimes slightly dentate; *areoles* round 2–3mm in diameter, felt brown but with age turning grey, spacing 10–15mm; *spines* 15–25, 10–20mm long, brownish-yellow when young, ash grey with age, straight, acicular, spreading. Central spines are weakly differentiated from radials but a little thicker. **Terminal brachyblast** rudimentary and undifferentiated from the stem except the last few millimetres of the stems turn brown and become a little woody in age. Spines are still present although a little shorter than typical for normal growth. **Flower** (from protologue) nocturnal, 50–65mm long and 30–46mm wide, usually borne singularly or in small groups (2–3) from the apex of the stem;

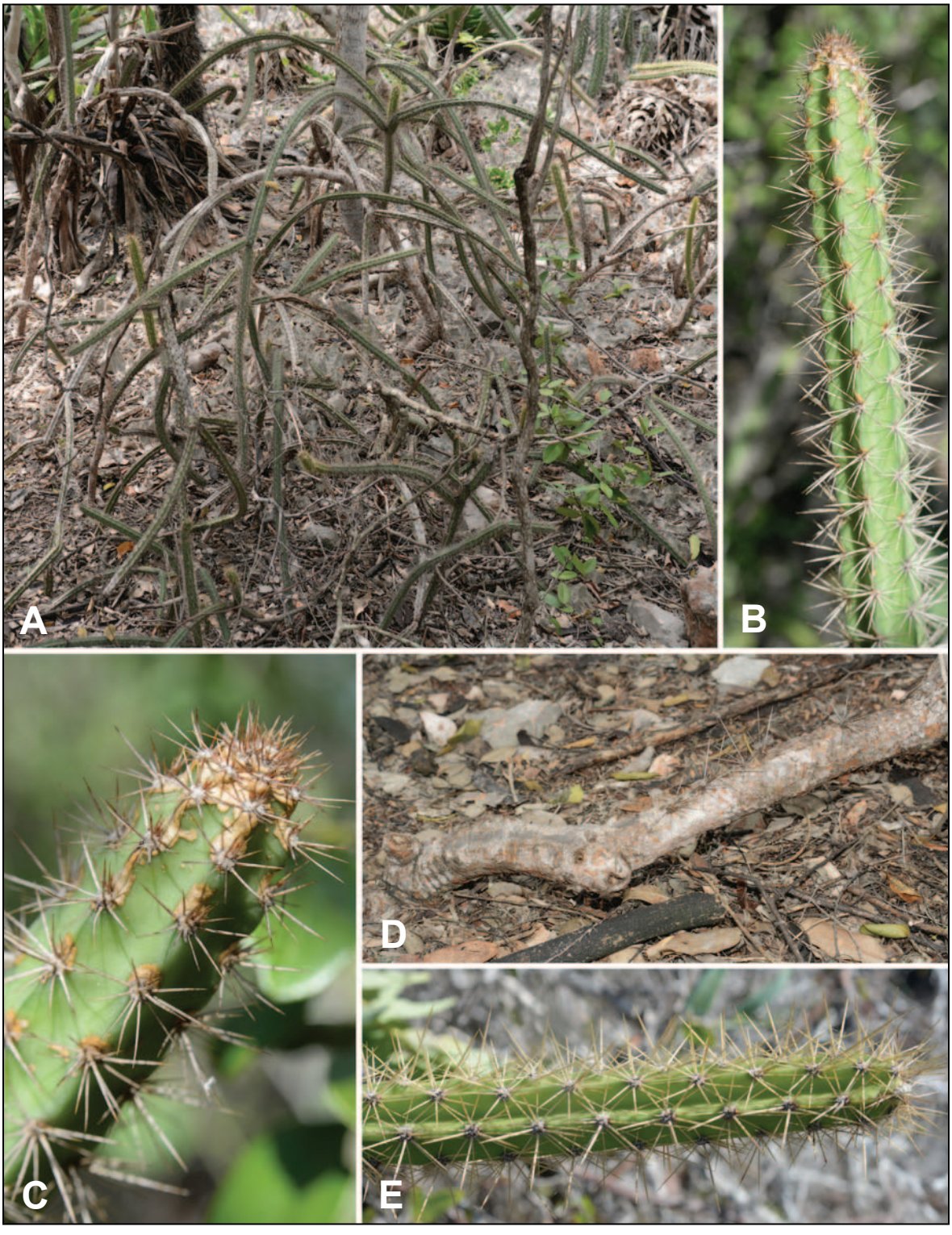


Figure 20. *Leptocereus demissus* DOMINICAN REPUBLIC. Province Pedernales. West of Pedernales, 100m (*Hoxey* 1865.01). **A–**Typical plant with arching and trailing stems. **B** to **C–**Stem with rudimentary terminal brachyblast. **D–** Thin woody trunk. **E–**Close up of stem and spination.

Figure 21. *Leptocereus demissus* DOMINICAN REPUBLIC. Province Pedernales. West of Oviedo, 150m (*Hoxey* 1956.01). **A–**Mature specimen with numerous branches. **B–**Stem segment with terminal brachyblast. **C–**Ripe fruit with a plum-red pericarp and strong spination.

Figure 22. *Leptocereus demissus* DOMINICAN REPUBLIC. Province Pedernales. Path to Trudillé, south-west of Oviedo, 150–190m (*Hoxey* 1956.01). **A** to **B–**Large growing plants reaching 4m tall with numerous branches. **C–**Stem and ripe fruit with a plum-red pericarp.

receptacle-tube obconical in shape, gradually expands without constrictions to 25–28mm wide at the rim, green; *areoles* rounded, 2–2.5mm, spaced 8–11mm, yellowish-brown felt; *spines* 7–17, 4–11mm long, straight, acicular, brownish; *nectar chamber* oblong, 8.6–9mm long and 5.5–10mm wide; *style* 34–37mm long and 1–2mm diameter, white; *stigma lobes* 9–10, 6–9mm long; *stamens* numerous, white, 7–15mm long; *anthers* 1mm long, cream; *perianth segments* recurved at anthesis. **Fruit** ovoid-globular 55–65mm long, 45–50mm wide; *pericarp* smooth, epidermis plum-red, sometimes a little ribbed towards the apex with persistent areoles. Flesh very firm, 10mm thick, lime green; *areoles* 2mm in diameter, dark brown felt, 15–20mm spacing; *spines* 18–20–(30), 5–10–(15)mm long, straight, stiff, unequal lengths, light brown. Seeds are contained within a very mucilaginous pulp. **Seed** ovoid, slightly flattened, 2.2–2.6 × 1.3 × 1.0mm, matt black, slightly rugose; *testa* with large (10µm wide) high-domed cells with partially pointed apex; *cells on the hilum-micropylar border* small (5µm wide) and flat; *hilum* 1.0 × 0.3mm, oblique, edge brown.

Distribution and habitat: *Leptocereus demissus* is of restricted distribution and only known with certainty from the Bahoruco Peninsula, east and south-east of Pedernales in the extreme south-west of the Dominican Republic, growing on coral limestone in a xerophytic woodland. We know *L. demissus* from several small scattered populations growing up to an elevation of 220m although one population on the trail from Los Tres Charcos, west of Oviedo to the coastal village of Trudillé is very extensive with many plants which extend almost to the coast. The distribution inland is restricted by less arid conditions where *L. demissus* is replaced by *L. velozianus*. The distribution of *L. demissus* extends right up to the Haitian border (we encountered it within 500m of the frontier) so the species may also grow there. Nevertheless, to date, it has not been reported from Haiti.

Discussion: When we first encountered *L. demissus* at various localities near the highway from Oviedo to Pedernales (Figures 20–21) we invariably found plants growing underneath trees or bushes producing thin sprawling stems which are incapable of supporting themselves to any height without external help. More recently we have discovered a large population of plants, as mentioned above, on the path to Trudillé (Figure 22). These plants grow to much bigger proportions forming bushes to 3m tall with large numbers of self-supporting stems. The stems are slightly thicker than found elsewhere and the larger plants form a small woody trunk to 50mm in diameter. The above description of the plants takes into account this population and hence differs a little from that of the protologue.

Leptocereus demissus appears to be shy to flower and we have never observed flowers nor buds in habitat and only found occasional fruits. We noted that drooping stems, when they touch the ground, will root and produce new shoots. If the original stem later dies, then a new plant is formed. We wonder if this is the principal method of reproduction and that populations consist of a single or a small number of clones. Perhaps this explains the poor fruit production or lack of evidence of flowering which may only occur sporadically during favourable climatic conditions. We noted fully mature fruits turn a plum-red colour (Figures 21C and 22C) and that green pigment is absent. This fruit colour is unique for *Leptocereus* species in Hispaniola and is in disagreement with the protologue (Areces, 2017: 121). Perhaps this is a variable character in this species or Areces did not have fully mature fruits available for study.

Plants reported from near Oviedo (*Majure* 5972) are considered to be *L. demissus* (Majure et al., 2021: 27). The illustrations (Majure et al., 2021: Figure 5) show a plant with a deep green epidermis, 4 or possibly 5 ribs, crenate rib margins, and 12–15 spines. All these characteristics conflict with *L. demissus* which has grey-green stems, 6–7 ribs, straight or slightly dentate rib margins, and a higher spine count. We do not believe these plants are *L. demissus* and they have been misidentified. Majure et al. (2021: 20–21) conclude that *L. demissus* can have straight or crenate rib margins but we disagree. All *L. demissus* we know have straight or slightly dentate ribs margins. Based on a comparison of the stem, seed and seedling morphology (Figure 3–4) of plants found near Oviedo with other *Leptocereus* species we believe they are better classified as *L. velozianus*. Unfortunately, Majure et al. (2021) use this misidentified collection from Oviedo as the only sample of *L. demissus* in a molecular study and concludes this species has a close relationship with *L. velozianus*.

Typification of *Leptocereus demissus*: We could not find the holotype at JBSD and the herbarium staff were not aware of its existence (pers. comm. in February 2018). Majure et al. (2021: 221) and Barrios & Majure (2022) also report that neither the holotype nor any of the isotypes could be found. The lectotype designated by Guiggi (2020: 1) is original material as defined by Article 9.4(b) and stands as the type unless the holotype comes to light.

The epitype designation by Barrios & Majure (2022: 221) is said by the authors to have been made 'for the species name to tie it with a physical specimen' but an epitype is intended to be as an interpretative type when the type is 'demonstrably ambiguous and cannot be critically identified for purposes of the precise application of the name to a taxon.' (Article 9.9). Contrary to Article 9B.2 the authors do not state in what way the lectotype is ambiguous such that epitypification is necessary. The epitype specimen selected originates in an area where *L. demissus* and *L. velozianus* grow in close proximity and possibly the epitype may not represent the same taxon as the lectotype. We have only observed *L. velozianus* within five kilometres of Oviedo, the stated locality of the epitype, and know *L. demissus* from approximately ten kilometres from Oviedo. Careful examination of the epitype specimen is required to determine its affinity.

Iconography: Hunt et al. (2006b: Figures 19.4 and 19.5) as *L. weingartianus*. Areces-Mallea (2017: Figures 4 and 7–9).

Additional specimens examined: DOMINICAN REPUBLIC. Province Pedernales: Cabo Rojo, near the point No. 7 of the Concession, *Veloz* et al. 945 (JBSD 92113). 18 kilometres from Oviedo on the road to Pedernales, 1 May 1998, *Villardebó* s.n. (JBSD 92110). North west of Manuel Golla, 150m, 10 January 2022, *Hoxey & Gdaniec* 109 (GIB). North west of Manuel Golla, 150m, 10 January 2022, *Hoxey & Gdaniec* 110 (GIB). Path to Trudillé, 150–200m, 13 January 2022, *Hoxey & Gdaniec* 111 (GIB).

4. *Leptocereus velozianus* Clase, Y.Encarn., Peguero & Majure, PhytoKeys 172: 23 (2021) ≡*Neoabbottia veloziana* (Clase, Y.Encarn., Peguero & Majure) Guiggi, Cactology 5 (Suppl. 12): 2 (2021).

Type: DOMINICAN REPUBLIC. Province Independencia: Sierra de Bahoruco, Parque Nacional Sierra de Bahoruco, Puerto Escondido, Rabo de Gato, 433m, 14 May 2019, *Majure* 7843 (Holotype: JBSD, Isotype: FLAS).

Plant forms a small tree 2–4m tall with a well-defined woody trunk 1–2m tall and 60–80(–100)mm in diameter, with scattered spines or spineless. Branches are generally sparse, self-supporting, occasionally upright but usually pendent. **Ultimate stem segments** shiny green, to 0.4–1m long and 20–30(–35)mm in diameter; *ribs* 4–5, thin, 10–12mm tall, 2–4mm wide; *rib margins* strongly crenate, 3–4(–5)mm difference between upper and lower undulations; *areoles* round, 3mm in diameter, felt brown but with age turning grey, spacing 15–20(–25)mm, situated in the lowest part of the rib between crenations; *spines* 10–15, 12–25mm long, straight, acicular, brown-grey or grey with darker tip plus two shorter thinner parallel spines at the base of the areole 4–6mm long. The radial and central spines are weakly differentiated. **Terminal brachyblast** small (below 5mm in diameter) felted region later woody at the apex of the stem. **Flower (**from protologue) nocturnal, *c*.76mm; *hypanthium* oblong in shape, and spiny; *spines* c.4, c.8mm long; *nectar chamber* 8mm wide; *style* c.30mm long; *stigma lobes* 8, pale green; *stamens* numerous, white, 13–15mm long; *perianth segments* greenish-white. **Fruit** ovoid-globular 55mm long, 45mm wide; *pericarp* smooth, but a little ribbed towards the apex, yellowish-green, 8mm thick with very firm flesh; *areoles* persistent (firmly attached), 2mm in diameter, dark brown felt, 15–20mm spacing; *spines* 12–18, 5–10mm long, straight, brown. Seeds are contained within a very mucilaginous pulp. **Seed** ovoid, slightly flattened, 3.2–3.4 × 1.8–2.0 × 1.2–1.4mm, matt black; *testa* with large (15μm wide) medium-domed cells with rounded apex; *cells on the hilum-micropylar border* small (5μm wide) and flat; *hilum* 1.3 × 0.7mm, oblique.

Distribution and habitat: *Leptocereus velozianus* is reported from the dry seasonal forest of the northern slopes of the Sierra de Bahoruco (Majure et al., 2021: 24). Unlike most species of *Leptocereus* in Hispaniola, except for *L. weingartianus,* this species is not restricted to low elevations. We can extend the elevational range given in the prologue slightly to 90–450m from our observations. We have found the species at four localities to the north of the Sierra de Bahoruco, two of which are illustrated in Figures 23–24. At one of these, we found it growing sympatrically with *L. paniculatus* and at another (Figure 2A) it grows with *L. weingartianus*. Another population (Figure 25) that we assign to this species is from south of the Sierra de Bahoruco, near Oviedo, which other authors have included in *L. demissus* as outlined in the entry for *L. demissus.* All these populations consist of relatively low numbers of individuals that are widely scattered. We found plants close to Jimaní on the Haitian border and this species may be present in Haiti although, to date, it has not been recorded from there.

Discussion: When we encountered this species in habitat before the publication of the protologue, we thought it was an undescribed taxon because we could not place it with any described species. We note the plants have a shiny green epidermis (Figures 23E and 24C) which is unusual in

Figure 23. *Leptocereus velozianus* DOMINICAN REPUBLIC. Province Independencia. Puerto Escondido, 470m (*Hoxey* 1939.04, close to the type locality). **A** to **B–**Large mature specimen, 4m tall with a trunk 100mm in diameter. **C–**Pendent stem. **D–**Fruit. **E–**Stem segment with crenate rib margins.

Figure 24. *Leptocereus velozianus* DOMINICAN REPUBLIC. Province Independencia. south-west of Jimaní, 150m (*Hoxey* 1941.06). **A** to **B–**A mature specimen in partially cleared woodland. **C–**Stem segment with crenate rim margins.

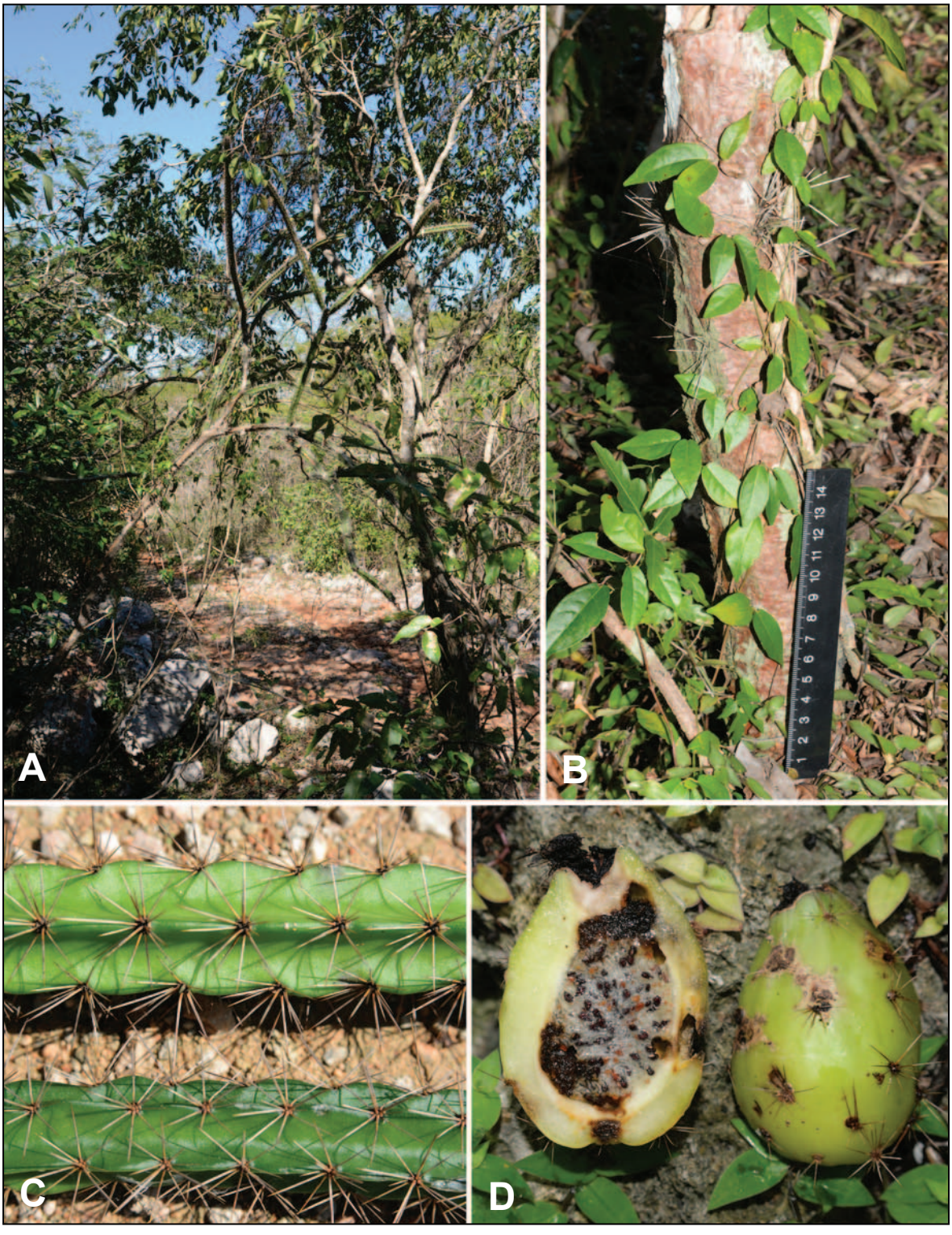


Figure 25. *Leptocereus velozianus* DOMINICAN REPUBLIC. Province Pedernales. Southwest of Los Tres Charcos, west of Oviedo, 100m, **A** to **B–**Mature specimen, 4m tall with trunk 60mm in diameter (*Hoxey* 1946.03). **C–**Stem segments with crenate ribs (*Hoxey* 1426.01). **D–**Fruit, partially parasitised (*Hoxey* 1867.01).

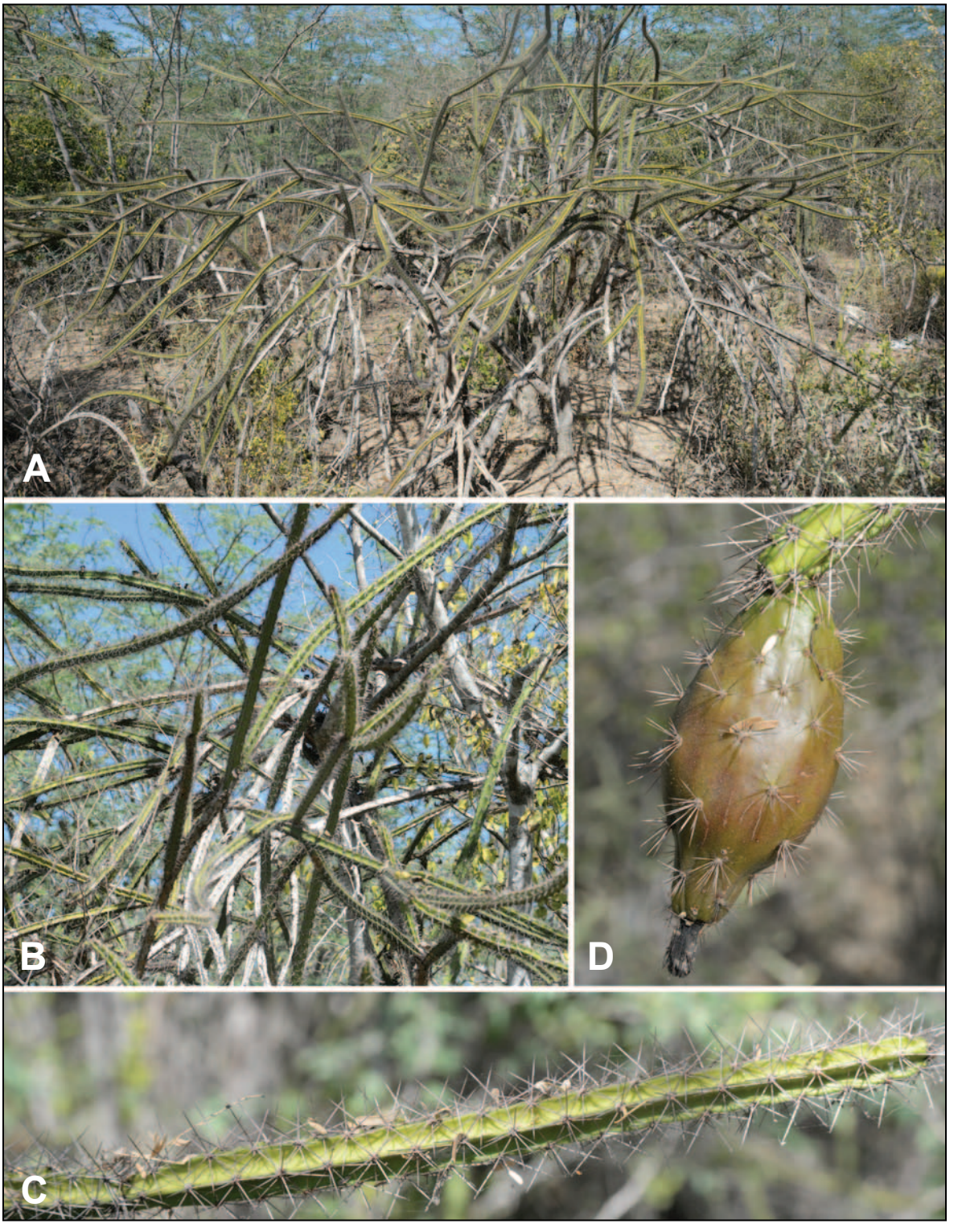


Figure 26. *Leptocereus weingartianus* DOMINICAN REPUBLIC. Province Independencia. East of El Limón, 40m (*Hoxey* 1944.01,). **A** to **B–**Mature specimen with numerous thin stems. **C–**Stem segment with slightly crenate rib margins. **D–**Mature fruit.

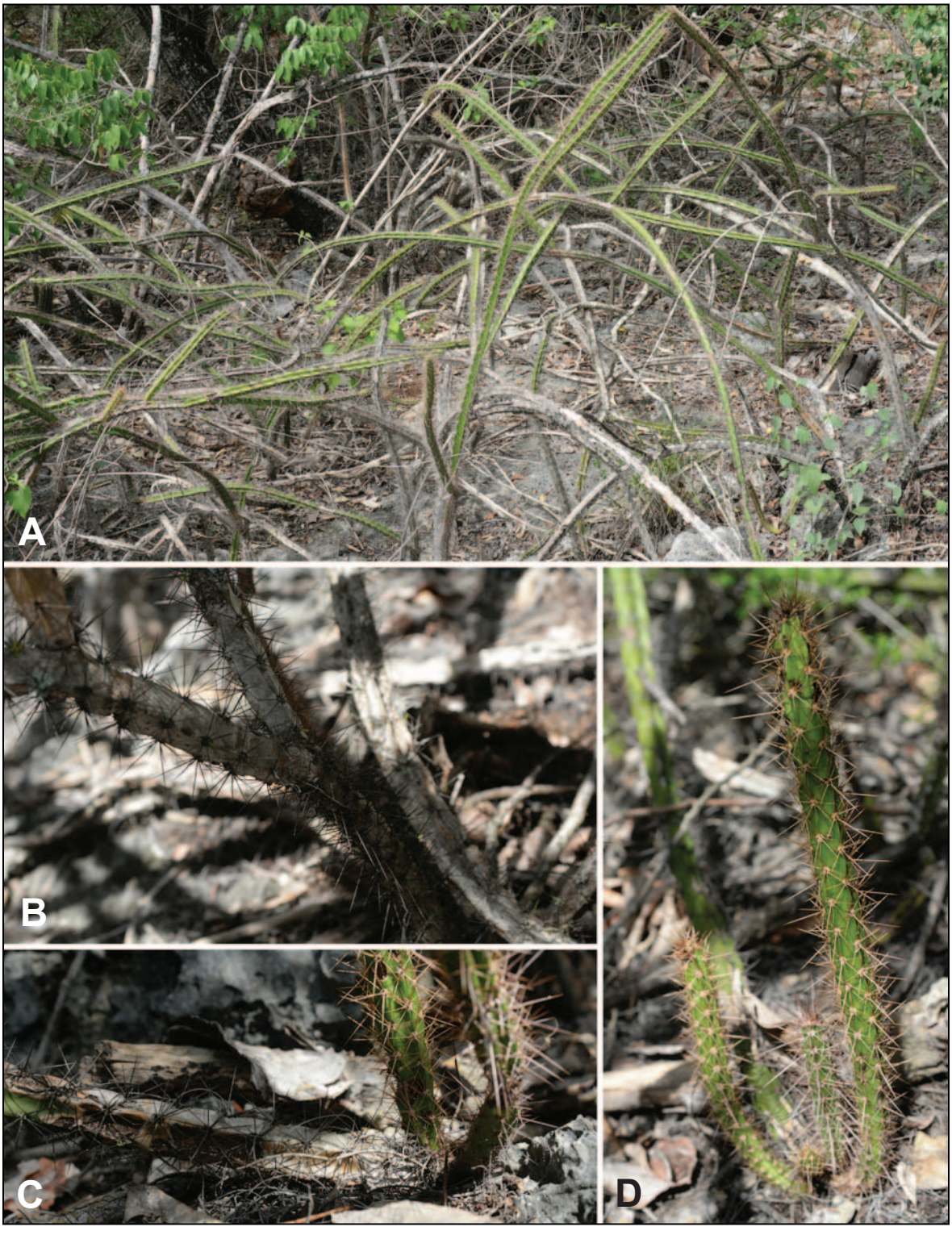


Figure 27. *Leptocereus weingartianus* DOMINICAN REPUBLIC. Province Independencia. Puerto Escondido, 440m (*Hoxey* 1869.01). **A–**Mature specimens with numerous thin stems growing on dogtooth limestone in thin soils. **B–** Thin woody trunk, *c.*50mm in diameter. **C** to **D–**New shoots grow where stems touch the ground and root.

Leptocereus species of Hispaniola. Most species have a grey-green or green epidermis with a matt surface. The only other taxon we found with a similar epidermis is *L. rosei*, a species described in this paper but with straight rib margins and much longer and thinner stems which are not self-supporting.

Iconography: Majure et al. (2021: Figures 2–3), Majure et al. (2021: Figure 5) as *L. demissus*.

Additional specimens examined: DOMINICAN REPUBLIC. Province Independencia. Sierra de Bahoruco, Municipio Duvergé, Puerto Escondido, at a place called Rabo de Gato, on the way to Cañada de Pedro Bello, 26 June 2013, *Clase et al.* 8004 (JBSD 124606). Sierra de Bahoruco, Municipio Duvergé, Puerto Escondido, at a place called Rabo de Gato, on the way to Cañada de Pedro Bello, 400m, 27 July 2017, *Clase et al*. 10202 (JBSD 129859). Sierra de Bahoruco, Municipio Jimaní, going from El Limón, a place called Guzmán, 200–300m, 27 July 2017, *Clase et al.* 10205 (JBSD 129855). 3 kilometres west of El Limón, 100m, 9 January 2022, *Hoxey & Gdaniec* 107 (GIB). **Province Pedernales.** Oviedo, Sierra de Bahoruco, Municipio Oviedo, at a place called Fondo Paradí, Parque Nacional Jaragua, 86m, 3 February 2016, *Majure* 5972 (JBSD 127087). West of Oviedo, 90m, 11 January 2022, *Hoxey & Gdaniec* 107 (GIB).

5. *Leptocereus weingartianus* (E.Hartmann) Britton & Rose, Cactaceae (Britton & Rose) 2: 77 (1920) ≡*Cereus weingartianus* E.Hartmann, Monatsschr. Kakteenk. 14: 155 (1904) ≡*Neoabbottia weingartiana* (E.Hartmann) Guiggi, Cactology 5(Suppl. 9): 3 (2020).
Lectotype (designated by Guiggi 2020: 3): HAITI. Photograph in Hartmann (1904: 155), reproduced here in Figure 30A.
Epitype (designated by Guiggi 2020: 3): HAITI. Petite Gonave Island, 9–10 July 1920, *Leonard* 5256 (NY 00948113).

Plant with long arching stems, supported by other vegetation or drooping when not supported, with a woody trunk, to 1m long and 30–50mm in diameter, usually spiny. Lower branches are also woody to 30mm in diameter. **Ultimate stem segments** 1–2m long and 10–15mm in diameter, epidermis bright green; *ribs* 4–5(–6), 4–6mm high with straight or slightly crenate margins, undulations about 1mm tall; *areoles* circular, 2–3mm in diameter, spacing 12–20mm, felt brown, fading to grey with age, situated in the lower part of the rib crenations; *spines* 10–12(–15), 10–20(–25)mm long, straight, acicular, brown, sometimes two additional shorter spines, 5mm long, thinner, and parallel, emerging from the base of the areole. **Terminal brachyblast** forms at the end of the stem, felted, later woody, up to 10mm long, slightly narrow than the stem, initially with several short weak spines, later absent. **Flower** (based on *Majure* 6464) nocturnal, 50–55mm long and 20mm in diameter, usually borne singly or in small groups (2–4) from the terminal brachyblast or adjacent areoles; *pericarpel* 10mm long and 10mm wide, green; *areoles* 1–2mm in diameter with dark brown felt. Spines 0–4, very short, 2–3mm long; *hypanthium* 30mm long and 15mm wide at the rim, green, and slightly ribbed; *areoles* 2–3mm in diameter with dark brown felt; *spines* about 10, 5–8mm long; *stigma lobes* 8–10; *anthers* 1mm, cream; *perianth segments* whitish-cream, about 30, 8–10mm long and 5–6mm wide. **Fruit** ovoid, 70mm long and 35mm wide, green with a reddish-brown hue, smooth without ribs, apex thinner, elongated and slightly ribbed; *pericarp* 6–8mm thick, seed cavity 45mm long and 20mm wide. Seeds in a mucilaginous pulp; *areoles* 1.5–2mm in diameter, dark brown felt, spacing 10–15mm situated in a slight indentation in fruit, weakly persistent; *spines* 5–10mm long, about 10 in lower areoles and about 15 in upper areoles, straight, acicular, grey-brown, with darker brown tip, not overlapping with spines on adjacent areoles; *dried flower remains* when attached, black, 30mm long with spines, similar to but slightly shorter, than on pericarp. **Seed** oval, slightly flattened, 3.0 × 2.0–2.2 × 1.3mm, matt black; *testa* with large (15–20μm wide) medium-domed cells with rounded apex; *cells on the hilum-micropylar border* small (5μm wide) and flat; *hilum* 1.4 × 0.6mm, oblique.

Distribution and habitat: This species is known from several localities in the vicinity of Lago Enriquillo (Figure 26) and on the northern slopes of the Sierra de Bahoruco (Figure 27). It appears to be a relatively widespread although infrequent species with further populations known from the Sierra Martín García (Figure 28) and Cerro San Francisco (Figure 29A–C). We found a few plants in a sterile condition growing on limestone rocks north of Port-au-Prince (Figure 29D–E) in Haiti which is the closest to the epitype locality that we have observed this species. *L. weingartianus* has a very wide elevational range of 40–800m, the upper value the highest reported for any *Leptocereus* taxon. The species also appears to be unspecialised concerning substrate. Some populations are found on limestone-derived soils in flat terrain, but others are on exposed karstic limestone rocks such as Petite Gonave Island (the epitype locality), coast north of Port-au-Prince

Figure 28. *Leptocereus weingartianus* DOMINICAN REPUBLIC. Province Barahona. Sierra Martín García, 780m (*Hoxey* 1446.01). **A–**The thin stems are supported by the surrounding vegetation. **B** to **A–**cluster of three mature fruits. **C–**Terminal brachyblast. **D–**This population has more pronounced crenations on the rib margins.

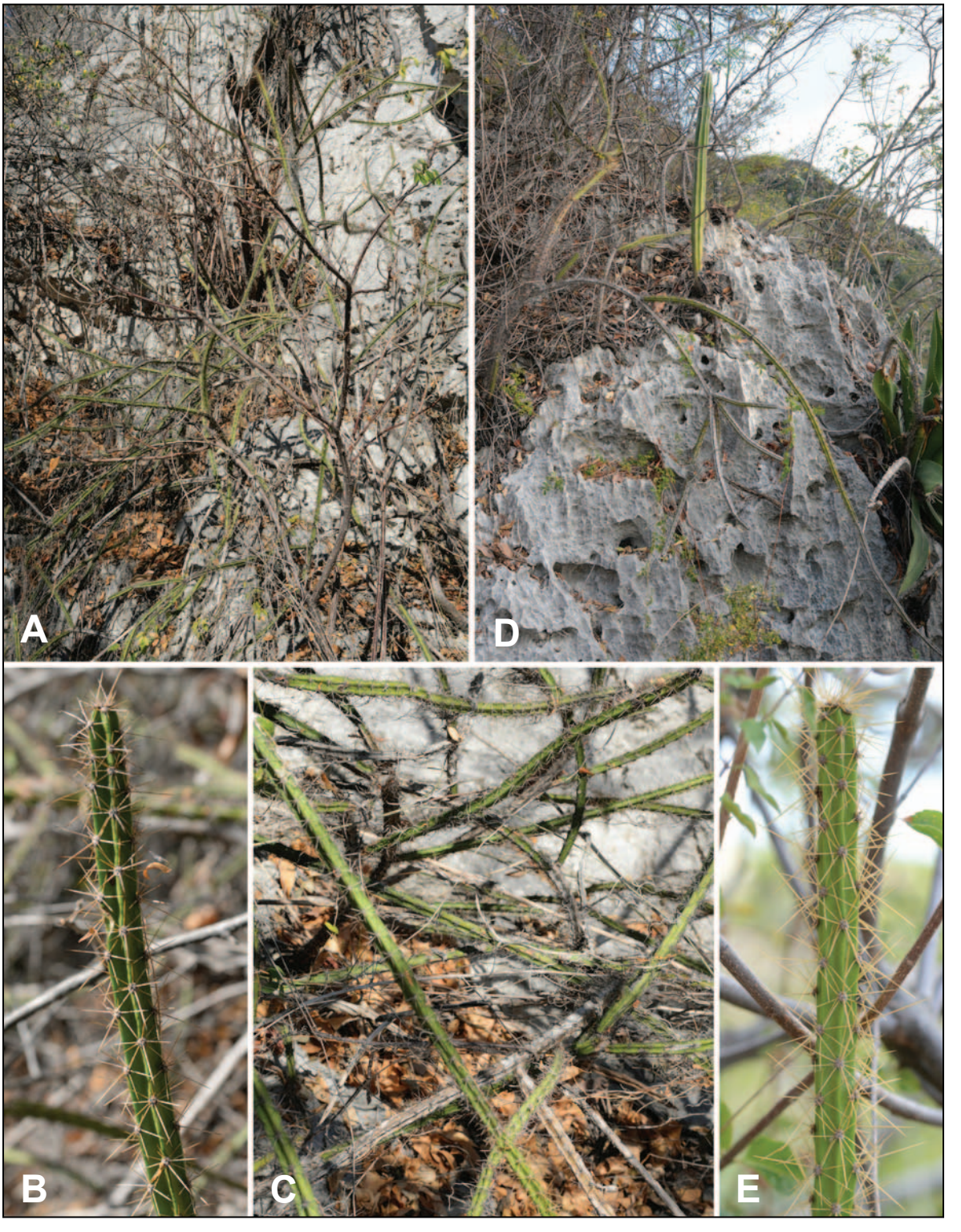


Figure 29. *Leptocereus weingartianus*, populations growing on dogtooth limestone rocks. **A** to **C–**DOMINICAN REPUBLIC. Province Elías Piña. Cerro de San Francisco, Bánica, 410m (*Hoxey* 1934.01). **D** to **E–**HAITI. Department Ouest. Coastal hills north of Port-au-Prince, 300m (*Hoxey* 1280.01).

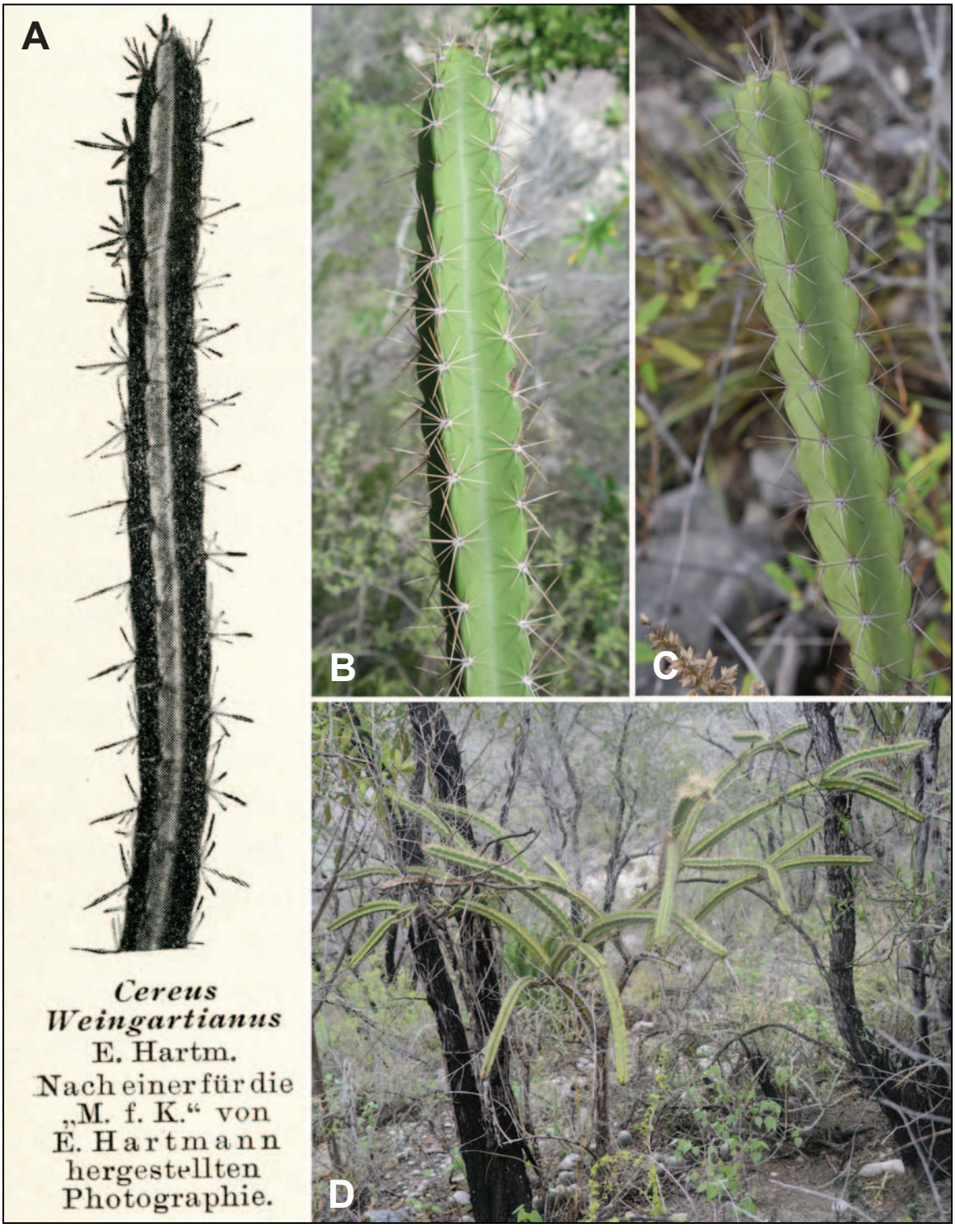


Figure 30. A–Lectotype of *Leptocereus weingartianus* (≡*Cereus weingartianus*) from Hartmann (1904). **B** to **D–** Immature specimens of *Leptocereus paniculatus*. DOMINICAN REPUBLIC. Province Independencia. Above La Descubierta, on the road to Los Pinos, 180m (*Hoxey* 1860.01).

(Haiti) and Cerro San Francisco (Dominican Republic). The surrounding vegetation is usually dry woodland, sometimes well developed with a dense canopy but can be quite sparse and dominated by other xerophytic plants.

Discussion: Typically, we found *L. weingartianus* grows in small discrete populations which consist of a small number of individual specimens even though they can contain a large number of stems. We observed *L. weingartianus* frequently grow roots when the apex of a drooping stem makes contact with the ground (Figure 27C–D) and fresh stems are formed. We have only observed this character in one other Hispaniola *Leptocereus* (*L. demissus*). This may indicate asexual reproduction is commonplace and populations may consist of a single or a small number of clones.

L. weingartianus can look similar to *L. velozianus* but after finding both growing together (Figure 2A) it is clear there are two distinct taxa involved. The plants on the Sierra Martín García are a little different from those elsewhere with more pronounced crenations on the rib margins (Figure 28D). This is a high elevation population which may be the reason for this difference. The plants in this population also had numerous fruits which appear solitary or in a small group (Figure 28B) from areoles close to the apex of the stems or from a terminal brachyblast (these consist of a small brown extension to the stem with a few closely spaced areoles).

Identification of *L. weingartianus*: *Cereus weingartianus* was described from a juvenile plant grown in Germany, raised from imported seed (Hartmann, 1904: 155). The origin of the material is stated to be Haiti and the epithet commemorates Wilhelm Weingart who had been sent plants and a photograph by Hartmann for evaluation. He thought it to be an undescribed species (Weingart, 1905: 6–9) and Hartmann subsequently published the new name in his honour. However, the following year Weingart had second thoughts after comparing the material in his possession with the illustration of *Cereus assurgens,* the type species of the genus *Leptocereus*, in Schumann (1897–1898: Figure 33). He concluded that they were conspecific and thus considered *Cereus weingartianus* a synonym of *Cereus assurgens*. Britton & Rose (1909: 437) list *Cereus weingartianus* as a 'species of unknown generic relationship' and state 'known only from the type plant'. It is only later that Britton & Rose (1920: 77–78) include *Cereus weingartianus* within the genus *Leptocereus.* They came to this conclusion based on material obtained by Rose near Azua (*Rose* 3941) in 1913. Specimens from this collection have four ribs, the same as *L. weingartianus* which may have been the primary reason for Britton & Rose to conclude this material is *Cereus weingartianus.*

Urban (1920–1921: 461) declined to follow Britton & Rose and did not accept the genus *Leptocereus* nor the name *Cereus weingartianus* and continued to use the name *Cereus assurgens* for this Hispaniola plant. Barker & Dardeau (1930: 244) in a flora of Haiti, follow the classification of Britton & Rose with *Leptocereus* accepted as a good genus including one Hispaniola species: *L. weingartianus.* Werdermann (1931: 234) again did not accept the genus *Leptocereus* and was unsure if *Cereus weingartianus* was a distinct species. He had material of the Rose collection but could not satisfy himself if it was different from *Cereus assurgens* and included the Hispaniola plant under that name.

Following Britton & Rose, Moscoso (1941: 78) accepted the genus *Leptocereus* and although he listed *L. weingartianus* he did not consider it distinct from *L. assurgens* because he included *L. assurgens* as a synonym under *L. weingartianus*. This is not permissible because *L. assurgens* is the older name and should have been used instead (Article 11.4). However, two years later, Moscoso (1943: 404) had a change of heart and listed both species separately.

Since the middle of the twentieth century, most authors (for example Backeberg. 1958–1962: 1960; Anderson, 200: 395; Hunt et al., 2006a: 144; Acevedo-Rodríguez & Strong 2012: 1062; Lodé, 2015: 329 and Hunt, 2016: 146) have accepted the genus *Leptocereus* and used the name *L. weingartianus* for a Hispaniola species that is distinct from the Cuban *L. assurgens*. The application of this name has followed Britton & Rose (1920: 77–78) and has been applied to any *Leptocereus* from Hispaniola which was not one of the two tree-sized species: *L. paniculatus* and *L. undulosus*.

Areces-Mallea (2003: 469) was the first to suggest there may be more than one taxon involved under the name *L. weingartianus* with the proposal of a subspecies: *L. weingartianus* subsp. *demissus* which was later published as *L. demissus*. Recently another new name *L. velozianus* appeared, yet the precise identity of *L. weingartianus* has never been satisfactorily resolved. The application of the name by Britton & Rose, based on a single collection from Azua (Dominican Republic), has been followed without any critical analysis. Surprisingly it has never been questioned if the plant found at Azua is the same taxon as the seedling plant in Germany with Haitian origins.

Figure 31. The holotype of *Leptocereus rosei* (*Clase, Sidoti & Possley* 6824, JBSD 123172).

When the name *Cereus weingartianus* was published in 1904 the *Leptocereus* of Hispaniola were unknown botanically. Even the two large growing species, *L. paniculatus* and *L. undulosus*, were only known from the illustrations produced 200 years beforehand by Plumier (1689–1697) and published in Burman (1755–1760). It was not until the 1920s that these species were encountered again in habitat, herbarium material was collected and further information published (Britton & Rose, 1921, 1925).

The type of *Cereus weingartianus* is clearly stated to be a cultivated seedling and we can assume it had yet to reach maturity and had not flowered. Nevertheless, the stem morphology has been compared with mature habitat specimens. Surely it would be beneficial to compare it with seedling plants and in particular with the most commonly encountered *Leptocereus* in Haiti, *L. paniculatus?*

During our observations of *Leptocereus* in Hispaniola, we observed seedlings of *L. paniculatus* at various localities. Unlike all other species of *Leptocereus* on the island, this plant has a wide distribution and is found in large numbers. The species is also reproducing well and seedlings of various sizes can be found relatively easily. As a small seedling, it grows as a single thin upright stem with four ribs in an almost square cross-section. The spination is very weak. When the plant reaches 300–500mm tall the stem becomes thicker, the four ribs become wing-shaped with noticeably more crenate margins. The plant also starts to branch at this size and develops a more robust spination with the lower part of the stem turning woody. Britton & Rose (1921: 4) also noted that a young *L. paniculatus* has four ribs. Although they did not elaborate further, there are clear similarities between the stems and spination of *L. paniculatus* at this age and the lectotype illustration of *Cereus weingartianus*. Table 3 summarises and compares the characteristics from the protologue description of *Cereus weingartianus* and observations of seedling specimens of *L. paniculatus*. Figure 30 reproduces the lectotype illustration together with juvenile stems of *L. paniculatus* from seedlings less than one metre tall.

It is also likely that the seed of *L. paniculatus* would have been collected in Haiti near Port-au-Prince where *L. paniculatus* can still be found today and was probably very common in the early twentieth century. It is one of the dominant species of the dry thorny woodland and cannot be overlooked. Compare this with other species of *Leptocereus* in Haiti which are of restricted distribution, found in much smaller numbers in more remote localities, and are not present in the vicinity of Port-au-Prince. For example, Plumier (1689–1697) failed to record any *Leptocereus* other than *L. paniculatus* in this area although he must have explored extensively at a time when the vegetation was significantly less degraded by human activity. It seems inconceivable that the seed of *L. paniculatus* did not reach Europe before any other, much less accessible, *Leptocereus* species of Haiti. The morphology of juvenile and mature stems of *L. paniculatus* are very different, so it is unsurprising that nobody at the start of the twentieth century could appreciate that the cultivated seedlings were conspecific with the drawing of a tree-sized cactus by Plumier (1689–1697: volume 3. t.21) which at that time was the only known record of *L. paniculatus* in Europe. There is no record of the type material of *Cereus weingartianus* flowering which is consistent with it being *L. paniculatus*, which has to grow to large dimensions to flower. We have never heard of this species flowering in greenhouse cultivation in northern Europe, whereas other *Leptocereus* can flower quite easily and at a relatively young age and small size (Hans Frohning, pers. comm.).

Therefore, we conclude that the type of *L. weingartianus* was a seedling *L. paniculatus*. Interestingly, there is a specimen (NY 01495770) annotated 'Cereus assurgens Gris. K. Sch 140 Kuba, Exemplar von W. Weingart in Oct. 1905'. The 'K.Sch 140' refers to the illustration in Schumann (1897–1898: Figure 33) captioned 'Cereus assurgens'. This specimen consists of some small fragments of stem and a few spine clusters and it is almost certainly material of *Cereus weingartianus* supplied by Weingart which would have originated from the same batch of seeds as the lectotype specimen. However, it cannot be considered original material because it is dated after the publication of the protologue.

Typification of *Leptocereus weingartianus*: Areces-Mallea (2017: 121) designated a neotype for *Cereus weingartianus* (≡*L. weingartianus*) but this is unnecessary because the illustration in the protologue can be considered original material (Article 9.4) and is acceptable as a lectotype. This illustration was designated as the lectotype by Guiggi (2020: 3). Guiggi also designated an epitype but contrary to Rec. 9B.2 he does not state why the holotype is ambiguous such that epitypification is necessary. Unfortunately, the epitype specimen selected by Guiggi consists of several sterile stems. The purpose of an epitype is to allow precise application of the name when the type is ambiguous which this specimen fails to do. It is a *Leptocereus* but we do not believe

Figure 32. *Leptocereus rosei* DOMINICAN REPUBLIC. Province Azua. 2km south of Las Guanábanas, 250m (*Hoxey* 1230.01, close to the type locality). **A–**Long stem segments clamber through vegetation. **B–**Stems hang pendently when not supported. **C–**Mature fruit attached to flowering terminal flowering brachyblast.

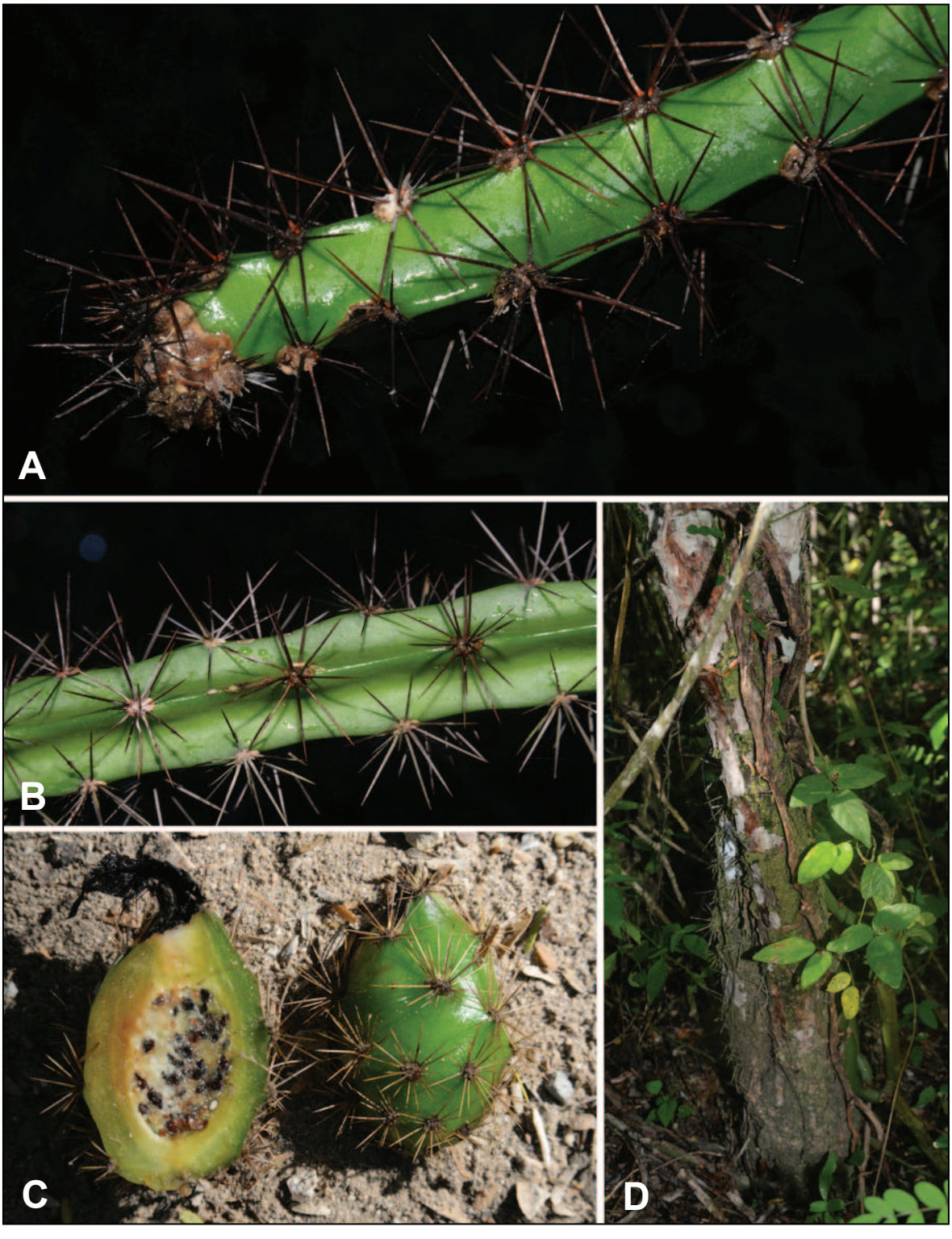


Figure 33. *Leptocereus rosei* DOMINICAN REPUBLIC. Province Azua. 2km south of Las Guanábanas, 250m (*Hoxey* 1930.01, close to the type locality). **A–**Stem with terminal brachyblast. **B–**Stem segment with slightly dentate rib margins. **C–**Sectioned fruit. **D–**Woody trunk, approximately 50mm in diameter.

it is the same taxon as the lectotype (as outlined in the discussion above) yet it appears impossible to challenge or reject it because 'The author who first designates an epitype must be followed' (Article 9.20). It would be extremely useful to visit Petite Gonave Island to examine living and preferably fertile material to understand the precise application of the name *L. weingartianus*. Meanwhile, we follow Majure et al. (2021) and apply the name *L. weingartianus* to the thin-stemmed *Leptocereus* found in central-southern Haiti and the Dominican Republic.

Iconography: Majure et al. (2021: Figures 9A–B and 9E–I).

Additional specimens examined: DOMINICAN REPUBLIC. Province Azua. Sierra Martín García, September 1976, *Liogier* 25277 (*JBSD* 08258). **Province Barahona.** Sierra Martín García, c.0.6 kilometres north-east of Cruce de Vicente Noble, north-east c.11.2 kilometres from Highway 44, 755m, 13 November 2016, *Majure* 6464 (*JBSD* 128219). Parque Nacional Sierra de Bahoruco, Puerto Escondido, Rabo de Gato, 433m, 13 May 2019, *Majure* 7850 (*FLAS* 272925). Sierra Martín García, 780m, 14 January 2022, *Hoxey & Gdaniec* 115 (GIB). **Province Elías Piña.** Cerro San Francisco (south side), outside the town of Bánica south of Pedro Santana, 490m, 14 May 2019, *Majure* 7863 (FLAS 272923). **Province Independencia:** Sierra de Bahoruco, *c.*1.5 kilometres east of El Limón on Highway 46 south of Lago Enriquillo, 43m, 13 May 2019, *Majure* 7839 (*FLAS* 272924). East of El Limón, 40m, 9 January 2022, *Hoxey & Gdaniec* 108 (GIB).

6. *Leptocereus rosei* Hoxey & Gdaniec **sp. nov.**
Type: DOMINICAN REPUBLIC. Province Azua: Municipio Sabana Yegua, towards San Juan, approximately 600m before Las Guanábanas, 241m, 30 July 2011, *Clase, Sidoti & Possley 6824* (Holotype: *JBSD* 123172 annotated as *Leptocereus* and reproduced here as Figure 31).

Plant with long scrambling and scandent stems, supported by other vegetation or drooping when not supported, with a woody trunk, 40–60mm in diameter, usually spiny. Lower branches are also woody to 20mm in diameter. **Ultimate stem segments** to 5m long, thin, 10–15mm in diameter; *ribs* 4(–5), straight or slightly dentate, (never crenate), 6–8mm high; *areoles* 3–4mm in diameter, spacing 15–20mm, felt brown; *spines* 10–12, 12–15mm long, straight, acicular, brown, sometimes two additional shorter spines, 5mm long, weaker, and parallel, emerge from the base of the areole. **Terminal brachyblast** form at the end of the stem, felted, later woody, about 10mm long, initially with several short weak spines but later absent. **Flower** reported to be 40mm long by Britton & Rose (1920: 77). *Spines* (from dried flower remains) c.6, c.6mm long, light brown. **Fruit** elongated ovoid, 55mm long and 30mm wide, bright green, smooth without ribs; *pericarp* 6–8mm thick, seed cavity 30mm, long and 15mm wide. Seeds in a mucilaginous pulp; *areoles* 3mm in diameter, dark brown felt, spacing 15–20mm, formed on a slightly raised part of the fruit; *spines* c.20, 10mm long, straight, acicular, light brown, overlapping with spines on adjacent areoles; *dried flower remains* black, 15mm long, with spines, attachment point 6mm wide, total length 15mm with spines, similar to but slightly shorter than on fruit. **Seed** oval, slightly flattened, large, 3.4 × 2.0–2.2 × 1.4mm, matt black; *testa* crested with large (10–15µm wide) low-domed cells with a rounded apex; *cells on the hilum-micropylar border* small (5µm wide) and flat; *hilum* 1.8 × 0.7mm, oblique, edge brown

Diagnosis: Differs from all other *Leptocereus* subgenus *Neoabbottia* species except *L. weingartianus* by having very thin stems (10–15mm in diameter). The rib margins are straight or slightly dentate and never crenate, a character which is only shared with *L. demissus* but that species has 6–7 ribs (4 or very occasionally 5 ribs for *L. rosei*). The epidermis has a shiny green lustre which is only seen elsewhere in *Leptocereus* subgenus *Neoabbottia* in *L. velozianus* but that species has much thicker (20–30mm compared with 10–15mm in diameter) self-supporting stems. with strongly crenate rib margins. Uniquely *L. rosei* has stems that can reach many metres long (5m+) which are unable to support their own weight and instead rely on surrounding vegetation or are pendant when not supported.

Etymology: The specific epithet '*rosei*' commemorates Dr Joseph Nelson Rose (1862–1928) an American botanist who discovered and made the first collection of this species. He is best known as the co-author of the four-volume work *The Cactaceae* (1919–1923), a monograph of the cactus family written in conjunction with Dr N. L. Britton.

Distribution and habitat: *Leptocereus rosei* is endemic to the Dominican Republic and we only know it from a single site (Figures 32–33), made known to us by the collection *Clase, Sidoti & Possley* 6824 which we designate as the type, approximately fifteen kilometres west of Azua, growing on a non-rocky substrate of sand and clay in seasonally dry woodland. Britton & Rose (1920: 78) also say it was rare and they only knew it from two places near Azua. We searched extensively

Figure 34. The holotype of *Leptocereus bayahibensis* (*Salazar, Peguero & García* 317, JBSD 72719).

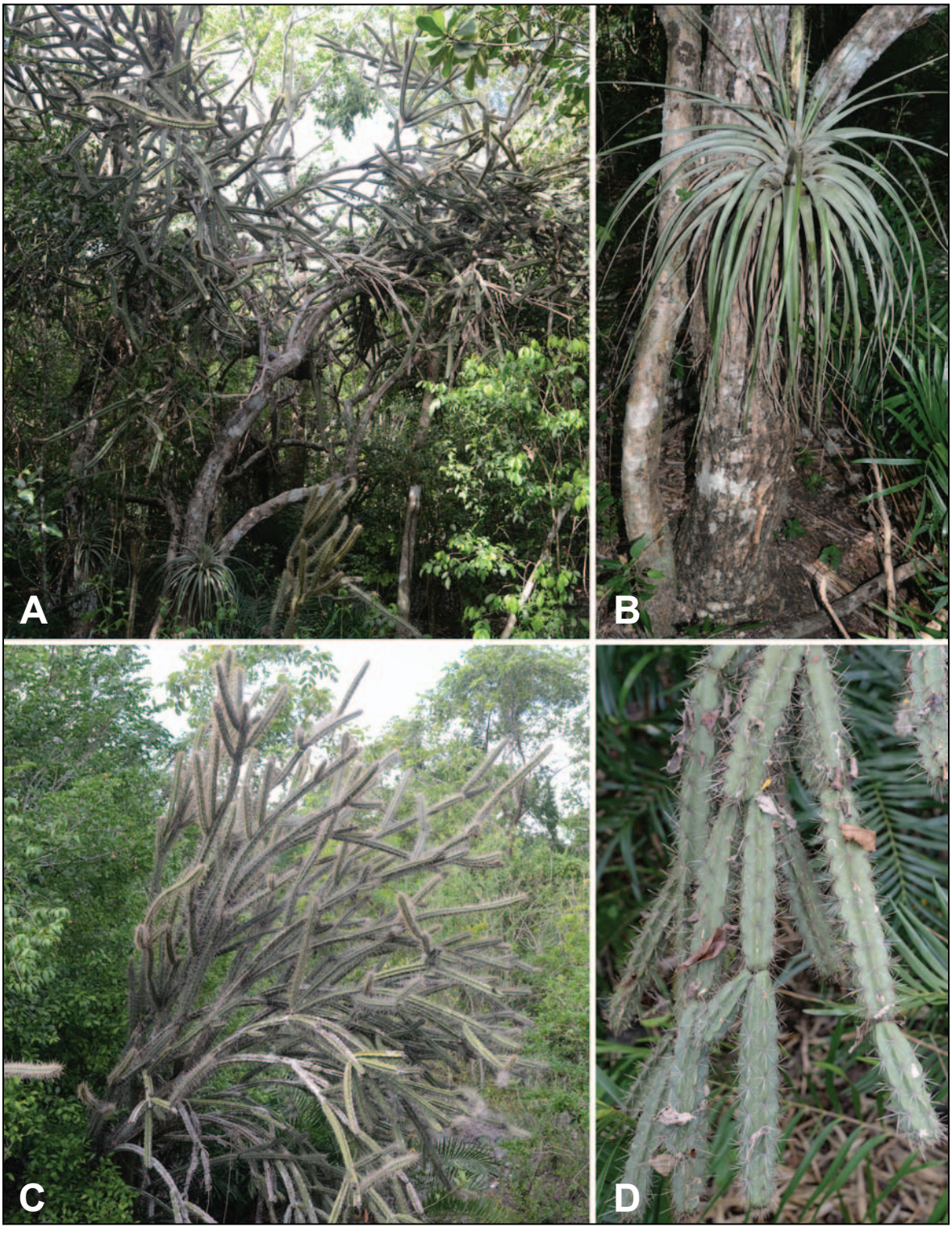


Figure 35. *Leptocereus bayahibensis* DOMINICAN REPUBLIC. Province La Altagracia. North of Bayahíbe, 30m (*Hoxey* 1850.02). **A** to **B–**Large tree-sized specimen, 5m tall with a trunk 200mm in diameter. **C–**A bushy specimen. **D–**Stem segments hang pendently.

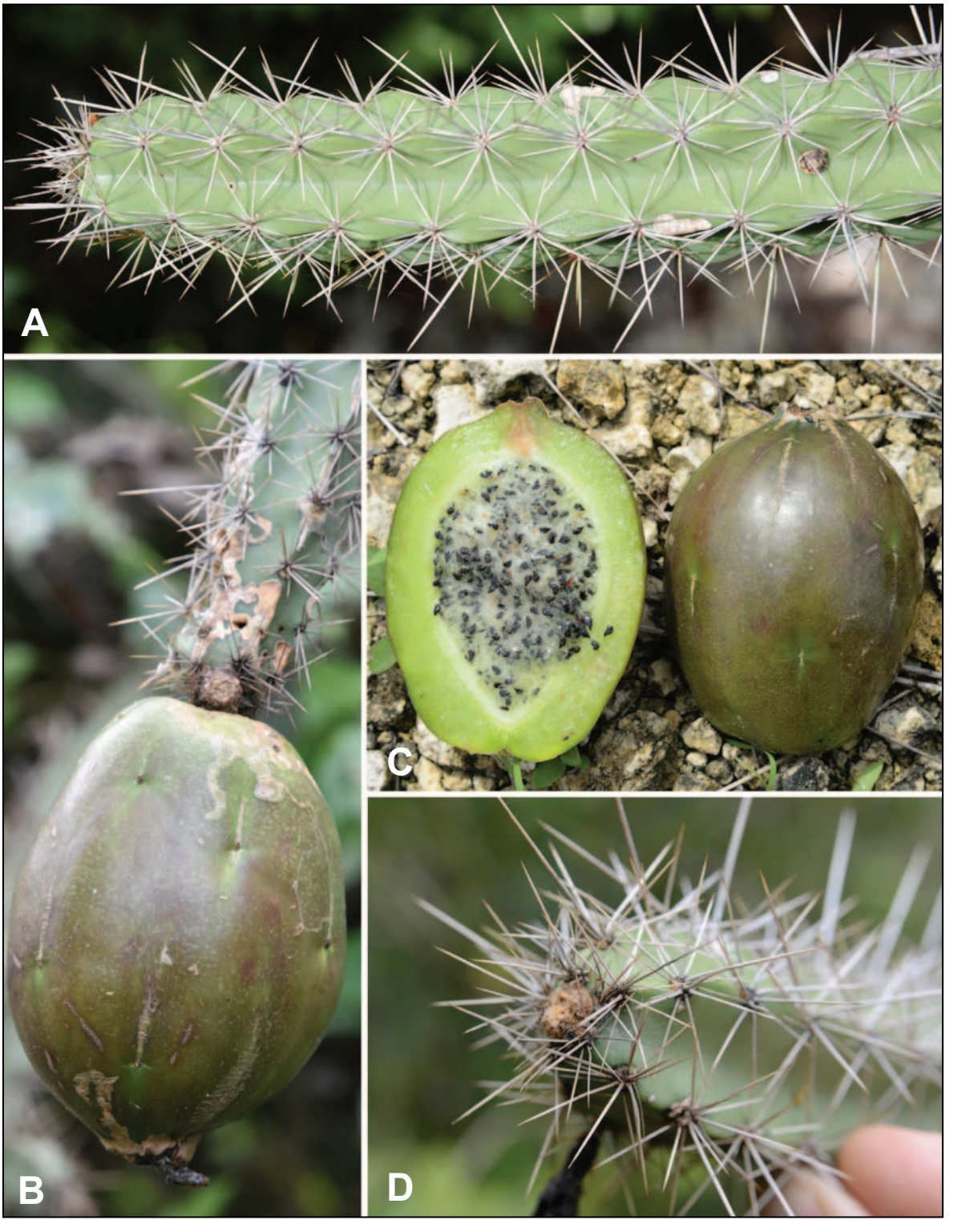


Figure 36. *Leptocereus bayahibensis* DOMINICAN REPUBLIC. Province La Altagracia. North of Bayahíbe, 30m (*Hoxey* 1859.05). **A–**Terminal stem segments with crenate rib margins. **B** to **C–**Nearly spineless mature fruit. **D–** Terminal brachyblast, a well-developed felted region.

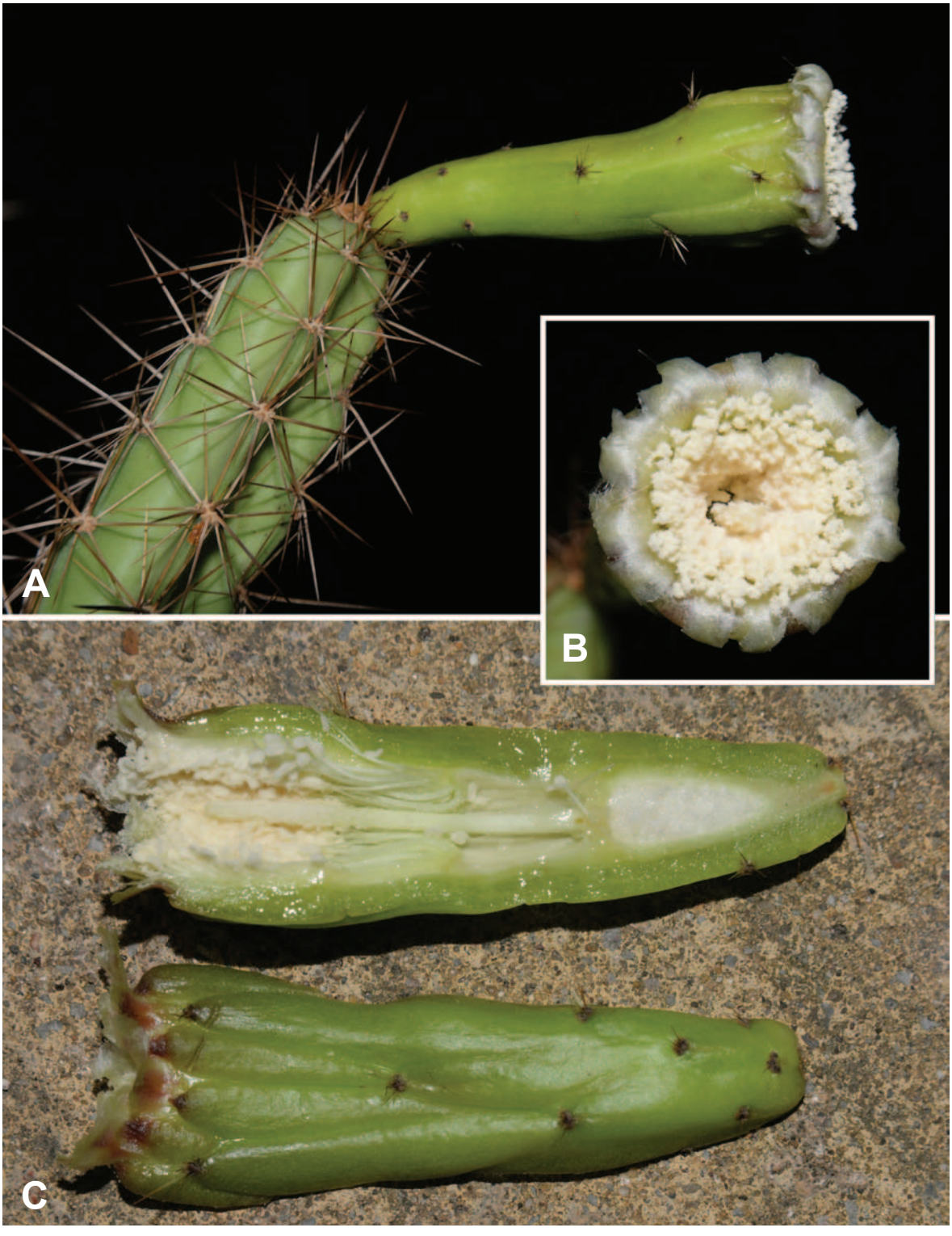
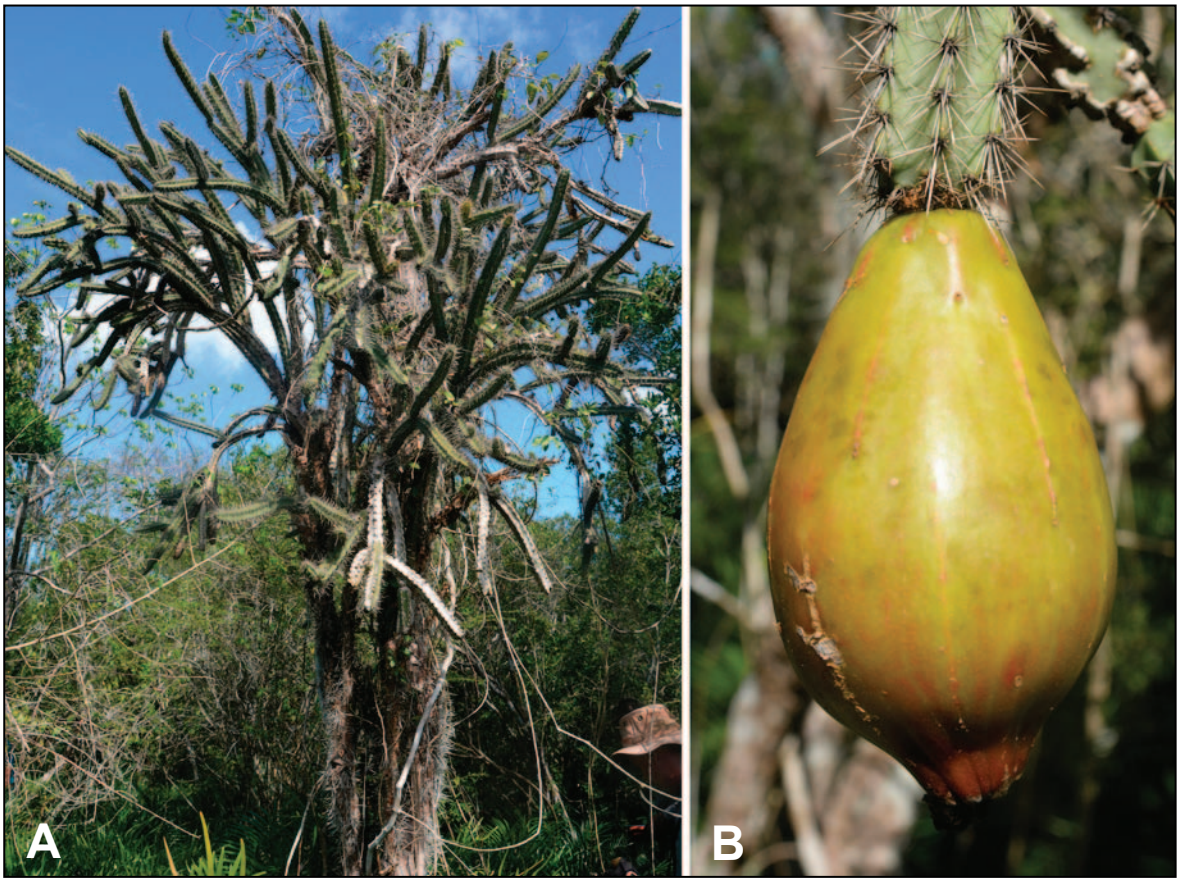


Figure 37. *Leptocereus bayahibensis* DOMINICAN REPUBLIC. Province La Altagracia. North of Bayahíbe, 50m (*Hoxey* 1459.01). **A** to **C–**Flower 55mm long, the pericarpel and hypanthium with a few weakly spined areoles.



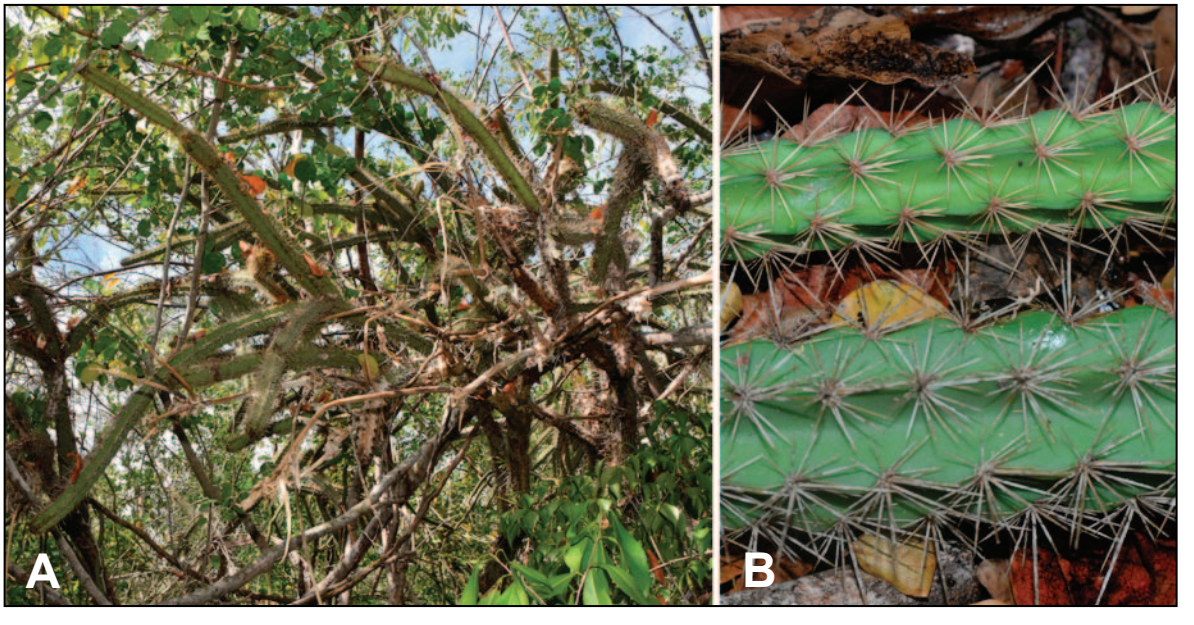


Figure 38. (above) *Leptocereus bayahibensis* DOMINICAN REPUBLIC. Province La Altagracia. Coastal woodland south of Bayahíbe, 10m (*Hoxey* 1978.01). **A–**Mature specimen. **B–**Terminal stem segment with fruit. **Figure 39.** (below) *Leptocereus bayahibensis* DOMINICAN REPUBLIC. Province La Altagracia. North coast of Isla Saona, 10m (*Hoxey* 1976.03). **A–**Mature specimen in dense woodland. **B–**Stem segments.

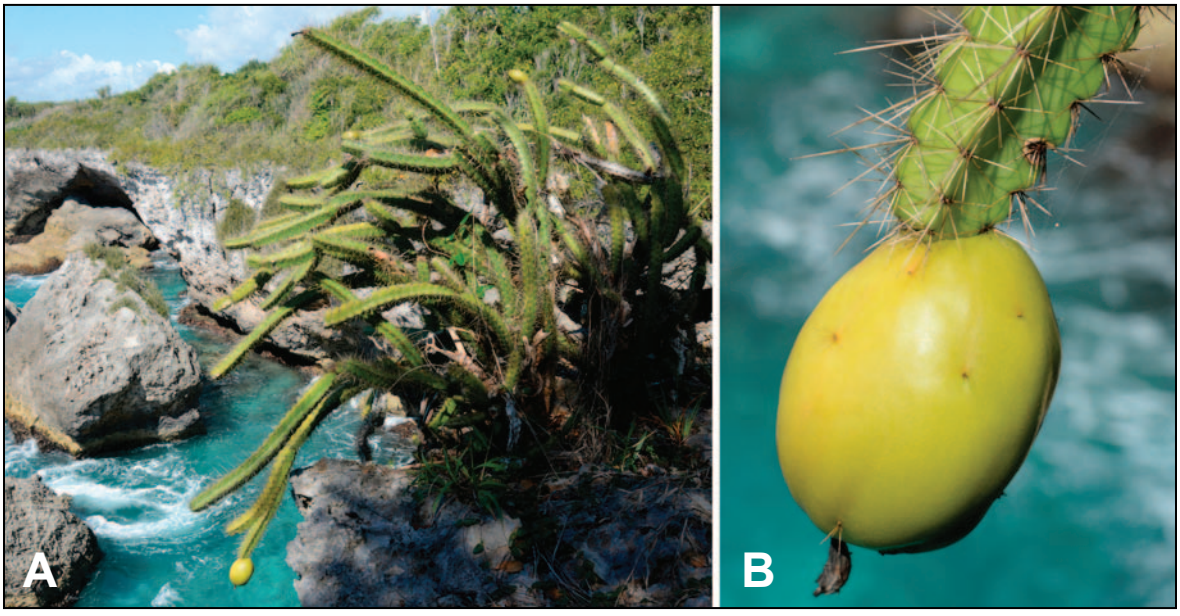


Figure 40. *Leptocereus bayahibensis* DOMINICAN REPUBLIC. Province La Altagracia. Coastal cliffs west of Punta Cuevita, 10m (*Hoxey* 1979.01). **A–**Mature specimen **B–**Fruit.

near Azua but failed to find this plant. Probably expansion of the town and agriculture over the last century has destroyed the Rose localities. Further fieldwork is urgently required to determine the range and distribution of this species which may be of conservation concern.

Discussion: This species was first collected by Rose in 1913 at Azua. Britton & Rose (1920: 77) considered this collection conspecific with *L. weingartianus* but as has already been discussed above we believe this to be an error. In our classification *L. weingartianus sensu* Britton & Rose is *L. rosei*. Majure et al. (2021: 32–34) also incorporate this taxon within their concept of *L. weingartianus*.

A remarkable feature of *L. rosei* is the very thin but long stems which we observed reach over 5m in length. Britton & Rose (1920: 77) state they grow even longer to 8–10m long. This species is adapted to grow within a relatively dense woodland environment and uses the surrounding vegetation to support itself (Figure 32A) and to allow the stems to reach sunlight. The low rib count is useful to reduce self-shading and the thin stems can be produced more rapidly than thicker stems to reach the light quicker. Thin stems are less suitable to store water but Britton & Rose (1920: 77) state the plant has tuberous roots which help support the plant during times of drought. The rib margins are straight or slightly dentate (Figure 33A–B), a feature only shared with *L. demissus* but we do not believe the two species are closely related. The shiny lustre of the epidermis is a noticeable feature and is only shared with *L. velozianus*. The seeds of the two species are also broadly similar and larger than all other species in *Leptocereus* subgenus *Neoabbottia*. We, therefore, tentatively consider *L. rosei* most closely related to *L. velozianus* and not *L. weingartianus*. *L. velozianus* and *L. rosei* are separated by over seventy kilometres and the significant differences in stem morphology and growth form amply distinguish the two species.

Iconography: Britton & Rose (1920: Figure 112) as *L. weingartianus*.

Additional specimens examined: DOMINICAN REPUBLIC. Province Azua: Azua, March 1913, *Rose* 3941 (NY 01495814, *US* 00190020, US 00190021, HMGBH (illustrated in Guiggi & Mariotti 2019: Figure 10)). 2 kilometres south of Las Guanábanas, 250m, 6 January 2022, *Hoxey & Gdaniec* 105 (GIB).

7. *Leptocereus bayahibensis* Hoxey & Gdaniec **sp. nov.**

Type: DOMINICAN REPUBLIC. Province La Altagracia: Parque Nacional del Este, Sector Guaraguao, 18°19.5'N 68°47'W, 21 January 1986, *Salazar, Peguero & García* 317 (Holotype: *JBSD* 72719 annotated as *Leptocereus weingartianus* and illustrated here as Figure 34; Isotype: NY 01495812).

Plant an upright shrub or small tree, 2–5m tall. Fully developed specimens within a forest environment have a well-developed woody trunk to 1.5–2.5m and 200–250mm in diameter with occasional spine clusters. Other plants in more open situations are smaller, from upright shrubs to small trees. **Ultimate stem segments** numerous with a green epidermis, self-supporting but eventually drooping, 1m long and 25–40mm in diameter; *ribs* (5–)6(–7), 10–15mm high, crenate margins, undulations about 2–3mm tall; *areoles* ovoid, 4mm wide and 3mm high, deep reddish-brown felt, later white, spacing 15mm situated in the lower part of the rib crenations; *spines* 15–20, 12–25mm long, straight, acicular, brown, golden-brown to brown when young, grey with age, sometimes two shorter spines to 8mm long, parallel spines emerge from the base of the areole. **Terminal brachyblast** felted structures about 10–15mm wide, about half the width of the stem, with densely packed areoles with small spines 1–2mm long, which are usually obscured by the felt. Rarely, and in extreme age, these structures reach 20–30mm long and become woody without felt where the areoles and spines are clearer to see. **Flower** single or in small groups (2–4) at the end of the stems, nocturnal, opening after dark and remaining open until after dawn the following morning, 50–60mm long and 15mm wide. Cut surfaces begin to darken a few minutes after being exposed to the atmosphere; *pericarpel* 20–25mm long and 10–14mm wide, green, with a few areoles; *areoles* small, 1mm in diameter, dark brown felt, spacing 5mm, sometimes with 2–3 very short, 1mm long and weak, dark brown spines but often spineless; *hypanthium* 35mm long and 15mm wide, green, or reddish-green, 3mm thick with fused sepals, about 16 with small dark-coloured scales; *areoles*, small, 1mm in diameter, with dark brown felt, spineless or with 2–3 very short, weak, dark brown spines, to 1mm long; *nectar chamber* 8–10mm long and 8mm wide, tapering to 5mm at either end*; style* 18–22mm long and 2mm diameter, cream-coloured; *stigma lobes* 10–12, to 5mm long, not exserted beyond flower tube; *stamens* numerous, 10mm long at top of the nectar chamber to 5mm long at the rim, slightly greenish; *anthers* 1mm, cream; *outer perianth segments* 3–5mm long, reddish-brown to greenish-brown, slightly fleshy, recurved at anthesis; *inner perianth segments* creamy-white, recurved and barely extending beyond tube, 5mm and 5mm with rounded apex, about 16. **Fruit** ellipsoid or pear-shaped, wider towards the apex, 70–100mm long and 50–60mm maximum width. Cut surfaces start to discolour a few minutes after being exposed to the atmosphere; *pericarp* smooth, green, or brownish-green, 10–12mm thick; *dried flower remains* black, 10–12mm long, sometimes absent leaving a blackened scar at the apex, 20mm wide, 3–4mm deep; *areoles* about 16, 1–2mm in diameter, light brown felt, persistent, remaining firmly attached to the fruit even at maturity, widely spaced, 20–30mm; *spines* often absent but when present up to 10–15, golden-brown, thin, straight, 2–5mm long. **Seed** oval, flattened, 2.4–2.7 × 1.4–1.6 × 0.8mm, matt black; *testa* with large (15µm wide) medium-domed cells with rounded apex; *cells on the hilum-micropylar border* small (5µm wide) and flat; *hilum* 0.8 × 0.3mm, oblique.

Diagnosis: Differs from all other species in *Leptocereus* subgenus *Neoabbottia* of Hispaniola except for *L. paniculatus* by the very short spines, only 1mm long, on the flower tube. *L. bayahibensis* can easily be distinguished from *L. paniculatus* by the thinner stems (25–40mm compared with 60–100mm) and only reaching a height of 2–5m compared with 6–10m in *L. paniculatus*.

Etymology: The specific epithet '*bayahibensis*' refers to the settlement of Bayahíbe where easily accessible specimens of this species can be found in the woodland on the road out of town.

Distribution and habitat: This species is endemic to the Dominican Republic and restricted to the Province La Altagracia in the east of the country. It is common in the coastal dry woodland around Bayahíbe (Figures 35–37), growing on generally flat coral limestone substrates with little soil, up to an elevation of 50m, We only know it from coastal localities within approximately two kilometres of the sea. We encountered a coastal population (Figures 38) about fourteen kilometres south of Bayahíbe which is only accessible by boat and also on the north coast of Isla Saona (Figure 39). The species can probably be found all along the coast from Bayahíbe to Boca de Yuma, where we observed plants growing in the forest at the top of low limestone cliffs. There is an interesting small population (Figure 40) of *L. bayahibensis* near Punta Cuevita, east of Boca de Yuma growing on exposed limestone cliffs directly above the sea. There are further populations of *L. bayahibensis* in coastal areas near Punta Cana (Figure 41), at the extreme eastern tip of the Dominican Republic, in a somewhat different environment. Here they inhabit a narrow band of low vegetation between the coast and woodland beyond. The plants at Punta Cuevita and Punta Cana are generally smaller in stature compared to the Bayahíbe population due to the lack of a forest canopy and more exposed situations.

Discussion: The seasonally dry forests in the east and south-east of the Dominican Republic

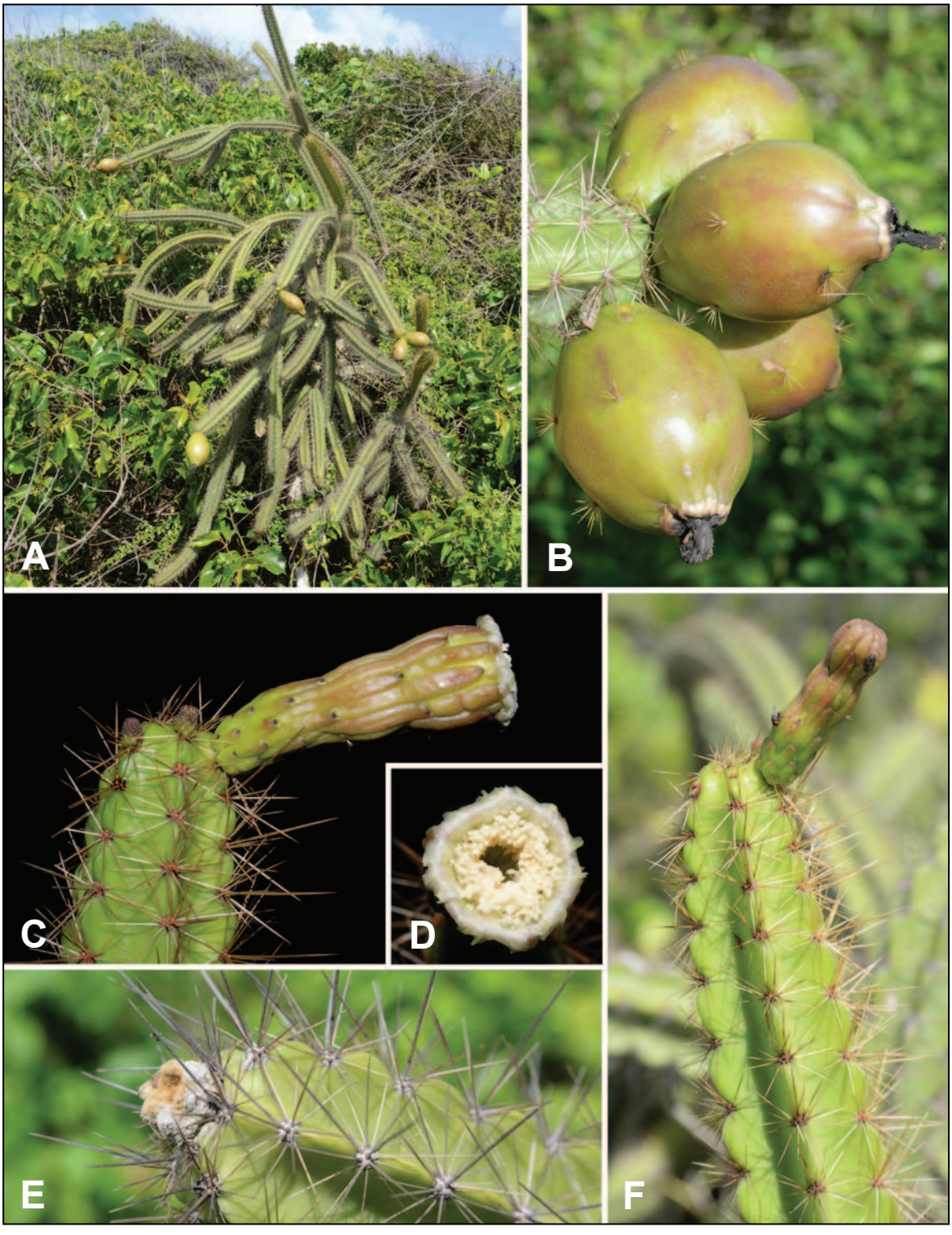


Figure 41. *Leptocereus bayahibensis* DOMINICAN REPUBLIC. Province La Altagracia. Punta Cana, 10m (*Hoxey* 1848.01). **A–**Mature specimen in fruit. **B–**Weakly spined fruits. **C** to **D–**Flower with almost spineless pericarpel and hypanthium. **E–**Terminal brachyblast. **F–**Stem with flower bud.

Figure 42. *Leptocereus cremnophilus* DOMINICAN REPUBLIC. Province Samaná. Loma el Frontón, 20m (*Hoxey* 1842.01). **A–**Mature specimen at top of a cliff (*Hoxey* 1455.03). **B** to **C–**Specimens on coastal rocks (*Hoxey* 1456.01). **D–**Specimens on a cliff face (*Hoxey* 1843.02).

are separated from similar habitats elsewhere in Hispaniola by wetter environments that are generally unsuitable for cacti. Some cactus species that are widespread elsewhere in Hispaniola are also found in this eastern area, for example *Leptocereus undulosus, Selenicereus trigonus* (Haw.) S.Arias & N.Korotkova and *Consolea* species, but many are absent such as *Cylindropuntia caribaea* (Britton & Rose) F.M.Knuth, *Harrisia divaricata* (Lam.) Backeb., *Mammillaria prolifera* (Mill.) Haw., *Pilosocereus polygonus* (Lam.) Byles & G.D.Rowley, *Stenocereus fimbriatus* (Lam.) Lourteig and *Melocactus* species. This likely indicates this region has not been directly connected to other dry areas of Hispaniola for some time and maybe acted as a refuge for xerophytic species during the Pleistocene climatic oscillations. Instead, there are several endemic species restricted to this region–*Leuenbergeria quisqueyana* (Alain) Lodé, *Pilosocereus excelsus* Hoxey & Gdaniec and *Leptocereus bayahibensis*. *L. bayahibensis* is isolated from all other species of *Leptocereus* subgenus *Neoabbottia* by approximately 120 kilometres.

Leptocereus bayahibensis has been known for some time (Fleming 1984) but was classified under the name *L. weingartianus* (Areces-Mallea, 2003; Areces-Mallea, 2017; Majure et al., 2021). This is quite surprising as this species grows to large dimensions (Figure 35A) with a robust woody trunk (Figure 35B), quite unlike other taxa previously assigned to *L. weingartianus.* We do not believe it is closely related to *L. demissus*, *L. velozianus*, *L. rosei* or *L. weingartianus* which do not form large tree-sized plants and have distinctly different seeds. Some characteristics suggest that *L. bayahibensis* is closer to *L. paniculatus* which also grows to large tree-sized proportions. Similarities include the terminal brachyblasts which are well differentiated from the normal branch segments (Figures 36D and 41E). The flowers of the two species also share several common characteristics such as absent or, if present, very short and weak spines on the hypanthium and small petals which are strongly recurved and only slightly extend beyond the end of the flower tube (Figures 37 and 41C–D). The fruits are equally very weakly spined (Figures 36B–C, 38B, 40B and 41B). However, the seed characters do not support such a close relationship between the two.

L. bayahibensis grows approximately 200 kilometres east of the closest *L. paniculatus* populations and within a wetter environment with denser vegetation. The intervening region between the two species is unsuitable for either species to become established. Majure et al. (2021) did not sequence this species in the molecular study but did include it within their concept of *L. weingartianus*.

Iconography: Areces-Mallea (2017: Figures 2–3) as *L. weingartianus*. Fleming (1984: Figures 6–7) as *L. weingartianus.* Lodé (2015: 640, three unnumbered illustrations) as *L. weingartianus*.

Additional specimens examined: DOMINICAN REPUBLIC. Province La Altagracia. Bayahíbe, La Romana, 1–5m, 21 February 1976, *Liogier & Liogier* 24907 (JBSD 07768, NY 01495813). Cabo Engaño, 14 May 1980, *Mejía & Zanoni* 6299 (JBSD 015509, JBSD 016556). 2 kilometres south of Cabo Engaño, 20 July 1989, *Hager & Sánchez* 556 (JBSD 069604). 5 kilometres south of the La Romana–Higuey highway, on the way to Bayahíbe, 2 January 1995, *Areces-Mallea* 6348 (NY 00948306, NY 00948338, NY 00948356, NY 00948377). Parque Nacional del Este, on the route to La Cueva de José María, Guaraguao, 1–30m, 28 April 2001, *Veloz & Cedeño* 2648 (JBSD 109384). Cap Cana, 50m, 22 January 2022, *Hoxey & Gdaniec* 118 (GIB). Coast 14 kilometres south of Bayahíbe, 10m, 23 January 2022, *Hoxey & Gdaniec* 119 (GIB). 5 kilometres west of Punta Cuevita, 10m, 24 January 2022, *Hoxey & Gdaniec* 120 (GIB).

8. *Leptocereus cremnophilus* Hoxey & Gdaniec **sp. nov.**

Type: DOMINICAN REPUBLIC. Province Samaná: Samaná Peninsula, Cape Samaná, 0–100m, 25 March 1921, *Abbott* 1191 (Holotype: NY 01495820; Isotype: US 00048113).

Plant a small tree or upright shrub 1–3m tall, with a woody trunk 0.5–1.5m tall to 100mm in diameter. Branches numerous, self-supporting, initially upright but eventually drooping. Branches frequently form numerous small shoots to 10mm wide from areoles near the apex which are probably deciduous and have evolved as a method to facilitate asexual reproduction. **Ultimate stem segments** 0.3–1m long and (35–)40–45mm in diameter. The flesh does not turn black when exposed to the atmosphere; *ribs* (4)5–6, triangular in cross-section (box-shaped cross section with 4 ribs) about 12mm wide at the base and 3–5mm wide at the apex; *rib margins* crenate, approximate 3mm difference in the height of the undulations; *areoles* dark brown felt, 4mm in diameter, spacing 15mm; *spines* 10–20(–25) mm long, 15–18, straight, acicular, radials and centrals are poorly differentiated, yellow-brown fading to grey-brown, just overlapping between clusters. **Terminal brachyblast** cylindrical, 10–20mm long and 15mm in diameter, felted

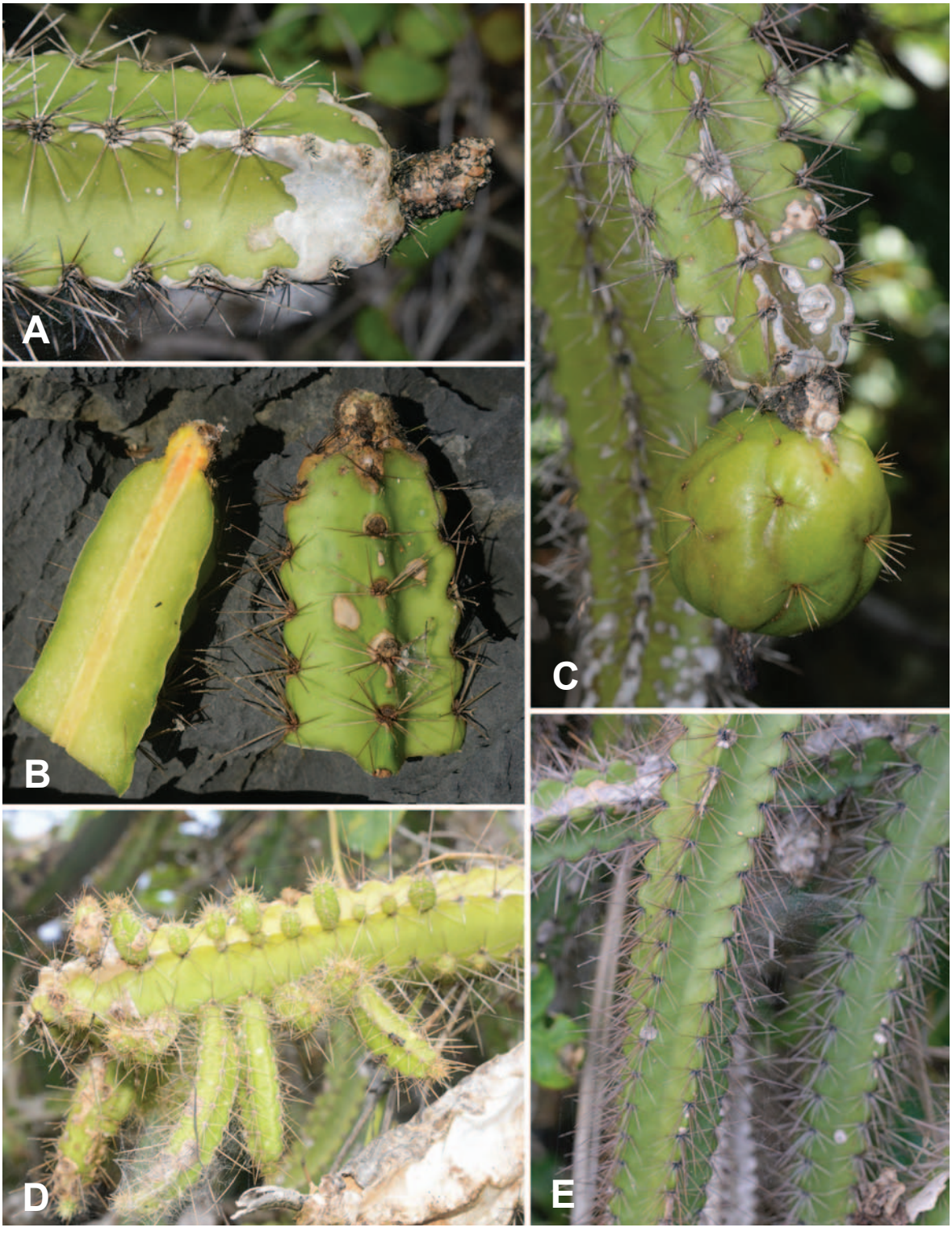


Figure 43. *Leptocereus cremnophilus* DOMINICAN REPUBLIC. Province Samaná. Loma el Frontón, 20m (*Hoxey* 1842.01). **A** to **B–**Terminal brachyblasts. **C–**Fruit. **D–**Proliferating stem. **E–**Typical stem.

Figure 44. *Leptocereus cremnophilus* DOMINICAN REPUBLIC. Province Samaná. Loma el Frontón, 20m (*Hoxey* 1842.01). **A–**Mature stem with flower buds but lacking terminal brachyblast. **B** to **C–**Flower.

but spineless, eventually turning woody with age, lacking chlorophyll. Flowers appear from areoles on normal stems near the apex or from the brachyblasts. **Flower** 60mm long and 12–15mm wide. Cut surfaces do not discolour; *pericarpel* 25mm long and 10mm wide, small brown areoles 1mm in diameter, spacing 5mm. Spines are very short to 1mm or absent; *ovary* 15mm long and 5mm wide, tapering towards the base; *nectar chamber* elongated 10mm long and 5mm wide; *hypanthium* is 30mm long and 10–12mm wide; *areoles* 1mm in diameter, dark brown felt, about 10–12, spacing 15mm, situated in slight depressions; *spines* c.8, 3–4mm long, straight, yellow-brown; *style* 25mm long, 1mm wide, white; *stigma lobes* about 10, 6mm long; *stamens* numerous 8–15mm long, emerge from 18mm of the flower tube above the nectar chamber with a gap of 5mm until a ring of stamens at the top of the tube, 5mm long; *anthers* cream; *outer perianth segments* 3–5mm long, reddish-brown to greenish-brown, slightly fleshy, recurved at anthesis; *inner perianth segments* creamy-white, recurved and barely extending beyond tube, 5mm long and 5mm wide with rounded apex, about 16. **Fruit** almost spherical, about 60mm in diameter, and yellow-green at maturity; *pericarp* about 10mm thick, smooth but a little ribbed towards the apex; *areoles* 2mm in diameter, brown felt, 20–25mm spacing, non-persistent and often absent; *spines c.*15, to 10mm long, golden-brown, straight but flexible; *flower remains* 15mm long, black but often absent leaving a black scar on the top of the fruit 10mm wide and 5mm deep. Seeds are contained in a pulp that is only slightly mucilaginous. **Seed** oval, flattened, 2.6–2.7 × 1.6 × 0.6mm, matt black; *testa* with large (20µm wide) high-domed cells with rounded apex; *cells on the hilum-micropylar border* small (5µm wide) and flat; *hilum* 1.0 × 0.4mm, oblique.

Diagnosis: Differs from *L. bayahibensis* on account of the smaller stature of the plants, the slightly thicker stems (35–45mm compared with 25–35mm) and longer spines on the flower tube (4–6mm compared with <1mm) and fruit (10mm compared with 2–5mm). Uniquely for *Leptocereus* subgenus *Neoabbottia* of Hispaniola, the plants can form numerous small shoots as a method to facilitate asexual reproduction. Also, the fruits only have a slightly mucilaginous pulp and the stem when cut does not discolour.

Etymology: The epithet '*cremnophilus*' derives from the Greek '*kremnos*' for a cliff and '*philos*' for friend or liking. This refers to the exclusive cliff-dwelling habitat of this species, which is unique for *Leptocereus* in Hispaniola.

Distribution and habitat: *Leptocereus cremnophilus* is of localised distribution and endemic to the Samaná Peninsula of the Dominican Republic. Unlike all other *Leptocereus* species in Hispaniola which favour dry forest environments on generally flat or gently sloping terrain, *L. cremnophilus* is mostly found on steep, almost vertical cliffs or coastal rocks growing in exposed situations (Figures 42–44). The rainfall of the Samaná Peninsula is high (2–2.5m per annum) and supports a humid evergreen forest unsuitable for cacti, except for the epiphytic species *Rhipsalis baccifera*. The only place xerophytic vegetation is present is on coastal cliffs made from a metamorphic marble derived from limestone. On these exposed rocks the conditions are suitable for cacti and other drought-resistant plants such as *Agave* and *Plumeria* species We only know *L. cremnophilus* from the east-facing cliffs of the Loma le Frontón, at the extreme eastern end of the Samaná peninsula, which rise about 100–150m out of the sea. *L. cremnophilus* is plentiful on the cliffs and grows in association with *Pilosocereus samanensis* Hoxey & Gdaniec, another narrow endemic to these cliffs. It is also reported from the nearby Cabo Cabrón (Salazar 2000: 142) but we have not been able to confirm this. *L. cremnophilus* is isolated from all other *Leptocereus* species by at least 120 kilometres and the closest populations are of *L. bayahibensis* near Punta Cana. The intervening region is not suitable for *Leptocereus* due to high rainfall and lack of suitable habitats.

Discussion: In addition to the unusual habitat there are three very interesting morphological characters which are not seen in other Hispaniola *Leptocereus*:

1. Specimens sometimes produce small stems from areoles that are no more than 10mm in diameter (Figure 43D). They are easily detached and appear to be an adaption to facilitate asexual reproduction. The small offsets can fall from the mother plant and root to grow into new individuals. Similar growths which evolved independently are seen in the genus *Acanthocereus*. Perhaps *L. cremnophilus* evolved this asexual method of reproduction due to the extreme environmental conditions of the cliff habitat. Compared with the forest environments of the other species, the cliffs offer little protection from the sun for developing seedlings and perhaps the asexual reproduction supplements sexual reproduction from seed in such difficult conditions.

2. The fruits have a pulp that is only mildly mucilaginous, unique for *Leptocereus* subgenus *Neoabbottia*. All other species have a very mucilaginous pulp. Possibly this indicates *L.*

Figure 45. *Leptocereus septentrionalis* DOMINICAN REPUBLIC. Province Monte Cristí. West of Monte Cristí, 90m (*Hoxey* 1837.01). **A** to **C–**Large mature specimen 8m tall with a crown of stems and a trunk 200mm in diameter. **D–** Terminal brachyblast. **E–**Fruits.

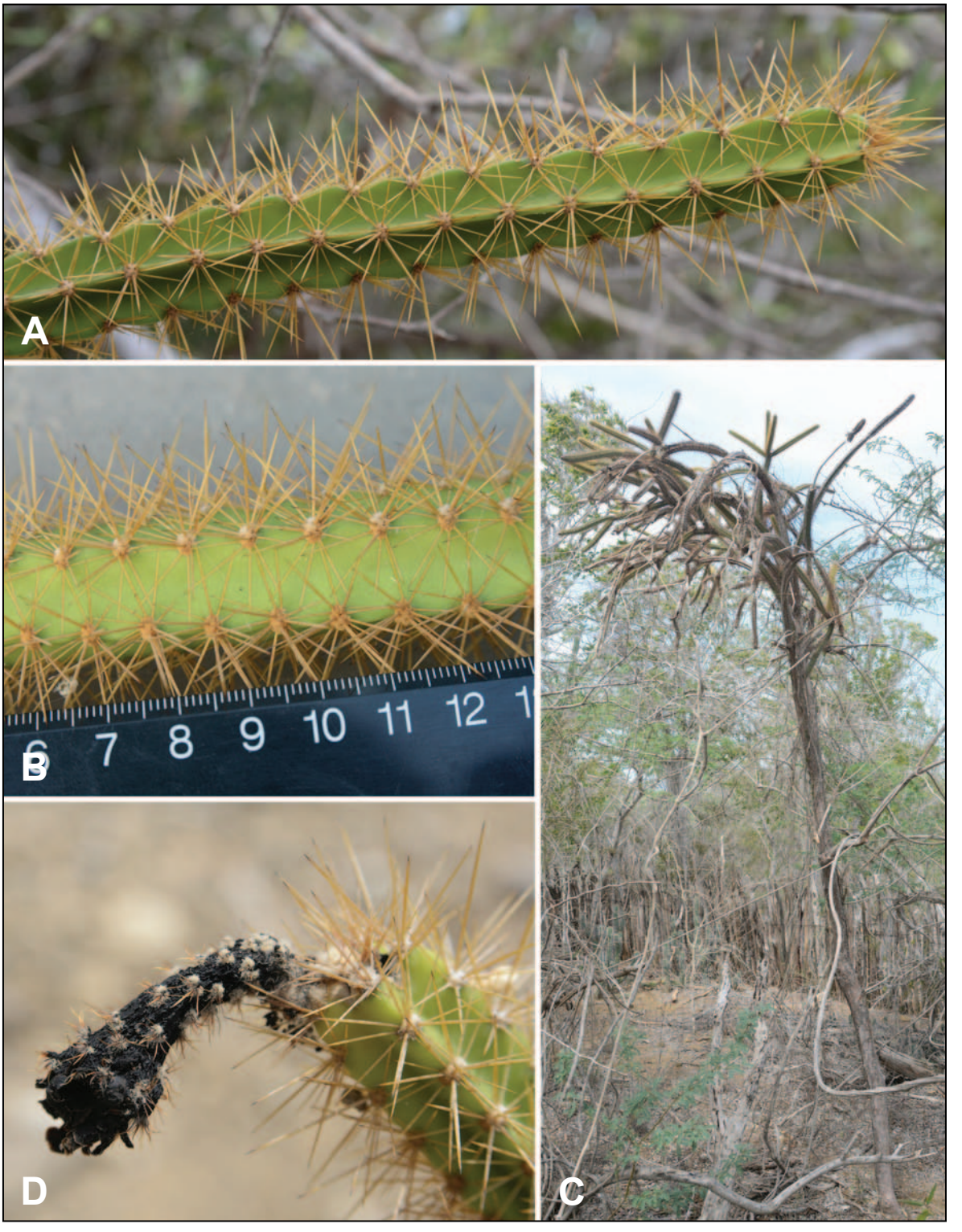


Figure 46. *Leptocereus septentrionalis* DOMINICAN REPUBLIC. Province Monte Cristí. West of Monte Cristí, 70m (*Hoxey* 1838.01). **A** to **B–**Typical branch with crenate rib margins and golden coloured spination. **C–**Mature specimen 4m tall in partially cleared woodland. **D–**Unfertilised flower remains.

cremnophilus has adapted to take advantage of a different seed dispersal vector because its cliff habitat may mean that the usual vectors are not able to access it so easily.

3. We also observed both stems and flowers do not discolour when cut open. This is a somewhat variable character in *Leptocereus* but all other Hispaniola species exhibit some degree of discolouring and darkening of exposed flesh.

We consider these characteristics together with the isolated distribution and unique habitat justify the acceptance of *L. cremnophilus* as a good species. Based on plant morphology we think *L. cremnophilus* is most closely related to *L. bayahibensis* and several features are in close agreement including the well-defined terminal brachyblasts (Figures 43A–B), flowers which have very short spines (Figures 44B–C) and the seed structure. The fruits are however a little different with longer spines (Figure 43C) although some specimens had mature fruits lacking spines. It is not clear if these never formed or had been dislodged from the fruit. The two species probably evolved from a common ancestor through allopatric speciation. Areces-Mallea (2003 and 2017) included this species within his concept of *L. weingartianus* and Majure et al. (2021) did not mention it at all.

Iconography: Areces-Mallea (2017: Figure 1) as *L. weingartianus*.

Additional specimens examined: DOMINICAN REPUBLIC: Province Samaná. La Boca del Diablo, south of Loma el Frontón, 10m, 17 January 2022, *Hoxey & Gdaniec* 88 (GIB).

9. *Leptocereus septentrionalis* Hoxey & Gdaniec **sp. nov.**

Type: DOMINICAN REPUBLIC. Province Monte Cristí: Monte Cristí, 23 February 1921, *Abbott* 1007 (Holotype: *US* 00048103).

Plant of variable sizes from upright shrubs (2–3m tall) to tree-sized specimens (8m tall) with a woody, spineless, trunk 3–4m tall and 200mm in diameter. A crown of numerous self-supporting but often drooping stems. Other specimens are shrubby 2–3m tall, with a short woody trunk and a smaller number of spreading and drooping branches. **Ultimate stem-segments** 0.5–2m long and 20–25(–30)mm in diameter, epidermis green. Cut surfaces blacken when exposed to the atmosphere; *ribs* 5–6(–7), 8–10mm tall; *rib margins* crenate, approximate 2mm difference in the height of the undulations; *areoles* ovoid, 3–4mm wide and 2–3mm long, spacing 10–15mm, white felt, situated in the lower part of the rib; *spines* 12–25mm long, 15–22, straight, acicular, spreading, radials and centrals are poorly differentiated, golden yellow and remaining so for some time before turning dark brown or grey on older stems, overlapping between adjacent areoles, sometimes two shorter, weaker, parallel spines appear from the base of the areole. **Terminal brachyblast** 10mm long and 15mm in diameter, spineless with white felt but brown and woody with age. Flowers appear from areoles on normal stems near the apex or from the brachyblasts. **Flower** unknown but based on unfertilised flower remains (Figure 46D) the hypanthium has areoles with grey-white felt and approximately 10 spines to 4mm long. **Fruit** elongated ovoid 60–80mm long and 40–50mm wide, smooth but slightly ribbed near apex, green with a slight yellowish hue; *pericarp* 10–12mm thick. Seeds in a mucilaginous translucent pulp; *areoles* 2–3mm in diameter, cream-white felt, spacing 15–20mm; *spines* 12–20, 6–15mm long, brown, a little flexible but straight, radiating in all directions equally, persistent; *dried flower remains* firmly attached, black, 10–12mm long, 15mm wide at the attachment point, with areoles and spines to 5mm long. Fruits singularly or occasionally in pairs, from the flowering brachyblast or areoles near the apex of the stems. **Seed** oval, flattened, 2.3–2.6 × 1.4 × 0.6mm, matt black; *testa* with large (15µm wide) high-domed cells with pointed apex (10µm high); *cells on the hilum-micropylar* border small (5µm wide) and flat. *Hilum* 1.0 × 0.5mm, oblique.

Diagnosis: Differs from *L. bayahibensis* and *L. paniculatus*, the only other species in *Leptocereus* subgenus *Neoabbottia* which grow to tree-sized proportions of 5m, by longer spines on the flower tube (4–6mm compared with 1–2mm) and fruits (6–15mm compared with 2–4mm).

Etymology: The specific epithet '*septentrionalis*' refers to the distribution of this species which is restricted to the north of Hispaniola (Latin adjective *septentrionalis* = northern).

Distribution and habitat: This species is only known from the north of Hispaniola and within five kilometres of the coast. It is found in two discrete populations which are separated by approximately 150 kilometres. The climate of the intervening region is probably too moist and thus unsuitable for *Leptocereus*. The type population (Figures 45–46) is restricted to the seasonally dry forests in the vicinity of Monte Cristí in the Dominican Republic, below an elevation of 100m, It appears to be scarce and of restricted distribution in the area. We know of two small colonies where large fully mature specimens can be found and some additional scattered specimens within the

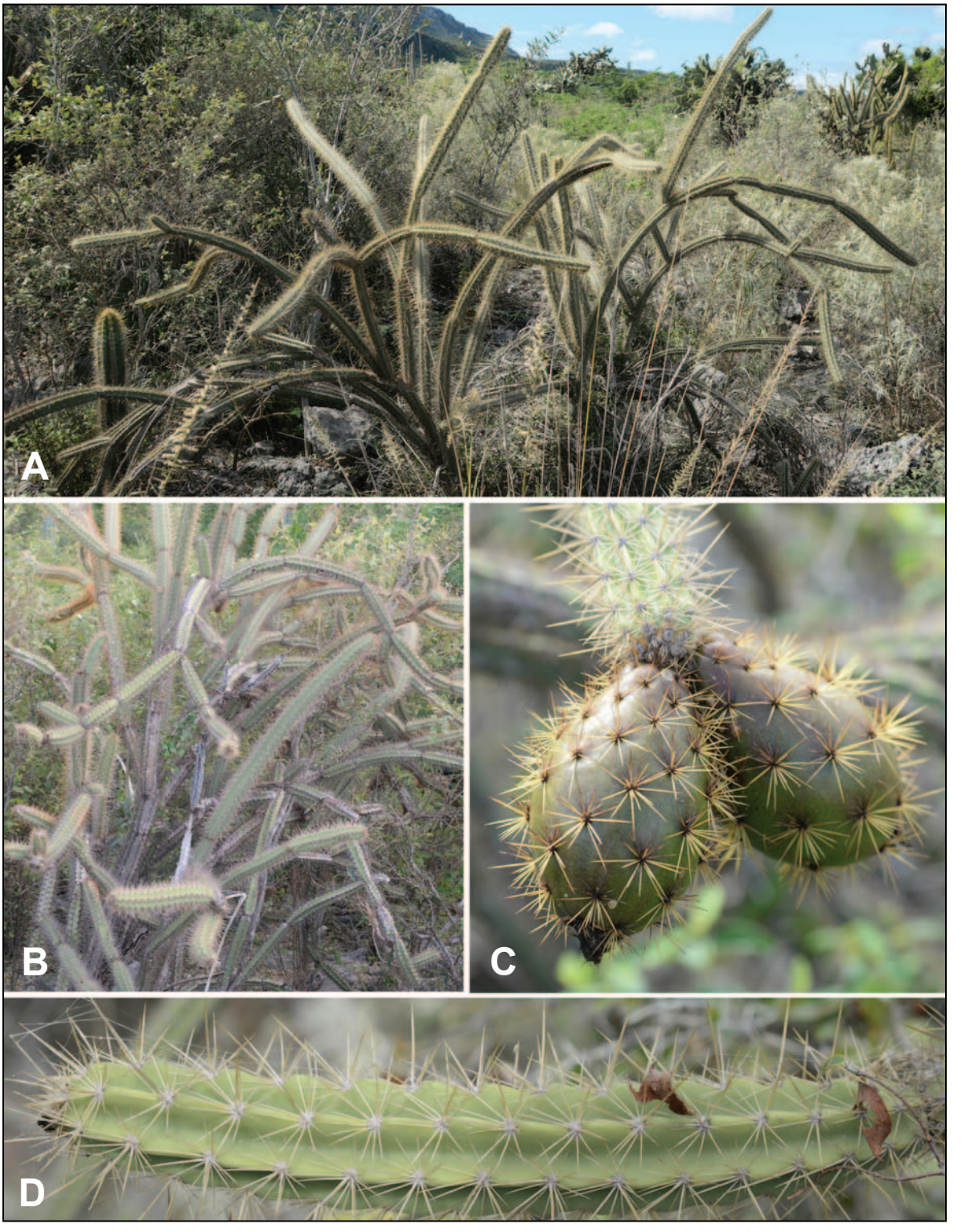


Figure 47. *Leptocereus septentrionalis* HAITI. Department. Nord-Ouest. Môle Saint Nicolas, 60–110m (*Hoxey* 1292.06). **A** to **B–**Mature specimen but retaining shrubby growth form without a well-defined trunk. **C–**Fruits, well-armed with spines. **D–**Stem with crenate rib margins.

Figure 48. *Leptocereus septentrionalis* HAITI. Dept. Nord-Ouest. West of Baie de Henne, 240m (*Hoxey* 1291.01) **A–**Mature specimen. **B–**Stem segment.

forest but all are within eight kilometres of each other. The populations are small with only a few individuals and only through chance did we find them. The second population (Figure 47), on the north coast of Haiti, is more extensive and extends from Port-de-Paix to Môle Saint Nicolas. We found one isolated population on the southern coast of the north-west peninsula near Baie de Henne (Figure 48) and suspect plants will be found in coastal areas from there until Môle Saint Nicolas. Again, these Haitian plants are found in small, fragmented colonies. They do not grow as large as the Monte Cristí plants probably because the surrounding vegetation has been modified by human activity and large trees are absent.

Discussion: We first encountered this species in Haiti where plants grow as shrubs reaching about 2–3m tall (Figure 47A). There is a relatively thin woody trunk not much thicker than the terminal branches which are self-supporting but tend to droop a little. The plants grow in relatively open situations on a solid coral limestone substrate. Erik Ekman was the first to take note of these plants and the material he collected (*Ekman* 4572) was identified as *Cereus maxonii* (≡*Cephalocereus maxonii*) by Werdermann (1931: 240). This is a mix-up with the intended name *Leptocereus maxonii*, because *Cephalocereus maxonii* is a completely different plant from Guatemala and is now considered (for example by Hunt et al. 2006a: 312) to be a synonym of *Pilosocereus leucocephalus* (Poselg.) Byles & G.D.Rowley. The plant found by Ekman is a *Leptocereus* species from the description in Werdermann (1931: 240) '3m, branches, spreading, 5(–6) ribbed; flower white, green on the outside; fruit olive-green ellipsoid, size of goose-egg, with groups of spines.' and confirmed by the specimen of *Ekman* 4572 at Kew Herbarium which consists of a stem fragment with crenate rib margins and a dried flower with spines. Both the specimen and description are consistent with the *Leptocereus* we found on the north coast of Haiti.

Near Monte Cristí in the Dominican Republic, we encountered a small population of similar-sized plants with stems indistinguishable from the Haitian plants. Although fruits were not present the plants had rudimentary terminal brachyblasts indicating they had flowered and one specimen had many small seedlings growing underneath it. We explored the area and we unexpectedly discovered several specimens of *Leptocereus* growing to 8m tall with thick woody trunks and a large crown of branches (Figure 45A–C). It was clear from the terminal stem morphology these were the same species as the smaller plants in the area and were fully mature individuals of some considerable age.

The large tree-sized *L. septentrionalis* grow in undisturbed woodland with a tree canopy about the same height as the plants. We speculate that the smaller plants we had seen are younger but are still mature and capable of flowering, growing where the tree canopy is not present. As with some other species of *Leptocereus* capable of growing to tree-sized proportions (for example *L. undulosus* and *L. bayahibensis*), the size obtained by specimens appears to be strongly dependent on environmental conditions. We believe specimens that grow in shady localities underneath the forest canopy grow larger than those in a more exposed situation with better access to the light at a smaller size.

1 Large trees (>6m) with thick trunk and crown of self-supporting stem segments……..…….. 2
1 Small trees (<6m), or erect or sprawling shrubs……..…….. 4

2 Stem segments <100mm diameter, 4–7 ribs ……..…….. 3
2 Stem segments>120mm diameter, 3–4 ribs. Flower and fruit spineless (Throughout Hispaniola in coastal areas)…….……. ***L. undulosus***

3 Stem-segments >50mm diameter, 4–6 ribs. Flower and fruit with spines (<4mm) (Lowlands of central Hispaniola and north-west Haiti)……..…… ***L. paniculatus***
3 Stem segments <40mm, spiny, 5–7 ribs. Flower-tube and fruit with spines >4mm long (North coast of Hispaniola) ……..... ***L. septentrionalis***

4 Small trees (3–5 m) or erect shrubs with self-supporting spiny stem segments <50mm ..…….. 5
4 Sprawling shrubs with scandent or climbing branches; stem segments not self-supporting 8

5 Flower tube with spines >2mm long. Fruit with spines >5mm long ……..…… 6
5 Flower tube with spines to 1mm long. Fruit with spines <5mm long (East and south-east Dominican Republic) ……..…… ***L. bayahibensis***

6 Stem segments 20–30mm, 4–7 ribs. Flower-tube with spines >4mm long ……..... 7
6 Stem segments 35–45mm, 4–6 ribs. Flower-tube with spines <4mm long. (Samaná Peninsula, Dominican Republic)……..…… ***L. cremnophilus***

7 Stems 20–30mm diameter, epidemis shiny green, 4–5 ribs. Flower tube with spines 8mm long. (Sierra de Bahoruco, south-west Dominican Republic) ……..... ***L. velozianus***
7 Stem segments 20–30mm diameter, epidermis matt green, 5–7 ribs. Flower-tube with spines <6mm long (North coast of Hispaniola) ……..……..…… ***L. septentrionalis***

9 Stem-segments 10–15mm diameter, ribs 4–5(–6) with straight or slightly crenate margins ..… 9
9 Stem segments 15–25mm diameter, ribs 5–7 with straight or slightly dentate margins (Bahoruco Peninsula, south-west Dominican Republic) ……..…… ***L. demissus***

9 Arching stem segments 1–2m long, ribs 4–5(–6) with straight or slightly crenate margins, green epidermis (West and south-west Dominican Republic and west coast of Haiti) ……..…….. ***L. weingartianus***
9 Climbing branches 5m+ long, ribs 4–5 with straight or dentate margins, shiny green epidermis (Vicinity of Azua, Dominican Republic) ……..……. ***L. rosei***

Key to the species of *Leptocereus* on Hispaniola. Note that *L. septentrionalis* appears twice in the key due to the frequent occurrence of plants that do not reach large dimensions yet are fully mature individuals.

The tree-sized plants of *L. septentrionalis* near Monte Cristí have fruits closely resembling those found in Haiti and without significant differences in ultimate stem-segment morphology including terminal brachyblasts and spination we consider them all one species. Seed and seedling morphology are also closely aligned. The region near Monte Cristí needs to be surveyed to better understand the range and population densities of this species. Presently we only know of a few mature individuals and *L. septentrionalis* may be of conservation concern if mature plants are as rare as we believe.

The seeds of *L. septentrionalis* point to a relationship with *L. bayahibensis* and *L. cremnophilus* but unlike either of those two species, the cells on the testa are pointed and not rounded. This feature is only shared with *L. paniculatus* and *L. demissus*. Seedling morphology also points to a relationship with these two species.

Iconography: Illustrations of this species have never previously been published.

Additional specimens examined: HAITI.

Species		*L. undulosus*	*L. paniculatus*	*L. demissus*
Growth form	Structure	Tree with a profusely branching crown of stem segments	Tree with a profusely branching crown of stem segments	Sprawling shrub with arching and trailing stems
	Total Height (m)	10	6–10	1–2(–3)
	Trunk height (m)	2–6	2–4	<1
	Trunk diameter (mm)	500	300–400	30–50
Ultimate stem segment (Figure 49A–C)	Length (m)	0.2–1	0.3–0.5	0.3–3
	Diameter (mm)	150	60–100	15–20
	Colour	Shiny bright green	Matt grey-green	<matt grey-green
	Number of ribs	3(–4)	4–6	(5–)6(–7)
	Rib margins	Strongly crenate.	Crenate	Straight or slightly dentate.
	Rib crenations (mm)	5–10	2–3	Absent
	Areole size (mm)	2–3 × 4–6	3 × 4	2–3 × 2–3
	Areole felt	White	White	Brown
	Areole spacing (mm)	30–40	20–25	10–15
	Spines number	0–3	15–25(–30)	15–25
	Spine length (mm)	0–20	5–20(–30)	10–20
	Spine colour	Pale grey with a darker tip	Brownish-yellow, grey with age	Brownish-yellow, grey with age
Brachy-blasts (Figure 50A–C)	Structure	Spineless with closely spaced areoles. Green, later woody and brown. Tapering towards the apex	Elongated cylindrical, spineless, closely spaced areoles, creamy white felt, later brown and woody	A short extension of the stem, turning woody and brown with age and with slightly shorter spines
	Length × Width (mm)	30 × 15	70–80 × 20	<5 × 12–20
Flower	Shape	Narrow tubular.	Cylindrical	Obconical
	Length × Width (mm)	150–200 × 15	50 × 15	50–65 × 30–46
	Areole size (mm)	Small	2	2–2.5
	Areoles felt	N/A	Light brown	Yellowish-brown
	Spines	0	0–3	7–17
	Spine length (mm)	N/A	0–2	4–11
Fruit (Figure 52A–C)	Structure	Globular, green, sometimes with a hypanthium-derived appendage	Ovoid-globular, green or reddish-green	Ovoid-globular, plum-red
	Length × Width (mm)	80 × 80	60–70 × 50–55	55–65 × 45–50
	Areole size (mm)	Small	Small	2
	Areoles felt	White	White or light brown.	Dark brown
	Spines	0	0–8, brown	18–30, brownish
	Spine length (mm)	N/A	4	5–10

Table 4A. Morphological comparison of *Leptocereus* of Hispaniola (*L. undulosus*, *L. paniculatus* and *L. demissus)*.

Species		*L. velozianus*	*L. weingartianus*	*L. rosei*
Growth form	Structure	Small tree with a sparse number of self-supporting stems	Long, arching and sometimes scandent stems	Long non-self-supporting scrambling and scandent stems
	Total Height (m)	2–4	3 (with external support)	5 (with external support)
	Trunk height (m)	1–2	1	1
	Trunk diameter (mm)	60–80	30–50	40–60
Ultimate stem segment (Figure 49D–F)	Length (m)	0.4–1	1–2	1–5
	Diameter (mm)	20–30	10–15	10–15
	Colour	Shiny deep green	Bright green	Shiny deep green
	Number of ribs	4–5	4–5(–6)	4(–5)
	Rib margins	Strongly crenate	Straight or slightly crenate	Straight or slightly dentate
	Rib crenations (mm)	3–4	0–1	Absent
	Areole size (mm)	3 × 3	2–3 × 2–3	3–4 × 3–4
	Areole felt	Brown	Brown	Brown
	Areole spacing (mm)	15–20	12–20	15–20
	Spines number	10–15	10–12(–15)	10–12
	Spine length (mm)	12–25	10–20(–25)	12–15
	Spine colour	Brown-grey or grey with a darker tip	Brown	Brown
Brachy-blasts (Figure 51D–F)	Structure	Small felted region, later woody	Felted, later woody, with several short weak spines but later absent	Felted, later woody, initially with short, weak spines but later absent
	Length × Width (mm)	<5 × <5	10 × 15	10 × 10–15
Flower	Shape	Oblong	Tubular	
	Length × Width (mm)	76 × ?	50–55 × 20	
	Areole size (mm)	?	2–3	
	Areole felt	?	Dark brown	
	Spines	*c.*4	*c.*10	*c.*6, light brown
	Spine length (mm)	*c.*8	5–8	*c.*6
Fruit (Figures 52D–F)	Structure	Ovoid-globular, yellowish-green	Elongated ovoid, green or reddish-green	Elongated ovoid, bright green
	Length × Width (mm)	55 × 45	70 × 35	55 × 30
	Areole size (mm)	2	1.5–2	3
	Areoles felt	Dark brown	Dark brown	Dark brown
	Spines	12–18, brown	10–15, grey-brown	*c.*20, light brown
	Spine length (mm)	5–10	5–10	10

Table 4B. Morphological comparison of *Leptocereus* of Hispaniola (*L. velozianus*, *L. weingartianus* and *L. rosei*).

Species		*L. bayahibensis*	*L. cremnophilus*	*L. septentrionalis*
Growth form	Structure	Tree or upright shrub with a profusely branching crown of stem segments	Small tree or shrub with a profusely branching crown of stem segments	Tree or shrub with a profusely branching crown of stem segments
	Total Height (m)	2–5	1–3	8
	Trunk height (m)	1.5–2	0.5–1.5	3–4
	Trunk diameter (mm)	200–250	100	200
Ultimate stem segment (Figure 49D–F)	Length (m)	1	0.3–1	0.5–2
	Diameter (mm)	25–40	(35–)40–45	20–30
	Colour	Green.	Green.	Light green.
	Number of ribs	(5–)6(–7)	(4–)5–6	5–6(–7)
	Rib margins	Crenate	Crenate	Crenate
	Rib crenations (mm)	2–3	3	2
	Areole size (mm)	3–4 × 3–4	4 × 4	3–4 × 2–3
	Areole felt	Reddish-brown	Brown	White
	Areole spacing (mm)	15	15	10–15
	Spines number	15–20	15–18	15–22
	Spine length (mm)	12–25	10–25	12–25
	Spine colour	Golden-brown to brown, grey with age	Yellow-brown fading to grey-brown	Golden yellow to dark brown
Brachy-blasts (Figure 51G–I)	Structure	Cylindrical, densely packed areoles with short spines. In age woody without felt	Cylindrical, spineless, felted eventually turning woody with age	Short extension, spineless white felt eventually turning woody with age
	Length × Width (mm)	20–30 × 10–15	10–20 × 15	10 × 15
Flower	Shape	Tubular	Tubular	Tubular?
	Length × Width (mm)	50–60 × 15	60 × 12–15	55 × 18
	Areole size (mm)	1	1	2–3
	Areole felt	Dark brown	Dark brown	Cream-white
	Spines	0–3, dark brown	*c.*8, yellow-brown	*c.*8, brown
	Spine length (mm)	1	3–4	4–6
Fruit (Figure 53)	Structure	Ellipsoid or pear-shaped, green or reddish-green	Almost spherical, green, sometimes yellowish	Elongated ovoid, green or yellowish-green
	Length × Width (mm)	70–100 × 50–60	60 × 60	60–80 × 40–50
	Areole size (mm)	1–2	2	2–3
	Areole felt	Light brown	Brown	Cream white
	Spines	(0)–10–15, golden-brown	*c.*15, golden-brown	12–20, brown
	Spine length (mm)	2–5	10	6–15

Table 4C. Morphological comparison of *Leptocereus* of Hispaniola (*L. bayahibensis*, *L. cremnophilus* and *L. septentrionalis*).

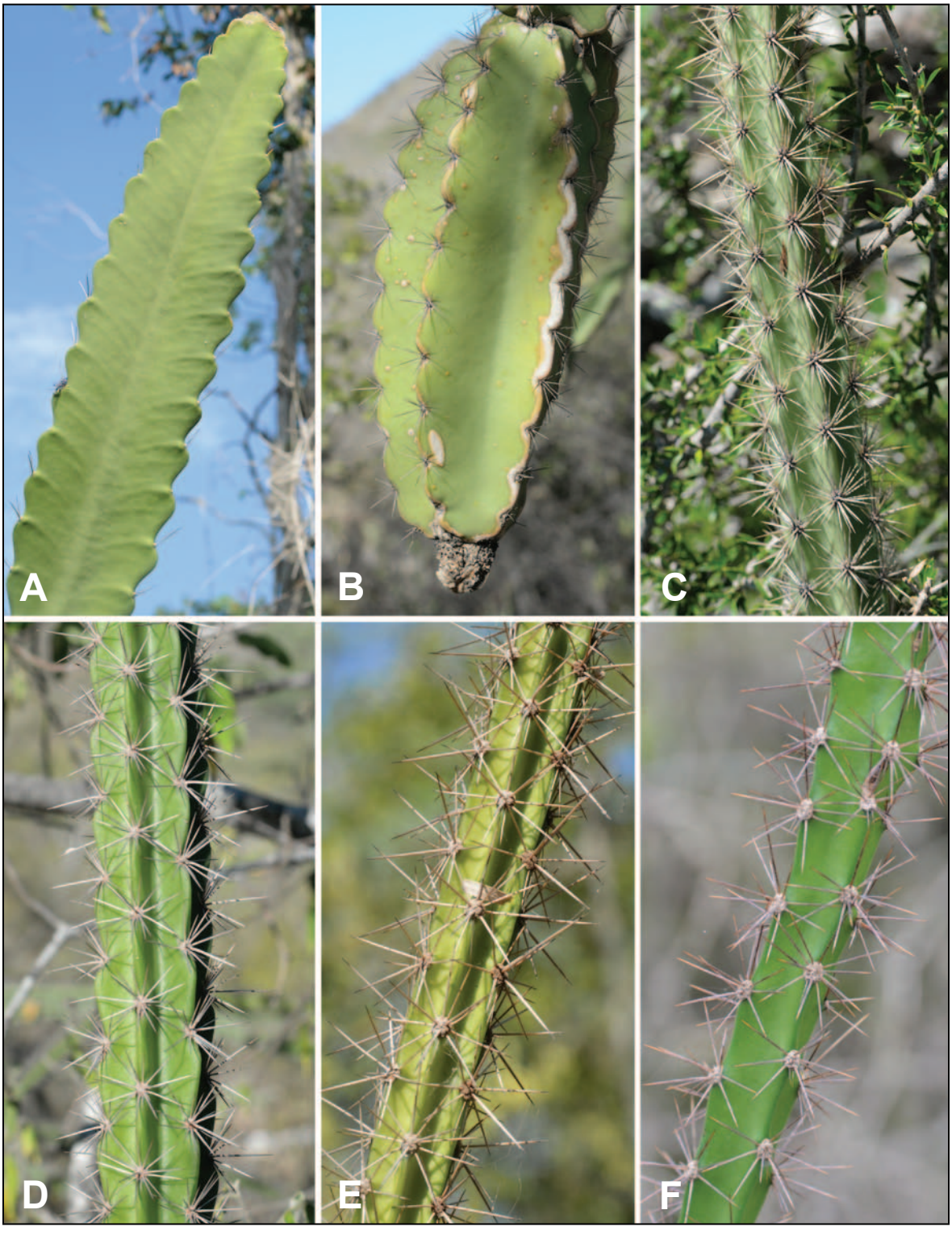


Figure 49. *Leptocereus* stem morphology. **A–***L. undulosus* (*Hoxey* 1965.01). **B–***L. paniculatus* (*Hoxey* 1941.04). **C–***L. demissus* (*Hoxey* 1428.02). **D–***L. velozianus* (*Hoxey* 1941.06). **E–***L. weingartianus* (*Hoxey* 1944.01). **F–***L. rosei* (*Hoxey* 1930.01).

Figure 50. *Leptocereus* stem morphology. **A–***L. bayahibensis* (*Hoxey* 1978.01). **B–***L. cremnophilus* (*Hoxey* 1455.03). **C–***L. septentrionalis* (*Hoxey* 1838.01).

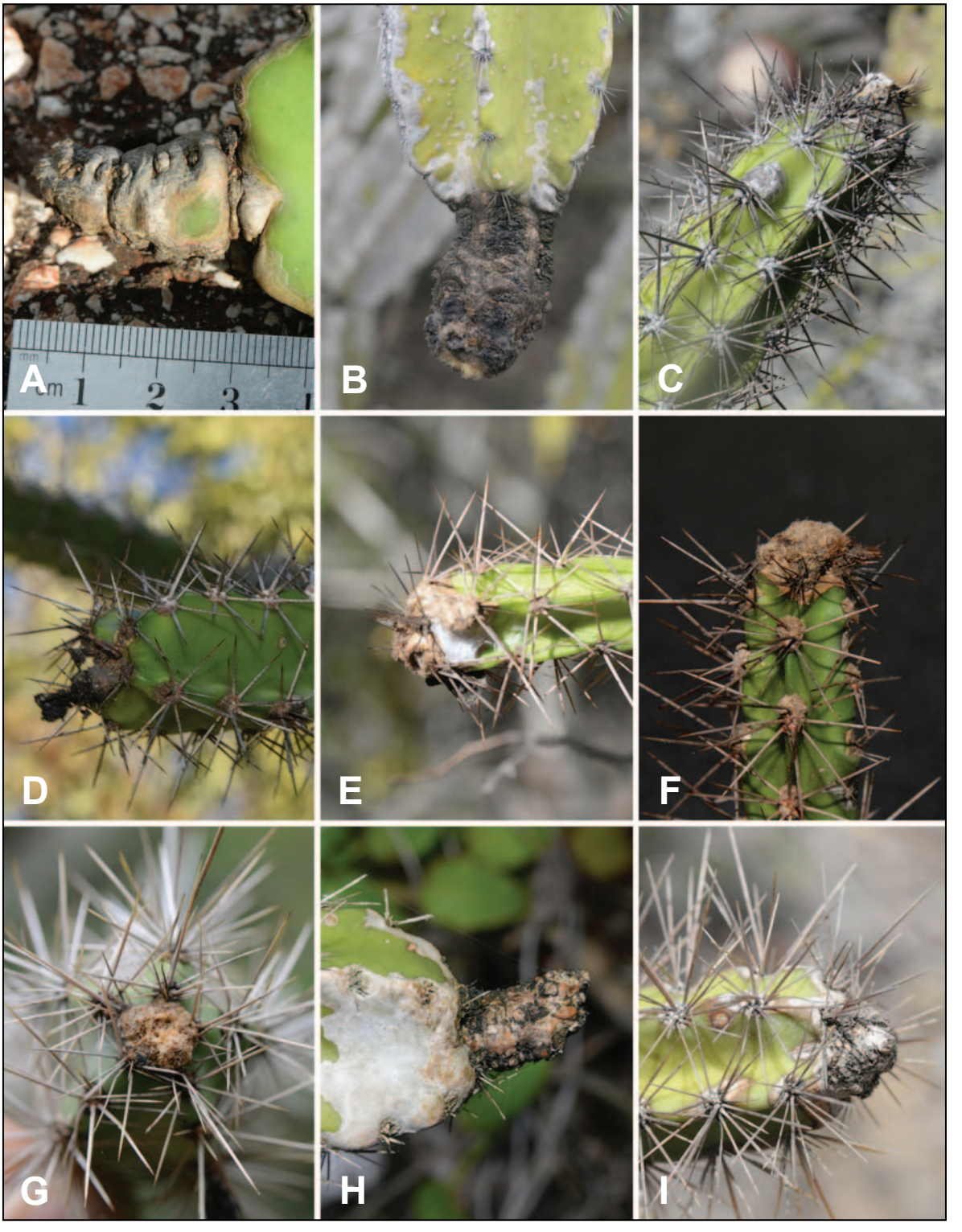


Figure 51. *Leptocereus* terminal brachyblast morphology. **A–***L. undulosus* (*Hoxey* 1435.02). **B–***L. paniculatus* (*Hoxey* 1421.03). **C–***L. demissus* (*Hoxey* 1952.07). **D–***L. velozianus* (*Hoxey* 1939.04). **E–***L. weingartianus* (*Hoxey* 1943.04). **F–***L. rosei* (*Hoxey* 1852.01). **G–***L. bayahibensis* (*Hoxey* 1459.05). **H–***L. cremnophilus* (*Hoxey* 1456.01). **I–***L. septentrionalis* (*Hoxey* 1837.01).

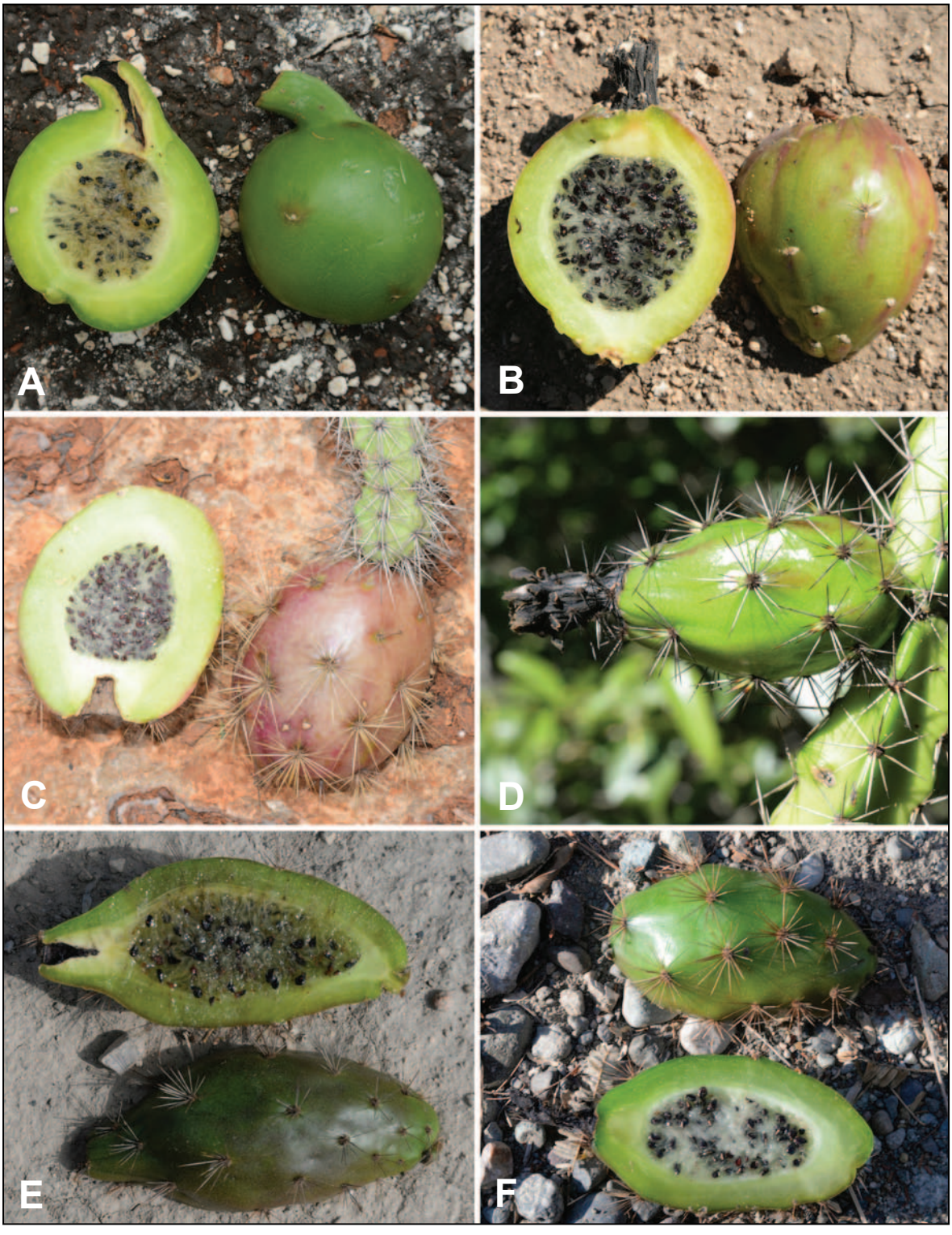


Figure 52. *Leptocereus* fruit morphology. **A–***L. undulosus* (*Hoxey* 1865.01). **B–***L. paniculatus* (*Hoxey* 1308.01). **C–***L. demissus* (*Hoxey* 1956.01). **D–***L. velozianus* (*Hoxey* 1939.04). **E–***L. weingartianus* (*Hoxey* 1944.01). **F–***L. rosei* (*Hoxey* 1930.01).

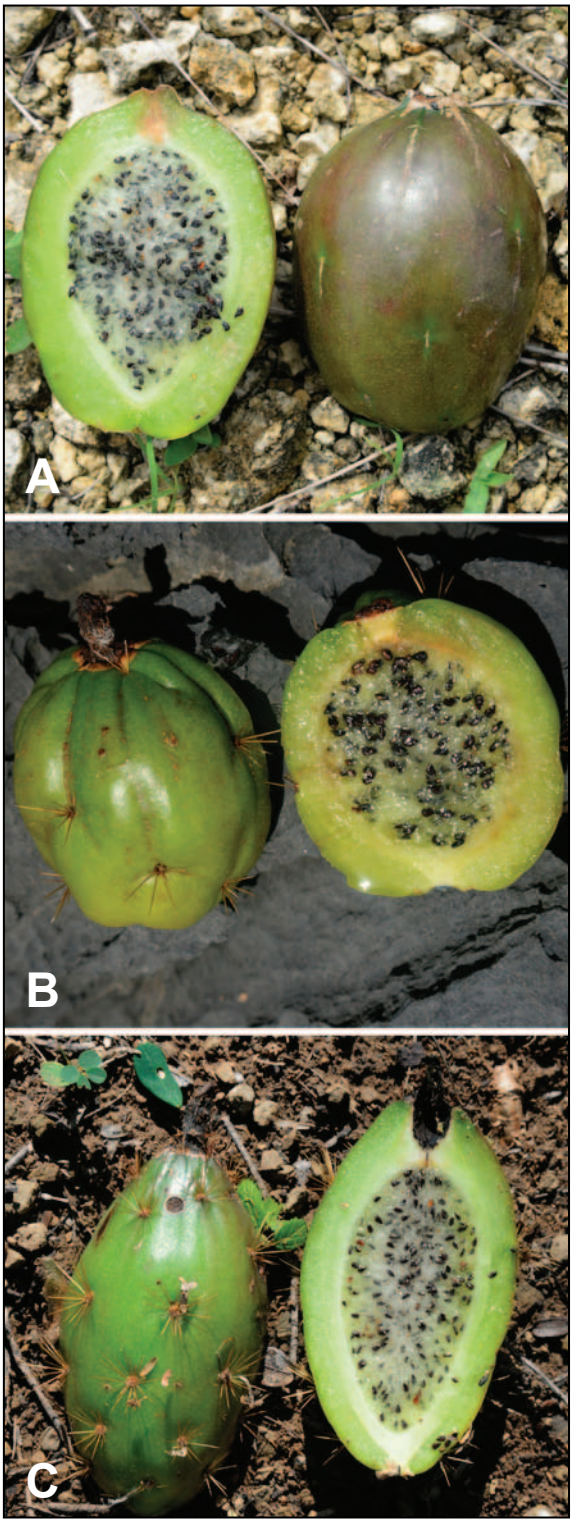


Figure 53. *Leptocereus* fruit morphology. **A–***L. bayahibensis* (*Hoxey* 1979.01). **B–***L. cremnophilus* (*Hoxey* 1842.01). **C–***L. septentrionalis* (*Hoxey* 1970.01).

Department Nord-Ouest. Presqui ile du Nord-Ouest, Port-de-Paix, 5 July 1925, *Ekman* 4572 (*K* 000251793). Môle Saint Nicolas, on the road to Jean Rabel, 19 January 1995, *Areces-Mallea 6815* (NY 00948350, NY 00948379). Môle Saint Nicolas, 60m, 13 January 2017, *Hoxey* et al 81 (GIB). East of Jean-Rabel, 30m, 14 January 2017, *Hoxey* et al 82 (GIB). **DOMINICAN REPUBLIC. Province Monte Cristí.** West of Monte Cristí, 110m, 19 January 2022, *Hoxey & Gdaniec* 117 (GIB)

Morphology

Summary of the Species of Leptocereus on Hispaniola

Table 4 which is split over three pages summarises the key morphological characters of all nine species of *Leptocereus* found on Hispaniola. The tabulated text is supplemented by Figures 49–53 which illustrate stem, flowering brachyblast and fruit morphology for all species.

Acknowledgements

We thank El Medio Ambiente, especially Mercedes Peguero Mendez, Rosanna Guzmán and Victoria Cáceres, for collection permits and CITES papers for this work. We appreciate the collaboration between the Jardín Botánico de Santiago and Gibraltar Botanic Gardens including help facilitating fieldwork and guidance on obtaining all documents. We are grateful to Yuley Encarnacion Piñeyro for permission to visit JBSD to examine and photograph herbarium specimens of cacti and we wish to acknowledge Dr Keith Bensusan (Director Gibraltar Botanic Gardens) for his support of our work in the Caribbean. We are indebted to Keith together with Graham Charles, Nigel Taylor, Roy Mottram and the reviewers, who all supplied useful comments on the manuscript. Additionally, we thank Roy and Graham for supplying images for inclusion in this paper.

The study was funded by a Royal Horticulture Society Bursary, a Cactus and Succulent Society of America Research Grant, a Gibraltar Government Scholarship Grant (PhD), Gibraltar Botanic Gardens and the authors.

References

Acevedo-Rodríguez, P. & Strong, M.T. (2012) Catalogue of seed plants of the West Indies. *Smithsonian Contributions to Botany* **98**: 1–1192.

Alberts, A. (compiler & ed.) (1999) *West Indian iguanas: status survey and conservation action plan*. Gland, Switzerland and Cambridge, UK. IUCN/SSC West Indian Iguana Specialist Group, IUCN.

Anderson, E.F. (2001) *The cactus family*. Portland, Timber Press.

Areces-Mallea, A.E. (2003) *Leptocereus (A. Berger) Britton and Rose: a monographic study of a West Indian genus of Cactaceae (Cactoideae). Inferences from morphological and molecular data.* Ph.D. Thesis. City University of New York, New York.

Areces-Mallea, A.E. (2017) *Leptocereus demissus*, a new species from southwestern Hispaniola. *Cactus and Succulent Society Journal (US)*, DR(3): 115–121.

Backeberg, C. (1955) *Dendrocereus* and *Neoabbottia*. *Cactus and Succulent Society Journal (US)* **27**(2): 48–53.

Backeberg, C. (1958–1962) *Die Cactaceae, Handbuch der Kakteenkunde*. Jena, Gustav Fischer Verlag.

Barker, H.D. & Dardeau, W.S. (1930) *Flore d'Haiti*. Port-au-Prince, Haiti.

Barthlott, W. & Hunt, D.R. (2000) Seed diversity in the Cactaceae subfamily Cactoideae. *Succulent Plant Research* **5**: 1–173.

Barrios, D., Arias, S., González-Torres, L.R. & Majure, L.C. (2020) Phylogeny and taxonomy of the genus *Leptocereus* (Cactaceae) inferred from chloroplast markers and morphoanatomical evidence. *Plant Systematics and Evolution* **306**(63): 1–15.

Barrios, D., & Majure, L. C. (2022). Types and typifications of the Antillean endemic genus *Leptocereus* (Cactaceae). *Brittonia* **74**(3): 219–226.

Barrios, D. and Mancina, C.A. (2017) *Dendrocereus nudiflorus* (Cactaceae): pasado, presente y futuro de un anacronismo en peligro de extinción según modelos de nicho climático. *Revista del Jardín Botánico Nacional* **38**: 119–132.

Berger, A. (1905) A systematic revision of the genus Cereus Mill. *Missouri Botanical Garden Annual Report* **16**: 57–86.

Berger, A. (1929). *Kakteen: Anleitung zur Kultur und Kenntnis der wichtigsten eingeführten Arten*. Stuttgart, E. Ulmer.

Britton, N.L. & Rose, J.N. (1909) The genus *Cereus* and its allies in North America. *Contributions from the United States National Herbarium* **12**(10): 413–437.

Britton, N.L. & Rose, J.N. (1920) *The Cactaceae. Descriptions and illustrations of plants of the cactus family* **2**. Washington, Carnegie Institute.

Britton, N.L. & Rose, J.N. (1921) *Neoabbottia*, a new cactus genus from Hispaniola, with four plates. *Smithsonian Miscellaneous Collections* **72**(9): 1–6.

Britton, N.L. & Rose, J.N. (1925) The Tree-cactuses of the West Indies. *Journal of the New York Botanical Garden* **26**(310): 217–221.

Burman, J. (1755–1760) *Plantarum americanarum. Amstelaedami,* Sumtibus Auctoris.

Censky, E.J., Hodge, K. & Dudley, J. (1998) Over-water dispersal of lizards due to hurricanes. *Nature* **395**: 556.

De Fraine, E. (1910). The seedling structure of certain Cactaceae. *Annals of Botany* ***24****:* 125–175.

Ekman, E.L. (1928) Plants Observed on Tortue Island, Haiti. *Arkiv för Botanik* **22A**(9): 1–61.

Ekman, E.L. (1930) A list of plants from the island of Gonâve, Haiti. *Arkiv för Botanik* **23A**(6): 1–73.

Fleming, C.D. (1984) Notes on some cactus species of the Dominican Republic. C*actus and Succulent Journal (US)* **56**(3): 125–130.

García, R. & Castillo, D. (1994) Ecologia, status y usos de *Neoabbottia paniculata* (Cactaceae) Endemica de la Isla Española. *Moscosoa* **8**: 53–64.

García, R., Mejía, M., Peguero, B., Salazar, J. & Jiménez, F. (2002) Flora y vegetación del Parque Nacional del Este, República Dominicana. *Moscosoa* **13**: 22–58.

Guiggi, A. (2020) New Circumscription and Combinations in the tribe *Leptocereae* Buxbaum *sensu G*uiggi (C*actaceae-Cactoideae*) from the Caribbean Region. C*actology* **5** (Supplement 9): 1–6.

Guiggi, A. (2021) New Combinations in the Re-evaluated Tribe L*eptocereae B*uxbaum *sensu* Guiggi (C*actaceae-Cactoideae*) from Dominican Rep. C*actology* **5** (Supplement 12): 2.

Guiggi, A. & Mariotti, M. (2019) J. N. Rose exsiccata collection (Cactaceae) in Herbarium Mortolensis (HMGBH): Revision and typification. *Bradleya* **37**: 191–200.

Hartmann, E. (1904) C*ereus weingartianus* E. Hartm. (nova species), in E. Dams Von der Kakteen-Ausstellung in Düsseldorf. *Monatsschrift fur Kakteenkunde* **14**(1): 155–158.

Hernández-Hernández, T., Hernández, H.M., De-Nova, J.A., Puente, R., Eguiarte, L.E. & Magallón, S. (2011) Phylogenetic relationships and evolution of growth form in Cactaceae (Caryophyllales, Eudicotyledoneae). *American journal of botany* **98**(1): 44–61.

Hunt, D.R. (1979) *The Genera of the Cactaceae* reprinted from Hutchinson, J. (1967) *The Genera of Flowering Plants* 2: 427–467. Oxford, Oxford University Press.

Hunt, D.R. (2006) *CITES Cactaceae checklist. Third Edition. Kew,* Royal Botanic Gardens.

Hunt, D.R. & Taylor, N.P. (1986) The genera of the Cactaceae: towards a new consensus. *Bradleya* **4**: 65–78.

Hunt, D.R. & Taylor, N.P. (1990) The genera of the Cactaceae: towards a new consensus. *Bradleya* **8**: 85–107.

Hunt, D.R. & Taylor, N.P. (1991) Notes on miscellaneous genera of Cactaceae. *Bradleya* **9**: 81–92.

Hunt, D.R., Taylor, N.P. & Charles, G. (eds.) (2006a) *The New Cactus Lexicon. Text.* Milborne Port, England, dh Books.

Hunt, D.R., Taylor, N.P. & Charles, G. (eds.) (2006b) *The New Cactus Lexicon. Atlas of Illustrations.* Milborne Port, England, dh Books.

Lamarck, J.B. (1783–1785). *Dictionnaire encyclopédique de botanique. Tome Premier.* Paris.

Leuenberger, B.E. (1984) *Neoabbottia paniculata* (Lam.) Britton & Rose. *Kakteen und Andere Sukkulenten (Berlin)* **35**(5): 104–105.

Lodé, J. (2015) *Taxonomy of the Cactaceae* **1**. Barcelona, Spain, Editions Cactus Adventures.

Majure, L.C., Encarnación, Y., Clase, T., Peguero, B., Ho, K. & Barrios, D. (2021) Phylogenetics of *Leptocereus* (Cactaceae) on Hispaniola: clarifying species limits in the *L. weingartianus* complex and a new species from the Sierra de Bahoruco. *PhytoKeys* **172**: 17–37.

Marshall, W.T. (1937) Notes by Wm. T. Marshall in Cuban Cacti (ed. De Giménez, E.C.). C*actus and Succulent Journal (US)* **9**(1): 12–13.

Marshall, W.T., Bock, T.M. & Haselton, S.E. 1941. C*actaceae: With Illustrated Keys of All Tribes, Sub-tribes and Genera*. Pasadena, Abbey Garden Press.

Mauseth, J.D., Terrazas, T. & Loza-Cornejo, S. (1998) Anatomy of relictual members of subfamily Cactoideae, IOS Group 1a (Cactaceae). *Bradleya* **16**: 31–43.

Moscoso, R.M. (1941) Las Cactáceas de la Flora de Santo Domingo. *Anales da la Universidad de Santo Domingo* **5**(1): 58–90.

Moscoso, R.M. (1943) C*atalogus Florae Domingensis. Parte 1. Spermatophyta*. New York, Universidad de Santo Domingo.

Mottram, R. (2002) Charles Plumier, the King's Botanist–his life and work. With a facsimile of the original cactus plates and text from *Botanicon Americanum* (1689–1697). *Bradleya* **20**: 79–120.

Mottram, R. & Hoxey, P. (2020) An evaluation of the cacti of Charles Plumier (1646–1704). *The Cactician* **13**: 1–99.

Pasachnik, S.A. & Martin-Velez, V. (2017) An evaluation of the diet of Cyclura iguanas in the Dominican Republic. *Herpetological Bulletin* **140**: 6–12.

Plumier, C. 1689–1697. B*otanicon Americanum seu historia plantarum in Americanis insulis nascentianum* **1–30**. Paris, Paris Natural History Museum.

Reppenhagen, W. (1979) Karibische Impressionen 2. Haiti und seine Kakteen. *Kakteen und Andere Sukkulenten (Berlin)* **30**(1): 16–19.

Salazar, J., Peguero, B. & Veloz, A. (2000) Flora de la Península de Samaná, República Dominicana. *Moscosoa* **11**: 133–188.

Schumann, K. (1897–1898) *Gesamtbeschreibung der Kakteen (Monographia Cactacearum)*. Neudamm, J. Neumann.

Spencer, J. L. (1955). A cytological study of the Cactaceae of Puerto Rico. *Botanical Gazette* **117**(1), 33–37.

Taylor, N.P. (2021). Notes on cultivated *Pereskia quisqueyana* and related species (Cactaceae). *Bradleya* **39**: 69–110.

Taylor, N.P., Hoxey, P., & Gdaniec, A. (2021). *Dendrocereus* Britton & Rose – one species or two?. *Bradleya* **39**: 16–22.

Turland, N.J., Wiersema, J.H., Barrie, F.R., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Kusber, W., Li, D., Marhold, K., May, T.W., McNeill, J., Monro, A.M., Prado, J., Price, M.J. & Smith, G. (2018) *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017*. Koeltz Botanical Books.

Urban, I. 1920–1921. Flora Domingensis. *Symbolae Antillanae* **8**: 1–860.

Veloz, A. & Peguero, B. (2002) Flora y Vegetación del Morro de Montecristi, República Dominicana. *Moscosoa* **13**: 81–107.

Weingart, W. (1905) Cereus Weingartianus E. Hartm. *Monatsschrift für Kakteenkunde* **15(1):** 8–9.

Werdermann, E. (1931) Die von E.L. Ekman in Westindien, besonders auf Cuba und Hispaniola gesammelten Cactaceae. *Repertorium specierum Novarum Regni Vegetabilis* **29**: 222–243.