

# NEOHAITICEREUS

## A NEW SUBGENUS FOR THE REDISCOVERED *CEREEAE* DEPICTED IN PLUMIER'S PLATE 26 OF THE *BOTANICON AMERICANUM*

In 1998 herbarium and field studies in the West Indies resulted in the rediscovery of the baffling Haitian *Cereeeae* depicted in Charles Plumier's plate 26 of his *Botanicon Americanum* (1689–1697). Typified upon Burman's copied tab. 195, f. 1 corresponding to Plumier's famous plate 26, this species was named and described in 1830 under *Cereus* by A. H. Haworth as *C. serruliflorus*. It was always difficult to accommodate this cactus among the subgenera of *Cereus* as circumscribed in eds. Hunt & Taylor (1990, 1992). Consequently, a new subgenus of *Cereus* is hereby proposed for this taxon, *Neohaiticereus*, alluding to Haiti, its only site of occurrence. With a unique combination of fluted, mucilaginous stems with 10 to at least 17 ribs; flowers striate-angled, recurved, with long-exserted style and stamens; indehiscent fruits that are pendant at maturity and enclose rostrate seeds with a papillose-tuberculate exotesta lacking interstitial pits, *Neohaiticereus* stands as a monospecific subgenus of *Cereus*. A detailed morphological description of this taxon is provided in addition to accounts of palynology, seed and epidermal surface morphology. *Cereus haitiensis* Franck & Peguero (2017) is treated as a synonym of Haworth's earlier name *C. serruliflorus*.

**Keywords:** West Indies, Haiti, Cactaceae, *Cereus* (subg. *Neohaiticereus*) *serruliflorus*

### Introduction

During the 17<sup>th</sup> century, many missionaries were nature-loving enthusiasts who visited faraway lands with the aim of studying the biological world without neglecting their religious duties. One of these missionaries with an extraordinary flair for plants was Friar Charles Plumier (1646–1704), a noble member of the Franciscan Catholic monastic order of Minimists. Commissioned by the French authorities of his time, Plumier visited the Caribbean Islands in the late 17<sup>th</sup> century, mainly between 1689 and 1695.

On his second voyage, in 1693, Plumier traveled extensively in what is now the Republic of Haiti, where he collected, described and depicted numerous new, outlandish trees, shrubs and herbs, among which there were several remarkable cacti. Plumier's plant collections were seemingly lost at sea, but a vast number of his sketches and illustrations survived to modern times. Excellent accounts of the life and contributions of this remarkable 17<sup>th</sup> century monk can be found in Urban (1920), and more recently in Mottram (2002).

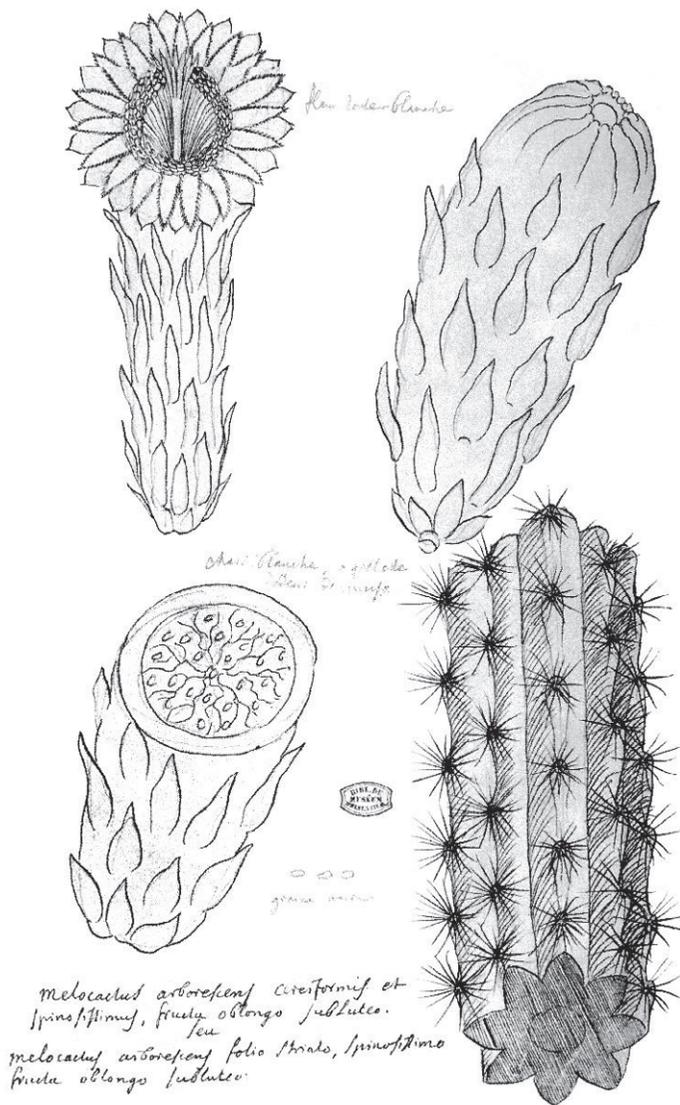
Plumier's botanical masterpiece was his still unpublished *Botanicon Americanum* (1689–1697), an eight-volume collection of hand-written texts and 1219 plates currently kept at the Museum of Natural History in Paris. Because of the enormous value of the informa-

tion contained in this *magnus opus*, several arrays of handmade copies of plants portrayed in his *Botanicon* were made in the eighteenth century, one of the best known was the so-called *Codex Boerhaavianus*, a set of 508 drawings now deposited in the library of the University of Groningen in the Netherlands. Other copies were acquired by the Royal Botanical Gardens at Kew, U.K., and the British Museum (Natural History).

The *Codex Boerhaavianus* was eventually acquired by the Dutch botanist Johannes Burman to be used as a prime reference for his *Plantarum Americanum Fasciculus*, a descriptive treatise of selected West Indian plants published between 1755 and 1760 containing a set of 262 plates issued in 10 parts. Since Burman did not have access to Plumier's original text, he accompanied the drawings copied from Boerhaave's *Codex* with his own botanical descriptions. In the absence of preserved plant material, Burman's copies gained much appreciation because they were the only ones truly available to the most notorious botanists of the eighteenth and nineteenth centuries, except for Lamarck, who worked directly with the original drawings of Plumier. Many of Burman's plates, all circuitously copied from the plants that were originally depicted by Plumier, served as types for the taxa that they represented.

The identification of the 24 cactus taxa originally illustrated by Plumier — or their handmade copies — has occupied famous scholars such as Linnaeus (1753), Lamarck (1783–1785), Haworth (1830), and De Candolle (1828). This arduous task continued through

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**1.** The polemical plate 26 (vol. 6) of Plumier's *Botanicon Americanum* depicting an open flower with serrulate, acuminate perianth segments and two young fruits, one of them sectioned. Compared to the live material, the bract-scales of both flower and immature fruits look exceedingly large.

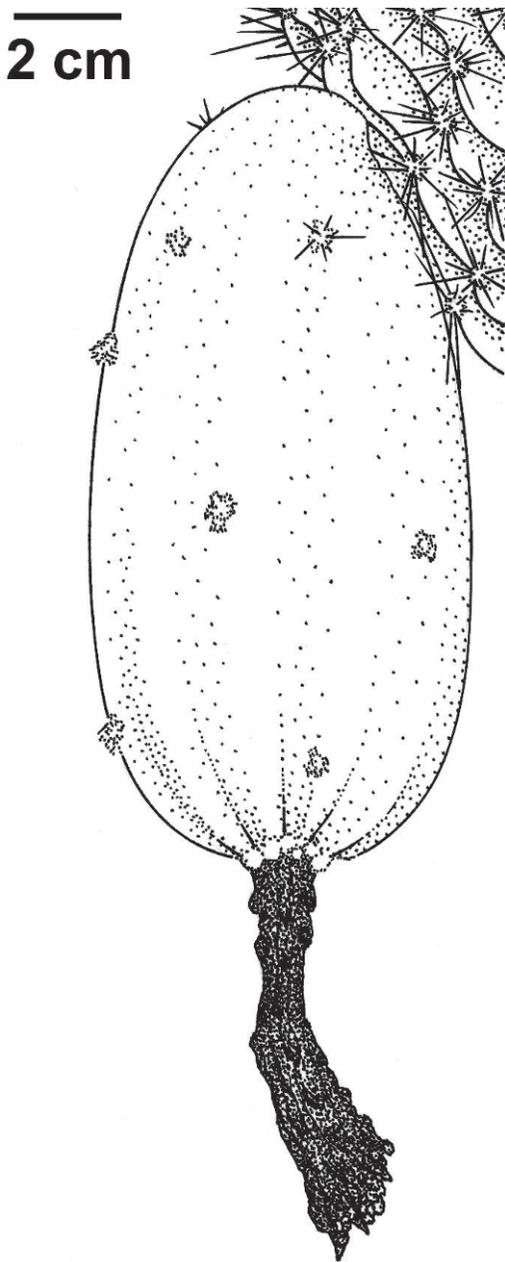
the twentieth century with Urban (1902, 1920), Britton and Rose (1919–1923), Hunt (1984), Lourteig (1991), and Mottram (2002). Although to this day much has been accomplished, the depiction of some confusing flower and fruit characters in various plates has prevented their definite identification. Mottram (2002) speculated that Plumier eventually had to call upon his memory to complete some of his schematic drawings.

Modern-day identification of plate 26 in volume 3 of Plumier's *Botanicon Americanum*, doubtfully assumed by some contemporary botanists to portray a

*Harrisia* species from Haiti and not a different *Cereus*-related genus, is an example of depiction that required corroboration. To make the *Harrisia* hypothesis plausible, Hunt (1984: 43) assumed that Plumier may have mistakenly drawn the stamens of a section of a flower-bud as though they were ovules (or seeds) embedded in a funicular matrix (Fig. 1), and Mottram later subscribed to this opinion (Mottram 2002). Hunt himself did not seem very convinced of his assumption when he commented (1984: 40) that the identity of plate 26 “urgently require verification.” What if Plumier was right and what Hunt and Mottram believed to be a sectioned flower was, in fact, an elongated young fruit with all its bract scales — exaggeratedly depicted — still attached? If we just consider the original written description accompanying plate 26: *Melocactus arborescens folio striato spinosissimo fructu oblongo subluteo*, we must conclude that the drawings cannot represent a *Harrisia* species for the reason that there is no *Harrisia* with oblong, elongated fruits (Britton & Rose 1920; Areces-Mallea, 1980; Franck, 2012; Fig. 2).

The mysterious plant portrayed in Plumier's plate 26 (corresponding to 159, 3: 53 in the Kew copy, and 188, tab. 195, f. 1 in Burman's *Plantarum Americanum*) was named and described according to modern taxonomic rules under *Cereus* by A. H. Haworth (1830), as *C. serruliflorus*.

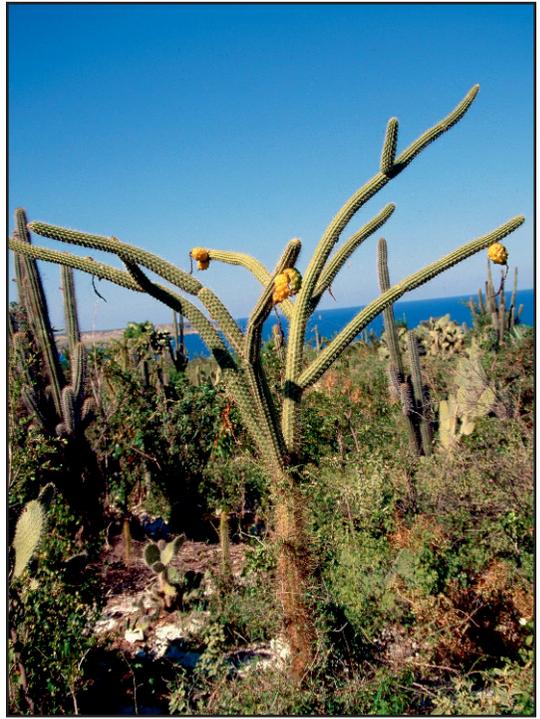
The type of the species was based upon Burman's copied tab. 195, f. 1. Convinced that this plant was a *Harrisia* (doubtless because of its “*Harrisia*-like” fluted stems), Lourteig (1991) combined Haworth's “*Cereus*” with this genus, becoming *Harrisia serruliflora*, a dubious taxon that has remained controversial ever since (A. R. Franck did not recognize the species in his 2012 synopsis of the genus *Harrisia*). Mottram (2002: 90) considered plate 26 to correspond with *Harrisia divaricata* (Lam.) Backeb., a true *Harrisia* species earlier described by Lamarck (1785) with nearly rounded fruits that are strongly tuberculate in youth. The fruit



2. Mature pendant fruit of the rediscovered *Cereae* of NW Haiti, with its apex sinuate-folded like Plumier's depiction of plate 26. Drawing by the author from a fruiting specimen at Môle St. Nicolas.

features of *H. divaricata* from Hispaniola, clearly and separately depicted in Plumier's plates 23 and 24 of the *Botanicon*, and in Burman's 187, tab. 193 of his *Plantarum Americanum*, exclude the possibility of plate 26 being conspecific with this taxon (Figs. 3–4).

Curiously, by mid nineteenth century, a *Harrisia*-like cactus collected overseas was being cultivated in the Botanical Garden at Caen, France. In 1843 — or



3. *Harrisia divaricata* (Lam.) Backeberg. Habit of a fruiting specimen in the dry coastal terraces of Môle St. Nicolas, NW Haiti. Corresponds to Plumier's plate 3:23.



4. *Harrisia divaricata* (Lam.). Mature, nearly spherical fruit on a plant growing along the banks of the Yaque del Norte river in the Dominican Republic, near the Haitian border. Corresponds to Plumier's plate 3:24.

perhaps earlier — a similar plant was reported to be in cultivation in the cactus collection of the French botanist M. de Monville (1794–1863). Lacking flowers or fruits, this notable 17–19-ribbed plant was described as *Cereus hermentianus* by Monville (1859), who named it after M. Herment, at the time the chief-gardener in Caen. Nearly forty years later, C. A. Lemaire transferred Monville's species to the genus *Pilocereus*



5. Fruit of *Cereus repandus* at Curaçao, Netherlands Antilles.

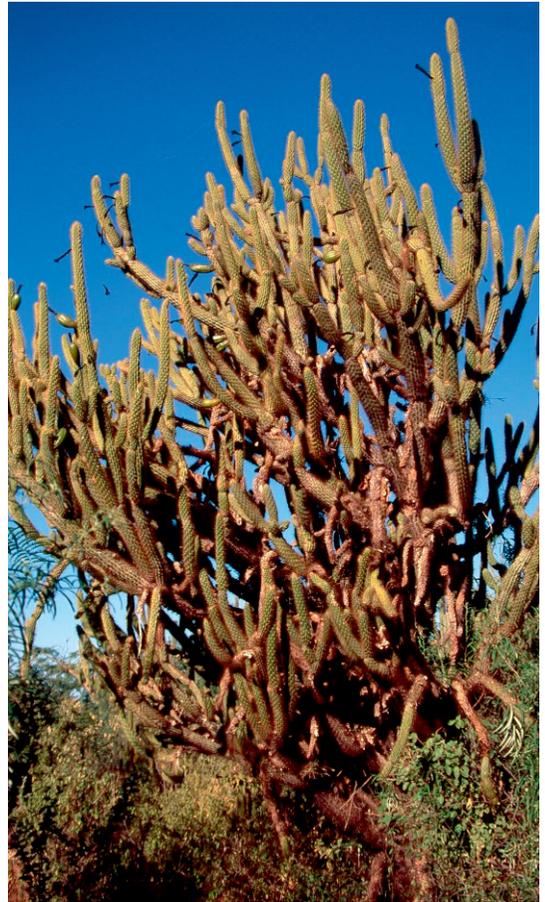
(Weber, 1898). According to Weber (1898), *Pilocereus hermentianus* (Monv.) Lem. was originally gathered in Haiti, a former French colony.

Since the genus *Pilocereus* was untenable, being based upon the same type as *Cephalocereus*, Monville's puzzling plant was successively re-named *Cephalocereus hermentianus* (Monv.) Britton and Rose (1909), and *Pilocereus hermentianus* (Monv.) Byles and Rowley (1957). To this day, the binomial *Cereus hermentianus* has not been applied with certainty to any live or preserved cactus specimen, a reason why the World Checklist of Selected Plant Families still refers to it as an "unresolved name."

It seemed as though Britton and Rose (1919–1923) doubted the existence of a "19-ribbed cactus" in Hispaniola, in both Haiti and the Dominican Republic, but nevertheless admitted the possibility that further explorations on the island may prove its occurrence there. In 1920 W. L. Abbott and E. C. Leonard spent time gathering cacti for Britton and Rose (1921) in the Haitian Cul-de-Sac region, an arid plain east of Port-au-Prince where Plumier had extensively collected. Despite all efforts, Abbott and Leonard could not locate the mysterious 19-ribbed *Cereaceae*.

## 20<sup>th</sup> century collections

In 1925, shortly after Britton and Rose published *The Cactaceae* (*op. cit.*), the intrepid Swedish botanist E. L. Ekman apparently found the elusive plant at two different locations, one of which, the Cul-de-Sac plain, was the very same place where Plumier seemed to have encountered it in the late 17<sup>th</sup> century. This locality had been previously explored, though unsuccessfully, by Abbott and Leonard five years earlier. Although Ekman's 11–14-ribbed specimens nos. 4446 and 5377 matched many characters depicted by Plumier in



6. Ramoso habit of an old 5 m tall tree of Plumier's masked *Cereaceae* of plate 26, at Môle St. Nicolas.

plate 26 and corresponded well with the description of Monville's *Cereus hermentianus*, no one at the time suggested a possible connection among them. Werdermann (1931), who specifically studied Ekman's findings in Haiti, associated these plants with *Cereus repandus* (L) Miller, a very different columnar cactus from the Netherlands Antilles, Grenada and northwestern South America, with dark-red fruits and thicker stems 10 to 20 cm. in diameter (Fig. 5).

Among the last 20<sup>th</sup> century scholars to collect the Haitian veiled cactus was E. C. and G. M. Leonard, who, in 1929, saw fertile specimens on the same remote cape — now called Môle St. Nicolas — where Columbus landed on 6 Dec. 1492 during his first voyage to the New World. Leonard and Leonard annotated on their collected specimens n. 13311 and 13682, now deposited at the U.S. National Herbarium, that their elongated fruits were yellow and pendant at maturity, a very distinguishing feature of this taxon. However, the specimens were determined to be *Cephalocereus nobilis* (Haworth) Britton and Rose,



7. Relatively slender, fluted stem segment of the same plant shown in Fig. 6.

an identity that was reaffirmed in 1969 (as *Pilosocereus nobilis* (Haworth) Byles & Rowley) in a US herbarium note by D. H. Nicolson and R. A. Defilippis. Whether being or not conspecific with *P. royenii* (L.) Byles & Rowley, *P. nobilis* cannot correspond to Plumier's plant because it has strongly ribbed stems, densely hairy flowering areoles, and very different, reddish, depressed-globose fruits. After Leonard & Leonard, only two other collections were made in Môle St. Nicolas before the end of the 20<sup>th</sup> century: one by T. Zanoni *et. al.* in 1985 who thought he had collected a *Harrisia* species, and that of myself, in 1998.

While working at the New York Botanical Garden, I came across Ekman's and Leonard's Haitian collections deposited in Stockholm (S) and Washington D.C. (US) respectively. In examining them, I knew that the only way to fully understand their identity, and perhaps decipher the mystery behind Plumier's controversial plate 26, was to travel to northwestern Haiti and collect living specimens for study. Opportunity arose in Dec. 1998 to explore Môle St. Nicolas and the dry coastal terraces



8. Close-up of a stem segment showing the crenate rib edges bearing areoles in the depressions.



9. Nyctigamous flower of *Cereus* (subg. *Neohaiticereus*) *serruliflorus* during maximum anthesis. Photographed by the author at Môle St. Nicolas on Dec. 28, 1998.



10. Erect, immature fruit showing the typical keels that run longitudinally on its surface.

between the Môle and Jean Rabel, in the *Département du Nord-Ouest* of Haiti. To my surprise, the multi-ribbed cactus with fluted stem segments and elongated fruits not only existed, but it was rather common in the mostly cut-over dry forests and thickets of the Môle

Table 1. Differences between the Haitian *Cereus* subg. *Neohaiticereus* Areces and *Cereus* subg. *Oblongicarpi* (Croizat) Hunt & Taylor.

Character		<i>Neohaiticereus</i> , subg. nov.	<i>Cereus</i> , subg. <i>Oblongicarpi</i>
Habit		Densely branched tree, very ramose	Tree-like with upright branches, not very ramose, or sparsely branched shrub
Stem segments		Relatively slender, fluted, highly mucilaginous	Rather thick and sturdy, lacking mucilage
Ribs		Numerous (up to 17), very low, not cross-furrowed	Few, elevated, markedly cross-furrowed
Stem areoles		Tufted when young with a pale yellow felt but no trichomes	Provided with long trichomes in youth
Flowers	Shape	Recurved, slightly or not constricted above the pericarpel	Straight or nearly so, noticeably constricted and forming a well-defined zone above the pericarpel
	Tube and pericarpel	Striate-angled, scales bearing tufts of white axillary wool	Terete in cross-section, scales with naked axils
	Perianth limb	Relatively wide, their segments linear to narrowly triangular, tapering gradually towards the tip	Narrow, their segments rectangular to oblanceolate, rounded, obtuse or acute at apex
	Stamens	Extended 1–1.7 cm beyond the floral throat	Stamens and style at the floral throat level or slightly exerted, otherwise inserted
	Style	Long-exserted, to 2.5–4.2 cm beyond the floral throat	Short-exserted, less than 1 cm beyond the floral throat
Fruits	Color and disposition	Yellow and pendant at maturity	At maturity green or greenish, and erect
	Surface	marked with small longitudinal keels separated by round sinuses	Lacking longitudinal keels and sinuses
	Spination	Sometimes with clusters of 5–15 spines on their lowermost areoles	Always unarmed
	Funicular pulp	Greenish-gray to grayish, very mucilaginous	White, not mucilaginous
	Floral remains	Persisting to maturity	Deciduous (but persisting in controversial <i>Cereus mortensenii</i> )
Seed exotesta		Papillose-tuberculate, lacking interstitial pits	Not papillose-tuberculate, with interstitial pits

area. Fortunately, my arrival in the 27 Dec. coincided with a massive blooming of the population (Figs. 6–10).

The ensuing collection of live material and consequent study of Môle St. Nicolas's population proved that it corresponded to the puzzling plant pictured in Plumier's plate 26 and tab. 195, f. 1 of Burman's *Plantarum Americanum*. The floral pericarpel, and the greenish developing fruits, both of which are patently elongated, bear bract-scales a bit like the ones shown in the mentioned drawings, though the size of the scales in the artwork is totally exaggerated (artistic license on a rather sketchy illustration or calling upon a mixed-up memory to complete the drawing?). As the young fruit enlarges and matures, the bract-scales tend to wither away and often drop; the full-grown fruits gradually turn from green to a vivid citrine-yellow color. At this point they start to lean down by gradual softening of their bases, until

they hang vertically on the stems, a position that they maintain for quite some time (Fig. 2). This is a distinguishing feature that was not recorded by Plumier probably because he never got to see fully ripened fruits, only "*subluteus*" — sub-yellow, unripe ones, perhaps with their tiny bract-scales still attached. The assumption that the sectioned organ in the famed Monk's depiction of plate 26 is a flower-bud and not a young (green) fruit with its bract-scales still in place, is misleading and erroneously favored the *Harrisia* hypothesis.

Since most vegetative characters of the 1998 Môle St. Nicolas collection matches well the original description of Monville's *Cereus hermentianus*, I am most inclined to consider it conspecific with this 17–19-ribbed taxon, at present dubiously referred to as *Pilosocereus hermentianus* (Monv.) Byles and Rowley (1957). The greatest number of ribs I could count in

the stem segments of all 13 live individuals examined at the Môle was 17, but since this character is a bit variable, it is by no means impossible that larger sampling of the population will yield the higher count of 19 referred to by Monville (1859). Nevertheless, the binomial *C. hermentianus* cannot be used to nominate the species because Haworth (1830) provided an earlier name (*Cereus serruliflorus*) for the plant portrayed in tab. 195, f. 1 of Burman's *Plantarum Americanum*, which obviously corresponds to Plumier's famous plate 26.

### Generic affiliation

The genus *Cereus* Miller (1754), to which the outlandish *Cereaceae* from Môle St. Nicolas has been referred to by some authors, was treated by the IOS Working Party with rather ample generic limits to contain, in subgeneric combinations, four other genera: *Subpilocereus*, *Monvillea*, *Ebneria* and *Mirabella* (Hunt & Taylor, eds., 1992). This complex ranges from northern South America and nearby islands, to northern, eastern and southern Brazil, Uruguay and Paraguay, from sea level, through eastern Andes of northern Argentina and Bolivia at up to 2,600 m.

The Haitian taxon has medium-sized flowers and elongated fruits which are to some extent evocative of those of *Cereus* subgen. *Oblongicarpus*, as circumscribed by Hunt & Taylor, 1992, but this resemblance is superficial. In some important respects, Plumier's plant differs substantially from all members of this subgenus (see Table 1). Nonetheless, if by subscribing to the broadening trend of *Cereus* adopted by Hunt & Taylor (1992) we were to conserve this cactus in *Cereus s. lat.*, it would have to be within a subgenus of its own. Because it does not tie in with any recognized subgenera of *Cereus*, it is proposed as a new one, *Neohaiticereus*, alluding to its only site of occurrence. With a unique combination of slender, fluted, internally highly mucilaginous stems; 10 to at least 17 notably low, crenate ribs; flowers recurved, striate-angled on surface, with serrulate segments and exceedingly long-exserted style and stamens; indehiscent fruits that are cylindrical and pendant at maturity, with small, rather deciduous bract scales subtending woolly areoles that may eventually bear clusters of 5–15 spines in their lowermost areoles, and a fruit containing a very mucilaginous, greenish-gray funicular pulp enclosing dark brown rostrate seeds with a papillose-tuberculate exotesta lacking interstitial pits, subgenus *Neohaiticereus* vindicates its claims to independent standing among other *Cereus* to include an isolated species constrained to NW and Central Haiti.

That it characterizes another supra-specific unit of the astounding cactus flora of the West Indies, cannot be doubted.

### *Cereus* Miller 1754 subgen. *Neohaiticereus* Areces, subgen. nov.

*Inter subgenera genus Cereus* Miller 1754 *sensu* Hunt & Taylor 1992 *squamae florum parvae carnosae et fructibus elongatis ad subgen. Oblongicarpus* (Croizat) Hunt & Taylor 1992 *accedens, sed rami teretes extus striati costis redactis, floribus arqualis tubo atque pericarpello demum striato-angulatis, stylis perigonium nimis superantibus, fructibus maturis pendulis seminibus haud foveatis sed undique dense papilloso-tuberculatis ab ea recedens.*

*Typus subgeneris: Cereus serruliflorus* Haw. *species adhuc unica*, C. Plumier vol. 3, pl. 26 *Bot. Am.*, ramus exclusus.

*Cereus serruliflorus* A. H. Haworth *Phil. Mag.* 37: 113, 1830.

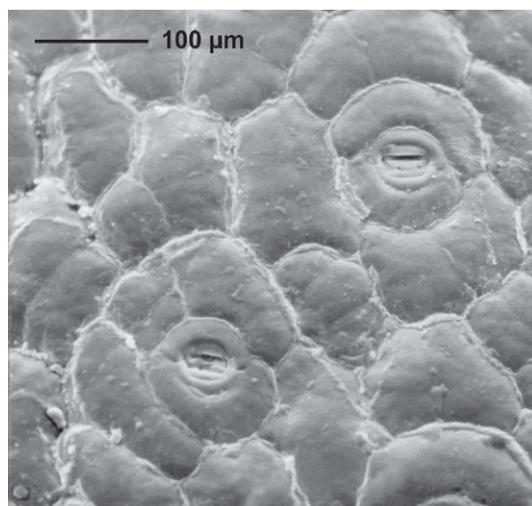
**Neotype**, here designated: HAITI. Grand Cul de Sac, between Port-au-Prince and Léogane, in hot, dry woods. Plant portrayed in September 1689–1690, or 1693, by Charles Plumier in plate 3: 26 of his *Botanicon Americanum*, with the exclusion of the drawing of the *Harrisia*-like stem segment, to avoid confusion.

**Synonyms:** *Harrisia serruliflora* (Haworth) Lourteig in *Bradea* 5(44): 408, 1991. Plumier's plate 26 was designated as the neotype of *C. serruliflorus* Haw. by Lourteig (1991), prior to its recombination to *Harrisia* — as *H. serruliflora* (Haw.) Lourteig, by the same author, *op. cit.*

*Cereus haitiensis* Franck & Peguero (2017) *Phyto-neuron* 2017–29: 1–17.

**Plant** a small tree up to 3–4 (–5) m, very ramose. **Trunk** distinct, short, cylindrical, branched above its base, up to 15–20 cm in diam., in cross section terete or nearly so, the vascular cylinder moderately woody, densely armed with long, deflexed, brownish-yellow spines up to 12–14 cm long, often banded with transverse brown stripes. **Main branches** diverging at 30°–45° angles, 0.25–1 (–1.5) m long, 5–10 cm diam. **Stem segments** curving upwards, fluted, slender, (3–) 3.5–4.5 (–5) cm diam., up to 1.5 m in young plants, those of older individuals more often composed of several shorter joints (7–) 10–70 (–90) cm long, mucilaginous. **Ribs** (10–) 12–15 (–17), low, (6–) 7–9 mm high,

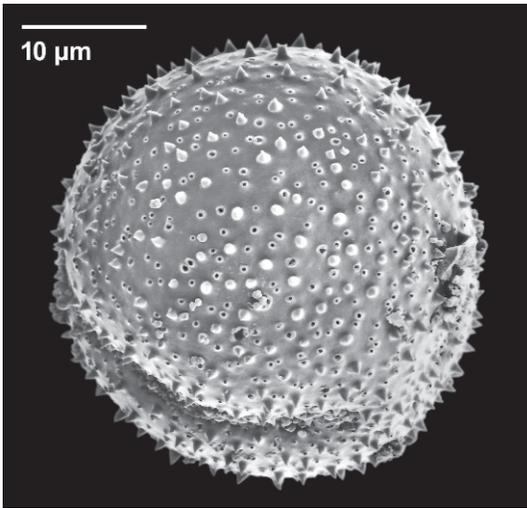
4–7 (–9) mm wide at base, the narrowly rounded and deeply crenate edge bearing the areoles in the depressions, the sinuses straight, acute. **Areoles** mostly orbicular or transversely elliptical-orbicular, to 3–4 (–4.6) mm in diam., 1.3–1.7 (–1.9) cm apart, tufted when young with a pale yellow felt later becoming tawny, and provided with (12–) 15–20 (–22) spines. **Spines** diverging, slender, acicular, (0.1–) 0.2–0.3 (–0.5) mm diam. at base, translucent pale yellow in youth, later becoming yellowish-brown, with their growing bases of a whitish-yellow color; central spines usually (2–) 4–8, 1.8–3 (–4.5) cm long, those of old joints longer, more numerous and frequently banded with transverse brown stripes; radial spines somewhat smaller, 0.6–1.8 (–2) cm long. **Flower buds** bulging at tip and apiculate at early stages of development, in age becoming acute, the stigma often protruding from within the appressed perianth segments and becoming fully visible 2–3 days before anthesis. **Flowers** on most areoles of the stems within the upper 2–3 m of the plant, medium-sized, narrowly funnel-shaped, recurved, striate-angled on surface, (6.4–) 6.7–7.1 (–7.3) cm from throat to base, (4.6–) 5–6.5 (–7.2) cm broad when fully expanded, for a single night nyctigamous; **pericarpel** 2.6–3.4 x 1.2–1.4 cm, elongated, striate-angled in cross-section, green, lustrous, with few triangular bract-scales (0.5–) 1–3 mm long bearing a small tuft of ivory-whitish wool in their axils; tube marginally striated, 3.3–4.1 x 1.2–1.4 cm at base, somewhat curved downwards, for the most part gradually widening to 2.5–3 cm at apex, sometimes slightly constricted beneath and above the nectar chamber, green, with few disperse, narrowly triangular 1.5–5 mm long purplish bract-scales with their tips tinted with a vivid red color, subtending small, nearly inconspicuous axillary tufts of ivory-whitish wool; **perianth limb** relatively wide but strongly reflexed during anthesis; segments (26–) 28–31 (–34) widely arrayed, narrowly triangular to linear, tapering gradually towards the slightly acuminate apex, finely and irregularly serrulate at margin, 2–3 (–3.3) cm x 4–5 (–6) mm, greenish below, wine-colored above the middle, the inner ones not differentiated from the outer ones except in their somewhat smaller width and paler color; **nectar chamber** cup-shaped, striate, 1.1–1.7 cm long, 3–7 mm broad at base, widening to 9–12 mm above; stamens numerous, (1.3–) 1.8–3 cm long, exserted, the upper ones extended 1–1.5 (–1.7) cm beyond the flower throat during anthesis, filaments capillary, whitish, anthers of a diluted yellowish-salmon pink color, linear-oblong to linear, 3–5 mm long; style long-exserted, including the stigma (6.4–) 6.9–7.3 (–7.5) cm long, 1.5–2



**11.** Scanning electron microscopy (SEM) photograph of the epidermis of a mature stem segment of *Cereus* (subg. *Neohaiticereus*) *serruliflorus* (Areces 6795 NY) after removal of the wax covering.

mm thick, extended 2.5–4 (–4.2) cm beyond the flower throat and 1.5–2.6 cm beyond upper stamens, greenish-white to whitish, not tapering upwards; stigma lobes (11–) 14, linear, erect or nearly so, cream-colored to yellowish, 7–9 mm long; ovary locule narrowly obconic in longitudinal section, 1.5–2.4 cm long, 2.2–3 mm wide at base, 4–7 mm above. **Fruits** indehiscent, elongated, at first green, erect, and cylindrical, its surface marked with 10–12 longitudinal keels separated by round sinuses, with sparse triangular bract-scales to 3 mm long that often wither and drop before maturity, each bearing a tuft of persistent ivory-whitish wool in their axils, later leaning down by way of softening of basal tissues, (9–) 9.5–12 (–13) cm long, 5–6.5 cm wide at maturity, hanging vertically on the stems, cylindrical to cylindrical-obovate, keels and sinuses becoming less apparent, vivid citrine-yellow, unarmed or sometimes with clusters of 5–15 spines 6–12 mm long on lowermost areoles, surface smooth, sinuate-folded at apex where the entire, persistent black floral remnant 2–4 mm inserts into the thickened fruit wall; **fruit wall** 6–8 mm thick, yellowish-green; funicular pulp greenish-gray to grayish, very mucilaginous (Figs. 6–10).

**Stem epidermis** consisting of large tabular cells 98–201  $\mu\text{m}$  long, 76–93  $\mu\text{m}$  wide, mostly polygonal in outline, with a relatively low profile when seen in cross-section. Anticlinal walls mostly obtuse-angular to nearly straight, outer periclinal walls smooth, slightly curved outwards. Stomata 9–11 /  $\text{mm}^2$ , randomly oriented and evenly distributed at the epidermal level over the entire rib and sinus surfaces.

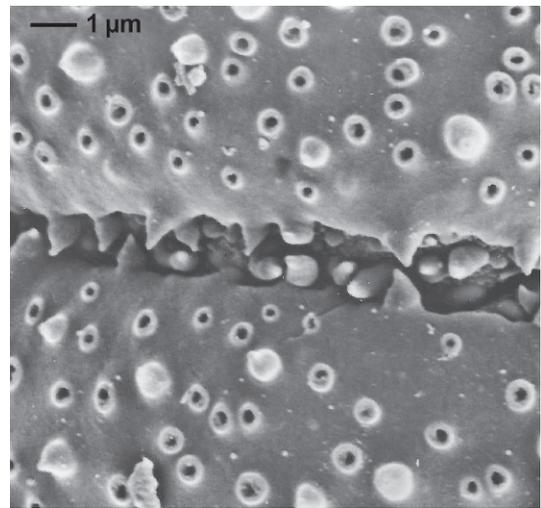


**12.** SEM photo of a typical 3-colpate pollen grain of *Cereus* (subg. *Neohaiticereus*) *serruliflorus* (Areces 6795 NY).

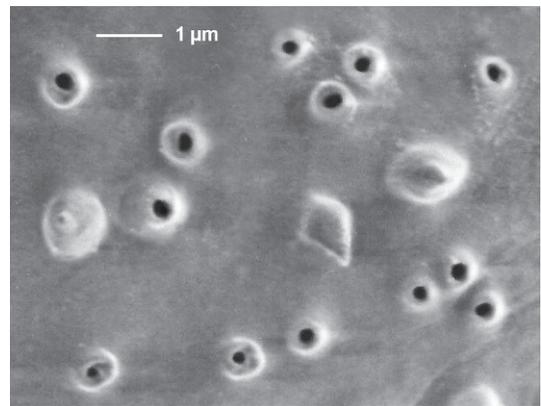
Fully-developed parallelocytic stomatal apparatus consists of a series of 4–6, C-shaped subsidiary cells gradually increasing in size from the center outwards, the outer partially overlapping the ends of the inner, all functional: no flawed, imperfect stomatal cell arrangements detected. (Fig. 11).

**Pollen** spinulate 3-zonicolpate corresponding to the “*Cereus*” type of Leuenberger (1976a, 1976b). Grains are spheroidal, with a range of equatorial and polar diameters varying from 36.2–55.2 μm to 37–55.1 μm, respectively (mean polar/equatorial diam. ratio 1.01). **Equatorial outline** (ambitus) nearly circular, **colpi** (ectocolpi) long, sharply pointed at either end. The distance between the ends of adjacent ectocolpi is 17.1–27.5 μm. In unacetolyzed grains a colpus membrane is visible. **Apocolpium diameter** is 20.3–32.1 μm, with a mean ratio of the distance between the ends of adjacent ectocolpi to the equatorial diameter of 0.49 (apocolpium index). **Exine** fully tectate, 2.5–3.3 μm thick. **Tectum surface** with conical spinules of identical height and basal width (1.5–2 μm), with minute punctae 0.2–0.3 μm wide, each encircled by a raised rim. The number of punctae per 100 μm<sup>2</sup> of tectum surface is 20–23, whereas the number of spinules is much lower: 4–10 (Figs. 12–15).

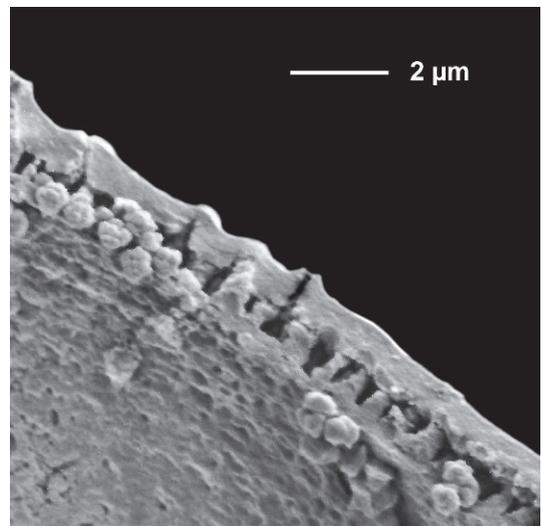
**Seeds** laterally flattened, tear- to mussel-shaped (*miesmuschelförmige*, in Barthlott & Voit’s 1979 terminology), with an oblong hilum cup forming a well-developed rostrum (dorsal region of compressed hilum cup). The dark brown **exotesta** is typically convex and papillose-tuberculate. The elongated **papillae**, which have minute cuticular folds on surface, are closely spaced and cover the entire seed coat except for the



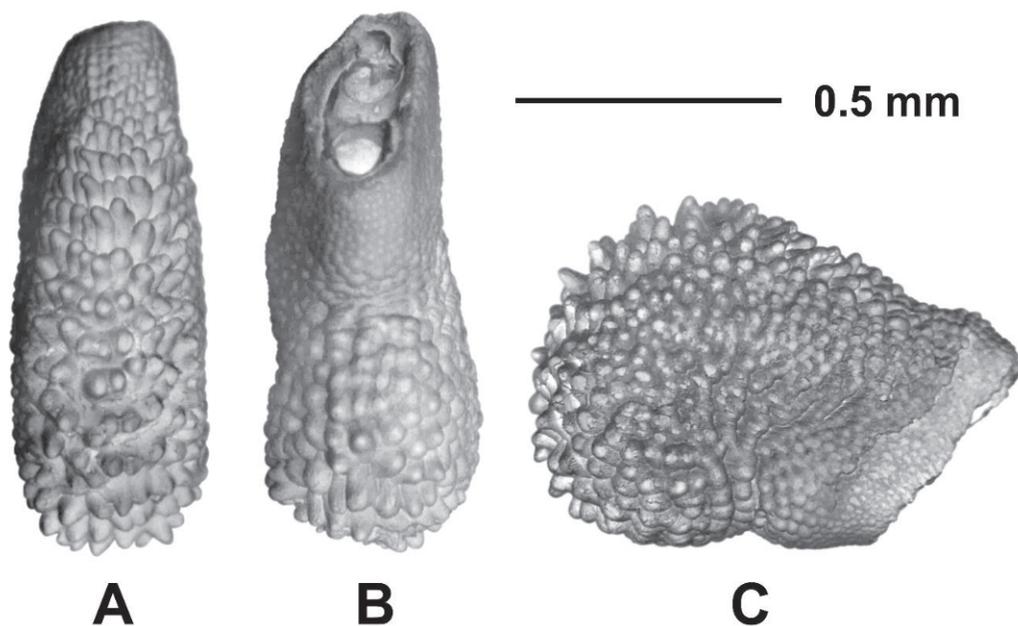
**13.** SEM photo of the pollen grain colpus, exposing the delicate colpus membrane.



**14.** SEM photo of the pollen grain surface showing details of the spinules and punctae.



**15.** SEM photo of a sectioned pollen grain, showing the exine with its perforated tectum.



**16.** Scanning electron microscopy (SEM) photo of a typical papillose-tuberculate seed of *Cereus* (subg. *Neohaiticereus*) *serruliflorus* (Areces 6795 NY). **A** dorsal view; **B** ventral view; **C** lateral view, showing a well-defined colliculate rim with minute, nearly rounded broad elevations.

sharply demarcated hilum-micropylar rim that is not papillose-tuberculate but colliculate. Cell boundaries are rounded in outline with no recognizable lines of demarcation. There are no interstitial pits (*lacunae interstitiales*) amid the papillae and certainly not traces of ariloid structures or strophioles derived from the funicular tissue (Fig. 16). In a 20-seed sample (Areces 6795 NY), the angle that the hilum forms with the long axis of the seed varies from 19° to 46°. Other quantitative measurements of this seed assortment are summed in Table 2.

### Geographic distribution

*Cereus* (subg. *Neohaiticereus*) *serruliflorus* is restricted to the Republic of Haiti. In the past, the species was probably well-distributed on three administrative divisions (provinces), namely the *Département du Nord-Ouest*, the *Département du Centre*, and the *Département de l'Ouest*. Nowadays, most surviving specimens seemed to be allocated in the mainly cut-over dry forests and thickets of Môle St. Nicolas, and in the dry coastal terraces between the Môle and Jean Rabel, in the *Département du Nord-Ouest*.

### Herbarium specimens examined

HAITI: Plants of Haiti, Vicinity of Môle St. St. Nicholas, arid thickets W of Môle gorge, fr., Feb. 16, 1929, *E. C. Leonard* & *G. M. Leonard* 13311 (US);

idem, Feb. 13–19, 1929, *E. C. Leonard* & *G. M. Leonard* 13311 (GH); Plants of Haiti, Vicinity of Jean Rabel, arid thicket along Môle road, fl., fr., March 3, 1929, *E. C. Leonard* & *G. M. Leonard* 13682 (US); Plants of the West Indies, Haiti, Cul-de-Sac plain, Croix-des Bouquets, low limestone hills, not very common, fl., fr., Dec. 18, 1925, *E. L. Ekman* 5377 (S); Plants of the West Indies, Haiti, Presqu'Île du Nord-Ouest, road from Jean Rabel to Môle St. Nicolas, near Môle St. Nicolas, terrace mountain, quaternary coral limestone, arid region, fr., July 3, 1925, *E. L. Ekman* 4446 (S); Haiti: Presqu'Île Nord-Ouest, Dept. Nord-Ouest, 5.5 km al nordeste de Môle St. Nicolas, en la carretera costera a Jean Rabel, fl. seca, Feb. 1985, *T. Zanoni*, *M. Mejía* & *J. Pimentel* 33542 (JBSD); Haiti, Département du Nord-Ouest, Presqu'Île du Nord-Ouest, coral limestone terrace 2 km NE to Môle St. Nicolas, on the road to Jean-Rabel, in xeromorphic cactus woodlands, fl., fr., Dec. 28, 1998, *A. E. Areces* 6795 (NY, HAJB).

### Discussion

After having collected and studied the polemical *Cereeae* portrayed four hundred years ago in Plumier's plate 3:26 of his *Botanicon Americanum*, the veiled plant is regarded as an isolated *Cereus* of rather uncertain affinity that could well support independent

**Table 2.** Quantitative seed characters of *Cereus* (subg. *Neohaiticereus*) *serruliflorus* measured in 20 randomly selected seeds from a specimen collected 2 km NE to Môle St. Nicolas (Areces 6795 NY). Dimensions reported are averages.

CHARACTER	
Length of seed	978 $\mu\text{m}$
Breadth of seed	542 $\mu\text{m}$
Ratio length to breadth	1.8
Thickness of seed	341 $\mu\text{m}$
Length of hilum measured internally (excl. rim)	374 $\mu\text{m}$
Width of hilum at middle (excl. rim)	137 $\mu\text{m}$
Diameter of largest lateral exotesta cell	39 $\mu\text{m}$
Diameter of largest dorsal exotesta cell	59 $\mu\text{m}$
Ratio of dorsal to lateral exotesta cell diameter	1.5
Angle between the hilum plane and the long axis of the seed	19°–46°

subgeneric status. On rediscovering the plant in 1998, I erroneously believed that it represented an undescribed species and so I described it in my unpublished 2003 PhD. dissertation. Since my studies of the Haitian *Cereae* were never formally published, I had time to reconsider its precise taxonomic position, with additional data collected elsewhere. A. R. Franck et. al., who had access to my unpublished dissertation, subscribed to my original idea and published a new species under the name *Cereus haitiensis*, discounting the Haworth publication of 1830. I consider that Haworth's *Cereus serruliflorus* based on the plant sketched in Burman's tab. 195, f. 1 (which corresponds to Plumier's famous plate 26) should not be rejected as the correct name of the species. To avoid confusion, Plumier's plate 26 of his *Botanicon* — excluding the depicted *Harrisia*-like stem segment — is treated as the Neotype of the species, herein designated. Despite the exceedingly large bract-scales of the floral tube, 4–5-times larger than normal, Plumier's sketched flower shows a combination of triangular-serrulated, acuminate perianth segments and long-exserted style unlike that of other cactus species of Hispaniola. This should clarify the confusion surrounding the identity of the Haitian *Cereae* portrayed by the 17th century monk.

Why this plant remained hidden for so long, sufficient to hinder and/or mislead the interpretation of its actual taxonomic position, may be explained by several reasons. First, was its secluded existence in one of the most remote and inaccessible corners of Haiti, the *Département du Nord-Ouest*. This dry isolated peninsula, with its rugged landscape, never exerted a great pull on plant scholars of the 19<sup>th</sup> and 20<sup>th</sup> centuries,

so very few collections of this plant has been made. Instead, it was the Cul-de-Sac plain — where Plumier had extensively collected — which captivated the attention of most botanists willing to venture to Haiti, a region where *Cereus* (subg. *Neohaiticereus*) *serruliflorus* seemed to have always been scarce. The audacious Ekman was one of the few that visited Haiti's northwestern cape in 1925 were, to this day, the plant is still common because it benefits from the removal of forest hardwoods by locals. Unfortunately, his first-rate collections of *Cereus* (subg. *Neohaiticereus*) *serruliflorus* near Môle St. Nicolas, and in Croix-des Bouquets, were not immediately associated with the elusive plant portrayed in Plumier's plate 26, but with the much thicker-stemmed *Cereus repandus* (L) Miller, a rather distinct columnar cactus with red fruits that does not occur in Haiti (Werdermann 1931). Likewise, the Leonard's fertile collections of 1929 in Môle St. Nicolas were also misidentified as *Pilosocereus nobilis* (Haworth) Byles & Rowley, an even more different columnar species bearing reddish, depressed-globose fruits.

Another reason that contributed to the neglect of Plumier's original finding seemed to have been its overall resemblance to the Hispaniolan endemic *Harrisia divaricata*, a 2–3 m tall shrub with a rather open, diffuse crown of widely divergent stems that are, like *Cereus* (*Neohaiticereus*) *serruliflorus*, fluted and slender, about 3–4 cm thick. In sterile condition, the novel subgenus here described can be easily dismissed as *H. divaricata*, a species that, in addition to resembling, is sympatric with *Cereus* (*Neohaiticereus*) *serruliflorus* in the *Department du Nord Ouest*, and rather common in nearly all scrubs and dry forests of both Haiti and the Dominican Republic. The field resemblance between these unrelated species is more noticeable in young plants, since old, mature *Neohaiticereus* trees are larger, to 5 m tall, their habit is much more ramose, and their branches and young stem segments tend not to grow with the *Harrisia*-like, open, diffuse pattern.

Dry herbarium collections of *Cereus* (subg. *Neohaiticereus*) *serruliflorus* which are shrunken and distorted, may be mistakenly taken for *Harrisia* when lacking reproductive organs. *Harrisia divaricata* has 9–11 stem ribs, a number that falls within the range of the Haitian *Cereus* who has 10–17 (–19?) ribs. Considering that correct identification of a 10–11-ribbed *exsiccata*

without flowers or fruits is always a bit uncertain, it is by no means impossible that a thorough study of all sterile herbarium specimens of *Harrisia* collected in Hispaniola, would uncover some *Cereus* (*Neohaiticereus*) *serruliflorus* individuals.

Finally, *Cereus* (*Neohaiticereus*) *serruliflorus* seems to have a definite flowering period in the dry season, ranging from December to early March, a time when few botanists are willing to spend time in the drought-deciduous scrubs and cactus woodlands of Haiti. Anytime during this 14-week period several massive and synchronous blooming episodes occur. At the peak of the flowering cycle, perhaps 40–50% of all seasonally-produced flowers open during one single night, a clandestine event that is easy to miss. Fruits seem to grow quickly and are fully formed in the same dry winter period. These peculiarities of the seasonal life cycle of the bewildering *Cereaceae* may also add to why the species has been overlooked for so many years.

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