

Investigation article

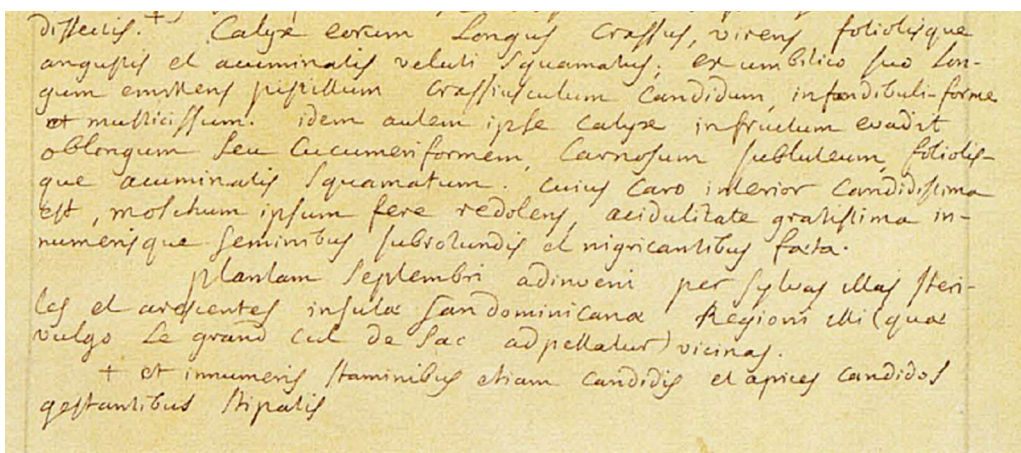
Mystery in Haiti:

What was really *Cereus serruliflorus* Haworth?

Joël Lodé (France)

There is still great confusion today about *Cereus serruliflorus* Haworth, native of “San Dominicana, the Grand Cul de Sac” as shown in Plumier (San Dominicana is the Latinized name for Santo Domingo, also called Hispaniola, encompassing today the Dominican Republic and Haiti) where we find the region known as Grand Cul de Sac.

How can this be possible that several botanists who have succeeded each other for more than a century and a half, have not been able to recognize the plant as a precise taxonomic entity, and that we have sometimes shunted from *Cereus* to *Pilosocereus*, passing by *Harrisia* and *Leptocereus*, genera that are actually found in the neighbouring Dominican Republic, and partly in Haiti?



Description extract of '*Cereus serruliflorus*' by Plumier (*Botanicon Americanum*, 1689-1697).

It is not only the probable mix of Plumier's drawings (Plate 26 of his *Botanicon Americanum* (1689-1697 or 1693) that provoked this impossibility of allocating this taxon to a single unit, a single genus, since several botanists went to check the plants in the field, including our two contemporary and specialized botanists



Our Cereus mystery. In my opinion, it is of hybrid origin, now stabilized, is no doubt. This is another example of reticulate evolution.

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Alberto Areces Mallea and Alan Franck ... So what is it?
We had previously:

Cereus serruliflorus Haworth, *Phil. Mag.* 37: 113. 1830. This was changed as *Harrisia serruliflora* (Haw.) Lourteig, in *Bradea* 5(44): 408 (1991).

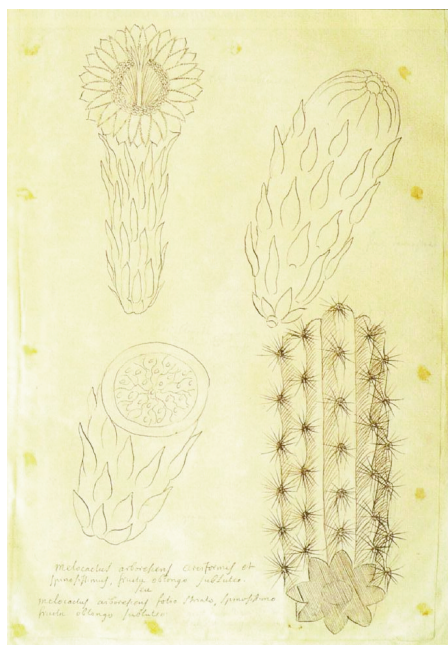
Since then, it has been synonymized with
Harrisia divaricata (Lamarck) Backeb. *Cactaceae* (Backeberg) IV. 2101 (1960).

However, a legitimate doubt remains about its real identity, the description itself leaving no doubts, at least in the name that has been given to this taxon: “serruliflorus”, having saw-like flower (margins), which is a typical discriminatory element. This detail is important enough as the taxon cannot be confused with a species of the genus *Harrisia*, whose inner tepals are never serrate. There are two species whose inner tepals are irregularly denticulate: *H. gracilis* and *H. fragrans* (= *H. simpsonii*) (Britton & Rose 1920), but they are not present on Hispaniola.

*Cereus haitiensis** A.R.Franck & Peguero
2018 is the name currently accepted by
Kew Science on the net.

For the moment, personally, I do not have any opinion for *Cereus haitiensis* or for *Cereus serruliflorus*, because there have been too many unknowns since the beginning. I will deliberately leave aside the taxonomy to be interested in the morphology of this taxon that I will call ‘*Cereus serruliflorus* / *haitiensis*’.

At first glance, with such a habit and looking at the stems, I thought it might be a hybrid between *Harrisia* and *Cereus*. After a quick search on the genus *Leptocereus*, which is extant on the island, I realized that many



Drawing of the putative “*Cereus serruliflorus*” in Plumier’s *Botanicon Americanum* (1689-1697).

*Also, an invalidated name *Cereus haitiensis ex* Schelle exists which is of horticulture origin which could be more confusing for being a perfect homonym, although the Art.53.1 of ICN (2012) unfortunately allows that; however, in my opinion, it should have been better to discard this name by choosing another..



Left to right: *Harrisia* sp. © JL, “*Cereus haitiensis-serruliflorus*”, *Leptocereus weingartianus* © A. Areces-Mallea, © Gérard Ardisson.



The flowering buds of *Cereus repandus* (not found in Haiti) are bulbous like that of our *Cereus* "mystery" on the right.

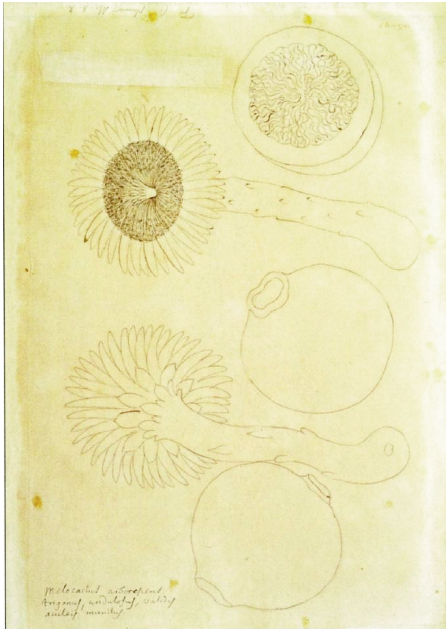
Leptocereus have crenate stems, a somewhat anarchic habit, and therefore *Leptocereus* could be involved in this hybrid. It was my first approach. There are two *Leptocereus* on Hispaniola: *Leptocereus weingartianus*, the type of which is native of Haiti, shrubby, and *L. paniculatus*, which is arborescent and could have given rise to the “hybrid” in question. Both are crenate.

The flowers of some species of *Leptocereus* are quite similar to that of ‘*Cereus serruliflorus* / *haitiensis*’, except for the pericarpel, very spiny in *Leptocereus* although the spines can be deciduous when the fruit is ripe. No comparison is possible with *Cereus* Miller, but the hybridization could have modified the flower, although these are pure suppositions. In *L. weingartianus*, the stem has mucilage, the seeds are rostrate and papillose; ‘*Cereus serruliflorus* / *haitiensis*’ is described with a stem containing mucilage and the seeds are also rostrate and papillose, much closer to a species of *Leptocereus* than a species of *Cereus* (see photo)

One thing is certain: neither the flower nor the seeds are a morphological reference to the genus *Cereus*. So, why was this taxon included in *Cereus*? The fruit is similar, can it be enough? The genus *Cereus sensu lato* is currently paraphyletic (Franco *et al.*, 2017), and it would be necessary to be able to separate some entities that were previously included, to see more clearly, rather than grouping any taxon looking alike in a catch-all called *Cereus* for convenience; Biodiversity does not regroup: it creates opportunities. Or rather, it creates new entities



The shrubby habit of *Leptocereus weingartianus* recalls our *Cereus* “mystery” rather well. © Christian Defferrard



Drawing of Plumier supposed to represent *Dendrocereus undulosus*: if the fruit is correct, the flower is quite far from reality (see photo on right).; therefore, it is plausible to believe that that the flower of "*C. serruliflorus* / *haitiensis*" is also partially erroneous.

The flower bud of '*Cereus serruliflorus/haitiensis*' before anthesis is typical, elongated, glabrous, and it forms like a fist stretched and closed at the tip, the same as we can find in *Cereus repandus* (with fimbriate flowers, see photo) from Curaçao, but also in *Monvillea* and *Praecereus*, genera that I did not dare to move in Tax. of Cact. vol 1-2, but that some would like to see included in the genus *Cereus*. Is this a simple convergence of form or a real characteristic of relationship? We do not have a definitive answer yet. Personally, I think that the only serious clue is that the descriptor has said the flower of this plant has been given the epithet "*serruliflorus*"; it is the only flower with this characteristic in the region. The picture of the flower by Areces-Mallea is clear and without doubts. In *Harrisia*, the flower bud before anthesis is elongated and pointed. The problem is the typification from Plumier's plate that does not match.

Except perhaps for the colour, the fruit has nothing to do with *Harrisia*, also the flower; the ovoid fruit of '*Cereus serruliflorus* / *haitiensis*' is typical of that of *Cereus repandus* (Morton 1967) from Curacao, and *Praecereus*, both taxa which are not extant on Haiti. However, the fruit wall is very thick in '*haitiensis-serruliflorus*', as in *Cereus repandus* but also other taxa, although it is probably not relevant. Finally, there is one more element to consider: the fruit of *Leptocereus weingartianus* is quite similar to that of our mysterious cereus, and keeps the remains of the dried perianth as in '*Cereus serruliflorus* / *haitiensis*'.

I had the opportunity to obtain seeds of *Cereus*, *Harrisia*, *Pilosocereus*, *Praecereus* and *Leptocereus* for my work Taxonomy of Cactaceae vol. 3-4 . The article of Areces-Mallea shows a decisive photo of seeds of *Cereus 'haitiensis-serruliflorus'*, which are rostrate and papillose to tuberculate.

Thus, I passed my seeds to "facial recognition", and the verdict quickly fell: nothing to do with the seeds of *Harrisia*, *Cereus*, *Praecereus* or *Pilosocereus* which are ruminated, foveolate, or tuberculate. The seeds of *Cereus 'haitiensis-serruliflorus'*



Cereus 'haitiensis-serruliflorus'



fl. & fr.

© A. Areces-Mallea



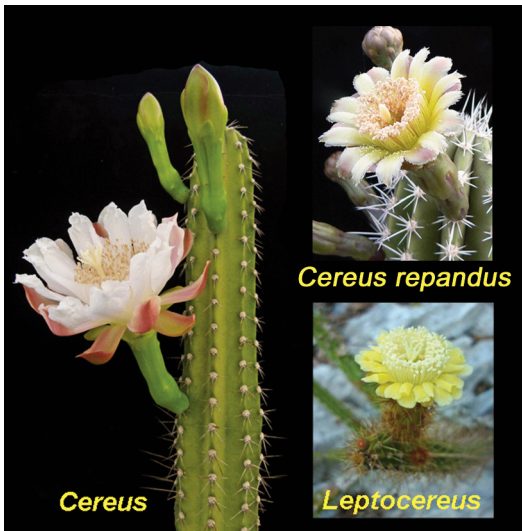
Harrisia



Dendrocereus undulosus



Præcercus



Cereus repandus

Cereus

Leptocereus

left: *Cereus* sp.; above right: *C. repandus* (not found in Haïti) and *Leptocereus assurgens* to compare

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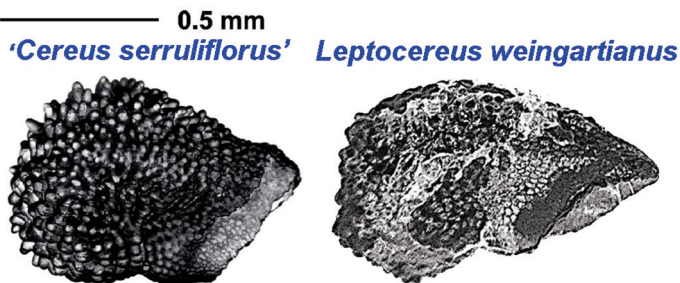
Pilosocereus

are rostrate and papillose to tuberculate. It remained for me to examine those of *Leptocereus*; they are all tuberculate except those of *Leptocereus paniculatus* and especially those of *L. weingartianus*, the two species which are on Hispaniola and which are rostrate and papillose to tuberculate, like those of *Cereus 'haitiensis-serruliflorus'*. Here we are! For me, who has been studying them for over 25 years, seeds are one of the most reliable characteristics after DNA.

If they are quite far from those of other genera present on the island, the seeds of *Leptocereus weingartianus* match quite well those of *Cereus 'haitiensis-serruliflorus'*, they are both papillose- tuberculate, are obviously not identical, their shape is nevertheless quite similar and they are covered with mucilage, also present in the fruit pulp of *Cereus 'haitiensis/serruliflorus'*. This are not concrete



Harrisia divaricata ISI 93-10, Barahona, Dom. Rep.; ***Cereus fricii*** AP1116.93; ***Praecereus saxicola*** JH.. s.n.; ***Pilosocereus polygonus brooksianus*** JMA, Baconao, Cuba; ***Pilosocereus swartzii*** RS, Palisades, Port Royal, Jamaica; ***Praecereus euchlorus jaenensis*** GC, Jaen, Perú.



The closest appearance of the seed is that of ***Leptocereus weingartianus***

evidence, but additional elements to help me think that one of the parents of this plant is probably a *Leptocereus*. Moreover, it is also the opinion of Guiggi (2018) whose conviction is that “*Serrulatocereus serruliflorus*” has a closer relationship with *Leptocereus* and *Harrisia* than *Cereus* Miller.

So let's look again at the species extant in Haiti (and Santo Domingo which are both political entities of a single island called Hispaniola) and which are often sympatric. Which other cactus taxa exist in Haiti, since the '*Cereus haitiensis*' presented by Franck is the same plant as that of Areces-Mallea who considers it to be '*Cereus – subgenus Neohaiticereus- serruliflorus*'. This is the only clue, with the serrulate flower, of which we are absolutely certain. The problem that remains is the drawing of Plumier, which shows a pericarpel with large scales, which is not the case of *Cereus 'haitiensis-serruliflorus'* growing there. Whether imagined or such a plant has disappeared are only conjectures. It is better to abandon the idea of attaching any drawing of a plant to make it a type, and better create it from of a well defined type, corresponding to the plant in question with e.g. that of Ekmann 4446 (see below), the oldest material that is 100% reliable.

I also agree with Areces-Mallea (2018) about the assumption that the sectioned organ is a flower bud and not a fruit which is obviously erroneous. The other Plumier plates all show a fruit of every species with a sectioned fruit, so it makes sense, even if this fruit is still immature.

From what I observed, we have a poorly known, but nevertheless prospected area of Haiti (by Abbott, Ehrenberg, Ekman, Leonard, Nash for example, but also Ritter and even Reppenhagen), where we can find: *Harrisia divaricata*, *Leptocereus paniculatus*, *L. weingartianus*, *Pilosocereus polygonus* and *Stenocereus fimbriatus*. There are even some plants in the background photo behind the '*Cereus haitiensis*' of Franck's article in Figure 4, which could be well *Pilosocereus polygonus* and *Stenocereus fimbriatus*...

Cereus serruliflorus was once considered synonymous with '*Cereus repandus*' in the sense of Britton & Rose (II, 1920 p.18) previously known in Curaçao, Aruba and Bonaire, and which does not fit Werdermann's description, which is based on the herbarium material of Ekmann 4446 and 5377, and which I repeat here:

« Hispaniola: Civ. Haiti: Presqu'île du Nord-Ouest, near Môle St.-Nicolas, in arid region (terrace mountains) (3. Jul. 1925 - Ekmann n. 4446; 3-4 m high, profusely branched, branches nearly as long as the main trunk, upwards bent, 14 ribbed; spines yellowish; fl. not seen; fruits ellipsoid, size of duck eggs, perfectly smooth, olive green (greenish-yellow) ; pulp greyish, seeds black ».

« Hispaniola: Civ. Haiti : Plaine Cul-de-sac, Croix-des-Bouquets, Hab. Juon, low limestone hills (18 Jul.. 1925 - *Ekman* n. 5377; 4-5 m tall, brown shaped, many branched, branches straight, erect, as long as main trunk, 11-13 ribbed; fl. white, brownish on the outside; fruits perfectly smooth, indistinctly ca.10 ribbed, elongated pear-shaped, olive-green, seeds nearly black in a grey-green pulp”.



Leptocereus weingartianus, with a fruit that loses its spines when ripe.
Bayahibe, Dom. Rep. © C. Defferrard

In fact, there is confusion between *Cereus repandus* (fruit first green, then dark purple red when ripe) of Curacao and *Cereus 'haitiensis-serruliflorus'*, whose fruit has about the same elongated obovoid shape and is smooth, thick-walled, first green, but which becomes lemon yellow when ripe, and which keeps me in my hypothesis that there is something of *Harrisia* in this taxon most likely from the reticulated evolution. What Werdermann described and Ekman collected under the numbers *Ekman* 4446 and *Ekman* 5377 are actually our mysterious *Cereus*! Other collections of this mysterious *Cereus* took place on 16 Feb. 1929 (n°13311), then, 3 Mar. 1929 (n°13682) by *E.C. Leonard & G.M. Leonard* under the name of *Cephalocereus nobilis*. On 2 Feb. 1985, *T. Zanoni et al.* n°33542, identified as *Harrisia* sp. Alessandro Guiggi (2018) quote an edifying fact, that of the

reassessment of herbarium sheets: the specimens of Leonard & Leonard are determined as cf. *Leptocereus* sp. by N.P. Taylor, while those of Ekman (4446) and Zanoni (33542) are evaluated as *Harrisia* sp. by Taylor and Hjertson.

In my opinion, if there is so much confusion, so much varied morphological data, this is because it seems that we could be in the presence of an episode of reticulate evolution, with hybrids more or less stabilized, some fertile and having the characteristics of their parents. Since then, some have disappeared because they have not been able to cope with the necessary conditions for their survival and have had to face unforeseen situations (drought, cyclones, single or extremely rare plant, non-reproduction of the event, etc.). One of them resisted, could reproduce and constituted a small population, obviously still very localized: it is one of the possible forms of speciation.

In other words, always in my personal opinion, we are dealing with a probable example of introgression, followed by a backcrossing giving a plant with characteristics of both parents, and able to reproduce. It is still, in my opinion, a plant that should be given a new name of genus if it does not have sufficient characteristics to be included into any one of the genera known in Haiti, especially because it could probably be a “new creation of nature” and therefore a plant that may be genetically close to one or the other. With such confusion we are unable to locate it, hence the descriptions are changeable, doubtfully determined and hastily reworked for a taxon finally unclassifiable in the current state. Here are some of the names attributed to our ‘mysterious *Cereus* since Plumier (around 1689-1693):

Cereus serruliflorus (sensu Haworth, 1830),
Cereus hermentianus (sensu Monville, 1859) (doubtful, described with up to 19 ribs),
Cereus repandus (sensu Ekman, 1925 – based on Ekman 4446),
Cephalocereus nobilis (sensu E.C. Leonard & G.M. Leonard, 1929, n° 13311-13682),
Cereus repandus (sensu Werdermann, 1931 – based on Ekman 4446)
Cereus repandus (sensu Hummelinck, 1937 – based on Ekman 4446),
Harrisia sp. (sensu T. Zanoni, 1985, based on T. Zanoni et al. 33542),
Leptocereus sp. (sensu Taylor, 2004 – based on Leonard & Leonard 13311, 13682),
Harrisia sp. (sensu Hjertson & Taylor, 2004, based on Ekman 4446 et Zanoni et al. 33542),

And changes began to run:

Cereus haitiensis (sensu Franck & Peguero, 2017),
Neohaiticereus serruliflorus (sensu Areces-Mallea, 2018, as a subgenus),
Arecesocereus haitiensis (sensu Wisnev 2018, as a subgenus),
Serrulatocereus serrulatus (sensu Guiggi 2018, as a genus)...

What's next ?...

It is possible that at the time of the first observations of Plumier in the late 1690s, there were some intergeneric hybrids that did not survive, or were not able to reproduce, or for other unknown reason as I implied above. This could explain the large confusion of that time of the supposed 19 ribs of the plant or the huge scales on the drawing of Plumier. In my opinion, the Ekman herbaria are the only first documents that can be authenticated and are therefore valid for this taxon.

Since no DNA study of the species extant on the island has yet taken place, I have satisfied myself with observations of the phenotypes, however understanding that convergence of form may alter this simplified vision, and that the analogies do not specify in any way the relationship. Nevertheless, for species that live sympatrically, it is impossible not to make a connection and this is what I did to support my proposal. The first vision I had of this plant when I read the article of Franck (the one I read first) and the photos is that the photographed plant is a stabilized hybrid. derived from reticulate evolution.

Cacti from this area eventually have flowers with fimbriate inner tepals, hence the name "fimbriatus" for one of them (*Stenocereus fimbriatus*). The *Pilosocereus* may also present this kind of corolla, but the pericarpel is naked: difficult to take outer tepals for scales. We are desperately looking for a pericarpel with such scales.

This serrulate flower corresponds well to a known plant, lost, found, but poorly described and probably confused because of a mixture of herbaria material, all this beautiful world in the same bag: we open the bag, and that's the result! Or the drawing of the flower is, until evidences of the contrary, a montage of two parts not belonging to the same plant: the pericarpel and the corolla. "The scales are a little big, but it's still OK ...".

No, it cannot be OK: we cannot take the flower only, nor obviously the rest that belongs to a little of all cacti that grow in Haiti! Unless the taxon described disappeared, and was an infertile hybrid...

There remains possibly a fourth solution: starting on new bases with a type (which exists, that of Franck) and a new name. The description is worthwhile, since it describes this new taxon, but we should not refer to Plumier or anything before Ekman, except to say that the confusion is such that we must abandon the idea of putting together a puzzle that we does not have all the pieces, and that in addition, we have the pieces of another or more in the place!

Everything is, in my opinion, a question of name, and the four proposed names all referring to this mixed-up drawing, are absolutely to be avoided. More, since the confusion has gone up in just one year! A DNA study will be absolutely essential for all the taxa of the genus *Cereus* as well as the satellite genera and of course, our mystery *Cereus*. For the moment, the most recent molecular studies (Franco *et al.*, 2017) show a paraphyletic *Cereus* genus, but do not pretend to propose any taxonomic changes. Although their works are really interesting on this subject and allow a better idea of the genera to include within or exclude from *Cereus* Miller, our Mystery *Cereus* not being present in their study, this one does not allow to bring new elements.

A new name will finally be needed for this so singular cactus, which could be the future floral symbol of Haiti, a cactus that lives in extreme conditions, but remains standing and living despite adversity, and continues to be a mystery for the rest of the world.

BIBLIOGRAPHICAL REFERENCES:

- Alvarado-Sizzo Hernán, Alejandro Casas, Antonio González-Rodríguez, Hilda Julieta Arreola-Nava & Teresa Terrazas. 2019. *Clave dicotómica y distribución del complejo de especies de Stenocereus griseus (Cactaceae)*. Revista Mexicana de Biodiversidad 90.
- Areces-Mallea Alberto. 2018. *Neohaiticereus a New Subgenus for the Rediscovered Cereeae Depicted in Plumier's Plate 26 of the Botanicon Americanum*. Cactus and Succulent Journal 90(2), 107-118.
- Britton & Rose. 1920. *The Cactaceae II*. Carnegie Institution, publ. no. 248, Washington, D.C.
- Franco Fernando Faria, Gislaine A. Rodrigues Silva, Evandro M. Moraes, Nigel Taylor, Daniela C. Zappi, Cecylia Leiko Jojima, Marlon C. Machado. 2017. *Plio-Pleistocene diversification of Cereus (Cactaceae, Cereeae) and closely allied genera*. Botanical Journal of the Linnean Society, Vol. 183(2): 199–210.
- Franck, A.R., B. Peguero, W. Cineas, and B. Jestrow. 2017. *A new species of Cereus s.str. (Cactaceae) endemic to Haiti*. Phytoneuron 2017-29: 1-17.
- Guiggi Alessandro. 2018. *Serrulatocereus Guiggi, a new proposed Genus for the recent re-evaluated Cereus serruliflorus*. (24 Sept 2018).
- Hodge W.H. 1943. *The Vegetation of Dominica*. The Geographical review, vol. XXXIII, nr.3.
- Lack Andrew J., Caroline Whitefoord, Peter G.H. Evans & Arlington James. 1997. *Dominica, Nature Island of the Caribbean Illustrated Flora*. 88 pp. Ministry of Tourism, Commonwealth of Dominica.
- Morton Julia F. 1967. *Cadushi (Cereus repandus Mill.), a useful cactus of Curaçao*. Econ. Bot. (1967) 21: 185.
- 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.
- Werdermann Erich. 1931. *Die von E. L. Ekman.† in Westindien, besonders auf Cuba und Hispaniola gesammelten*. Feddes Repert. 29(11-20) : 222-243
- Wisnev Michael A. 2018. *Arecesocereus a New Subgenus of Cereus*. Cactus & Succulent Journal 90(3): 222-223. (1st Sept 2018).