

IDENTITY AND NEOTYPIFICATION OF *CEREUS MACROGONUS*, THE TYPE SPECIES OF THE GENUS *TRICHOCEREUS* (CACTACEAE)

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Abstract: This paper clarifies the identity of *Cereus macrogonus* Salm-Dyck, the type species of the genus *Trichocereus* (Berger) Riccob., and specifies its synonyms and affinities. It is also intended to contribute toward stabilizing the generic nomenclature. An examination of Salm-Dyck's original description of *C. macrogonus* leads to an interpretation of the species, very plausibly of Peruvian origin, as a cactus which was later also named *Trichocereus peruvianus* Britton & Rose. A Neotype is designated that is consistent with the protologue. That interpretation coincides with the use of this name (*C. macrogonus*) in the botanical literature and in horticulture, which has been adhered to up to now. *Trichocereus pachanoi* Britton & Rose is here presented as a variety of *T. macrogonus* (Salm-Dyck) Riccob.: *T. macrogonus* var. *pachanoi* (Britton & Rose) S.Albesiano & R.Kiesling, nov. comb., and a lectotype for it is designated.

Resumen: Esta nota aclara la identidad de *Cereus macrogonus* Salm-Dyck, especie tipo del género *Trichocereus* (Berger) Riccob., también se establecen sus sinónimos y afinidades, y contribuye a la estabilidad nomenclatural del género. Del estudio de la descripción original se interpreta que la especie, muy posiblemente originaria del Perú, fue también llamada más recientemente *Trichocereus peruvianus* Britton & Rose y se designa un Neotipo que coincide con el protólogo. Esta identidad concuerda con el uso del nombre (*Cereus macrogonus*) en la literatura botánica y en horticultura, el cual se ha mantenido hasta el presente. *Trichocereus pachanoi* Britton & Rose es aquí considerada una variedad de *T. macrogonus* (Salm-Dyck) Riccob.: *T. macrogonus* var. *pachanoi* (Britton & Rose) S.Albesiano & R.Kiesling, nov. comb., y se designa un lectotipo.

Keywords: Cactaceae, *Cereus macrogonus*, nomenclature, South America, *Trichocereus*, typification.

HISTORICAL BACKGROUND

THE GENUS *TRICHOCEREUS*

Trichocereus has a basically Andean distribution, extending from Ecuador through Peru, Bolivia, Chile and southeastern Argentina, to the Atlantic coast. The plants have cylindrical stems, robust (mostly more than 9 cm in diameter), ribbed, branching from the base (cespítose), or possessing a definite trunk (arborescent), or, more exceptionally, creeping, with large, conical, robust flowers (from 15 to 30 cm long, but uncommonly as small as 7 cm), white, sometimes yellow, more rarely red or of intermediate colors. The receptacle is densely covered with hairs, and the fruits are very juicy. Up to the beginning of the twentieth century, *Trichocereus* species were treated as part of the collective genus *Cereus*.

Berger (1905) made an important contribution to the segregation of the components of *Cereus* by creating several subgenera (most of them later elevated to generic level by other authors). He recognized

14 species within his new subgenus *Trichocereus*, one of which is: "*C. (Trichocereus) macrogonus* Salm-Dyck. l.c. 115.- Andes?".

A few years later, Riccobono (1909: 236) elevated *Trichocereus*—among others of Berger's subgenera—to generic level, including in it only two species: *T. macrogonus* (Salm-Dyck) Riccob. and *T. spachianus* (Lem.) Riccob.

Britton and Rose (1920) adopted the genus *Trichocereus*, enlarging it to include a total of 19 species, and designating *Cereus macrogonus* as the type species. This designation has been followed up to now by all authors (Castellanos and Lelong 1938: 399, 1943: 87; Kiesling 1978: 281; Hunt 1967: 453; Madsen 1989: 27; Anderson 2005: 215; Hunt et al. 2006: 90).

After the creation of the genus, a few authors failed to accept it, keeping the species in *Cereus* instead: but most adopted the genus *Trichocereus* until Friedrich (1974) subsumed it under *Echinopsis*. However, this opinion of Friedrich was not shared by a number of other later authors (Rundel 1974: 86–88; Leuenberger 1976: 96, 130; Kiesling

1978: 263–330; Rauh 1979: 197–198; Ritter 1980: 437–456, 559–567, 1981: 1324–1329; Gibson and Nobel 1986: 161–163, 172–173; Bregman 1992: 218, 221; Kiesling 1999: 485–488; Eggli 1984: 203, 205; Perea 2005: 149–172; Trevisson and Demaio 2006: 65–66; Kiesling et al. 2008: 1826–1829). *Trichocereus* and *Echinopsis* are indeed closely related, but most of the species can be assigned clearly and without difficulty to one or the other of these two genera, using the morphological characters in the following key:

A. Plants 0.5 to 12 m tall, with branches as tall or nearly as tall as the central stem. Stems cylindrical, including basal branches. Flowers nocturnal or diurnal, campanulate. Receptacle wide, conical, with hairs dense on receptacular areoles, and scales on receptacle generally somewhat numerous, closely spaced or overlapping. Fruits juicy. Wood fibrous, hard*. Mostly occurring in the Andes, from Ecuador to Argentina and Chile *Trichocereus*

A'. Plants 0.1 to 0.3 m tall (except for adults in *E. leucantha* complex and *E. ayopayana*, which normally reach no more than 1 m, rarely up to 1.5 m). Stems (including basal offsets) globular, never cylindrical, when young and adult (except, again, for *E. leucantha* complex and *E. ayopayana*). Flowers mostly nocturnal, funnellform. Receptacle wider at the ovarian zone and narrower at the tube; hairs on receptacular areoles sparse, and scales on receptacle mostly few, with considerable space separating them. Fruits semidry. Wood without fibers, soft, with wide-band tracheids*. Mostly occurring in eastern South America, with some species in the Andes of Argentina and Bolivia *Echinopsis*

* References to the wood after Mauseth and Plemmons (1998), and Mauseth (2004).

Furthermore, the combined analyses of molecular and morphological characters indicate that *Trichocereus* is monophyletic and distinguishable from *Echinopsis* (Albesiano and Terrazas, 2012, this volume of *Haseltonia*).

Cereus/Trichocereus macrogonus

Cereus macrogonus was described by Salm-Dyck (1850: 203), who wrote an extensive description. His protologue lacks any information about flowers and place of origin, but provides several vegetative characters, which taken together can be applied to only one species of the whole family Cactaceae.

The names *Cereus macrogonus* and *Trichocereus macrogonus* have been applied frequently in botanical and horticultural books, as well as in trade catalogs, from the time of Salm-Dyck's (1850) publication on-

ward throughout the nineteenth and early twentieth centuries. Later, the use of the specific epithet *macrogonus* may have decreased because the descriptions of *Trichocereus pachanoi* and *T. peruvianus* by Britton and Rose (1920), in their cornerstone monograph, encompassed large subsets of the group of plants that had previously been known as *T. macrogonus*. But despite that, many authors and horticulturists still employ the name *Trichocereus macrogonus* for a very well known species used as grafting stock. The most recent monographs recognizing *Trichocereus macrogonus* (under *Echinopsis*), are those of Anderson (2001, 2005), although he also recognized *Echinopsis pachanoi* and *E. peruviana* as distinct species.

From the original description of *C. macrogonus* (Fig. 1), the characters which we consider important are: the number of ribs (6–7), their thickness and very obtuse, rounded shape in transverse section, as well as their glaucous color; and a transverse dermal furrow just above each areole. Areoles are ca. 2.5 cm apart, situated on the raised surface of each rib, basal to a transverse furrow in the rind of the rib (the shape and depth of the furrow and its distance above the areole varying among populations and even among individuals within a population).

Spinination in the young areoles consists of 7–9 radials and one central; but in old (basal) ones there are 18–20 spines, some of them (3–4) thicker than the others, ca. 1 cm in length, and brown. The number of spines of the basal areoles given by Salm-Dyck is higher (nearly double) compared to that in the plants now cultivated under this name, but variation in the number and size of spines is very much affected by light intensity and other environmental conditions. Cultivated plants can show from zero to 10 spines at different areoles on the same branch. Wild plants have many more: *T. santaensis* Rauh & Backeb. and *T. chalaensis* Rauh & Backeb. (see below) look like wild plants of the same species, but show denser spinination.

After Salm-Dyck, the only references to *C. macrogonus* in the nineteenth century (except for Schumann's, see below) were made by Labouret (1853: 352), Rümpler (1886: 706), who only repeated Salm-Dyck's information, and Weber (1899), who gave a short description of a plant that had flowered, evidently a *Trichocereus*, given the size and hairiness of its flowers.

Based on flowers produced by mature plants after the original description, nearly all subsequent botanical authors have used the specific epithet *macrogonus* to refer to a *Trichocereus* species (under *Cereus*: Weber 1899; Berger 1904, 1905; as *Trichocereus*: Riccobono 1909; Schelle 1926; Borg 1937, 1951; and as *Echinopsis*: Hunt 1989, 1992, 1999; Anderson 2001, 2005), as also did authors of books on horticulture (see below for a more complete list).

Only one author, K. Schumann, in 1890 and 1897–1898, used the name *Cereus macrogonus* for a species from Brazil, which is currently listed under the genus *Pilosocereus* (Fig. 2). As Schumann worked at the Berlin Botanical Gardens, from whence Salm-

tis, tuberculatis, aut interrupte ac cristatim costatis. Tertia tandem in hortis adhuc rara, pro subvarietate *nana* præcedentis habenda est; ei simillima, sed partibus omnibus diminutis et caule ramosissimo vix poll. 6-8 alto.

(59.) *C. MACROGONUS* *H. Berol.* *C.* caule erecto columnari subglaucescenti-læteviride 6-7 angulato, costis turgidis obtusissimis apicem versus obrepandis ad pulvillos crenato-plicatis et colore intensius viride arcuatim notatis, pulvillis confertis griseo-tomentosis, aculeis rigidis abbreviatis brunneis, in pulvillis junioribus 8-10, in senioribus 18-20, erecto-patulis, 3-4 validioribus. (*Nob.*)

Caulis hucusque 8-10 pollicaris, diametro fere bipollicari. Costæ rotundatæ, farctæ, superne ad pulvillos plicatæ et arcu viridiore notatæ. Pulvilli lin. 3-4 distantes parvuli, grisei. Aculei primo subregulariter dispositi, 7-9 radiantes cum centrali 1; sed mox (aculeis novis enascentibus) sine numero ac ordine normali erecto-patuli, graciles, brunnei, 3-4 paulum validioribus, lin. 5 longis.

Fig. 1: Excerpt of the Salm-Dyck (1850) publication with the original description of *Cereus macrogonus*.

Dyck supposedly received his specimen, there must be some possibility that he had original plants and may have been correct. Schumann first used that name in Martius's *Flora Brasiliensis* (1890). The plant he described and illustrated there at that time did not have all the attributes mentioned in Salm-Dyck's description, such as the furrows above the areoles, and perhaps he was influenced solely by the color of the epidermis and the number of ribs—but see below about Krainz (1975).

Schumann's assignment of the specific epithet *macrogonus* to a species now considered a *Pilosocereus* species was rejected by Berger (1904), who also gave a complete description of the plant, which corresponded to a *Trichocereus* species and furthermore complied with the protologue. The fact that Berger devoted a special note to refute the use of the name by so great an authority as Schumann is very significant. Berger based his argument on the earlier description by Weber (1899), and on plants culti-

vated in botanical gardens near the Mediterranean Sea. That strongly suggests that the widely cultivated plant corresponds to a *Trichocereus*. In his 1929 book, Berger again briefly mentioned Schumann's mistake.

When Schumann (1897-1898) published in fascicles his monograph of the family, *Cereus macrogonus* (1898: 121-122) was maintained as the concept of his previous publication in *Flora Brasiliensis*. However, in a comment following the description of *Cereus bridgesii* (1898: 107-108), he mentioned "it is very similar, if not the same, as *Cereus macrogonus*". *C. bridgesii* is a species of known origin (near La Paz, Bolivia), and has always been considered as part of *Trichocereus* since the creation of this subgenus and later genus. Additionally, Schumann did not incorporate *Cereus macrogonus* in the subgenus *Pilosocereus* (now the genus *Pilosocereus*), surely because his classification was based on vegetative characters and because the species he was considering does not have conspicuous long hairs on the stem areoles.

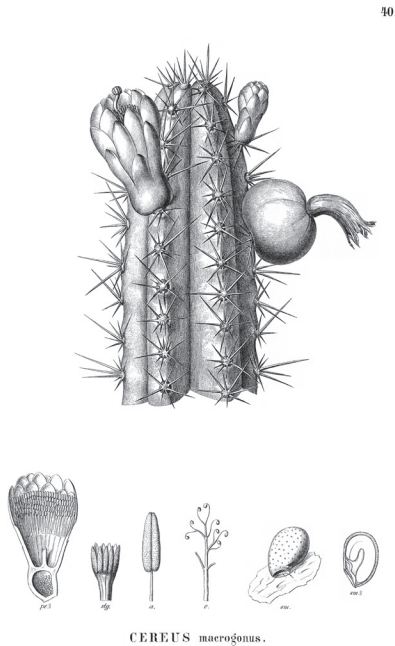


Fig. 2: Illustration of *Cereus macrogonus* in Schumann, *Flora brasiliensis* (1890), surely a *Pilosocereus* species, according to the current conception.

Britton and Rose (1920) designated *C. macrogonus* as the type species of the genus *Trichocereus*, included it in the key, and wrote a description of it. Simultaneously, they described *T. peruvianus* and *T. pachanoi*. We, on the other hand, regard those three names as conspecific (see immediately below). Britton and Rose (1920) also considered that the species mentioned by Schumann (1890, 1898) as *Cereus macrogonus* was mistaken by him, and that in reality it corresponds to *Cephalocereus arrabidaei* (Lem.) Britton & Rose, now *Pilosocereus arrabidaei* (Lem.) Byles & Rowley. The same opinion was taken later by Werdermann (1942: 98 and 108).

In our opinion the three names (*Trichocereus macrogonus*, *T. pachanoi* and *T. peruvianus*) correspond to only one species because of the glaucous epidermis of the stems, the low number of ribs (6–9, but rarely as low as 4), which are obtuse, near 2 cm high and 2.5 cm wide, with furrows immediately distal to the areoles, and dull seeds, which have a dorsal crest. Although these characters are variable within and among populations, we consider the degree of variability to merit infraspecific recognition. These character states can also be present in other taxa of the subfamily Cactoideae, but not all combined. The noticeable differences in some morphological characters (see the taxonomic key above) and in geographic distribution warrant the differentiation at the level of variety of *T. macrogonus* var. *macrogonus* (= *T. peruvianus*), and *T. macrogonus* var. *pachanoi* (= *T. pachanoi*).

Schelle (1926, Fig. 19) not only described, but also illustrated, *Cereus macrogonus*. Although the clarity of reproduction of the photo is poor, it depicts a cultivated columnar cactus with a few (ca. 5) wide obtuse ribs and apical flowers, and can be readily identified as a *Trichocereus* species of the group we are considering.

Borg (1937: 134, 1951: 180) provided a longer description of *T. macrogonus*, but also mentioned Argentina and Bolivia as being its countries of origin. He noted its use as grafting stock.

Rauh (1958) made no reference to *T. macrogonus* in his book on Peruvian cacti, but described some very closely related species (see next paragraph).

The publications of Backeberg and Knuth (1936) and Backeberg (1966) mention *T. macrogonus*, but add no more information than was previously known. The second reference is strange, because Backeberg had published an earlier note (Backeberg 1941) where he had reported that he himself had found wild plants of *Trichocereus macrogonus* in the wild, in Peru, and after more than a page of text and a clear photo, had made the clear synonymy *Trichocereus macrogonus* (S.-D.) Ricc. = *T. peruvianus* Br. et Rose. We cannot know if he had subsequently changed his opinion or simply forgotten his own note. In his larger work, Backeberg (1959) presented as a wild form of *T. macrogonus* an illustration of a plant found by Werner Rauh in central Peru. It exhibits more robust spination than is found in cultivated plants. In the same book other very similar species are included, among them *T. santaensis* Rauh & Backeb. from northern Peru (with a very clear illustration), *T. chalaensis* Rauh & Backeb. from southern Peru, and also *T. peruvianus* and *T. pachanoi*—all very closely akin to *T. macrogonus* as judged by our concept. However, we find in that work no reference to his 1941 note, nor to his trip to Peru and his own finding of *T. macrogonus* in the wild there.

Krainz's reference (1975) is confusing. Under the heading *Trichocereus macrogonus*, he described a *Trichocereus* species that agrees with the original description, and provided a photo of a specimen, cultivated at his own institution in Switzerland, that shows a big flower and surely corresponds to *Trichocereus*. But he also includes two other photos, of plants cultivated at a Spanish garden, showing fruiting stems which seem to correspond to a *Pilosocereus* species, judging from their depressed, dehiscent fruits. Very likely he was mixing up different plants under that name, as Schumann appears to have done (*vide supra*). Krainz also followed Schumann's information from 1890, mentioning Rio de Janeiro, Brazil, as the area of origin of the plant.

As already pointed out, the name *C. macrogonus* was consistently used throughout the late nineteenth and early twentieth centuries. Even more recently, the names *Cereus macrogonus*, *Trichocereus macrogonus*, and *Echinopsis macrogona* have been utilized—and indeed are still being utilized—both by trained botanists (Berger 1929: 136; Borg 1937: 135 and 1951: 180; Rowley 1974: 96, when subsuming the

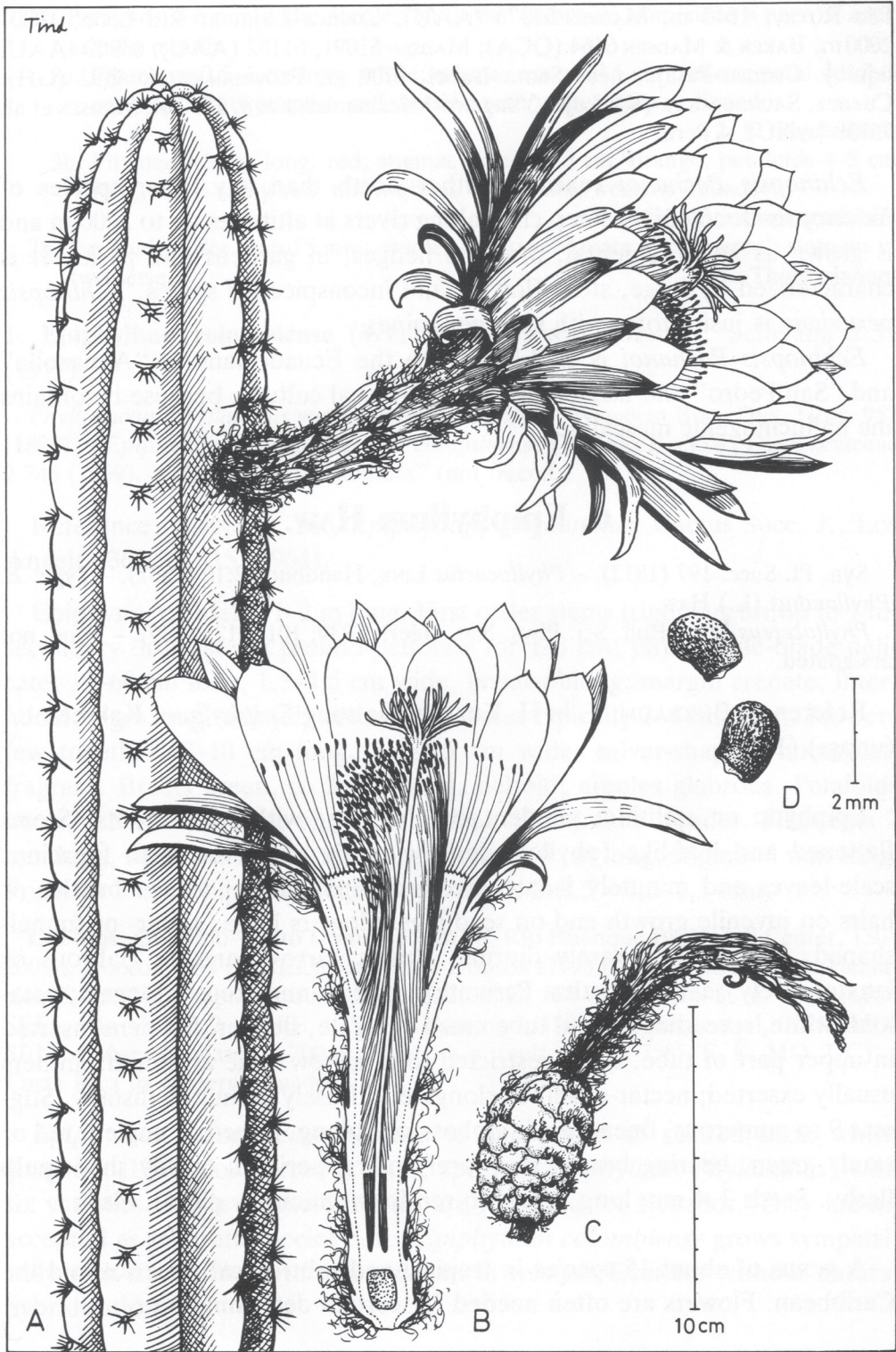


Fig. 3: Illustration from Madsen (1989) of *T. macrogonus* var. *pachanoi* (as *Echinopsis pachanoi*). A. Flowering stem. B. Longitudinal section of flower. C. Fruit. D. Seeds.



Fig. 4: *Trichocereus macrogonus* cultivated at a rural house in northern Chile (between Vallenas and Ovalle). Photo by Daniel Schweich.



Fig. 5: Neotype of *Trichocereus macrogonus* as seen at the Tropicos website of the Missouri Botanical Garden; www.tropicos.org/Image/85856 on 30 Oct. 2011.

species under *Echinopsis*; Krainz l. I. 1975 unpagued; Hunt 1992: 57, 138 and 1999: 190; Anderson 2001: 272 and 2005: 235) and in the horticultural literature (Rothers 1923: 44, 124; Schelle 1926: 19, 105; Petersen 1927: 32, 71; Kupper 1929: 66; Houghton 1931: 116; Backeberg and Knuth 1936: 203; Backeberg 1941; Backeberg 1959: 1119 and 1966: 438, inter alia; Ríha and Subík 1981: 180; Hunt 1989: 239; Innes 1990: 146; Mordhorst 2008: 218), as well as in trade catalogs (e.g., Haage 1927: 10 and 1938: 4, inter alia; Kreuzinger 1935: 38; Wenzel 1937: 4; Holly Gate Nurseries 1977/78: 4; Abbey Garden 1981: 38; Veg Saatzucht Zierpflanzen Erfurt 1979: 5; Köhres 1986: unpagued). These references demonstrate that the epithet *macrogonus* is still in use.

Some of the publications also offer illustrations, e.g., Schelle (1926, Fig. 19), Backeberg (1959, Fig. 1075) and Anderson (2001: 273 and 2005: 235). Hunt (1989) made a reference to an illustration published by Haustein, in *Der Kosmos-Kakteenfürher* 131 (1983); this illustration is consistent with our identification of the species, except that Brazil is given as country of origin, surely following Schumann's 1890 opinion. Most of the references mentioned above highlight the remarkably glaucous epidermis and the use of the species as a good grafting stock.

In his very recent book, Ostolaza (2011) recognizes both *Echinopsis pachanoi* and *E. peruviana*, differentiated only by the more robust spination and

ostensibly higher concentration of alkaloids in *E. peruviana*, which had been found by him in the Lima region (apparently as a wild plant).

Related taxa

As mentioned, Britton and Rose (1920) described as two new species: *Trichocereus peruvianus*, which in our opinion is the selfsame species as *C. macrogonus* (and even the same variety), and *Trichocereus pachanoi*. Our concept interprets this latter as an infraspecific variant of the same species, based on the different number and size of spines. The authors included a good description, illustration, indication of place of origin, and cited a type specimen for both. Thus, later authors frequently use the well-defined binomial *T. peruvianus*, but not so frequently the prior name *T. macrogonus*. This close relationship between *T. macrogonus* and *T. peruvianus*—and even their synonymy—has been mentioned by several authors, including Backeberg and Knuth (1936: 203), although in some publications Backeberg did not uphold this opinion. Later Madsen (1989) also considered both as only one species. Ritter (1981: 1324) proposed *T. peruvianus* as a form of *T. pachanoi*, based on field observations, where he saw populations morphologically intermediate between the two taxa. Ritter did not allude to *Cereus* (or *Trichocereus*) *macrogonus* in his work.

Madsen (1989) described and illustrated "*Echinopsis pachanoi*" in detail (Fig. 3), giving *T. peruvianus* as a synonym; but the only reference in his work to *Cereus macrogonus* was that name as the type species of *Trichocereus*. The illustration of *E. pachanoi* (his Fig. 7) is very clear, and its fully comprehensive description shows great concordance with Salm-Dyck's original description of *Cereus macrogonus*, although with a wider range of variation. Both Ritter and Madsen studied the plants and their variability in the field. We consider their agreement on the affinity of *T. peruvianus* and *T. pachanoi* to be plainly evident and a signal confirmation of our viewpoint.

Anderson (2001: 272 and 2005: 235) described and illustrated *T. macrogonus*, but also gave *T. pachanoi* and *T. peruvianus* (all under *Echinopsis*) as separate species. His photo of *T. macrogonus* agrees with our concept of the species, but the origin given is Bolivia. The mention of Bolivia as the country of origin for this plant can perhaps be based on some anthropological literature (e.g., Schultes and Hoffmann 1979). Anderson did not compare nor give any key to differentiate the species.

In the last comprehensive study published on the Cactaceae (Hunt et al. 2006), both *Echinopsis peruviana* and *E. pachanoi* are given as recognized species. The name "*Echinopsis macrogona*," however, is listed in Appendix III (p. 322): "*Unreferred names*," in the category of "Names whose original application is indeterminate or debatable." Hunt et al. state (p. 97)—without explanation—that "Modern descriptions [of *E. macrogona*] deviate from the original, and the name may be misapplied..." A previous Hunt refer-

Key to the varieties

- A. Spines of the older areoles 18–20, 3–4 of them prominent, longer, stronger, and more robust (ca. 5 cm long, 1 mm in diameter). Plants up to 5 m tall, branches erect or ascending; stems stouter, 16–20 cm in diameter. *T. macrogonus* var. *macrogonus*
- A'. Spines of the older areoles often absent or few: 3–7, all similar (ca. 1–2 cm long, and less than 1 mm in diameter). Plants up to 2–4 m tall; stems erect, becoming parallel; stems more slender, 6–11(–15) cm in diameter; *T. macrogonus* var. *pachanoi*

ence to *Echinopsis macrogona* (1989), included the same doubt, but likewise failed to provide a basis for it. One plausible supposition could be that this judgment derived from observations made at plant nurseries or amateurs' greenhouses. It should be noted that the recent book (Hunt et al. 2006) is written for a broad audience, and contains neither keys nor discussion about the relationships of the species, and in this case neglected to mention the true name (or names) of the plant(s) which is "said to be a good grafting stock." When Hunt evokes an undescribed "*Echinopsis macrogona* hort.," the implication is that the plant in cultivation does not correspond to the description of Salm-Dyck. Neither does Hunt clarify what is the true sense of *Cereus macrogonus* of Salm-Dyck, which is precisely the object of this paper.

The presence or absence of spines and their size have been taken by different authors as the principal characters for differentiating *T. peruvianus* from *T. pachanoi*, but these are inconsistent characters. The original description of *T. pachanoi* mentioned the variability of the spines, from no spines to 3–7 spines up to 1–2 cm long, as can be seen in the type specimens at NY and US. Schultes and Hoffmann (1979: 154) noted that *T. pachanoi* has no spines when cultivated, but develops them under wild conditions. We encountered the same experience after moving a cultivated plant of *T. macrogonus* from a relatively shady situation to a more exposed one (SA & RK, pers. obs.). A more consistent finding is that the spines of plants in populations of *T. peruvianus* are larger and stronger than the ones of *T. pachanoi*, as is evident from the bibliographic references of all the authors who studied these plants in the wild, and from the herbarium specimens. The species key, descriptions and photos of Britton and Rose note that *T. peruvianus* is shorter in stature (2–4 m, but up to 5 m in nature) than *T. pachanoi* (3–6 m, but up to 7 m in nature) and its branches are not so close and parallel, but more arched.

ETHNOBOTANY

Under the local Spanish common name of "San Pedro", but also the indigenous "achuma" or "huachuma", or the botanical names *Trichocereus pachanoi* and *T. peruvianus*, this plant is very widely known for its hallucinogenic properties (Schultes and Hoffmann 1979: 154–155; Anderson 2001: 47). Ritual uses of this cactus were practiced long before the Spaniards arrived in South America, as is depicted on pre-Columbian Peruvian ceramics and other ar-

chaeological objects. Ostolaza (1995: 76–82) gave an extended analysis of the San Pedro plant in Peruvian archaeology. For Bolivia, Cárdenas (1969: 367–370) mentions *T. pachanoi* only as cultivated. It had been used in Peru as a narcotic for therapeutic purposes before the Spaniards arrived, as proven by a very early archaeological reference (ca. 1300 years B.C., Anderson 2001: 46).

At present this cactus is part of Peruvian shamanic syncretic ceremonies of healing and magic, although its significance is diminishing over time. Schultes and Hoffmann (1979: 154–155), describe the plant as cultivated in Ecuador, Peru and Bolivia, which explains the references to those countries throughout the botanical literature of the twentieth and twenty-first centuries.

Anderson (2001) also referred to *E. peruviana*, recorded by him as "San Pedro macho," perhaps due to its more developed spines, as an equivalent source of alkaloids, and he alludes to a "rare" four-ribbed form of "San Pedro" that was believed to have "special healing properties." Anderson, citing Davis (1983), further added that the plant was domesticated along the coast, but originated from higher elevations. Anderson plausibly had information from Ostolaza publications and personal communications, but that information also could have originated in popular belief or as interview data from shamans.

Some of the references to relative alkaloid levels among *Trichocereus* species in the cactus literature we have mentioned, were very plausibly based on some biochemical analyses of some individuals, but most such reports appear to be based on popular behaviors or shamanic communications. Although several different scientific publications had reported the content of alkaloids (particularly mescaline, the predominant psychoactive alkaloid) of the "San Pedro", only recently has a paper been published (Ogunbodede et al. 2010) with analyses made on several samples of mostly known origin, in a comparative way (similar sampling, the same techniques and instrumentation, etc.) The results reported in that paper suggest that the content of mescaline is higher in plants actually used by shamans than in other cultivated or wild plants. Also the highest mescaline concentration in the study was found in plants identified as *Echinopsis pachanoi*, and not in those identified as *E. peruviana*, although mescaline levels showed great variation among the various plants analyzed, including plants of the same complex of species under discussion here. There was no suggestion of any correlation between alkaloid concentration and rib number or other mor-

phological characters, but such correlations were not tested for. It seems reasonable to conclude that the plants used by shamans are cultivars selected by them.

At present it is difficult to determinate in an accurate way the true geographic origin of this widely cultivated species. In our opinion, based on the literature and herbarium specimens, the species is naturally distributed in high valleys of Peru and perhaps northwestern Bolivia, but it is cultivated over a wider area, including Ecuador and N Chile (Fig. 4) (and we hear about it in northwestern Argentina, but cannot verify that). Wild plants are phenotypically different from the cultivated ones, and they have been given different names—by botanists, and likewise by the local people.

TAXONOMIC REMARKS

As a result of comparing the original description with the presently known *Trichocereus* species, we conclude that *C. macrogonus* Salm-Dyck is the same species known as *T. peruvianus*, and that it is conspecific with *T. pachanoi* but differentiable at a lower (infraspecific) level. Cladistic analysis of combined evidence, morphological and molecular (rpl16 and trnL-F), confirms the close relationship between specimens identified as *T. peruvianus* and those identified as *T. pachanoi* (Albesiano and Terrazas, 2012).

On the other hand, as mentioned, it is worth noting that Ritter (1981: 1324) and Madsen (1989: 27–28), the two authors who extensively observed the plants in the field, respectively consider *T. pachanoi* and *T. peruvianus* to be conspecific, distinguishable at the form level (Ritter 1981), and indistinguishable and thus synonymous (Madsen 1989). The paper of Ogunbodede et al. (2010) is also based on documented field samples plus cultivated ones; the quantitative phytochemical differences between the samples of *E. peruviana* and *E. pachanoi* in our opinion may be attributed to a broad range of phenotypic plasticity within a single species, which is more compatible with the taxonomic recognition of our two varieties, rather than two separate species.

NOMENCLATURE¹

Trichocereus macrogonus (Salm-Dyck) Riccob., *Boll. Reale Orto Bot. Palermo* 8: 236. 1909.

BASIONYM: *Cereus macrogonus* Salm-Dyck, *Cact. Hort. Dyck.* 1849: 203. 1850.

Neotype (designated here): Peru, Dpto. Junin, Prov. Tarma, between Acobamba and Palca, 2890 m, 1 Oct. 1982, D. Smith 2456 (SI, Neotype; MO, Iso-neotype, seen at the Tropicos website of the Missouri Botanical Garden: www.tropicos.org/Image/85856 [seen 30 Oct. 2011]). (Fig. 5).

Obs. We choose this specimen because it corre-

sponds closely with the original description of *Cereus macrogonus* except for the lower number of spines in young areoles (1 to 4, when the original description states 7–9 spines with an additional central). But, as explained, this is a variable character.

Stems erect, 2.5–5 m tall. Branches 6–15(–20 cm) diameter. Ribs at the base 7–8, obtuse, 2.5 cm wide, 2 cm tall, with a furrow, perpendicular to the axis of the rib, distal to each areole. Areoles circular, 6 mm diameter, all grey or dark brown. Spines acicular, 1–3 centrals, near 3.3 cm long, brown with black point; ca. 8 radial spines, 2–8 cm long. Flowers mostly near the stem apex, rarely at the apex, funnel-form, 21 cm long, densely covered by clear brown hairs; 2 cm in diameter at the ovary level; scales on the pericarp 1 cm long, green with brown apex, scales on the tube 2.5 cm long, green or yellowish-green with brown apex; tepals 9 mm long, mostly yellowish-green or pale yellow with brown longitudinal lines, rarely deep pink; style green, 8 cm long; stigma yellow, 1 cm long. Seeds broadly ovoid (ratio of length to width = 1.3 to 1), small (0.9–1.1 mm long), dull, without keel, anticlinal walls of the testa straight.

Frequently cultivated in Peru, Ecuador and Bolivia as an ornamental, for fences, and for medicinal or magical purposes. Its most plausible wild origin is the medium to high valleys of the Peruvian Andes, at altitudes of 2000–3000 m.

Trichocereus macrogonus (Salm-Dyck) Riccob. var. *macrogonus*.

Basionym: *Trichocereus peruvianus* Britton & Rose, *The Cactaceae* 2: 136. 1920. Neotype, here designated: Peru, Dept. Matucana, vicinity of Matucana, 9 Jul. 1914, J. N. Rose and Mrs. J. M. Rose 18658, US 761324, isotype: NY 386193!

Other synonyms:

Echinopsis peruviana (Britton & Rose) Friedrich & G.D. Rowley, *IOS Bull.* 3 (3): 97. 1974.

Trichocereus pachanoi f. *peruvianus* (Britton & Rose) F. Ritter, *Kakteen in Südamerika* 4: 1324. 1981.

Echinopsis macrogona (Salm-Dyck) H. Friedrich & G.D. Rowley, *I.O.S. Bull.* 3(3): 96. 1974.

Cereus rosei Werd., in Backeberg, *Neue Kakteen*: 73: 101. 1931. (As a new name for *T. peruvianus* Britton & Rose, to avoid the homonym with *Cereus peruvianus* (L.) Mill.)

Trichocereus macrogonus (Salm-Dyck) Riccob. var. *pachanoi* (Britton & Rose) S. Albesiano & R. Kiesling, comb. et stat. nov.

Basionym: *Trichocereus pachanoi* Britton & Rose, *The Cactaceae* 2: 134. 1920.

Type: Ecuador, outskirts of Cuenca, 17 to 24 Sep. 1918, J.N. Rose, A. Pachano and G. Rose 22806 US (lost). Lectotype, here designated: Ecuador, outskirts of Cuenca, 17 to 24 Sep. 1918, J.N. Rose, A. Pachano and G. Rose 22806 (NY 386191). Note: this lectotype is a duplicate (isotype) of the original US

¹Other species apparently referable as subspecies, varieties or forms, like *T. chalaensis* Rauh & Backeb., *T. santaensis* Rauh & Backeb., or *T. bridgesii* (Salm-Dyck) Britton & Rose are not mentioned, pending the results of research in progress.

holotype. That holotype is apparently lost; a consultation with the US curator, Rusty Russell, in September 2008, revealed that the specimen had not been found in 1941, according to a note by the curator at that time, and has not been found since.

Synonyms: *Cereus pachanoi* (Britton & Rose) Werderm., in Backeb, *Neue Kakteen*: 73. 1931.

Echinopsis pachanoi (Britton & Rose) Friedrich & G. D. Rowley, *IOS Bull.* 3 (3): 96. 1974.

Other studied materials

Bolivia, Dpto. La Paz, Prov. Larecaja, Collabamba, 5 Nov. 2002, Kiesling et al. 10041 (LPB). Dpto. La Paz, Prov. Saavedra, 1433 m, 12 Sep. 2004. L. Cayola et al. 1533, 1534 (LPB).

N.b.: We are designating the variety *pachanoi* to differentiate the plants with a tendency to have small numbers of very small spines to no spines from the plants which tend to produce spines of larger sizes and different numbers. Even though this changeable character of spination also depends on environmental conditions, and although intermediates exist, the differences are noticeable and in some degree consistent enough to merit taxonomic recognition at the varietal level.

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