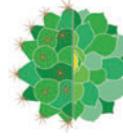


CactusWorld Special Issue

December 2020

# South American Cacti

Giovanna Anceschi and Alberto Magli



## Introduction

As an Editor, it is good to receive longer articles at times – something the more serious reader can get their teeth into. However, when the first article from these authors was designed and laid out, and it came to 24 pages, something had to be done.

Of course 24 pages would have filled almost half the Journal and so the idea of a Special Issue was considered. The same authors were able to write a second article on a similar theme – South America cacti – and so the Special Issue was born.

*CactusWorld* has always been a place for the publication of novel taxa (always after serious consideration and care not to publish names willy-nilly and at all cost), but has also provided a platform for new and alternate ideas of classification. This is the case in the Special Issue that you hold in your hands. Many will not

agree with the authors' proposals or their taxonomic suggestions, yet their ideas deserve to be heard.

They have hiked the hillsides and travelled the miles, and have spent many, many months in total in the field in South America, photographing, observing, studying and measuring the cacti in habitat. Back home, they have ploughed through the historic as well as the contemporary literature before coming to their conclusions. They have published their work in *Bradleya*, *Cactaceae Systematics Initiatives* and elsewhere, and it is an honour to publish their articles in this supplement.

And dear reader, if you find this all heavy going, at least you can enjoy the photos. Also be sure to check out their website:

<http://cactusinhabitat.org>

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All photographs by the authors.

Layout by Alice Vanden Bon

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# New circumscription of the concept of *Echinopsis* (*Cleistocactus*) *buchtienii* and the inclusion of *Cleistocactus tupizensis* sensu Backeberg in the *Echinopsis* (*Cleistocactus*) *nothohyalacantha* complex

## Introduction

Those who are not used to our taxonomic system might find the inclusion of *Cleistocactus* Lemaire in *Echinopsis* Zuccarini unusual. In practice, the



Fig. 1 *Echinopsis* (*Cleistocactus*) *nothohyalacantha* (*tupizensis* populations). Bolivia, Potosí, Tupiza, Puerta del Diablo, 3,000m, 2007-03-28, A&M 186

molecular evidence (Schlumpberger & Renner 2012: 1336, 1341, 1346; Anceschi & Magli 2013a, 22-29; 2013b, 31: 24-27), show that *Cleistocactus* turns out to be only one of the 15 genera within the tribe Trichocereae (Anderson 2001, 2005, 2011; Hunt et al. 2006) or subtribe Trichocereinae (Nyffeler and Eggli 2010) to be included in *Echinopsis* s.l. to achieve a well-supported monophyletic macro-genus *Echinopsis* (ML 100% bootstrap support, according to Schlumpberger & Renner 2012, 1336, 1341, 1346). If we want the contraposition between concepts such as: monophyletic versus polyphyletic and/or monophyletic versus paraphyletic, ie those used by modern systematics to define taxa with phylogenetic criteria, or monophyletic taxa exactly (ie natural in the sense of Hennig 1966), to have some meaning and not represent just an empty specialised terminology to be used in a discretionary way among ‘insiders’, then the qualitative criteria of these concepts as conceived by the author must be respected (ibidem, 146). In this regard, we recall that the concept of paraphyly did not exist before Hennig, with the exception of Naef, 1919 (Wiley & Liebermann 2011, 72; Anceschi & Magli 2018, 36: 74).

On this basis, the genera *Cleistocactus* and *Borzicactus* Riccobono, as currently conceived (remember that the second genus has been restored by Hunt (2013, Atlas: xii, xix, 208-213; 2016, 23-24, 147, 161), following Charles’s adaptation (2012, 26:14), from the last molecular studies (Schlumpberger & Renner 2012, 99 (8): 1342), do not correspond to natural clades (or monophyletic in Hennig’s sense). In fact to be



Fig. 2 *Echinopsis nothohyalacantha* (*tupizensis* populations). Bolivia, Potosí, Tupiza, Puerta del Diablo, 3,000m, 2007-03-28, A&M 186

monophyletic in accordance with the analysis (ibidem, 1347), the *Cleistocactus* s.s. clade (100% bootstrap support), should include *Vatricania guentheri*, *Cephalocleistocactus*, *Samaipaticereus*, *Weberbauerocereus*, *Yungasocereus* and *Cleistocactus*, but not *Borzicactus*; while the *Oreocereus* (*Borzicactus*) clade (99% bootstrap support), should include *Oreocereus*, *Borzicactus*, *Espostoa*, *Haageocereus*, *Matucana*, *Mila*, *Oroya*, *Pygmaeocereus* and *Rauhocereus*. On the contrary, based on the latest redefinitions of the aforementioned concepts by members of the cladistic school (the descendants of the phylogenetic systematics based on the ideas of Hennig, ie Nelson (1971), Farris (1974), Wiley & Liebermann (2011), the genera *Cleistocactus* and *Borzicactus* as interpreted by Hunt (2013) on the basis of Charles (2012, 26:14), both appear to be polyphyletic. Indeed, Nelson (1971: 472) defines paraphyletic as groups lacking one species or monophyletic group, and polyphyletic as groups lacking two or more species or monophyletic groups, while Wiley & Liebermann (2011, 82) following modern vertebrate zoologists, grant paraphyletic groups the lack of two species or monophyletic groups, consequently defining polyphyletic those lacking more than two species or monophyletic groups. So, as already specified, in accordance with both definitions of the concepts of paraphyly and polyphyly reported



Fig. 3 *Echinopsis nothohyalacantha* (*nothohyalacantha* populations). Argentina, Jujuy, Volcan, 2,100m, 2007-03-19, A&M 171



Fig. 4 *Echinopsis (Oreocereus) celsiana*. Bolivia, Potosí, Tupiza, Valle de los Machos, 2007-03-28, A&M 187

above, the genera *Cleistocactus* and *Borzicactus* as currently conceived are both polyphyletic, lacking five groups in the first and eight in the second in order to be considered monophyletic. A more practical approach, in wanting to continue to use phylogenetic criteria to distinguish taxa, in a framework that opposes the concept of monophyly with those of polyphyly and paraphyly sensu Hennig, (also on the basis of the evidence about the impossibility of continuing to recognise taxa on the distinction between floral characters and pollination syndromes, which have proved to be extremely labile when traced in the molecular phylogeny (Ritz et al. 2007; Lendel et al. unpubl. data; Nyffeler et al. unpubl. data; Nyffeler & Eggli 2010; Schlumpberger & Renner 2012; Anceschi & Magli 2013a)), we believe it is more correct (and elegant), to consider *Cleistocactus*, *Borzicactus* and the other genera of the Trichocereae/Trichocereinae involved in the analysis as 'Echinopsis groups with floral characters and/or pollination syndromes modified' (Anceschi & Magli 2013b, 31: 25).

To support further the phylogenetic hypothesis we have adopted, we highlight that of the 15 genera often cited to be assimilated in *Echinopsis* s.l., for the constitution of a monophyletic macro-genus *Echinopsis*, actually six of these are monotypic genera (ie composed of only one species): *Denmoza*, *Mila*,



Fig. 5 *Echinopsis tacaquirensis*. Bolivia, Potosí, Tupiza, Puerta del Diablo, 2007-03-28, A&M 188



Fig. 6 *Weingartia fidana*. Bolivia, Potosí, Tupiza, Puerta del Diablo, 2007-03-28, A&M 189

*Rauhocereus*, *Samaipaticereus*, *Vatricania* and *Yungasocereus*, and according to Hunt (2003, 15: 3) “The monotypic genus is a contradiction in terms.

Logically (or at least etymologically) the term genus implies a class or group of things of a lower order (in botany, species etc), ie a collection of things with common attributes.” Not to mention that two of the genera in question (*Oroya* and *Pygmaecereus*), are composed of only two species. It is therefore evident that the aforementioned transfer to *Echinopsis* involves in reality far fewer natural taxa than those which would seem initially implicated. On the basis of what has been highlighted, the accepted taxa protagonists in this article will be named in the text (apart from the first citation), only in their combinations in *Echinopsis*. Within the taxonomic system, it is time now to move from natural taxa intended as ranks, to natural taxa at the populational level in their habitats.

## The *Cleistocactus tupizensis* sensu Backeberg geographical extension

The first two protagonists of our story are *Echinopsis* (*Cleistocactus*) *buchtienii* (Backeberg) Anceschi & Magli and *Cleistocactus tupizensis* sensu Backeberg, reminding with regard to the second taxon, that Mottram’s suggestion (2002, 13:12), concerning the attribution of the basionym of *Cleistocactus tupizensis* (Vaupel) Backeberg to *Oreocereus celsianus* (Salm-Dyck) Riccobono, is now commonly accepted by most scholars (Hunt et al. 2006, text: 49; Leuemberger 2012, 27: 12-16; Lowry 2016, 34: 156-157), with the exception of Anderson & Egli (2011, 127). Equally diffused among the same authors (ibidem; Hunt 2016, 29; Lowry 2016, 34: 156), again with the exclusion of Anderson & Egli (2011, 127), is the idea that *C. tupizensis* sensu Backeberg (from now on *C. tupizensis*), is part of the synonymy of *E. buchtienii* (*Cleistocactus buchtienii* Backeberg in the cited literature), the first representing the southernmost populations in the area of the second taxon (Lowry 2016, 34: 163). Our first encounter with the populations of *C. tupizensis* (A&M 186) was in March 2007, during our second study trip in the South American continent (07 Nov 2006/01 Aug 2007). We were in Tupiza, Potosí, Bolivia, where without following specific indications, leaving the city walking in a south-western direction, we dedicated ourselves to



Fig. 7 *Echinopsis nothohyalacantha* (*tarijensis* populations). Bolivia, Tarija, Tarija, Portillo, 2011-06-03, A&M 525



Fig. 8 *Echinopsis nothohyalacantha* (*tarijensis* populations). Bolivia, Tarija, Tarija, Portillo, 2011-06-03, A&M 525



Fig. 10 *Echinopsis nothohyalacantha* (*nothohyalacantha* populations). Argentina, Jujuy, Volcán, 2,100m, 2007-03-19, A&M 171



Fig. 9 *Echinopsis nothohyalacantha* (*tarijensis* populations). Bolivia, Tarija, Tarija, Portillo, 2011-06-03, A&M 525



Fig. 11 *Echinopsis nothohyalacantha* (*nothohyalacantha* populations). Argentina, Jujuy, Volcán, 2,100m, 2007-03-19, A&M 171



Fig. 12 Carlos, Miguel and Alberto. Bolivia, Chuquisaca, Culpina, 2011-06-30

a series of surveys in the areas between the Puerta del Diablo, the Valle de Los Machos and the Cañon del Inca. Among these surveys, we found populations of *C. tupizensis*, whose distinctive character was immediately shown to be the evident and thin orange-red/dark-red spination, that mainly involves the upper



Fig. 13 *Echinopsis nothohyalacantha* (*tupizensis* populations). Bolivia, Tarija, Quebrada de Paicho Sur, 2011-06-29, A&M 564

part of its stem (Fig. 1). The orange tips of this taxon, which together with the rocky spires characteristic of that area, stood out against the blue sky, are one of the most vivid memories of that day (Fig. 2). The taxon was substantially distinguished by the aforementioned colour of the spines, as well as by a greater height of the stems, compared to the populations of *Echinopsis* (*Cleistocactus*) *nothohyalacantha* (the third protagonist of our taxonomic revision) which bear (on average) spines coloured from hyaline to straw yellow and orange at the top. This latter taxon was also detected by us in the same month (March) in Argentina, on the rocks of the pre-Puna arid valleys between



Fig. 14 *Echinopsis nothohyalacantha* (*tupizensis* populations). Bolivia, Tarija, Quebrada de Paicho Sur, 2011-06-29, A&M 564



**Fig. 15** *Echinopsis nothohyalacantha* (*tupizensis* populations). Bolivia, Chuquisaca, Culpina, Loc. Santa Rosa, 2011-06-30, A&M 575

Quebrada del Toro (Salta) in the south, and Quebrada de Humahuaca (Jujuy) in the north, see A&M 171, Volcán, 2100 m (Fig. 3), as we went up towards La Quiaca-Villazón (the two border towns between Argentina and Bolivia), in the direction of Tupiza. As this was the first time that we experienced these two taxa in their natural habitats, and having never before investigated the populations of *E. buchtienii* in the Cochabamba area, type locality of the taxon, ie T: BO, between Arque and Cochabamba, 2000m, [Buchtien?] (ZSS, fide Egli 1987/TSP 59: 35–36 (Hunt et al 2006, text: 45), in relation to the Tupiza populations, we relied on the understanding of the ICSG members (Hunt et al, 2006), who already at that time assimilated the populations of *C. tupizensis* in *C. buchtienii*.

Before leaving Tupiza, it is noteworthy to mention that in the course of the surveys conducted on 28 Mar 2007 south-west of the city, together with our first population of *C. tupizensis* and other sympatric taxa common in the area, such as *Echinopsis* (*Oreocereus*) *celsiana* (Salm-Dyck) Anceschi & Magli, A&M 187 (Fig. 4) (*Oreocereus* is also part of the genera indicated by the analysis as part of the new monophyletic macrogenus *Echinopsis*) and *Echinopsis tacaquirensis* (Vaupel) H. Friedrich & G.D. Rowley, A&M 188 (Fig. 5), we came across a population of *Weingartia fidana* (Backeberg) Werdermann growing on stony hills in the Puerta del Diablo area, A&M 189 (Fig. 6). Apart from the beautiful specimens making up the

population (see A&M 189, photos 1–21, in [cactusinhabitat.org](http://cactusinhabitat.org)), in our eyes it was merely a population of the taxon. Only after the publication of the materials relating to A&M 189 in our website (October 2010), and the attention that was subsequently focused on the population in question, did we learn that we had unknowingly found the ‘lost’ population of the type of *W. fidana*. Although the information on our web page was not so detailed, ie Bolivia, Potosí, Tupiza, Puerta del Diablo, our photos of the survey were quite explicit, and knowing for sure that by that time the population has been visited on several occasions, we feared for its fate. Since that



**Fig. 16** *Echinopsis nothohyalacantha* (*tupizensis* populations). Bolivia, Chuquisaca, Culpina, Loc. Santa Rosa, 2011-06-30, A&M 575

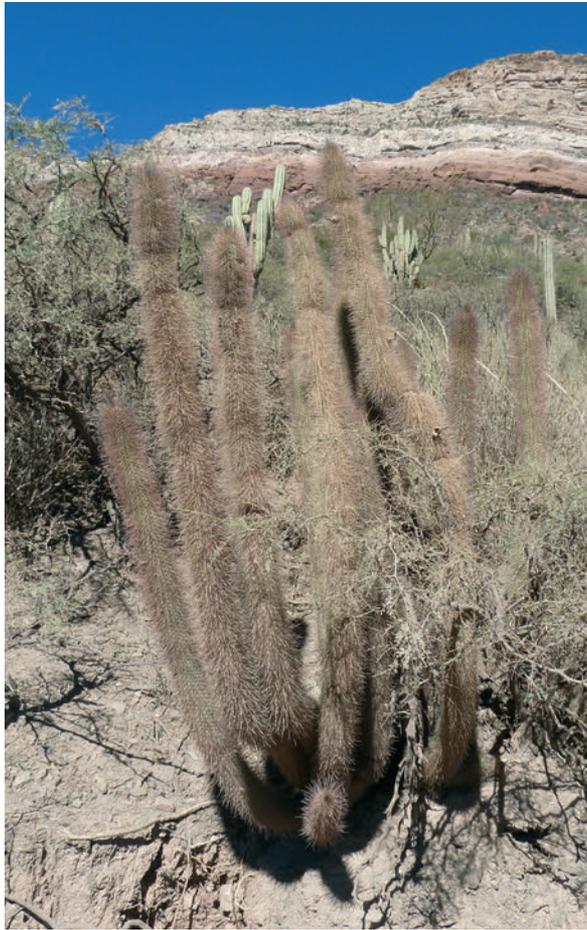


Fig. 17 *Echinopsis nothohyalacantha* (*tupizensis* populations). Bolivia, Chuquisaca, road to Culpina, 2011-06-30, A&M 581

event we have become more discreet about the information that accompanies the location of taxa in our publications, especially those judged to be 'rare'. In this regard, the reason for the almost maniacal importance that is usually given to the population of the type of a taxon escapes us, which we personally consider a population of the taxon, not **the** population of the taxon. As already reported in our latest booklet (Anceschi & Magli 2021, unpubl. data), regarding the attempt to limit the area of the type of *Gymnocalycium pugionacanthum* Backeberg ex H.Till by Meregalli & Kulhánek, for a 'better' definition of the species thus obtained, "in order that the science of classification has some meaning (ie that approaches something approximately true in nature) and performs some distinctive function, we believe it is fundamental that it is the type that must adapt to the natural populations, not the natural populations to the type. For example, the replacement of the idea of a type as currently conceived, ie based on a **single** individual, with another

that considers a **set** of individuals, would be more representative of the real variety of a natural species."

Returning to our research, the next step takes us to June 2011, during our fourth South American trip (15 Feb 2011/30 Dec 2011), a journey that will remain unforgettable in the panorama of our studies, having in fact travelled that year for 11 consecutive months with an average of about one move every three days. We were in Tarija, in the homonymous department in the extreme south-east of Bolivia, where between the 3rd and 22nd of the month we carried out three surveys on the rocks of the pre-Puna arid hills surrounding the city; two in the south-east of the city, Portillo (A&M 525) and El Angosto [Cañón de La Angostura] (A&M 537) localities and one immediately south, at the Dique San Jacinto (A&M 544), noting, as already published in our 2013 booklet (Anceschi & Magli 2013, 49) that the populations previously attributed to *Cleistocactus tarijensis* Cárdenas (Anderson 2001, 164) or *Cleistocactus hyalacanthus* subsp. *tarijensis* (Cárdenas) Mottram (Hunt et al. 2006, text 46) were nothing but (Figs. 7–9) the natural progression to the north, of the Argentine populations of *E. nothohyalacantha* (Figs. 10–11). In fact, the distinctive elements of *C. tarijensis* with respect to the southern populations consisted of fewer spines (about 20 versus 20–30) and a more northerly distribution in the province of Tarija, in Bolivia, compared to the provinces of Salta and Jujuy, the area of distribution of *E. nothohyalacantha* in Argentina (ibidem). However, apart from the labile morphological distinction based on the number of spines, where there is a transitional phase (ie the semaphoront with 20 spines per areole), common to both taxa, as demonstrated by the surveys of *E. nothohyalacantha* (as *Cleistocactus hyalacanthus*) in the Departments of Chuquisaca, Potosí and Tarija (see Ralph Martin's Cactus and Succulent Field Number Finder), there was evidence of detections of the 'Argentinian' taxon in a northerly direction, well beyond the department of Tarija. We underline that the same position was also taken a few years later by Lowry in his synopsis of the genus *Cleistocactus* (2016, 34: 148-186), which in fact sees *C. tarijensis* and *C. hyalacanthus* subsp. *tarijensis* included in the synonymy of *Cleistocactus hyalacanthus* (K. Schumann) Roland-Gosselin (ibidem: 163).

Fig. 18 (facing page, top) *Echinopsis nothohyalacantha* (*tupizensis* populations). Bolivia, Chuquisaca, Culpina, Com. Sajlina, 2011-06-30, A&M 585

Fig. 19 (facing page, bottom) *Echinopsis nothohyalacantha* (*tupizensis* populations). Bolivia, Tarija, between Tomayapo and Carmen del Obispo, 2011-07-02, A&M 608





**Fig. 20** *Echinopsis nothohyalacantha* (*tupizensis* populations). Bolivia, Chuquisaca, north-east of Tarabuco, Lamboyo, 2014-03-10, A&M 1007

During the same journey, Tarija was the starting point of an expedition to the north-west, beyond the Cuesta de Sama (the mountain overlooking the city), which lasted four days (29 Jun 2011–2 Jul 2011). We departed on a minibus, with our young drivers Carlos and Miguel (Fig. 12), with the goal of conducting a series of surveys in the habitats of the arid inter-Andean rocky valleys and pre-Puna and Puna rocky outcrops between the Cuesta de Sama, Iscayachi, San Antonio, Quebrada de Paicho Sur, Tomayapo and Carmen del Obispo (in the Tarija Department) and Camargo (base of the expedition), San Pedro, Culpina, and Tacaquira as the most extreme point to the north

(in the Department of Chuquisaca). During the surveys carried out in the areas involved in the expedition, we had the opportunity to observe that the populations we recognised in 2007 in Tupiza as *C. tupizensis* certainly extended at least up to Culpina, Chuquisaca, in a north-easterly direction, 105km as the crow flies from the Tupiza area. All the populations of the taxon in the areas visited: A&M 564, Quebrada de Paicho Sur (Figs. 13–14), A&M 575, Culpina, Loc. Santa Rosa (Figs. 15–16), A&M 581, road to Culpina (Fig. 17), A&M 585, Culpina, Com. Sajlina (Fig. 18), and A&M 608, between Tomayapo and Carmen del Obispo (Fig. 19), showed in most of the individuals the thin orange-red/dark-red spines in the upper part of the stem, typical of *C. tupizensis*. After the surveys conducted in 2011 north-west of Tarija, our operations involving the taxa covered by this article move forward to 2014, covering our fifth study trip (4 Nov 2013/1 Jun 2014). In fact, between 8 and 14 March, we were based in Tarabuco, Chuquisaca, Bolivia, also to clarify the alleged relations between two species of the genus *Parodia* Spegazzini, ie *Parodia prestoensis* F.H. Brandt and *Parodia tuberculata* Cárdenas, which grow in the valleys that extend in the four cardinal points from Tarabuco (ie in the direction of Presto in the north (*P. prestoensis*, *P. tuberculata*), Zudañes in the east (*P. tuberculata*), Icla in the south (*P. prestoensis*) and Sucre in the west (*P. prestoensis*, *P. tuberculata*). Also on this occasion during the surveys carried out in the pre-Puna rocky



**Fig. 21** *Echinopsis nothohyalacantha* (*tupizensis* populations). Bolivia, Chuquisaca, south-east of Tarabuco, 2014-03-13, A&M 1031



**Fig. 22** *Echinopsis nothohyalacantha* (*tupizensis* populations). Bolivia, Chuquisaca, south-east of Tarabuco, 2014-03-13, A&M 1031

slopes and the related arid inter-Andean rocky valleys, both north-east of Tarabuco, in the direction of Zudañes, see A&M 1007, Lamboyo (Fig. 20), then south-east towards Icla, A&M 1031 (Figs. 21–22) & A&M 1035 (Figs. 23–25), populations of *C. tupizensis* continued to appear. The taxon increasingly assumed the form of a dominant species, which with numerous populations, in turn rich in individuals, extended from the south of Tupiza, Potosí Department, in a northern direction, at least up to the district of the city of Sucre, in the Department of Chuquisaca, now at a distance of about 280km as the crow flies from the populations of the south.

We were starting to wonder where we would begin to encounter any evidence, that as conceived by the current literature (Hunt et al. 2006,

text: 49; Leuemberger 2012, 27: 12-16; Hunt 2016, 29; Lowry 2016, 34: 156 ), that the *Cleistocactus* of Tupiza was somehow related to the populations of *E. buchtienii*. At this stage we were looking for a transitional point that would justify the assimilation of a taxon (*C. tupizensis*), lower, <1.5 m (Anderson & Eggli 2011, 127) with a stem bearing a greater number of ribs, <24 (Backeberg 1977, 99; Anderson 2001, 164; Anderson & Eggli 2011, 127), lower, with more spines, <22 (Backeberg 1977, 99; Anderson 2001, 164–165; Anderson & Eggli 2011, 127), more fragile, of a dark red/orange-red colour in the upper part of the stem, in one (*E. buchtienii*) much higher, < c. 2.55m (A&M 1314, 2016, see description of the taxon below), with fewer ribs, <22 (Anderson & Eggli 2011, 117), more prominent, and fewer spines, <19 (Anderson 2001, 155; A&M 1306, 2016, see description of the taxon below), yellow, stronger, homogeneous in all parts of the stem, as shown by the image chosen to represent the taxon in Hunt et al. (2006, atlas: 202, fig. 202.3). On the other hand, the populations of *C. tupizensis* began to show an ever greater morphological similarity of stem, ribs and spination with the populations of the *E. nothohyalacantha/C. tarijensis* complex, the two taxa now forming another dominant species whose populations as already highlighted, extended from the provinces of Salta and Jujuy in Argentina to the areas bordering the city of Tarija in Bolivia, but with records of surveys far north of the ‘tarijeña’ area (see Ralph Martin’s Cactus and Succulent Field Number Finder).



**Fig. 23** *Echinopsis nothohyalacantha* (*tupizensis* populations). Bolivia, Chuquisaca, south-east of Tarabuco, 3,044m, 2014-03-13, A&M 1035



Fig. 24 *Echinopsis nothohyalacantha* (*tupizensis* populations). Bolivia, Chuquisaca, south-east of Tarabuco, 3,044m, 2014-03-13, A&M 1035

The only distinction between *C. tupizensis* and *E. nothohyalacantha* remained the more evident dark red/orange red colour of the upper part of the stems in the first taxon. For the elements of similarity between some individuals of the populations of the first taxon with those belonging to the populations of the second, compare: A&M 1007 (*C. tupizensis*), Bolivia, Chuquisaca, north-east of Tarabuco, Lamboyo (Fig. 26) with A&M 525 (*E. nothohyalacantha* (*tarijensis* populations), Bolivia, Tarija, Tarija, Portillo (Fig. 27); and again A&M 1007 (*C. tupizensis*), ibidem (Fig. 28) with A&M 544 (*E. nothohyalacantha* (*tarijensis* populations), Bolivia, Tarija, Tarija, Dique San Jacinto (Fig. 29). Meanwhile, we hoped to be able to reach a clarification about the real relationships between *E. buchtienii* and *C. tupizensis* during the same trip (2013–2014), and after Tarabuco, following the track of the Andean parodias, after having carried out surveys in the south (Turuchipa, Potosí) and to the north (Puente Arce, Chuquisaca) of the city of Sucre, following first Ruta 5 then, Carretera 23, we headed to Mizque in the Department of Cochabamba, to reach the capital where among the many planned surveys,



Fig. 25 *Echinopsis nothohyalacantha* (*tupizensis* populations). Bolivia, Chuquisaca, south-east of Tarabuco, 3,044m, 2014-03-13, A&M 1035



Fig. 26 *Echinopsis nothohyalacantha* (*tupizensis* populations). Bolivia, Chuquisaca, north-east of Tarabuco, Lamboyo, 2014-03-10, A&M 1007

some populations of *E. buchtienii* were also waiting for us, this time in the populational area of the type.

### The first encounter with *Echinopsis buchtienii*

Our first encounter with a population of *E. buchtienii* in the Cochabamba area took place a few days after our arrival in the city which we used as a base camp to carry out a series of surveys in the surrounding areas (31 Mar 2014 to 9 Apr 2014). In fact, on 3 Apr 2014, south-east of Cochabamba, in the locality of Cuchu Punata, at 2812m, together with our first population of *Parodia schwebsiana* (Werderm.) Backeberg, A&M 1109 (Fig. 30), we also encountered the first individuals of an *Echinopsis* (*Cleistocactus*) with a morphology attributable to *E. buchtienii* (A&M 1110a). In this sense the image chosen by Hunt et al. to represent the taxon in *NCL* (2006, Atlas: 202, fig. 202.3) is quite in line with the specimens detected on that occasion and subsequently in habitat (Fig. 31), except that the photo chosen by the authors shows an individual endowed with a slightly more “soft” spination compared to that found on average in natural habitats.

On the same day, we again encountered *P. schwebsiana* and *E. buchtienii*, and also on the hills south-east of Arani, 2,863m, where this time the population of



Fig. 27 *Echinopsis nothohyalacantha* (*tarijensis* populations). Bolivia, Tarija, Tarija, Portillo, 2011-06-03, A&M 525

*E. buchtienii* (A&M 1116) was visibly more numerous than the previous one. The characters that distinguish the taxon, ie a certain height, on average forming massive bushes (Fig. 32), the prominent ribs (Fig. 33), together with the strong yellow spination (Fig. 34), appeared to be quite homogeneous in all the individuals of the populations studied in habitat, but none of these showed some morphological similarity with the presumed ‘southern’ populations of the taxon, ie *C. tupizensis* (Fig. 35). During that journey, there were still so many populations that we had planned to visit (the species of the coastal desert of Peru were still waiting for us), that we had to suspend our studies of *E. buchtienii* in the Cochabamba area at the only two populations encountered then. One thing was certain though: our concepts of *C. tupizensis* and *E. buchtienii* had moved further and further away from each other, while that of the first taxon came closer and closer to that of *E. nothohyalacantha*. However, we had to consider that, while our knowledge of *C. tupizensis* and *E. nothohyalacantha* was already quite extensive in number of populations visited, that of *E. buchtienii* required further ‘ad hoc’ investigations in habitat. Consequently, the three taxa subjects of this research led us to our sixth trip (16 Nov 2015 to 2 Aug 2016), where among the four countries to visit (AR, BO, BR, UY), in Bolivia just three missions awaited us: 1) the reunion with the Acebey family, our fraternal friends in Tarija, 2) an in-depth study on the populations of



Fig. 28 *Echinopsis nothohyalacantha* (*tupizensis* populations). Bolivia, Chuquisaca, north-east of Tarabuco, Lamboyo, 2014-03-10, A&M 1007

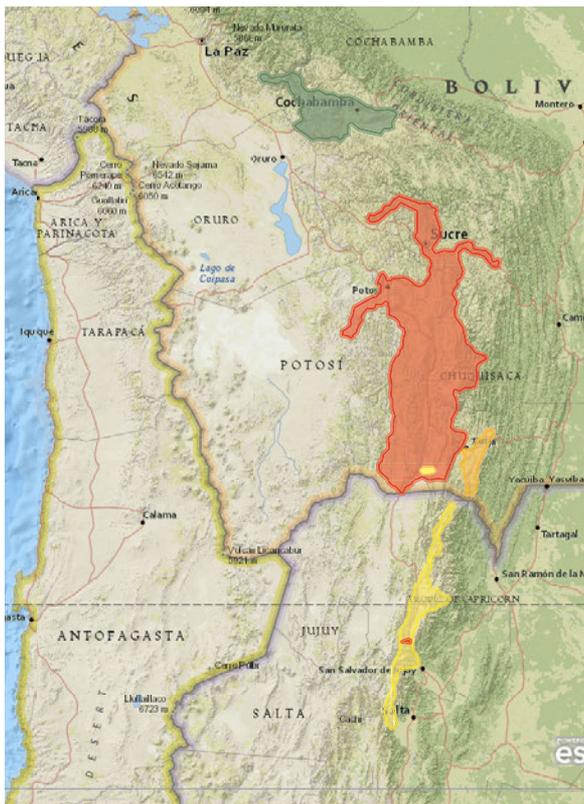
*E. buchtienii* in the areas adjacent the city of Cochabamba, 3) the study of the populations of *Parodia comarapana* Cárdenas, in Comarapa, Santa Cruz.

### ***Cleistocactus tupizensis* sensu Backeberg as part of the *Echinopsis nothohyalacantha* complex**

An initial confirmation of the close relationships between two of the three taxa in question came unexpectedly while we were crossing the Quebrada de Humahuaca (Argentina) for the third time, coming from San Salvador de Jujuy towards the La Quiaca-Villazón border. That year we had chosen the small village of Tumbaya, at the beginning of the Quebrada, to carry out a series of surveys in the area. Among these, was the search for possible new populations of *Parodia chrysacanthion* (K. Schumann) Backeberg, in addition to the detection of the conservation status of an historical population of the same taxon in the Volcán area, a few kilometres away from our base. It was Christmas Day 2015 (we stayed in Tumbaya from



Fig. 29 *Echinopsis nothohyalacantha* (*tarijensis* populations). Bolivia, Tarija, Tarija, Dique San Jacinto, 22-06-2011, A&M 544



Map 1. Extent of occurrence of: *Echinopsis* (*Cleistocactus*) *buchtienii* (22 locations, dark green); *Echinopsis* (*Cleistocactus*) *nothohyalacantha* (123 locations in total), *nothohyalacantha* populations (20 locations, yellow), *tarijensis* populations (15 locations, orange) and *tupizensis* populations (88 locations, red)



Fig. 30 *Parodia schwebsiana*. Bolivia, Cochabamba, south-east of Cochabamba, Cuchu Punata, 2,812m, 2014-04-03, A&M 1109

23 Dec 2015 to 27 Dec 2015, and we still remember with emotion those days spent observing the ceremonies dedicated to the ‘Navidad’ by the villagers), when, walking in a quebrada west of the village, to reach a population of large specimens of *Echinopsis pasacana* (F.A.C. Weber ex Rumpler) H. Friedrich & G.D. Rowley, A&M 1270 (Fig. 36), on an elevated plateau, climbing up to the plateau we came across some groups of *E. nothohyalacantha* (A&M 1269), a taxon as already previously noted, common in the area. The members of this population of the taxon were less common. In fact, in the same population (Fig. 37) growing side by side, were semaphoronts (Hennig, 1966: 6–7, 32–33, 63, 65–67), with the upper part of the stem bearing spines of a hyaline-straw yellow colour (Figs. 38–39), similar to the traditional concept of *E. nothohyalacantha*, with others having the same portion of the stem with orange-red/dark red spines (Figs. 40–41), closer to the concept of *C. tupizensis*. All this in an area, Tumbaya, in the Quebrada de Humahuaca, Jujuy (AR), which exclusively contains only *E. nothohyalacantha*. The tangible evidence of a repeatedly suspected merger between the morphologies of the two taxa was in front of our eyes. After the inclusion in *E. nothohyalacantha* of the populations of *C. tarijensis* or *C. hyalacanthus* subsp. *tarijensis* (Anceschi & Magli 2013, 49), with the new consideration given by the further addition of the already dominant *C. tupizensis*, *E. nothohyalacantha* has thus assumed the proportions of a dominant



Fig. 31 *Echinopsis (Cleistocactus) buchtienii*. Bolivia, Cochabamba, south-east of Cochabamba, Cuchu Punata, 2,812m, 2014-04-03, A&M 1110a



Fig. 32 *Echinopsis buchtienii*. Bolivia, Cochabamba, Arani, south-east of Arani, 2,863m, 2014-04-03, A&M 1116



Fig. 33 *Echinopsis buchtienii*. Bolivia, Cochabamba, Arani, south-east of Arani, 2,863m, 2014-04-03, A&M 1116

species in the evolutionary Darwinian sense, which with extended populations in turn composed of numerous individuals, following the arid inter-Andean rocky valleys and the pre-Puna and Puna rocky outcrops of the Andean ridge, extending from the west of Campo Quijano, at the beginning of the Quebrada del Toro, Salta, Argentina to the south, at least up to the areas bordering the city of Sucre, Chuquisaca, Bolivia to the north. Actually, various populations of the taxon stand out even further north of Sucre, up to the north of San Pedro da Buenavista, Potosí, Bolivia, as the extreme point of the taxon's range in a north-west direction (Map 1), with an extension of about 740km as the crow flies. It is noteworthy that in his synopsis of the genus *Cleistocactus* Lemaire (Cactaceae), Lowry (2016, 34: 157), in the comment on *C. buchtienii*, highlighted the greater proximity of the populations occupied by the taxon in the south of its distribution range (*C. tupizensis*) with *C. hyalacanthus*, rather than with those of the type of *C. buchtienii*, stating, "The plants to which the name *C. tupizensis* have been misapplied show considerable differences from the type [of *C. buchtienii*]. They are generally shorter in stature,



Fig. 34 *Echinopsis buchtienii*. Bolivia, Cochabamba, Arani, south-east of Arani, 2,863m, 2014-04-03, A&M 1116

have more ribs and more, often hyaline spines giving them a silver appearance... These characters give the plants an appearance similar to that of *C. hyalacanthus* (K. Schum.) Rol.-Goss. and it may be better to consider these southern populations under that name rather than here.” Despite this, however, the author decided to keep *C. tupizensis* sensu Backeberg among the synonyms of *C. buchtienii* (ibidem: 156). Even more unusual appears to be the fact that in the subsequent comment dedicated to *C. hyalacanthus*, Lowry (ibidem163), denies the previous affirmation about the proximity of *C. tupizensis* and *C. hyalacanthus* trying to produce a series of evidence relating to flower, spines and habitats, which would somehow distinguish the two taxa, using these words, “...plants of the southern *C. buchtienii* [*C. tupizensis*] tend to have centrals and radials of different but more or less constant length whilst those of *C. hyalacanthus* are quite variable. Otherwise location may be the only clue; plants of *C. hyalacanthus* are plants of the moister eastern slopes whereas *C. buchtienii* prefers the drier valleys further west.” We emphasise the marginality in the distinction of the spines, which are not particularly evident in the populations in habitat, are



Fig. 35 *Echinopsis nothohyalacantha* (*tupizensis* populations). Bolivia, Potosí, Tupiza, Puerta del Diablo, 3,000m, 2007-03-28, A&M 186



Fig. 36 *Echinopsis pasacana*. Argentina, Jujuy, Tumbaya, west of Tumbaya, 2,130m, 2015-12-25, A&M 1270

however, plausible in the context of the variability of a dominant natural species, so extended and variable that it turned out to be *E. nothohyalacantha*.

Regarding the difference in the habitats 'chosen' by the two taxa, we would like to underline (for the vast portion of their range that we visited), that the Quebradas where the typical *C. hyalacanthus* or *E. nothohyalacantha* grows in Argentina, are as dry as the areas close to Tarija where *C. tarijensis* grows, as are in turn the Andean valleys and the areas of pre-Puna throughout the *C. tupizensis* range, from Tupiza (Potosí) to the Paicho Valley (Tarija), up to the neighbouring areas of Tarabuco (Chuquisaca).

### ***Echinopsis (Cleistocactus) buchtienii*, a relatively dominant species**

Reaching this point, we lacked the in-depth knowledge on the populations of *E. buchtienii* in the Cochabamba area, in order to have a better definition of this third taxon. To confirm the picture that was taking shape, we point out that during the same trip, in travelling between the city of Tupiza (Department of Potosí) to that of Tarija (homonymous department) via Iscayachi, we were able to ascertain that the

populations of *C. tupizensis* from the south of Tupiza actually continue in the direction of the Paicho Valley (Tarija) and surrounding areas, through the Tojo Valley in a northerly direction towards Carrizal. Also that in an easterly direction, in the area between Tojo and Yunchara (already in the Tarija Department), populations of *C. tupizensis* are evident, in the most part composed of individuals with stems bearing orange-red spines, as usual, but also highlighting specimens with yellow spines very close to those of *E. nothohyalacantha*. In short, the same situation found in Tumbaya, but with inverted numbers, as we are already in the prerogative areas of the *tupizensis* populations.

After a break with our friends from Tarija, we finally reached Cochabamba on 23 Jan 2016, to devote ourselves to the study of *E. buchtienii*. In the area surrounding the capital, we carried out five surveys on the taxon; four east of Cochabamba, in the mountains north of Sacaba, between 2,809 and 2,950m (A&M 1306, A&M 1308, A&M 1309, A&M 1312), and one south of Cochabamba, on the road between Cochabamba and Santiváñez, at 2,900m (A&M 1314). In confirmation of our first hypotheses, all the



Fig. 37 *Echinopsis nothohyalacantha* (*nothohyalacantha* and *tupizensis* semaphoronts). Argentina, Jujuy, Tumbaya, west of Tumbaya, 2,130m, 2015-12-25, A&M 1269

populations visited showed rather homogeneous characters, in line with the previous two populations encountered in 2014, confirming a taxon with a habit that takes the form of a massive shrub (Figs. 42–43), <2.55m high (Fig. 44), stems with well raised ribs (Figs. 45–46) and areoles bearing strong yellow-brownish yellow spines (Figs. 47–48) on the whole stem (Fig. 49). No individual within the *E. buchtienii* populations in the Cochabamba area showed signs of proximity to the populations of the *E. nothohyalacantha* complex (*C. tarijensis* and *C. tupizensis* included). Contrary to the extensive territorial dominance of the *E. nothohyalacantha* complex as outlined above, *E. buchtienii* manifests itself as a relatively dominant species (ie dominant only in the areas adjacent to the city of Cochabamba, with some populations propagating in the north-west direction on the Morochata-Independencia line (always in the Department of Cochabamba), up to entering the Department of La Paz, in the areas of Pauca and Quime (both in the Inquisivi Province), as extreme points, respectively to the south and to the north, of the north-west diffusion of the taxon). The populations of *E. buchtienii* appear numerous, in turn

made up of numerous individuals in the area of endemism so circumscribed.

## Taxonomy

Following are the scientific descriptions of the two taxa which are the subjects of our revision, ie *E. buchtienii* and *E. nothohyalacantha* (including *C. tarijensis* and *C. tupizensis* sensu Backeberg), updated on the basis of the new evidence from this article. Descriptions are based on a mix that consider *Cactus Lexicon* (Backeberg, 1977), *The Cactus Family* (Anderson, 2001), *The New Cactus Lexicon* (Hunt et al., 2006), *Das Grosse Kakteen Lexicon* (Anderson & Eggli, 2011), A synopsis of the genus *Cleistocactus* Lemaire (Cactaceae) (Lowry, 2016), and also expanded by our field data [in square brackets]. Together with the new descriptions, we also include updated information on the distribution, biome, ecological region and habitat of the two taxa in question, deriving from the inclusion of *C. tupizensis* in the synonymy of *E. nothohyalacantha*, as well as from the circumscription of the populations of *E. buchtienii* to the sole areas of the Departments of Cochabamba and La Paz as indicated above.



Fig. 38 *Echinopsis nothohyalacantha* (*nothohyalacantha* semaphoront). Argentina, Jujuy, Tumbaya, west of Tumbaya, 2,130m, 2015-12-25, A&M 1269



Fig. 39 *Echinopsis nothohyalacantha* (*nothohyalacantha* semaphoront). Argentina, Jujuy, Tumbaya, west of Tumbaya, 2,130m, 2015-12-25, A&M 1269

## Biomes

The definition of biomes and ecological regions is based on Olson, et al., 2001. For a better understanding of the circumscription of ecological regions as currently conceived we also used: <https://ecoregions2017.appspot.com/>

## Occurrence data

The dataset of occurrence record (145 in total) of the two species and their main synonyms, was obtained using the following sources:

- a) A&M numbers 2005–2016,
- b) Ralph Martin's field number finder (<http://www.fieldnos.bcss.org.uk/finder.html> accessed from 2020/06/03 to 2020/06/15),
- c) GBIF.org (<https://www.gbif.org/species/search> accessed from 2020/06/04 to 2020/06/16),
- d) Lowry, M, 2016, 34: 156, Fig. 6 (LM 0452.02 only).

## Revised synonymy, scientific descriptions, habitat & distribution, ecological regions and biomes

1. *Echinopsis* (*Cleistocactus*) *buchtienii* (Backeberg) Anceschi & Magli



Fig. 40 *Echinopsis nothohyalacantha* (*tupizensis* semaphoront). Argentina, Jujuy, Tumbaya, west of Tumbaya, 2,130m, 2015-12-25, A&M 1269

Heterotypic synonyms to be transferred to *E. nothohyalacantha*: *C. tupizensis* sensu Backeb., *Kakteen-Freund* 3:124 (1934), non *Cereus tupizensis* Vaupel.

Description: habit forming a tall shrub [with a central stem and dense, erect branches, sometimes candelabra-like, <c.2.55m high], branches <5cm diameter. Ribs 12–22, [well defined], with V-notches above the areoles. Areoles brown-tomentose at first, <1cm apart. Spines: [awl-shaped, strong, brownish yellow, green yellow at the stem apex]. Central spines: [1-2] (-4), [usually directed downwards, 2.8]-3.5cm long. Radial spines [6-9](-15), 2 [-5.5]cm long. Flower barely open, tubular, directed upwards, with short, dense hair from the scalp axils, 5–8cm high × 0.9cm diameter, [fuchsia] to wine red, exerted green stigma and purple anthers, style not very prominent, stamens not or hardly outstanding. Fruit globular, 1–3cm in diameter, [green to reddish green, yellowish red when ripe, covered by scales with yellowish-brown bristles, REM persistent]. Seeds, 1.2mm, black, pitted.

Habitat and distribution: Arid inter-Andean rocky valleys, 2,000–4,025m.



Fig. 41 *Echinopsis nothohyalacantha* (*tupizensis* semaphoront). Argentina, Jujuy, Tumbaya, west of Tumbaya, 2,130m, 2015-12-25, A&M 1269



Fig. 42 *Echinopsis buchtienii*. Bolivia, Cochabamba, Sacaba, north of Sacaba, 2,822m, 2016-01-25, A&M 1308



Fig. 44 *Echinopsis buchtienii*. Bolivia, Cochabamba, between Cochabamba and Santiv  ez, 2,900m, 2016-01-25, A&M 1314



Fig. 43 *Echinopsis buchtienii*. Bolivia, Cochabamba, Sacaba, north of Sacaba, 2,880m, 2016-01-25, A&M 1309



Fig. 45 *Echinopsis buchtienii*. Bolivia, Cochabamba, Sacaba, north of Sacaba, 2,822m, 2016-01-25, A&M 1308

Ecological regions: Bolivian montane dry forest and Central Andean puna.

Biomes: Tropical and subtropical dry broadleaf forests and Montane grasslands and shrublands.

Occurrence: BO (LP, CB). Map 1.

2. *Echinopsis* (*Cleistocactus*) *nothohyalacantha* Anceschi & Magli (including *Cleistocactus tarijensis* C  rdenas and *Cleistocactus tupizensis* sensu Backeberg).

Heterotypic synonyms added: *C. tupizensis* sensu Backeb., *Kakteen-Freund* 3:124 (1934), non *Cereus tupizensis* Vaupel (transferred from *E. buchtienii*).

Description: habit shrubby with erect stems, branching basally, 60–150cm high. Stems (4)-[5.5–6.5cm diameter in the centre of the stem, 3.5–5.3cm towards the apex], fresh green. Ribs 14–24, low, obtuse, 3mm high. Areoles whitish. Spines thin, needle-like, projecting, hyaline or straw yellow, [from orange to dark red in the upper part of the stem in some



Fig. 46 *Echinopsis buchtienii*. Bolivia, Cochabamba, Sacaba, north of Sacaba, 2,880m, 2016-01-25, A&M 1309



Fig. 48 *Echinopsis buchtienii*. Bolivia, Cochabamba, between Cochabamba and Santiviáñez, 2,900m, 2016-01-25, A&M 1314



Fig. 47 *Echinopsis buchtienii*. Bolivia, Cochabamba, Sacaba, north of Sacaba, 2,809m, 2016-01-25, A&M 1306



Fig. 49 *Echinopsis buchtienii*. Bolivia, Cochabamba, between Cochabamba and Santiviáñez, 2,900m, 2016-01-25, A&M 1314

populations or individuals]. Central spines 2–4[-5], sometimes thicker than the radials, 2.5–4.5cm long, hyaline, straw yellow, [orange or dark red]. Radial spines (15-) 20–30, bristly, brittle, hyaline [to greyish]. Flower tubular, slightly curving, with little scales with sparse, short hairs, perianth parts spreadings, 3.5–4(-8)cm high × 0.5–0.7cm diameter, red to magenta. Fruit globose, 1.2–1.5cm diameter, [yellowish green] to light red [to yellowish brown], with scales [covered by white hairs, REM persistent].

Seeds from black, shiny to glossy, dark brown.

Habitat and Distribution: Arid inter-Andean rocky valleys and pre-puna rocky slopes, 1,700–3,500m.

Ecological regions: Bolivian montane dry forest and Central Andean puna.

Biomes: Tropical and subtropical dry broadleaf forests and Montane grasslands and shrublands.

Occurrence: AR (JY,SA); BO (CB,CQ,PO,TR). Map 1.

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## GLOSSARY:

**Hennig's concepts of monophyly, paraphyly and polyphyly** – The instruments provided by Hennig to recognise monophyletic groups, ie those that “...are subordinated to one another according to the temporal distance between their origins and the present; the sequence of subordination corresponds to the ‘recency of common ancestry’ of the species making up each of the monophyletic groups “ (Hennig, 1966: 83), are the characters that the author identified as synapomorphy. He considers the characters carried by the first ancestor (stem species) plesiomorphous, those derived during the process of transformation, and fixed on subsequent ancestors apomorphous. In the current species, the characters directly inherited from the first ancestor (plesiomorphous) are defined symplesiomorphous, while the characters derived from more recent ancestors (apomorphous), although not necessarily the most recent, are defined synapomorphous (ibidem, 89). So let us call synapomorphies a particular category of characters, ie those that distinguish a monophyletic group, which are inherited by all members of the group, or clade, from a recent common ancestor.

In the identification of these characters, it is essential to understand the distinction of those that are genuinely synapomorphous from:

- Those that are symplesiomorphous, which like the first, represent types of homologous characters, ie inherited from a common stem species.
- Those resulting from evolutionary convergence or parallelism (analogous characters), either morphologically similar in different species, but not derived from a common ancestor (due to convergence), or similar characters, absent in the stem species of a monophyletic group, occurred independently in the subsequent species (parallelism) (ibid., 117).

On the basis of the selected characters to identify groups, Hennig defines those where similarity is based on synapomorphy as monophyletic; those in which similarity is based on symplesiomorphy as paraphyletic; if the similarity is due to convergence then they are polyphyletic (ibidem, 146).

**Semaphoront** – see glossary of the previous article.

**Sympatric** – Two forms or species are sympatric\*, if they occur together, that is if their areas of distribution overlap or coincide. \*This term was coined by Poulton in 1903. (Mayr, 1942: 148).

# Introduction to the authors

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Giovanna Anceschi (b. Milan, Italy, 1963) and Alberto Magli (b. Bologna, Italy, 1960) decided to dedicate their lives to cactus in 2004.

The couple, who are based in Bologna, Italy, have been travelling and researching nonstop ever since, with a focus on field-based taxonomy. Since 2010, they have managed the comprehensive online archive [cactusinhabitat.org](http://cactusinhabitat.org), together with the publication of the related booklets (2010, 2013), dedicated to the documentation and

classification of cactus populations in Argentina, Bolivia, Brazil, Chile, Paraguay, Peru, and Uruguay. Their extended trips have produced notes and photography on more than 350 species in the wild.

They have contributed taxonomical studies on *Echinopsis* s.l. to *Cactaceae Systematics Initiatives* (2013) and on *Parodia* s.l. to *Bradleya* (2018) and *The Cactus Explorer* (2013–2014).

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Giovanna Anceschi and Alberto Magli. Bolivia, Santa Cruz, Comarapa, north of Comarapa, 2,159m, 2016-01-30

