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A putative *Oreocereus* x *Echinopsis* hybrid from southern Bolivia

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Abstract: Solitary plants of the putative intergeneric cross *Oreocereus celsianus* × *Echinopsis tarijensis* were found on two independent occasions in the same general region of S Bolivia (Dept. Potosí). The plants are described and illustrated. They are intermediate in general appearance and flower characters between the supposed parents, and appear to be sterile. The importance of intergeneric and interspecific crosses in the evolution of Cactaceae is briefly discussed, and the relative ease with which intergeneric hybrids can be artificially obtained in cultivation is contrasted with the apparent rarity of naturally occurring intergeneric hybrids. Based on available evidence, the impact of natural intergeneric hybridization on cactus evolution appears to be limited.

Zusammenfassung: Bei zwei unabhängigen Gelegenheiten wurde im selben Grossraum in Südbolivien (Dept. Potosí) je eine Einzelpflanze der vermuteten intergenerischen Kreuzung *Oreocereus celsianus* × *Echinopsis tarijensis* gefunden. Die Pflanzen werden beschrieben und abgebildet. Sie stehen im generellen Aussehen sowie bezüglich der Blütenmerkmale zwischen den vermuteten Elternarten, und scheinen steril zu sein. Die Bedeutung von intergenerischen und interspezifischen Kreuzungen für die Evolution der Cactaceae wird kurz diskutiert, und die Verhältnisse in Kultur mit verhältnismässig einfach künstlich erzielbaren intergenerischen Hybriden werden mit der offensichtlichen Seltenheit natürlich vorkommender Hybriden kontrastiert. Auf der Basis des vorhandenen Wissens erscheint der Einfluss natürlicherweise entstehender intergenerischer Hybriden auf die Evolution der Kakteen gering zu sein.

Resumen: Solitary plants of the putative intergeneric cross *Oreocereus celsianus* × *Echinopsis tarijensis* were found on two independent occasions in the same general region of S Bolivia (Dept. Potosí). The plants are described and illustrated. They are intermediate in general appearance and flower characters between the supposed parents, and appear to be sterile. The importance of intergeneric and interspecific crosses in the evolution of Cactaceae is briefly discussed, and the relative ease with which intergeneric hybrids can be artificially obtained in cultivation is contrasted with the apparent rarity of naturally occurring intergeneric hybrids. Based on available evidence, the impact of natural intergeneric hybridization on cactus evolution appears to be limited.

Introduction

Hybridization, both intergeneric (i.e. between species of different genera) and interspecific (i.e. between species of the same genus), is a well known fact in Cactaceae (e.g. Hawkes 1982, 1983, Rowley 1994, 2004a, 2004b). While there is a profusion of hybrids produced artificially in cultivation (some of them of horticultural importance as well as of great economic value, e.g. *Hatiora* ×graeseri, “Easter Cactus”, *Schlumbergera* × *buckleyi*, “Christmas Cactus”), the number of confirmed naturally occurring hybrids is surprisingly small.

Rowley (1994, 2004a) lists the known naturally occuring intergeneric hybrid combinations, and Rowley 2004b is a complete catalogue of known intergeneric hybrids, both naturally occurring or produced in cultivation. Intergeneric cactus hybrids are only known from subfamily Cactoideae, but not from Opuntioideae. In the few cases of natural intergeneric hybrids outside subtribe Trichocereinae, the number of hybrid individuals is always reported as small or very small (e.g. Bressler 2002 for ×*Myrtgerocactus*, of which 1-2 adult plants are known only, with sterile fruits; Bravo-Hollis 1978 for ×*Pacherocactus*, with a single adult plant only). An exception is a population of hybrids of *Neobuxbaumia* × *Cephalocereus* (Vite & al. 1996), which are again thought to be sterile.

In addition to these confirmed cases, hybrid

Figure 1 ×*Oreonopsis* individual at the Pampa Chuchuli locality. In the background a flowering specimen of *Echinopsis werdermanniana*.

Figure 2 Flower details of the Pampa Chuchuli plant.

Figure 3 Crown of the Pampa Chuchuli plant with many dry flower remains, but no fruits.

Table 1 (on pages 34 & 35):

Known intergeneric crosses in Trichocereeinae, based primarily on Rowley (1994, 2004a, 2004b). Rowley (2004b) also lists many additional hybrid combinations which are most unlikely to have ever existed, and these are omitted from this list. Entries are arranged alphabetically, with the parent coming first in alphabetical sequence listed as parent A (e.g. reports of *Echinopsis* × *Cleistocactus* are listed under *Cleistocactus* × *Echinopsis*). For the columns Parent A and Parent B, generic names are used as in the original publications, followed by the accepted generic synonym in brackets according to Anderson 2005. In the column Nothogenus, the original nothogeneric name is listed, with a referral to the nothogeneric name based on the classification of Anderson 2005. The hybrid sign is omitted for clarity.

Figure 4 ×*Oreonopsis* individual at the Abra Blanca locality.

Figure 5 Flowering ×*Oreonopsis* individual at Abra Blanca in top view.

Figure 6 ×*Oreonopsis* individual at the Abra Blanca locality, with last open flowers and many dry flower remains from this and the previous flowering period, but without fruits.

Figure 7 *Echinopsis tarijensis*, Pampa Chuchuli, photographed in late February with open flowers and developing fruits from the first flush of flowers around Christmas.

Figure 8 *Echinopsis tarijensis* produces an impressive flush of flowers towards the end of December. (Photographed at Torre Waykho)

Parent A	Parent B	Nothogenus	Wild	Reference
Acanthocalycium	Echinopsis	Acanthechinopsis		Rowley 2004b
Akersia (Cleistocactus)	Borzicactus (Cleistocactus)	Borkersia → Cleistocactus		Rowley 2004b
Akersia (Cleistocactus)	Oreocereus	Oreokersia → Cleistoreocereus		Hans & al. 2012
Bolivicereus (Cleistocactus)	Echinopsis	Not named → Cleistopsis		
Bolivicereus (Cleistocactus)	Matucana	Not named → Cleistocana		Hans & al. 2012: 269
Borzicactus (Cleistocactus)	Chamaecereus (Echinopsis)	Chamaeborzicactus nom. inval. = Chamaezicactus nom. inval. → Cleistopsis		Rowley 2004b
Borzicactus (Cleistocactus)	Cleistocactus	Cleistoborzicactus → Cleistocactus		Rowley 2004b
Borzicactus (Cleistocactus)	Denmoza	Borzimoza → Cleistoza		Rowley 2004b
Borzicactus (Cleistocactus)	Echinopsis	Borzinopsis → Cleistopsis		Rowley 2004b
Borzicactus (Cleistocactus)	Espostoa	Borzipostoa → Espostocactus	X	Ritter 1981, Rowley 2004b
Borzicactus (Cleistocactus)	Matucana	Not named → Cleistocana	X	Ritter 1981
Borzicactus (Cleistocactus)	Oroya	Borziroya → [unnamed]		Rowley 2004b
Chamaecereus (Echinopsis)	Cleistocactus	Cleistochamaecereus → Cleistopsis		Rowley 2004b
Chamaecereus (Echinopsis)	Echinopsis	Chameaecereopsis → Echinopsis		Rowley 2004b
Chamaecereus (Echinopsis)	Pygmaeocereus	Chamygmaeocereus → [unnamed]		Mordhorst 2007
Cleistocactus	Denmoza	Cleistoza		Rowley 2004a
Cleistocactus	Echinopsis	Cleistopsis		Rowley 2004b
Cleistocactus	Espostoa	Espostocactus	X	Ritter 1981, Rowley 2004b
Cleistocactus	Haageocereus	Cleistaageocereus		Mordhorst 2011
Cleistocactus	Matucana	Cleistocana	X	Ritter 1981, Rowley 1994
Cleistocactus	Oreocereus	Cleistoreocereus	X	Ritter 1981, Rowley 2004a

Parent A	Parent B	Nothogenus	Wild	Reference
Cleistocactus	Samaipaticereus	Cleipaticereus	X	Rowley 1994
Cleistocactus	Yungasocereus	Yungastocactus	X	Ritter 1981, Rowley 2004a
Denmoza	Echinopsis	Echinomoza	X	Rowley 2004a, Font & Pica 2001, Font 2004
Denmoza	Seticereus (Cleistocactus)	Setidenmoza → Cleistoza		Rowley 2004b
Denmoza	Trichocereus (Echinopsis)	Trichomoza → Echinomoza	X	Rowley 2004b
Echinopsis	Haageocereus	Echinaageocereus		Mottram 2008
Echinopsis	Harrisia	Harrisinopsis		Rowley 1982, Rowley 2004b
Echinopsis	Hildewintera (Cleistocactus)	Hildewintopsis (nom. inval., Art. H9.1) → Cleistopsis		Hans & al. 2012
Echinopsis	Lobivia (Echinopsis)	Echinobivia → Echinopsis		Rowley 2004b
Echinopsis	Oreocereus	Oreonopsis	X	Ritter 1981, Rowley 1994, Lowry 2000, Pinto & Kirberg 2009, Bates 2012
Espostoa	Haageocereus	Haagespostoa	X	Ritter 1981, Rowley 1982
Espostoa	Matucana	Espocana	X	Ritter 1981, Heath 1992, Rowley 2004
Espostoa	Rauhocereus	Unnamed	X	Ritter 1981
Espostoa	Weberbauerocereus	Weberbostoa	X	Ritter 1981, Rowley 1994
Haageocereus	Matucana	Unnamed		Hans & al. 2012: 265 ref. 690
Lobivia (Echinopsis)	Oreocereus	Oreobivia → Oreonopsis		Rowley 2004b
Matucana	Morawetzia (Oreocereus)	Not named → Oreocana		Hans & al. 2012: 268
Matucana	Oreocereus	Oreocana	X	Ritter 1981, Heath 1992, Rowley 2004a
Matucana	Oroya	Maturoya	X	Ritter 1981, Heath 1992, Rowley 2004a
Morawetzia (Oreocereus)	Arequipa (Oreocereus)	Moraquipa → Orcoereus		Baumgärtner 2012
Oreocereus	Trichocereus (Echinopsis)	Oreotrichocereus → Oreonopsis		Rowley 2004b
Oreocereus	Weberbauerocereus	Unnamed	X	Charles 2000, for Oreocereus tacnaensis

Appendix to Table 1

Triparental hybrids:
×*Cleistoechinocana*: → ×*Schickara*
×*Graeserara* Mordhorst 2011: *Cleistocactus* × *Echinopsis* × *Haageocereus*
×*Schickara* Mordhorst 2011: (= ×*Cleistoechinocana*) = *Cleistocactus* × *Echinopsis* × *Matucana*

Hybrids with one parent from outside tribe Trichocereeae:
Cleistocactus × *Echinocereus*: × *Cleistonocereus* (Rowley 2004a)
Echinopsis × *Aporocactus* (now syn. of *Disocactus*): ×*Aporechinopsis* → ×*Disonopsis* (Rowley 2004b)
Echinopsis × *Echinocereus*: ×*Echinocereopsis* (Rowley 2004b)
Echinopsis × *Epiphyllum*: ×*Echinophyllum* (Rowley 2004b)
Echinopsis × *Nopalxochia* (now syn. of Disocactus): ×*Echinopalxochia* → ×*Disonopsis* (Rowley 2004b)
Echinopsis (as *Chamaecereus* / as *Lobivia*) × *Parodia* (as *Notocactus*): ×*Chamecactus* = ×*Notolobivia* → ×*Echinoparodia* (Rowley 2004b)
Echinopsis × *Selenicereus*: ×*Seleniopsis* (Rowley 2004b)
Echinopsis (as *Lobivia*) × *Sulcorebutia* (Ritter 1981): ×*Weinganopsis* Rowley 1994
Harrisia (as *Eriocereus*) × *Cereus* (Ritter 1981): ×*Harricereus* (Rowley 1994)
Harrisia × *Selenicereus*: ×*Selenirisia* (Rowley 2004b)

status has been suggested for genera showing odd combinations of characters, as in the case of *Geohintonia* (Anderson 2001, Anderson 2005, Hunt & al. 2006) and *Pierrebraunia* (Hunt & al. 2006).

Whether hybridization (natural or man-made in cultivation) is intergeneric, or interspecific ("intrageneric") is to some extent dependent on the generic classification used, and this is especially true for genera such as *Echinopsis*, where narrow ("splitter's") and wide ("lumper's") circumscriptions compete.

Naturally occurring interspecific hybridization has been recorded relatively infrequently in the past, although there is a growing body of literature documenting individual cases (e.g. Powell & al. 1991, Lambert & al. 2006a, 2006b; see Machado 2008 for a synopsis). In general, natural interspecific hybridization appears to be of minor importance, unless we are willing to accept that the majority of cases has gone by unnoticed, as suggested by Mottram (2008).

The only exception to this finding are the genera *Opuntia* and *Cylindropuntia* of subfamily Opuntioideae. Within these genera, natural interspecific hybridization has been shown to be a fairly common phenomenon contributing significantly to the presently observed naturally occurring species diversity (Pinkava 2002). In horticulture, artificially produced interspecific hybrid combinations have frequently been produced with the aim to breed novel plants, but have also occurred accidentally in cultivated collections, and there is no overview of documented or suspected combinations of parents.

Intergeneric hybrids in Trichocereinae

Apart from the epiphytic cacti of tribe Phyllocacteae that gave rise to the "epicacti", artificially produced as well as spontaneous natural intergeneric hybrids are especially well known from the genera of Trichocereinae. While globose taxa of *Echinopsis* s.l. and their hybrids (e.g. the "Paramount hybrids", Mays 1997) involving species of formerly segregated genera (e.g. *Lobivia*, *Pseudolobivia*, now included as synonyms in *Echinopsis* on the basis of lexica such as Anderson 2001, Anderson 2005, and Hunt & al. 2006, but see Schlumpberger & Renner 2012 for new data suggesting an alternative treatment) have some general horticultural importance, there is a growing interest in intergeneric hybrids involving other genera of the subtribe, esp. amongst amateur growers on the European continent, and Mordhorst (2011) reports on some recently obtained novel generic combinations. This supplements Ritter (1981: 1514-1515) who lists the intergeneric combinations he found during his extensive travels in South America, but which mostly remain completely undocumented. The known intergeneric combinations are listed in Table 1 (page 34).

From this data, almost every bigeneric combination within Trichocereinae appears possible, adding many combination to the diagram of Rowley (1994). Since the hybrids obtained in cultivation in general are fertile, further breeding resulting in trigeneric combinations has been successfully tried (×*Graeserara*,×*Schickara*, Mordhorst 2011). At least in cultivation, the genera of Trichocereinae appear to form one large comparium (first suggested by Rowley 1994). This is in contrast to the situation encountered in nature, and Table 1 (page 34) clearly shows the minor number of known naturally occurring bigeneric hybrids.

Figure 9 Native bees are the most frequent visitors of *Echinopsis tarijensis* flowers, and individual bees often arrive at a time when buds are still closed (at Torre Waykho).

Figure 10 Native bee forcing itself into the flower bud that hardly started to open.

Figure 11 Cristate head of *Echinopsis tarijensis* with ripe fruits. The hole in one of the fruit is likely due to an ant attack (at Cerro Cieneguillas).

Figure 12 *Oreocereus celsianus*, Abra Blanca.

Figure 13 *Oreocereus celsianus* in full flower, at Pampa Chuchuli.

Figure 14 *Oreocereus celsianus* with rich fruit set, (Photograph taken at Pampa Chuchuli).

Figure 15 The hummingbird *Patagona gigas* visiting flowers of *Oreocereus celsianus* (Photograph taken at Cerro Tinajayoj, Tupiza, 3425 m).

Figure 16 Another specimen of *Patagonas gigas* visiting flowers or *Oreocereus celsianus* (Photograph taken at Churquipampa, Tupiza, 3322 m).

Moreover, Ritter (1981) does not comment whether the intergeneric hybrids he observed were fertile or not, and does not indicate whether he found whole hybrid populations, or merely isolated plants. There are no records of extensive intergeneric hybrid populations (perhaps with the exception of the hybrid "genus" *Neobinghamia* (involving hybrids between *Espostoa* as one parent, and *Haageocereus* or *Cleistocactus* as the other parent (Rowley 1994: 4)), and a suspected *Oreocereus* ×*Weberbauerocereus* hybrid (Charles 2000)), despite the fact that species from genera of this comparium are frequently growing sympatrically, and the few observations at hand report only few or even solitary individuals amongst a vast population of the parent taxa.

A case study from Bolivia

One of us (MG), during extended travels on foot in Bolivia between mid-January and the end of March 2011, recently on two occasions discovered a solitary individual at each place of a different-looking plant within or near extensive populations of *Oreocereus celsianus* to the E of Tupiza (locality 1: Pampa Chuchuli, 21.42325° S / 65.68097° W, 3475 m; locality 2: Abra Blanca,

Figure 17 Comparison of spination between parents and hybrid individuals.

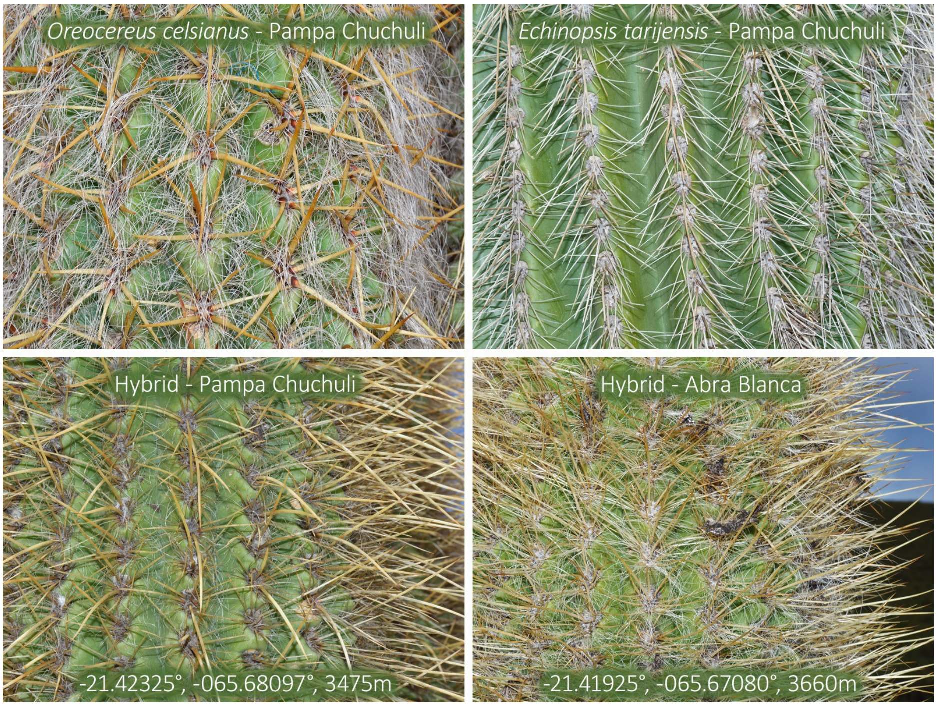

Figure 18 Comparison of spination between parents and hybrid individuals.

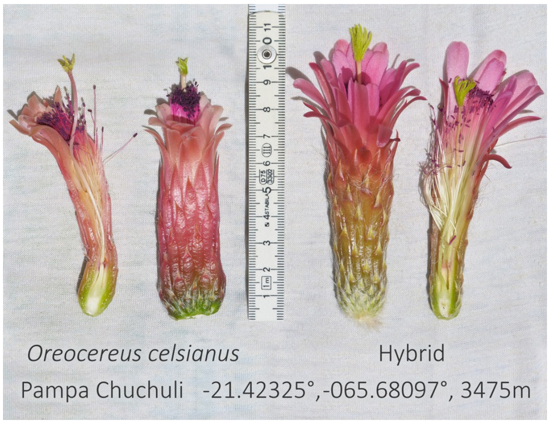

Figure 19 Comparison of flowers between *Oreocereus celsianus* and the hybrid. Due to the small number of *E. tarijensis* flowers, no photographic comparison that includes this species has been made.

21.41925° S / 65.67080° W, 3660 m; both localities visited several times in summer 2011).

Nearby occurring cacti are *Echinopsis werdermanniana*, *E. tarijensis* and *Cleistocactus buchtienii* (usually referred to *C. tupizensis*, but this is a misapplied name, see Leuenberger (2012)). A comparison of vegetative morphology as well as floral characters of the deviating plants with the sympatrically occurring taxa shows that the plants are intermediate between *Oreocereus celsianus* and *Echinopsis tarijensis* (see Figures 17,18 & 19), and most probably represent first-generation hybrids between these two species. It is thus another example of a taxon of ×*Oreonopsis* and confirms the casual report by Ritter (1080: 697, Ritter 1981: 1514).

The case is notable as the two supposed parents show different floral phenomenology: *Oreocereus celsianus* has typical ornithophilous flowers (Figures 13, 15 & 16), and Larrea-Alcázar (2007) and Larrea-Alcázar & López (2011) report the hummingbird *Patagona gigas* as the main pollinator, and 2 other species of hummingbirds as occasional pollinating visitors, and bees, wasps and moths as occasional but probably non-pollinating visitors. The flowers remain open for several consecutive days.

For *Echinopsis tarijensis*, we are not aware of any published observations. According to personal observations by MG, native bees, which are very common in the whole area, are the most frequent visitors (Figures 9 & 10), and no hummingbirds were observed at all. The flowers can remain open for up to 3 days as long as the weather is dry, but they close when it rains and do not open again. Considering the positioning of the flowers, hummingbird visits are not likely, as they prefer laterally porrect flowers as in *Oreocereus*, and corroborated by Schlumberger & Badano (2005), who observed that *Echinopsis atacamensis*, also with laterally porrect flowers is mainly pollinated by *Patagona gigas*, with wasps, bees and hawkmoths as occasional visitors.

The independent occurrence of the supposed hybrid in two localities is a definite sign that some degree of pollinator sharing between the two taxa occurs. We suspect that native bees are the pollen vectors.

The two specimens observed are remarkable as both of them flowered profusely, synchronous with their putative parents, but none of them produced any fruit, as observed on subsequent visits in the same summer. This is in contrast to the sympatrically occurring putative parents, which all produced abundant fruits at the time of the visit (Figures 11 & 14). This is a clear indication that there was no shortage of pollinators, and we conclude that the suspected intergeneric hybrids are sterile (at least female-sterile; pollen viability not investigated). The most likely explanation for this is that the parents have different chromosome numbers.

According to Schlumpberger & Renner (2012), *Oreocereus celsianus* is tetraploid (2n=44), while *Echinopsis tarijensis* (for which no counts are known) is likely diploid (2n=22) (and is placed in a clade with both diploid and tetraploid taxa by Schlumpberger & Renner 2012). The resulting hybrids would be triploid (2n=33), and triploids are generally sterile. (It should be noted that a hybrid *Oreocereus celsianus* × *Echinopsis ferox* from N Argentina was described as being without fruits, and having pollen-less anthers by Lowry (2000), suggesting complete sterility in this case, but no chromosome count for *E. ferox* is available).

Hybridization between the putative parent species appears, at least in S Bolivia, to be a rare event and MG, during his numerous hiking trips in the general area, never did encounter other examples of obvious hybrid plants. This is surprising since both putative parents are common in the region — *O. celsianus* indeed is the most common arborescent cactus of the area, and *E. tarijensis* forms dense stands of 100 m diameter and more. The flowering period of *O. celsianus* embraces almost the whole rainy season from late December to March. *E. tarijensis*, in contrast, produces its main flush of flowers in the period late December to early January, followed by 2 or 3 smaller flushes separated by about 3 weeks. Considering

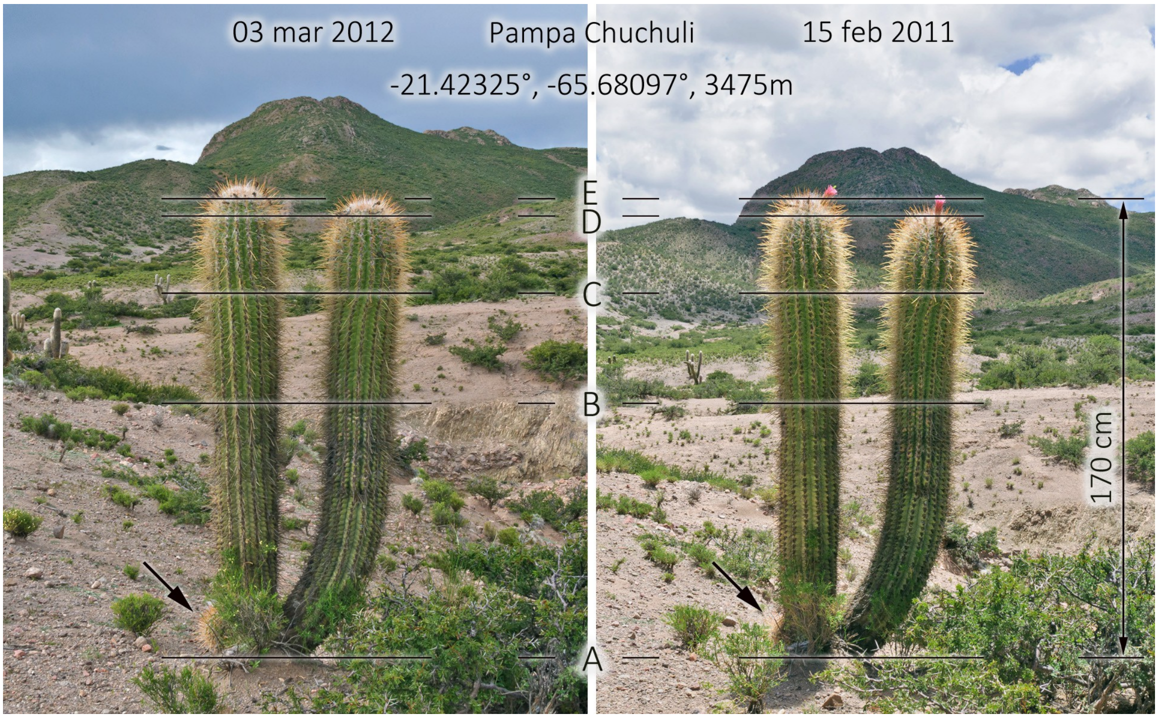

Figure 20 Photographic record of yearly growth of the ×*Oreonopsis* hybrid. The photographs were taken at a 54 week interval. The plant flowered in 2011, but not in 2012 probably as a result of the dry 2011 summer which left the plants with few resources for flowering in 2012. The comparison of the photographs indicates a substantial increase in stem diameter due to the wet 2012 summer. Both stems of the plant grew about 6 cm in the 54 week period.

the vast number of individuals of the putative parents, and their floriferous nature and overlap in flowering period, as well as the abundance of the suspected native bee pollinators, and the excellent fruit set of sympatrically occuring parents, the rarity of the putative hybrid is surprising.

Discussion

At present, the declared importance of hybridization in cactus evolution is merely speculative, and difficulties classifying the observed variability in nature (Mottram 2008) are not necessarily related to natural hybridization, but could also be associated with other ways of incipient speciation. Indeed, Schlumpberger & al. (2009) describe “dramatic among-population variation in floral traits” for *Echinopsis ancistrophora*, with apparent mis-matches between floral traits and observed pollinators. This is a clear indication that the 1:1-relationships we would prefer to see between floral syndromes on the one hand and pollinators on the other hand (see e.g. the diagram in Rowley 1994) are not always in existence, and that evolutionary changes to morphology and floral syndromes are likely to be comparatively rapid.

To explain the apparent rarity of hybrids, it could be theoretially speculated that hybrid fruits are regularly produced in many cases (though not in the example here described), but that the number of hybrid seeds is negligible in comparison with the abundant seed crop produced by the parents. Keeping in mind the generally low establishment rates of cactus seeds / seedlings, the observed rarity of hybrid individuals would be less surprising. This at least is the conclusion of Glass & Foster (1970) for an unnamed wild *Lemaireocereus* × *Myrtillocactus* hybrid.

Some authors argue that naturally occurring hybridization is an important facet in the intricate evolution of the diversity of flowering plants in general, and also contributes to the biodiversity of the cacti that exist today (Friedrich 1974, Machado 2008 and references there cited, Mottram 2008). While the existence of artificially produced intergeneric hybrids without doubt is a good indication of the close relationships between genera or groups of genera (and especially so if these hybrids are fully fertile), the small number of unambiguously confirmed and documented naturally occurring hybrids casts some doubt on the importance of the phenomenon for cactus evolution.

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