

# A putative intercladal *Echinopsis* s.l. (Cactaceae) hybrid from Andean Chile

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**Abstract:** A solitary plant of the putative intercladal cross *Echinopsis* (*Leucostele*) *atacamensis* subsp. *atacamensis* × *Echinopsis* (*Soebrensia*) *formosa* was observed in the contact zone of the mostly allopatric populations of the parent species in the Salar de Atacama region in the Chilean Andes. The plant is intermediate between the parents in its characters. It was found to be sterile, despite normal-looking anthers (with abundant pollen) and stigma. In addition, an apparently typical individual of *E. atacamensis* with yellow flowers has been found, but it remains unknown whether this is merely a flower colour variant, or whether hybridization could be involved.

**Resumen:** Se observó un individuo solitario de un supuesto cruce intercladal entre *Echinopsis* (*Leucostele*) *atacamensis* subsp. *atacamensis* × *Echinopsis* (*Soebrensia*) *formosa* en la zona de solape entre las poblaciones principalmente alopatricas de las especies progenitoras, cerca del Salar de Atacama en la zona norte de Chile. De acuerdo a sus características, la planta es morfológicamente intermedia entre sus progenitores y es estéril, pese al polen y al estigma de aspecto normal. Además se encontró un individuo aparentemente normal de *E. atacamensis*, pero con flores de color amarillo. Sin embargo no se pudo establecer en que medida se trata simplemente de una variación floral caprichosa no más o si está implicada alguna hibridización.

**Keywords:** Chile, Cactaceae, *Echinopsis*, hybrid

## INTRODUCTION

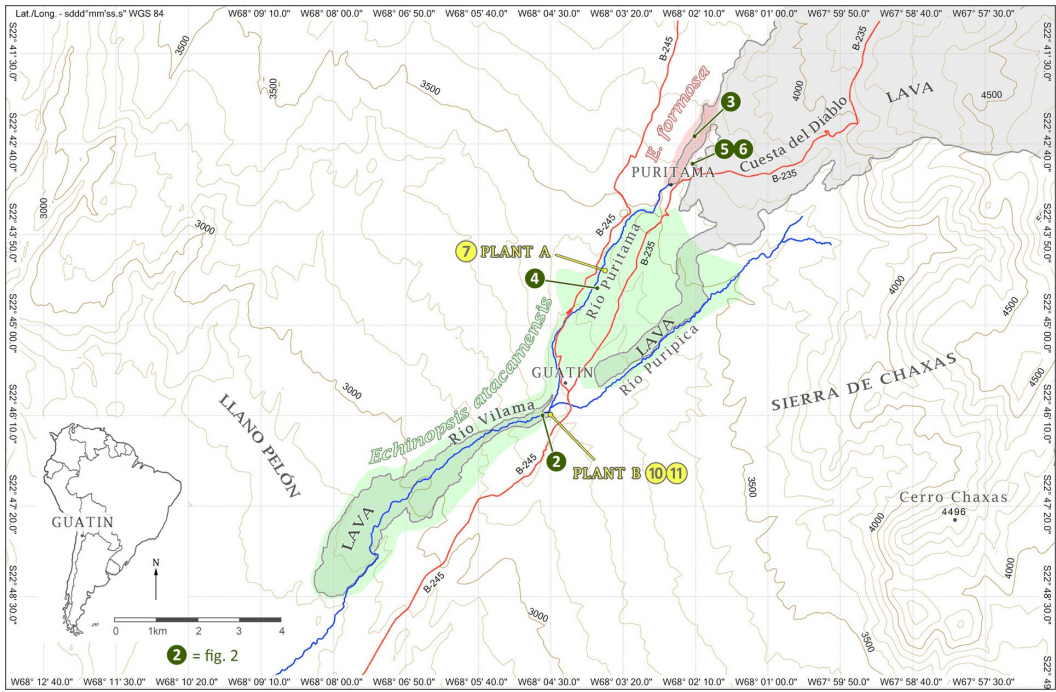
Hybridization between individuals of different species of cacti is a common occurrence, both at intergeneric (= between species of different genera) and intrageneric (= between species of the same genus) levels, and a profusion of such hybrids has been produced intentionally or accidentally in cultivation. Some are horticulturally more or less important, for example the Easter and Christmas cacti, to a lesser extent also the so-called Paramount hybrids of *Echinopsis* s.l. or the epicacti (or orchid cacti) from the *Disocactus-Epiphyllum* group of genera (Rowley 2017). Specialist hobby societies interested in hybrids of epicacti as well as *Echinopsis* s.l. (s.l. = *sensu lato* = "in the wide sense") exist, and their journals (*Bulletin of the Epiphyllum Society of America*, *Hybrid-Journal*) give an impression of the plethora of forms obtained in cultivation by repeated crosses and back-crosses, although often with poor or no documentation as to complete parentage.

In contrast to the ease with which hybrids are obtained in cultivation, well-documented cases of naturally occurring cactus hybrids are relatively few, and it appears that natural hybridization is overall of small importance (see Ritter (1981: 1514–1515) and Rowley (1994) for lists of known or suspected intergeneric natural hybrids) — unless we accept the view of Mottram (2008) that the majority of such hybrids have not yet been recognized as such. Hunt (2015) also argues that "odd" characters present in several monotypic genera of Cactaceae could be explained

by unrecognized hybridization in the evolutionary past. The notable exception to the general scarcity of natural hybrids are the genera *Cylindropuntia* and *Opuntia*, in which natural intrageneric hybridization is common and contributes significantly to the existing diversity of species in nature (Pinkava 2002).

Hybridization amongst species of cacti is especially prevalent in subtribe Trichocereinae, where numerous intergeneric hybrids are known, mostly from cultivation (Rowley 2017: 125; see Eggli & Giorgetta (2013) for a tabulation). Hybrids between species of Trichocereinae are generally fertile, making further breeding possible, including trigeneric hybrids (for examples see, e.g., Mordhorst 2011). This resulted in highly diverse multihybrids that include 4 or more different species amongst their parents (for examples see Hans & al. 2012). The ease with which hybrids are obtained in Trichocereinae led Rowley (1994, 2017: 101) to suggest to treat the group as one large comparium.

As far as we are aware, no exhaustive lists have been published for intrageneric cactus hybrids. Machado (2008) provided a synopsis of naturally occurring suspected intrageneric hybridization, and Powell & al. (1991) and Lambert & al. (2006a, 2006b) deal with selected cases in the genera *Echinocereus* and *Melocactus*, respectively. The picture relative to the occurrence of intergeneric vs. intrageneric hybrids is confounded to some extent by the existence of radically different classifications in use for the cactus family: Depending on the taxon-



**Figure 1.** Map of the study region, northeast of the Atacama Depression, in the area of the Guatín settlement. The positions of the photographs of Figs. 2–11 are indicated with numbers.

omy used, the circumscription of some genera varies widely (compare Hunt & al. (2006) with 124 genera, Nyffeler & Eggl (2010) with 130 genera, Hernández-Ledesma & al. (2015) with 139 genera, and Lodé (2015) with 177 genera). The more a splitter's classification is used, the more likely hybrids between species from closely related genera would be classified as intergeneric, while the very same combination of parent species becomes an intrageneric hybrid within the concept of a lumpers' classification. The genus *Echinopsis* s.l. is a good example — Hunt & al. (2006) and Anderson & Eggl (2011) use a wide circumscription (hence *Echinopsis* s.l.), while the recent molecular study of Schlumpberger & Renner (2012) finds *Echinopsis* s.l. as both polyphyletic and vastly paraphyletic relative to the majority of the remaining genera of subtribe Trichocereinae, and at least half a dozen clades of their phylogeny would have to be recognized at generic level to arrive at monophyletic units (see Schlumpberger 2012 for the necessary new combinations).

Most of the studied examples of natural hybrids (inter- or intrageneric) in Trichocereinae occur as solitary or almost solitary individuals ("isolated occurrences", Machado 2008), or are few in number (Eggl & Giorgetta 2013: 38, with references to exceptions). The  $\times$ *Oreopsis* hybrid (*Echinopsis tarijensis*  $\times$  *Oreocereus celsianus*) reported by us (Eggl & Giorgetta 2013) is a case in point — it occurs as two solitary individuals in separate mixed populations of the parent species, and appears to be sterile. The  $\times$ *Oreopsis* hybrid (*Echinopsis atacamensis*  $\times$  *Oreocereus leucotrichus*) reported by Pinto & Kirberg (2009) was a single plant found in a vast mixed population,

and it was also found to be sterile. In our subsequent report, we add a further example of such a natural hybrid form the *Echinopsis* (s.l.) comparium.

## MATERIAL AND METHODS

**Study site:** The study region is on the south-eastern slope of the Atacama Depression, roughly along the track B-245 from San Pedro de Atacama (Región de Antofagasta, Chile) to Machuca (Fig. 1). The region is dominated by wide lava fields, where young lava flows dating from the Pleistocene (20 kya and older) cover older volcanic ashes from the Pliocene (2.6–5.3 mya) when flowing from the Andean volcanoes towards the Atacama Depression. The longest of these young lava flows originates at the crest of the Andean Cordillera at almost 6000 m asl and descends to 2850 m asl, about 500 m above the salt flat Salar de Atacama. The lava flow is dissected by deep-cut valleys and narrow gorges, some of them with running water, but none of the water flows permanently reaches the bottom of the Atacama Depression. While the surrounding volcanic ashes are deeply weathered, generating a deep gravelly substrate, the lava flow consists of variously broken and fissured hard basaltic rocks (SERNAGEOMIN 2003). The site was visited for several days in November/December 2016 and March/April 2017.

**Study species:** *Echinopsis atacamensis* (Philippi) H. Friedrich & G. D. Rowley subsp. *atacamensis* (subsequently just referred to as *E. atacamensis*) forms a scattered population between 2800 and 3500 m asl (Figs. 2 & 4). Plants are usually solitary and to 4 m tall but can exceptionally grow to 9 m tall. Between



**Figure 2.** Forest of *Echinopsis atacemensis* subsp. *atacemensis* on the lava flow at Guatín, at the site of “Plant B”, with Sairecabur volcano (5970 m asl) at the horizon (3189 m asl, 10. Nov. 2016).



**Figure 3.** Population of *Echinopsis formosa* on the lava flow, at Puritama, associated with *Maihueniopsis camachoii*, *Cumulopuntia ignescens*, *Atriplex imbricata* and *Fabiana ramulosa* (3655 m asl, 8. Dec. 2016).

3500 and 3800 m asl, a dense population of *Echinopsis formosa* (Pfeiffer) Jacobi ex Salm-Dyck is present (Figs. 3, 5 & 6), consisting of solitary globose to shortly columnar branched or offsetting plants (sometimes with up to 12 and more offsets developing from old toppled columns, forming a dense group). The populations of the two species show no significant overlap (Fig. 1). Associated sympatric cacti on the lava flows are *Oreocereus leucotrichus*

(Philippi) Wagenknecht and *Cumulopuntia ignescens* (Vaupel) F. Ritter, and on the volcanic ashes *Maihueniopsis glomerata* (Haworth) R. Kiesling, while *M. camachoii* (Espinosa) F. Ritter is growing at both sites, and *Cumulopuntia sphaerica* (C. F. Förster) E. F. Anderson prefers sites on the lava flow near permanent water flows (but occurs in other ecological conditions outside the study area).



**Figure 4.** The typical, narrowly funnel-shaped white flower of *Echinopsis atacamensis* subsp. *atacamensis* (3347 m asl, 1. Dec. 2016).



**Figure 6.** The typical, shortly and broadly funnel-shaped flower of *Echinopsis formosa* (details as for Fig. 5).



**Figure 5.** A typical branched adult plant of *Echinopsis formosa* with shortly columnar main bodies (the larger is approximately 80 cm tall and 44 cm diam) and several still globose basal offsets, seen from the front (left photograph) and the rear (right photograph) sides (3633 m asl, 7. Dec. 2016).

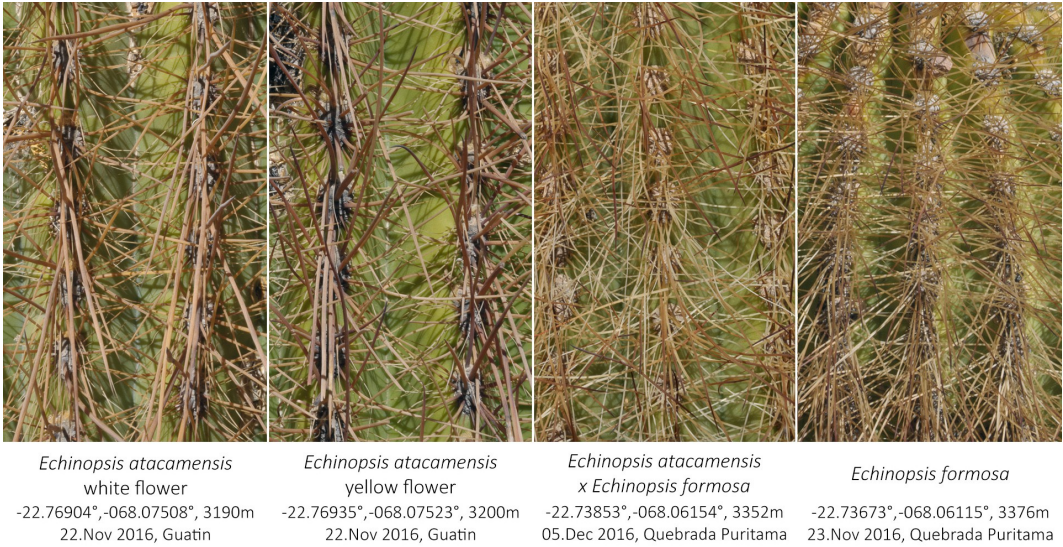
## RESULTS

Amongst the thousands of specimens of the completely allopatric study populations of the two *Echinopsis* species (Fig. 1), two plants presented special characteristics:

**Plant A (Fig. 7):** At 3345 m asl, a solitary unbranched specimen 1.85 m tall and 40 cm diam. was found close to a group of numerous typical, mostly unbranched, *E. atacamensis*, in the canyon of the Río Puritama where the first few specimens of *E. formosa* are occurring. None of the >1000 plants that make up the main population of *E. formosa*, located c. 3 km further along the canyon, has a similar growth form. The spination of the individual is reminiscent of typical *E. formosa*, except for the presence of more whitish, slender, bristly radial spines (Fig. 8), although differences in the spination between *E. atacamensis* and *E. formosa* are overall insignificant.



**Figure 7.** The apparently intermediate Plant A, 1.85 m tall and 40 cm diam. (3345 m asl, 1. Dec. 2016).



**Figure 8.** Comparison of the spination of *Echinopsis atacamensis*, *E. formosa* and the intermediate Plant A.



**Figure 9.** Comparison of the flowers of a typical *Echinopsis atacamensis* subsp. *atacamensis*, the intermediate Plant A and typical *E. formosa*. The insects on the flowers of *E. atacamensis* subsp. *atacamensis* and that of Plant A are different species of halictid bees (see text).

The flower (Fig. 9) showed the typical yellow colour of *E. formosa*, although a hint paler, and with less pronounced coppery-red tips of the outer petaloid perianth elements, but it is larger, with larger and more separately placed petaloid perianth elements, and shows a more pronounced and longer perianth tube. Two openings of flowers were observed at 24. Nov. and 1 Dec. 2016. Both had apparently normal-looking anthers with abundant pollen, and a normally developed style / stigma, but despite the presence of numerous individuals of halictid (Fig. 9) and megachilid bees, no fruit set was recorded at later visits (December 2016, March and April 2017). Also, none of the flowers that opened before did set seed, and the specimen is likely completely sterile.

**Plant B (Figs. 10 & 11):** Within a small "forest" of typical *E. atacamensis* at 3200 m asl (Fig. 2), an unbranched specimen of an otherwise apparently typical *E. atacamensis* was found that consistently

produced yellow flowers. A total of 3 flowers was observed on 10. Nov., 22. Nov. and 24. Nov. 2016, respectively. In addition to the flowers, about a dozen developing fruits were present on the specimen. Vegetatively, the plant falls entirely within the range of growth forms and spination variability exhibited by typical *E. atacamensis* (Fig. 8). Also the flower corresponds with typical *E. atacamensis* flowers as to disposition, size, shape and arrangement of the perianth elements, only the colour of the inner petaloid perianth elements — pale yellow — deviates.

**DISCUSSION**

Plant A described above most likely represents the hybrid *E. atacamensis* subsp. *atacamensis* × *E. formosa* and is gross-morphologically intermediate between its parents. Stem shape and size and rib number are intermediate (based on measured and



**Figure 10.** Plant B is apparently typical of an adult but still unbranched *Echinopsis atacamensis* subsp. *atacamensis* but differs by deviating pale yellow flowers (3200 m asl, 24. Nov. 2016).

published data) between the suspected parents (Table 1), and the flowers also combine characters of both putative parent species (Fig. 9). In the currently preferred classification of Anderson & Egli (2011) and Hunt & al. (2006), the plants conform to an intra-generic *Echinopsis* hybrid, while when applying the classification suggested by Schlumpberger & Renner (2012), it would be a *Leucosteles* × *Soehrensia* hybrid, viz. a hybrid between two rather distantly related clades within *Echinopsis* s.l. in the phylogeny suggested by these authors (Schlumpberger & Renner 2012). This could explain its sterility. Unfortunately, the chromosome numbers of the putative parents are not known with certainty (and a possible difference in ploidy level such as diploid vs. tetraploid) can thus not be used as additional explanation to explain the apparent sterility of the observed individual): Schlumpberger & Renner (2012) give  $2n=22$  for *E. formosa*, but the clade to which this wide-spread and polymorphic species belongs ("Helianthocereus clade" in their paper, *Soehrensia* when accepted as separate genus) also includes tetraploid species (e.g. *E. thelegonoides*, *E. candicans*). For the "E. atacamensis clade" (= *Leucosteles* when segregated at generic level), Schlumpberger & Renner (2012) list  $2n=22$  for both *E. chilensis* and *E. terscheckii*.

No data has been found in the literature about hybrids between species of the two clades involved, *Soehrensia* and *Leucosteles*. *E. atacamensis* especially is not usually grown in cultivation due to its large size and because it is slow-growing (at least under glass in the N hemisphere, pers. obs. UE), and flowering specimens are thus not easily available for hybridization experiments by dedicated growers. *Soehrensia*



**Figure 11.** Flower of plant B (details as for Fig. 10).

species are more commonly seen in cultivation, and a couple of artificially obtained hybrids are listed especially by Ito (1981, 1988), involving three different clades in *Echinopsis* s.l. (see Table 2). The present report is thus the first documented occurrence of a *Leucosteles* × *Soehrensia* hybrid within the *Echinopsis* s.l. comparium. The characteristics of the specimen are intermediate between the parents, and the single observed specimen likely is an F1 hybrid.

Plant B described above is more difficult to interpret. All characteristics of the specimen are completely compatible with *E. atacamensis* (see Fig. 8 for a comparison of spinations) except for the flower, which deviates by the yellow colour of the petaloid perianth elements. The flower colour of *E. atacamensis* is described as white with rosy hues by the relevant Chilean floristic works (Hoffmann & Walter

**Table 1:** Comparison of stem characteristics of *Echinopsis atacamensis* subsp. *atacamensis* and *Echinopsis formosa*. H&W 2004 = Hoffmann & Walter (2005); P&K 2009 = Pinto & Kirberg (2009); pers. obs. = own observations, relating to selected individuals of the study populations, while the published data are aggregate values for the flora regions covered.

Trait	Source	<i>Echinopsis atacamensis</i>	Hybrid (Plant A)	<i>E. formosa</i>
stem height (m)	P&K 2009	6 – 8		not covered
	H&W 2004	up to 7		up to 1.5
	pers. obs. <sup>1</sup>	3.7	1.85	0.8
stem branching	pers. obs.	old plants only, branches far above the base	solitary	old plants, from the base, often forming clumps with equal-sized heads
stem diameter (cm)	P&K 2009	30 – 60		not covered
	H&W 2004	up to 70		20 – 35
	pers. obs.	33	40	44
rib (number)	P&K 2009	20 – 35		not covered
	H&W 2004	20 – 30		27 –40
	pers. obs.	24	34	44

<sup>1</sup> The plant measured for *Echinopsis atacamensis* is that shown in Fig. 10, that for *E. formosa* in Fig. 5 left.

**Table 2:** Hybrids involving species of *Soehrensia*.

Nothogenus	Source	parentage according to the source publication		parentage according to the phylogeny of Schlumberger & Renner (2012)	
		parent 1	parent 2	parent 1	parent 2
<i>Cylindrosia</i>	Ito 1981: 643	<i>Cylindrolobivia huascha</i> var. <i>roseiflora</i>	<i>Soehrensia bruchii</i>	<i>Soehrensia</i>	<i>Soehrensia</i>
<i>Echinosis</i>	Ito 1988: 496	<i>Echinopsis kermesina</i>	<i>Soehrensia bruchii</i>	<i>Bridgesii Clade</i>	<i>Soehrensia</i>
<i>Soehrenantha</i>	Ito 1981: 646,	<i>Soehrensia bruchii</i>	<i>Cosmantha grandiflora</i> <sup>3</sup>	<i>Soehrensia</i>	<i>Soehrensia</i>
	Ito 1988: 685	<i>Soehrensia formosa</i>	<i>Cosmantha grandiflora</i> <sup>3</sup>	<i>Soehrensia</i>	<i>Soehrensia</i>
<i>Soehrenocylindra</i>	Ito 1988: 687	<i>Soehrensia bruchii</i>	<i>Cylindrolobivia vatteri</i> <sup>2</sup>	<i>Soehrensia</i>	<i>Echinopsis</i> s.s.
<i>Soehrenofuria</i>	Ito 1981: 649,	<i>Soehrensia bruchii</i>	<i>Furiolobivia nigra</i> <sup>1</sup>	<i>Soehrensia</i>	<i>Lobivia</i>
	Ito 1988: 687	<i>Soehrensia bruchii</i>	<i>Furiolobivia longispina</i> var. <i>nigra</i> <sup>1</sup>	<i>Soehrensia</i>	<i>Lobivia</i>
<i>Soehrenolobivia</i>	Ito 1981: 650, Ito 1988: 688	<i>Soehrensia bruchii</i>	<i>Salpingolobivia aurea</i>	<i>Soehrensia</i>	<i>Echinopsis</i> s.s.
<i>Trichopsis</i>	Ito 1988: 706–707	<i>Trichocereus thelegonus</i>	<i>Echinopsis kermesina</i>	<i>Soehrensia</i>	<i>Bridgesii Clade</i>
		<i>Trichocereus purpureopilosus</i>	<i>Echinopsis kermesina</i>	<i>Soehrensia</i>	<i>Bridgesii Clade</i>
no formal name	Hans & al. 2012: 112	<i>Soehrensia</i> sp.	<i>Trichocereus schickendantzii</i>	<i>Soehrensia</i>	<i>Soehrensia</i>

<sup>1</sup> Classification according to Anderson & Eggl (2011): *Echinopsis ferox*; 2) ditto.: *Echinopsis marsoneri*; 3) ditto.: *Echinopsis huascha*.

2005, Pinto & Kirberg 2009), and the latter authors in addition illustrate a white, a pale greenish-white and a pale yellowish-white flower from the N Chilean populations they studied. But even their pale yellowish-white flower is still very different from the clear yellow flowers observed on our study plant B (Fig. 11), which is absolutely unique considering that MG has observed thousands of flowers of *E. atacamensis* throughout its geographical range during the past 30 years. Plant B could be interpreted as a mere flower colour variant, extending the range of known flower colour variability of the species. In contrast, and purely speculatively, plants A and B could be interpreted as the result of reciprocal crosses between the same parent species. While F1 crosses are expected to be uniform irrespective of which species is the pollen donor, there is a small number of reports that this is not always the case. Griffith (2001) found that in Chihuahuan Desert *Opuntia* species, reciprocal crosses were not always pos-

sible between a given set of parents, and Montanucci (2015: table 3) found that reciprocal crosses between *Astrophytum capricorne* var. *capricorne* and *A. coahuilense* produced strikingly different seed numbers, and seedling survival (13% vs. 66.66%) also differed, indicating some asymmetry in crossing behaviour.

The presence of just 1 or 2 hybrid plants in our study region is in line with the other cases of natural hybridization known from Trichocereinae, which were also always limited to solitary individuals. In the case of our  $\times$ *Oreonopsis* hybrid (Eggl & Giorgetta 2013), the rarity of hybridization between the two sympatrically occurring parent species is explainable by different floral syndromes and thus pollinators. In the case reported here, the rarity is in addition explainable by the minimal overlap of the parent species at the study site, although the distance between the hybrids and the main population of the more distantly located parent is of the order of 3 km or less.

*Echinopsis atacamensis* is pollinated by the giant hummingbird *Patagona gigas*, and wasps, bees and hawkmoths are also recorded as occasional visitors by Schlumpberger & Badano (2005) and Moré & al. (2014) (both for subsp. *pasacana*). There are no published reports on the pollination biology of *E. formosa*, but the positioning of the rather short, broadly funnel-shaped flowers near the apex of the plant body, as well as their placement largely between or even partly covered by the densely arranged spines, makes them difficult to access for hummingbirds, as we previously mentioned for *E. tarijensis* (Eggli & Giorgetta 2013).

During numerous visits to the study region, MG observed 3 different species of halictid bees as visitors of cactus flowers. One (Fig. 9 left) appears to be restricted to *E. atacamensis* (and could be the main pollinator of the taxon in this part of Chile), the second to *Oreocereus leucotrichus*, while the third (Fig. 9 centre) appears to be less specific and was observed on both species of *Echinopsis* and the hybrid Plant B, as well as on flowers of *Maihueniopsis camachoi*. Black megachilid bees have also been commonly observed on the flowers of all these cacti. Since there is a partial overlap of anthesis between the two study species, the possibility for cross-pollination exists. The rarity of successful hybridization events can either be the result of very rare cross-pollination events (perhaps because there are few shared pollinators), or can be due to incompatibility barriers.

*Echinopsis atacamensis* and *E. formosa* both have very wide geographical ranges, with considerable general overlap, and outside Chile, several sympatric populations are known to the authors from N Argentina (Salta, Tucumán). Further cases of hybrids between the two parents are therefore likely to be in existence. But considering the hundreds of hours of spent in the field over the past 30 years at many appropriate places, hybridization appears to be of very sporadic and rare occurrence.

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