

Flowering phenology and preliminary observations on the pollination biology of South American cacti. Part 4: *Oreocereus leucotrichus*

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Abstract: The range of *Oreocereus leucotrichus* (Cactoideae: Trichocereae) extends from southern Peru to the Atacama depression in northern Chile. Based on three decades of observation of a population at its southern fringe of occurrence, we argue that there is a mis-match between pollination syndrome and the observed pollinators: the expected hummingbird visitors are absent from the study population region, and instead, the flowers are mainly visited by solitary bees *Caenohalictus dolator* (Halictidae) and *Colletes* sp. (Colletidae). Likely, the bee visitors are secondary pollinators that provide some resilience against reproductive failure as seen from the moderate fruit set. The flowers of *O. leucotrichus* in the study population show pronounced variability of style length, and the possible influence of the switch from hummingbird to bee pollination on this character is discussed.

Resumen: El área de distribución de *Oreocereus leucotrichus* (Cactoideae: Trichocereae) se extiende desde el sur de Perú hasta la depresión interandina del Salar de Atacama en el norte de Chile. Sobre la base de tres décadas de observación de una población en el límite sur de su área de distribución, constatamos que existe un desajuste entre el síndrome de polinización y los polinizadores observados: Los picaflores esperados están ausentes en la zona de la población estudiada, y en su lugar las flores son visitadas principalmente por abejas solitarias *Caenohalictus dolator* (Halictidae) y *Colletes* sp. (Colletidae). Es probable que las abejas sean polinizadores secundarios que proporcionan cierta resiliencia frente al fallo reproductivo, según se observa en la moderada fructificación. Las flores de *O. leucotrichus* en la población estudiada muestran una notable variación de longitud del estilo, y se discute la eventual influencia del cambio de polinización por picaflores a la polinización por abejas en este aspecto.

Introduction

The vegetations of semi-arid and arid landscapes in the Americas often include numerous species of Cactaceae, and many regions are characterized by iconic arborescent species of cacti such as *Pachycereus pringlei* (S. Watson) Britton & Rose (“cardón”, but this vernacular name is also used for several other cacti in North America) or *Carnegiea gigantea* (Engelmann) Britton & Rose (“saguaro”) in the Sonoran Desert of North America, or *Echinopsis atacamensis* (Philippi) H. Friedrich & G. D. Rowley (“pasacana” but also “cardón”, which in Andean South America is used as a general term for several other cacti) in the Andes of Bolivia, Chile and Argentina of South America. The family counts some 1900 species (Anderson and Eggli 2011, Korotkova et al. 2021; other sources have lower or higher numbers, depending on the classification used), the majority of which are outcrossing (Anderson 2001, Boyle 2003, Mandujano et al. 2010): the plants are self-incompatible and need a vector to transport pollen from the stamens

of one individual to the stigma of another conspecific individual. Since successful sexual reproduction is dependent on successful pollination, the study of pollination biology is an important facet in the study of the life history of any plant taxon.

Over time, a fascinating array of interrelationships between plants and their floral visitors and pollinators has been discovered, ranging from generalist systems with many pollinators from different animal groups servicing a given flower (which is then said to be unspecialized or generalized), to highly specific key-and-lock systems where a single pollinator organism is servicing the flower (which is then termed specialized) under investigation (Willmer 2011 and references there cited). Some of the most intriguing pollinator-flower interrelationships are even essentially mandatorily mutualistic, such as the well-known *Yucca* / *Yucca* Moth example (Powell 1984, Pellmyr 2003).

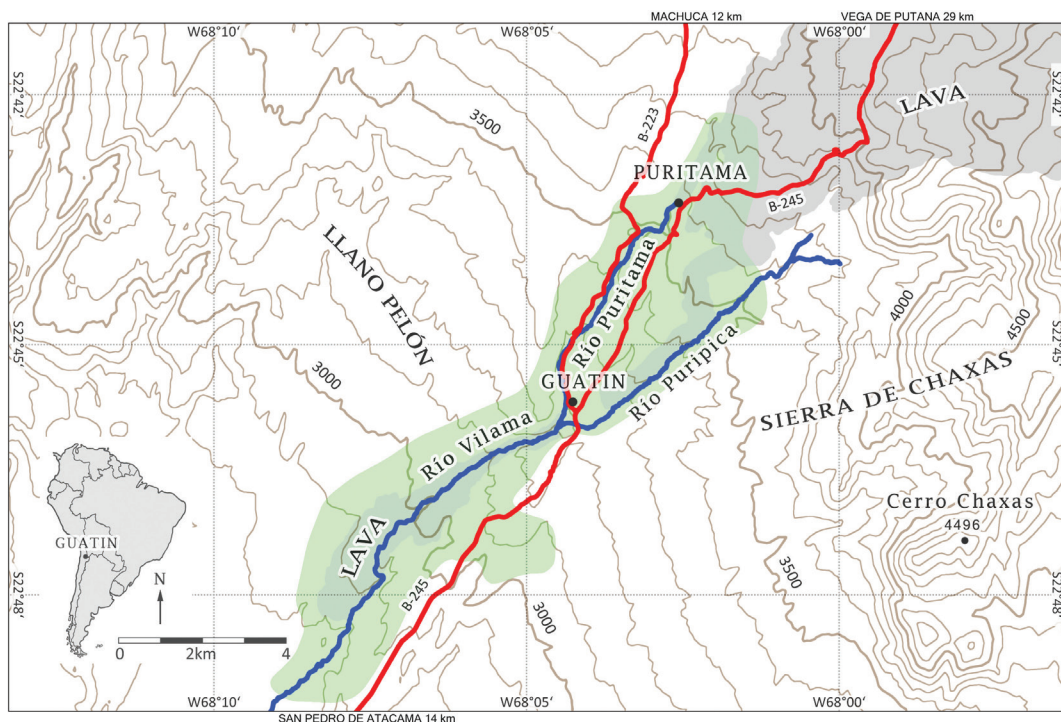


Figure 1. Map of the study region in the high Andes of northern Chile, above the Salar de Atacama, near the village of San Pedro de Atacama. Black dots represent the named settlements and mountain peak.

As individual studies of pollination and the involved pollen vectors accumulated over time, it became apparent that certain types of pollinators are correlated with certain characteristics of flowers. Soon, the concept of “pollination syndromes” emerged, culminating in the comprehensive overview by Faegri and van der Pijl (1971) (see also Willmer (2011), and Waser et al. (1996), Fenster et al. (2004) and Ollerton et al. (2007) for critical discussions of components of the principles). Because of the apparently good correlation between pollen vectors and floral syndromes (Rosas-Guerrero et al. 2014), such as hummingbirds favouring red tubular flowers, the previously defined syndromes began to become widely used as a substitute for the usually time-consuming direct observations of flowers and flower visitors (for cacti e.g. Porsch 1938, 1939, Rowley 1980). In recent years, evidence is accumulating, however, that the predictive power of the syndromes for a given pollinator is far from absolute, resulting in growing general criticism of the value of pollination syndromes, and indeed, Ollerton et al. (2009) found that almost no flowers fit the pre-defined pollination syndromes completely. The syndromes thus rather provide an uncorroborated hypothesis on possible pollinators, and detailed observations are needed to confirm the expected pollinator, or reject the assumption (such as hummingbird pollination for *Denmoza rhodacantha*, Egli and Giorgetta 2015;

Gorostiague (2016) records the hummingbird *Oreotrochilus leucopleurus* as pollinator for this species but does not produce any evidence or observations, so the mention is likely erroneous).

A major problem associated with the study of pollination biology is the difficulty to distinguish effective pollinators from mere flower visitors. Exclusion experiments are the approach of choice to identify effective pollinators, and to separate them from non-pollinating visitors (including nectar thieves and florivores). As a proxy, observations of feeding behaviour of the visiting animals, and the presence of pollen on those parts that are likely to touch anthers and stigmas, are used.

For cacti, a growing number of pollination biological studies (see Schlumpberger (2012) for an overview) suggest that mismatches between syndrome (i.e. expected pollinator) and the pollinator(s) observed in the field are not uncommon. Indeed, deviations from the conceptually favoured “key-and-lock”-relationships (= extreme specialization) are to be expected in vegetations with pronounced year-to-year variability in climate (especially rainfall) and the correlated variability of the pollinator fauna (Johnson and Steiner 2000) but also on theoretical grounds (Waser et al. 1996). Increased variability in pollinators linked to climatic variability over a latitude gradient was corroborated for a guild of N American columnar cacti (Valiente-Banuet et al. (2004)

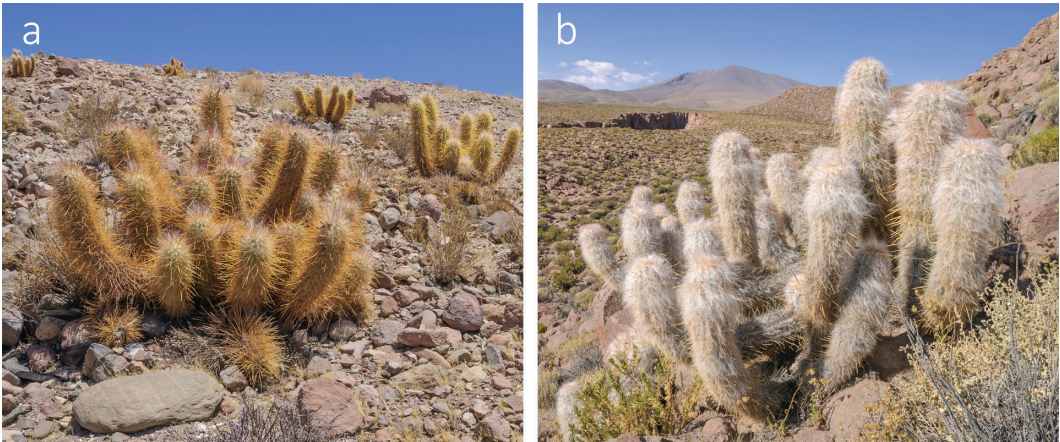


Figure 2. (A) The study population of *Oreocereus leucotrichus* at Guatin, 3018 m amsl, 11. Nov. 2018; (B) Plants at higher altitudes are more densely hairy, Quebrada Jorquencial, 3666 m amsl, 21. Nov. 2019.

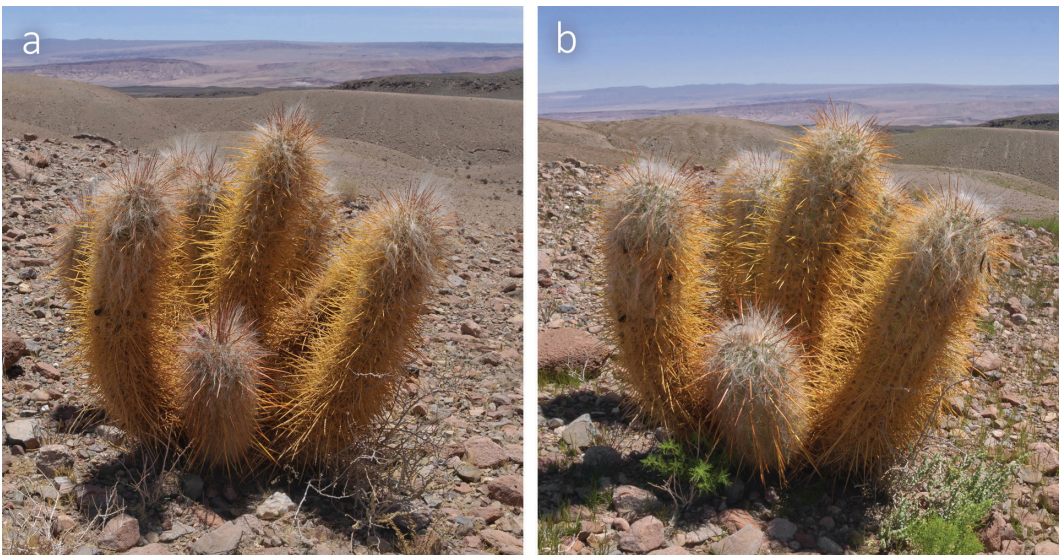


Figure 3. The same individual of *Oreocereus leucotrichus* at the end of the dry season after 19 months without rain (left, 17. Nov. 2016) and at the end of the rainy season (27. March 2017) at Guatin, 3033 m amsl.

and references there cited). In addition, some taxa have been found to differ as to pollination ecology over their range, e.g. the Chilean *Echinopsis chilensis* (Colla) H. Friedrich & G. D. Rowley, whose flowers are visited by hawkmoths at the S end of its range (Walter 2010) but by solitary bees at the N end of its range (Ossa Gómez and Medel 2011). For Argentinian *Echinopsis atacemensis* ssp. *pasacana* (F. A. C. Weber) G. Navarro with flowers seemingly adapted to nocturnal pollinators, a mismatch between expected and observed pollinators is also documented, and flowers are known to be visited by several species of solitary bees (esp. *Xylocopa ordinaria*), a social wasp (*Polybia ruficeps*), and occasionally by the Giant

Hummingbird *Patagona gigas*, as well as the hawkmoth *Manduca diffusa* (Schlumpberger and Badano 2005, Viana et al. 2001). For *Browningia candelaria* from Peru and Chile, Humaña et al. (2021) report that it is pollinated by the bat *Platalina genovensium* in S Peru and N-most Chile, but by the hummingbird *Rhodopis vesper* at the southern limit of its occurrence in Chile, and record seven insect species as additional flower visitors and potential pollinators. For the Argentinian *Echinopsis ancistrophora* Spegazzini, Schlumpberger and Raguso (2008) and Schlumpberger et al. (2009) found a pronounced lability of the expression of pollination syndromes at the population level, and in a previous study (Eggl

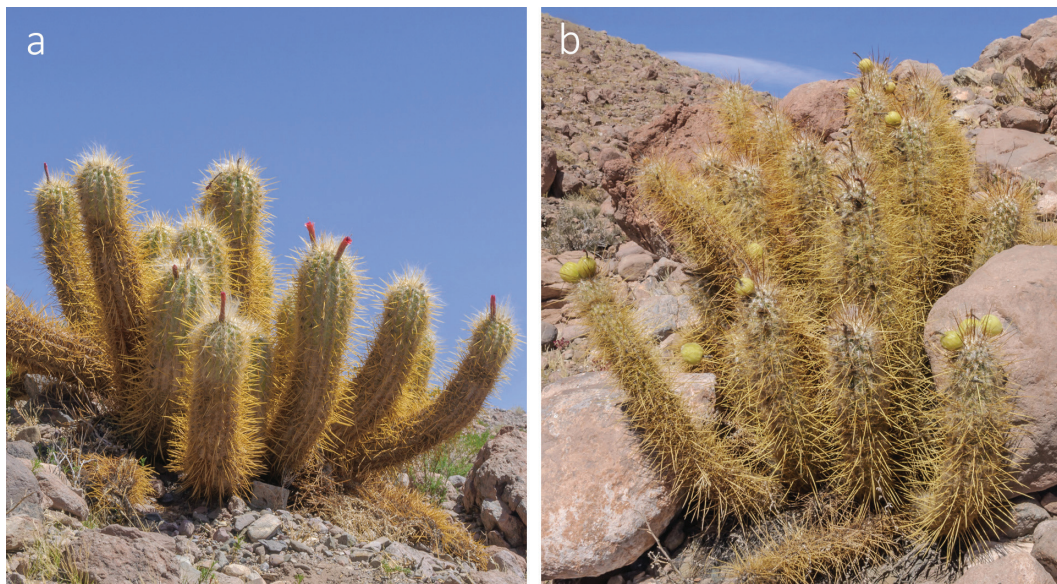


Figure 4. (A) Mature flowering individual of *Oreocereus leucotrichus* (Guatin, 2965 amsl m, 5. March 2013); (B) Mature fruiting individual of *Oreocereus leucotrichus* (Guatin, 2949 m amsl, 23. Nov. 2017).

and Giorgetta 2015), we showed that the expected pollinators (hummingbirds) are not visiting the flowers of *Denmoza rhodacantha* (Salm-Dyck) Britton & Rose at least in our study population.

Here, we report preliminary observations on the pollination biology of a further South American cactus, *Oreocereus leucotrichus* (Philippi) Wagenknecht, from the W slopes of the high Andes of S Peru and N Chile, which is generally thought to be hummingbird-pollinated on the base of the flower syndrome it exhibits, but confirmed observations of this are absent.

Material and methods

Study organism: *Oreocereus leucotrichus* (Philippi) Wagenknecht is a low growing shrubby cactus to 1 (exceptionally 2) m tall and with as many as ± 100 branches (Figs. 2 and 4). Its morphology is very variable in most aspects—stem diameter varies from 6–12 cm and the number of ribs from 10–18. The areoles are usually provided with long (5–10 cm), coarse, white hairs, 1–4 strong central spines to 11 cm (exceptionally to 30 cm, pers. obs. MG) and 5–10 shorter radial spines to 1.5 cm. The red, tubular zygomorphic flowers appear—typically for the genus *Oreocereus*—from at or near the stem apex. They reach 8–10 cm in length and after successful pollination, they are followed by the roughly globose, thick-walled green to pale green or yellowish-green fruits with 4–6 cm diameter, with a basal pore when separating from the plant (Fig. 12). The overall geographical range extends from Arequipa in S Peru to the region of the Salar de Atacama in N

Chile (Ritter 1980, Hoffmann and Walter 2005, Ostolaza 2014, Miesen et al. 2015, Hoxey 2017).

Study site: The study region is situated on the slope N of the Atacama depression, roughly 18 km NE of San Pedro de Atacama, near the Río Vilama and the shepherds' settlement of Guatin, at 3215 m amsl (Fig. 1). The site is at the southern fringe of the known geographical range of the study species. Associated succulents are the cacti (names according to Anderson and Egli 2011) *Cumulopuntia ignescens* (Vaupel) F. Ritter, *Cumulopuntia sphaerica* (C. F. Förster) E. F. Anderson, *Echinopsis atacamensis* (Philippi) H. Friedrich & G. D. Rowley subsp. *atacamensis*, *Echinopsis formosa* (Pfeiffer) Jacobi ex Salm-Dyck, *Maihueniopsis camachoii* (Espinosa) F. Ritter and *M. glomerata* (Haworth) R. Kiesling, the Aizoaceae *Tetragonia microcarpa* Philippi and the Montiaceae *Cistanthe celosioides* (Philippi) Carolin ex Hershkovitz and *C. amarantoides* (Philippi) Carolin ex Hershkovitz. Other perennial vegetation consists of several xeromorphic shrubs such as *Atriplex imbricata* D. Dietrich, *Ambrosia artemisioides* Meyen & Walpers, *Chuquiraga atacamensis* Kuntze and *Urmenetea atacamensis* Philippi, *Tiquilia atacamensis* (Philippi) A. T. Richardson, *Ephedra breana* Philippi, *Adesmia atacamensis* Philippi, *Krameria lappacea* (Dombey) Burdet & B. B. Simpson, *Tarasa operculata* (Cavanilles) Krapovickas, *Fabiana ramulosa* (Weddell) Hunziker & Barboza and *Solanum chilense* (Dunal) Reiche, *Acantholippia deserticola* (Philippi) Moldenke and *Fagonia chilensis* Hooker & Arnott. After prolonged rainfall, a short-lived, rich cover of annuals develops (termed “pasto de lluvia” by the locals). In the study region, rain occurs mostly during

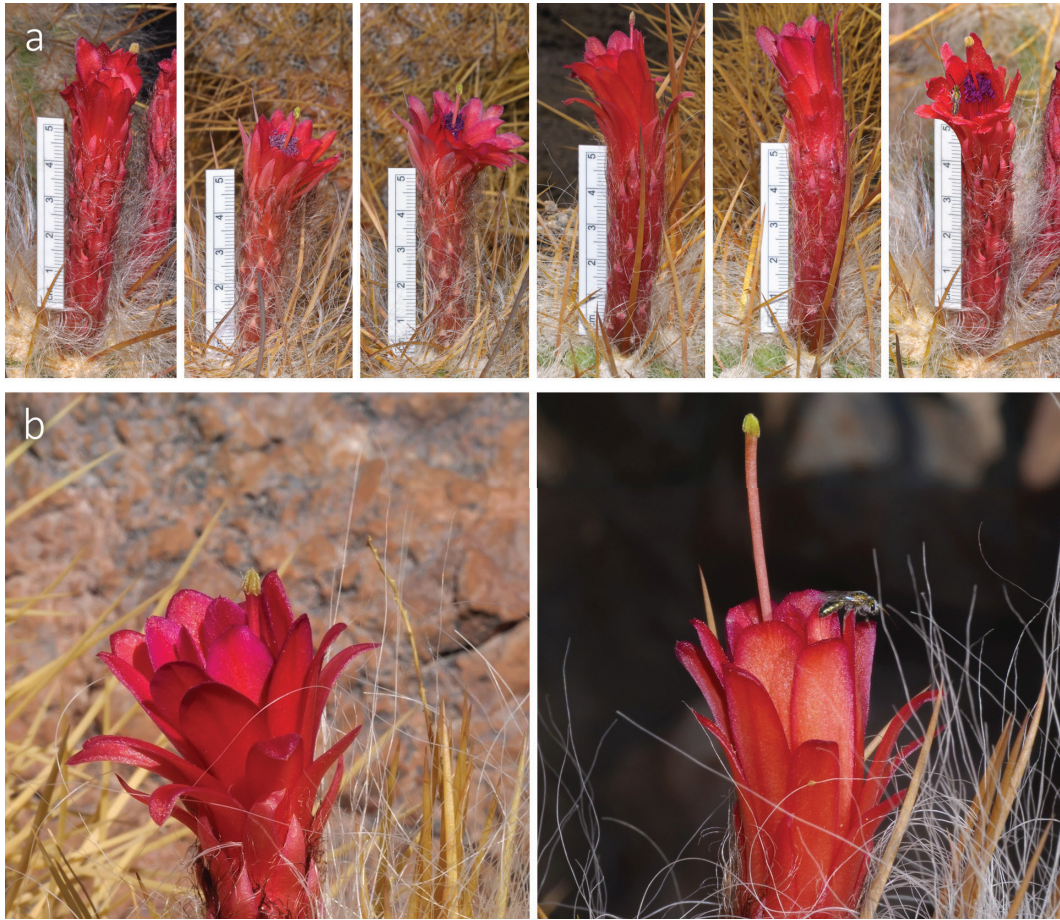


Figure 5. (A) Flower length variability of *Oreocereus leucotrichus* (S of Guatin, c. 3000 m amsl, 2011–2018); (B) style length variation (Guatin – Antofagasta, left 3070 m amsl, 14. Nov. 2019; right 2839 m amsl, 14. Nov. 2013).

summer and fall or winter, but is erratic with pronounced year-to-year differences. The dry season can extend to as much as 19 months, and rainfall events vary between intense stormy rains to week-long almost continuous drizzle (Eggle and Giorgetta 2020).

Study Methods: Numerous observations were made by MG in the late spring / early summers (October to December) and in late summers (March) during the past 30 years during regular study visits to the area. The studied plants were GPS-registered to allow repeat visits, and their flowering phenology, and flower and fruit visitors were documented with over 3000 photographs and videos. Observations were made during the whole day from dusk to complete nightfall by visual inspection, and were documented with photographs and videos. No voucher material has been collected, neither of the plant nor of the insect visitors; the identification of insects is made on the base of photograph using available published literature and contacts with specialists.

Results

General phenology: In the study area, *Oreocereus leucotrichus* grows both on basaltic lava rocks along the Río Vilama and its tributaries as well as on lava ash (rubble) of the adjacent hills and slopes, spanning an altitudinal range of 2750–3900 m amsl and preferring W aspects (Fig. 2). The study area spans two climatic zones: the lower, southern part is in the semi-arid climate influenced by the adjacent Atacama Desert to the west, with sporadic precipitation mostly falling in the summer months, while the higher, northern part is in the wetter and cooler climate of the Prepuna influenced by the adjacent high mountains to the east, with sporadic precipitation in summer and winter, sometimes with hail and snow. Plants from the lower altitudes (Fig. 2A) are distinctly less copiously hairy than those from higher altitudes (Fig. 2B). Plants show pronounced volume changes



Figure 6. Frontal view of flowers to show variation in flower characters of *Oreocereus leucotrichus* (31 photographs from Guatín, 2835 – 3122 m amsl, 4 photographs from Quebrada Jorquencal, 3619 – 3657 m amsl; 4 of them taken in October, 27 in November, 2 in December, 2 in March).



Figure 7. Flowers of *Oreocereus leucotrichus* are proterandrous: A and B show flowers at the first day of anthesis, with opened anthers and abundant light magenta pollen; C and D show flowers on the second day of anthesis, with empty purple anthers and more loosely arranged stigma lobes (all figures from Guatin).

between the dry and the wet period of the year (Fig. 3), similar to those reported by Eggli and Giorgetta (2020) for the sympatric *Echinopsis atacemensis*.

Flowering phenology: Flowering occurs between early October and early to mid-November, and irrespective of the hydration status of the plants, i.e. even strongly desiccated plants can produce flowers. A second flowering phase is sometimes observed at the end of summer late in March. The overall morphology and coloration of the flowers as well as the absence of human-detectable scent conform to the ornithophily syndrome. At anthesis, the flowers are about as long as the surrounding developing spines, i.e. the flower throat is directly accessible to incoming flying animals (Fig. 4A). Flowers vary considerably in overall length as well as in length of the style and thus the distance between anthers and stigma lobes (Fig. 5A), as well as in colour and disposition

of the perianth elements (Fig. 6). Flowers commonly open in late afternoon and then remain open day and night before they close and rapidly wilt on the third day, or more rapidly after successful pollination. Flowering is somewhat erratic, and even on large plants, only few (<4) flowers are open together, and some plants do not flower at all. Typically for the genus, the flowers are strongly proterandrous (Fig. 7): the anthers dehisce on the first day of anthesis, when the stigma lobes are still tightly closed together. On the second day of anthesis, the pollen has usually already been depleted, and the stigma lobes are arranged more loosely. Similar to the flowers of *Oreocereus celsianus* and *O. trollii* in Bolivia (pers. obs. MG), the pollen of *O. leucotrichus* shows a light magenta color and is collected by visiting female bees or serves as food for other insects, such as flies.

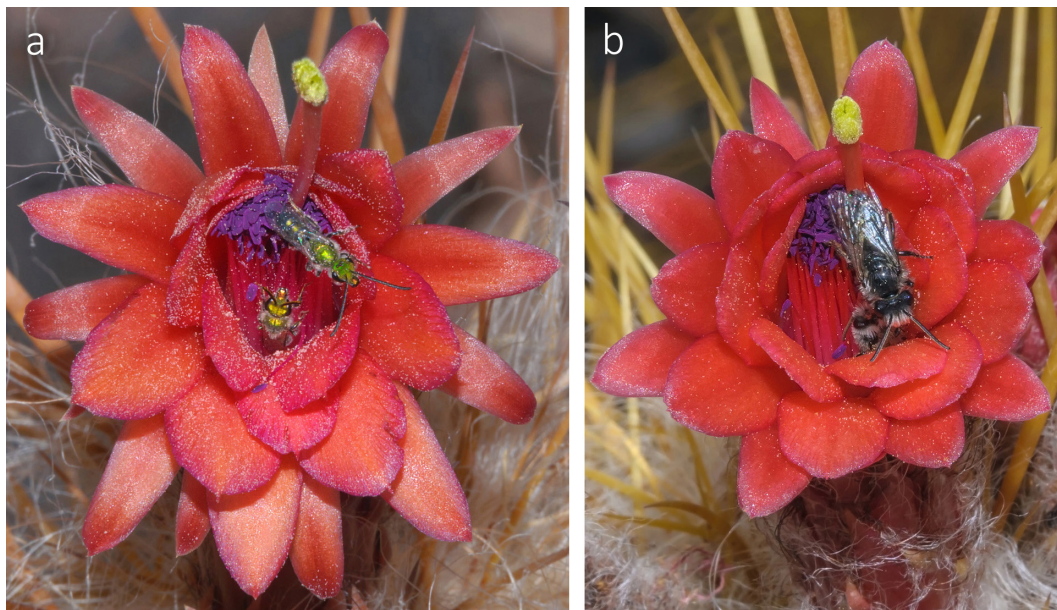


Figure 8. One pair each of the observed main pollinators (male individuals, characterized by long antennae, are at the top): (A) *Caenobalictus dolator* (Halictidae) (Guatin, 2991 m amsl, 10. Dec. 2013, 17:01); and (B) *Colletes* sp. (Colletidae) in the flowers of *Oreocereus leucotrichus* (female phase), where they meet for mating (Guatin, 3079 m amsl, 9. Nov. 2019, 16:59).

Flower visitors

Hummingbirds: No hummingbirds were ever recorded by MG on the flowers of *Oreocereus leucotrichus*. While the migrating Giant Hummingbird *Patagonas gigas* (Trochilidae) was regularly seen in the 1990s, and was observed to visit the flowers of *Echinopsis atacamensis* during the peak flowering period, it became progressively rarer in the past 20 years, and single individuals were last seen in the study area in the springs of 2014 and 2015. *Patagonas gigas* is known as a flower visitor of the Argentinian/Bolivian *Oreocereus celsianus* (Lemaire ex Salm-Dyck) Riccobono (Larrea-Alcázar and Lopez 2011; MG pers. obs., cf. Egli and Giorgetta 2013 [for Bolivia]), and the Bolivian *O. fossulatus* (Larrea-Alcázar et al. 2018). A sizable population of the migratory Giant Hummingbird *Patagona gigas* appears each spring coming from the north to nest and breed in the central regions of Chile, and retreats again in the fall. Since the observations of Charles Darwin in the year 1834 (Gould 1841), there have been repeated speculations as to where these birds winter, whether in Peru or even Ecuador. Until recently, ornithologists were unable to provide an answer (Ortiz-Crespo 1986). Recently, Williamson et al. (2024) established that *P. gigas* s.str. migrates southwards in the spring along the western slopes of the Andes, and migrates back in autumn along the eastern slopes of the Andes

to overwintering areas in central Peru, spanning a north-south distance of some 4000 km and an elevational range of 4100 m. We assume that the disappearance of the Giant Hummingbird from our study region is due to a small change of its migration towards the south, shifting somewhat to the east of our study area along the foot of the high cordillera, where dense stands of *Echinopsis atacamensis* bloom in spring, and likely provide a nectar resource exploited by the migrating birds (Williamson et al. 2024 merely note that the migration coincides with the flowering of *Weberbauerocereus weberbaueri* in Peru, and the breeding season with that of *Echinopsis litoralis* and *Eriocyce subgibbosa* in Chile, but have no further details of when the migration exactly occurs, and what energy resources are exploited during migration). The local disappearance of *P. gigas* is likely a consequence of the general deterioration of its habitat due to the drying up of watercourses and marshes caused by the overexploitation of natural water resources by the mining activities (copper, lithium) prevalent in the wider region of the Atacama Depression.

Insects: The most common insect visiting the flowers is the small, golden-green metallic sweat bee *Caenobalictus dolator* (Halictidae) (Fig. 8A), which collects pollen and also appears in pairs for mating in the flower. The same behavior is observed with a black plasterer bee *Colletes* sp. (Colletidae) (Fig. 8B),

of which several species are living in this area. When a pair of these bees meet at a flower, a veritable preceding love play is seen: they run after each other in the flowers, hide down in the tube or behind the petals, fly away and return. During their long romp, they also stir up the pollen, if there is any. It has been observed that, when approaching flowers with long projecting styles, these bees often first land briefly on the stigma, then jump down to the anthers, where they usually immediately slip down into the flower tube and remain there for minutes, presumably attracted by the scent of nectar. When collecting or feeding on pollen, however, they crawl around on top of the anthers, also touching the stigma of flowers that have short styles. Whether the degree of stigma exertion influences pollination success, was not investigated. A similar observation of insects landing on the stigma has already been described for *Echinopsis chiloensis* ssp. *litoralis* (Johow 1921).

Less frequently, the cactus bee *Trichothurgus aterrimus* (Megachilidae) (Fig. 9) can be observed, which prefers the flowers of the surrounding cushion-forming cactus *Maihueniopsis camachoii*. Furthermore, the long-horned bee *Svastra flavitarsis* (Apidae) is also seen, which visits any kind of flowers.

Other observed flower-visiting insects include Bombylid bee flies and Syrphid hoverflies, both of which feed exclusively on nectar and pollen and

which are also known flower pollinators (Raguso 2020). Further, the common and predominantly nocturnal desert grasshopper *Trimerotropis ochraceipennis* (Acrididae) often eats the stigma of the flowers, but sometimes also the petals. Of the flowers that typically open towards the evening, 30–50% lost the stigma lobes due to florivory by the following morning (Fig. 10). *Trimerotropis ochraceipennis* is a polyphagous band-winged grasshopper endemic to Chile and Peru. In our study area, florivory was observed on *Cumulopuntia ignescens*, *C. sphaerica*, *Maihueniopsis camachoii*, *M. glomerata*, *Echinopsis formosa* and *Oreocereus leucotrichus*.

Fruiting phenology: Fruit set has been observed to be very variable, and sometimes, abundantly fruiting individuals (Fig. 4B) are found next to completely sterile plants with only withered flower remains. Only ca. 20% of all flowers are estimated to produce fruits, but this varies from plant to plant. Fruits can be present simultaneously with flowers (Fig. 11) and have been found to be quite variable in shape and size (Fig. 12). When mature, they usually fall off the plant spontaneously (Fig. 4B). In the study region, the passerine birds *Sicalis olivascens* and *Phrygilus atriceps* (Thraupidae) are common. They feed mostly on the juicy fruits of *Echinopsis atacamensis* and *E. formosa*, and forage for seeds from *Oreocereus* fruits fallen to the ground. Further dispersal of *Oreo-*



Figure 9. The solitary bee *Trichothurgus aterrimus* on the flower of *Oreocereus leucotrichus* (female phase) (Guatin, 3027 m amsl, 2. Nov. 2015).

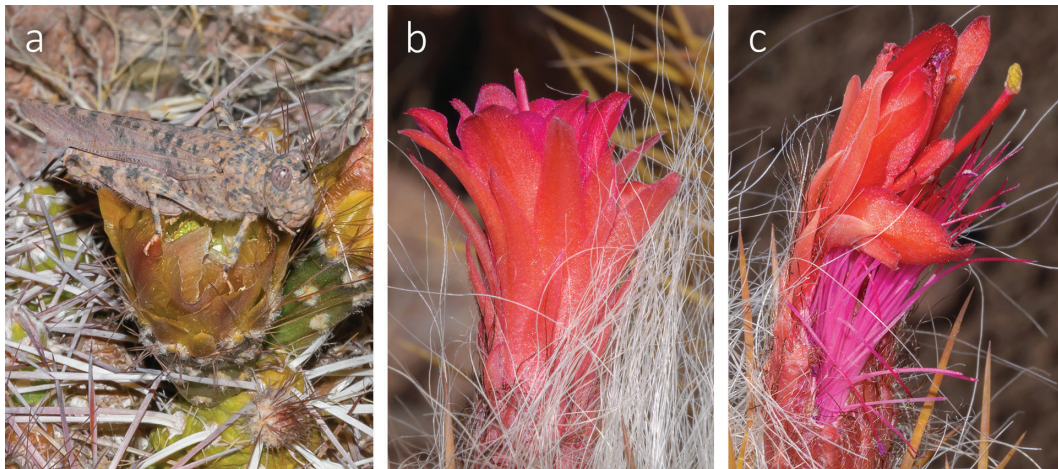


Figure 10. (A) The grasshopper *Trimerotropis ochraceipennis* (Acrididae) is a common florivore of *Oreocereus leucotrichus* and other sympatric cactus species; (B) The stigma and part of the style of this flower were consumed by the grasshopper; (C) Part of the perianth of this flower has been consumed by the grasshopper (A: Guatín, 2856 m amsl, 26. Nov. 2017; B & C: Guatín, 3114 m amsl, 28. Nov. 2013).

ereus seeds is perhaps by ants, although ants are not common in the study region. Moreover, seeds may become scattered when they escape from the pores of fallen fruits when these are blown around by the wind. Endozoochory involving seed-eating passerine birds has been described for several columnar cacti, with seeds recovered from bird feces having increased germination capacity in comparison to controls (León de la Luz and Dominguez Cadena (1991) for *Stenocereus gummosus*, Naranjo et al. (2003) for *Stenocereus griseus* and *Subpilocereus repandus*, Gomes et al. (2014) for *Cereus jamacaru*). Whether this mechanism is also in place for *Oreocereus leucotrichus* is unknown, however.

Discussion

Oreocereus leucotrichus is another example of a cactus species with a flower that is readily equated with a defined pollination syndrome (i.e. ornithophily), but where the expected hummingbird pollinator is not observed (contrasting its congeners *O. celsianus* and *O. fossulatus* in Bolivia, where hummingbirds were recorded as pollinators by Larrea-Alcázar and López (2011) and Larrea-Alcázar et al. (2018), respectively). Instead, two different bee species, the Halictid bee *Caenohalictus dolator* and the Colletid bee *Colletes* sp., were regularly observed as main visitors, and the Megachilid bee *Trichothurgus aterrimus* and the Apid *Suastra flavitarsis* as occasional and less frequent visitors. These bees collect or consume the pollen. By touching the stigma with their pollen-dusted bodies while walking around on the anthers or landing directly on it, they cause pollination of the flowers. The case of *O. leucotrichus* is especially

intriguing since its congeners *O. celsianus* and *O. fossulatus* have both been recorded as hummingbird-pollinated (Larrea-Alcázar and Lopez 2011, Larrea-Alcázar et al. 2018).

The Halictid bee observed on *O. leucotrichus* was also found as common visitor to the flowers of *Echinopsis atacamensis*, and Rojas and Toro (2000) describe it as generalist flower visitor for other parts of Chile. *Trichothurgus aterrimus* is a generalist bee and has been observed on the flowers of all sympatric cactus species (*Cumulopuntia ignescens*, *C. sphaerica*, *Echinopsis atacamensis*, *E. formosa*, *Maibueniopsis camachoii*, *M. glomerata*) of the study region. In addition, it has also been seen on *Chuquinaga atacamensis* and *Haploppappus rigidus* Philippi (both Asteraceae), likely visited for nectar and pollen for own consumption.

Halictid bees were also recorded as flower visitors for *Denmoza rhodacantha* in NE Argentina (Eggl and Giorgetta (2015), the observed visitor was recently identified as *Lasioglossum* sp. [Laurence Packer, pers. comm.] and *Browningia candelaris* in Chile (Humaña et al. (2021), observing *Caenohalictus* sp. and *Lasioglossum aricensis* aff.).

Similar to *Denmoza*, fruiting success was found to vary in *O. leucotrichus*, with only a fraction of flowers successfully turning into mature fruit. The overall low fruit set observed in *O. leucotrichus* (only about 20% of all flowers produce a fruit) could hypothetically indicate that bees are not the main pollinators and that pollen transfer is somewhat accidental, or that visits are comparatively rare as sympatric, simultaneously flowering other species of cacti are more rewarding or provide better matching attraction clues. To what extent florivory by *Trimerotropis* also has a negative effect on fruiting success remains unstudied.

There is no published information on the pollination of *O. leucotrichus* outside our study area (which is at the southern margin of its known geographical range), and it is quite possible that further north hummingbirds do visit its flowers. On this basis, bee pollination would be a “fallback” pollination system (i.e., bees are “secondary pollinators,” Rosas-Guerrero et al. 2014) that allows *O. leucotrichus* to reproduce in a region where its usual main pollinators (hummingbirds) are generally absent or have disappeared. The frequent occurrence of flowers with a short style that raises the stigma only slightly above the anthers may contribute to the success of this secondary “fallback” pollination, and it would be interesting to compare the variability in style length across the species’ range or, in our study area, to investigate whether pollination success correlates with style length — hypothetically, if short-styled plants show greater reproductive success, a gradual adaptation over several cactus generations would be expected, with gradual replacement of the “truly ornithophilous” flowers with long style by “more entomophilous” flowers with short style.

The presence of alternate pollinators highlights the importance of such fall-back mechanisms, but indeed even more that generalized pollination systems provide some resilience against reproductive failure in times of change. Indeed, Gorostiague and Ortega-Baes (2016) list 13 species of Cactaceae with flowers conforming to the ornithophily syndrome,

and which are visited both by hummingbirds as well as bees; they further speculate that among the total of 386 cactus species with flowers that exhibit the ornithophily syndrome in their superficial census, several might rely primarily on bees for pollination. One such example is *Cleistocactus smaragdiflorus* (Gorostiague and Ortega-Baes 2016: 68).

When red or predominantly red flowers are visited by bees, this raises the question of how they are attracted. While these seemingly hummingbird-adapted flowers are scentless to the human nose, the presence of olfactory stimuli that we are unable to detect is highly likely. In addition, the accessibility of the nectar has to be considered: the tubular flowers of *O. leucotrichus* have — typical for the genus, and for the ornithophilous syndrome as a whole — a well-defined nectar chamber at the bottom (Fig. 13), for whose morphology González et al. (2021) use the term “semi-closed”. The top of the chamber is formed by the basis of the filaments, which are fused into a “roof” with a central opening for the style. For the morphologically similar flowers of *Cleistocactus baumannii* and other bird-visited flowers, González et al. (2021) found that the nectariferous tissue is confined to the nectar chamber proper and does not extend to the filament bases. The nectar would thus be inaccessible to bees and other insects. It is highly likely, however, that the nectar spreads amongst the closely arranged filaments by capillarity when the chamber is completely filled, so that it becomes avail-



Figure 11. Buds, flowers and fruits can be present simultaneously (Guatin, 3083 m amsl, 28. Oct. 2017).

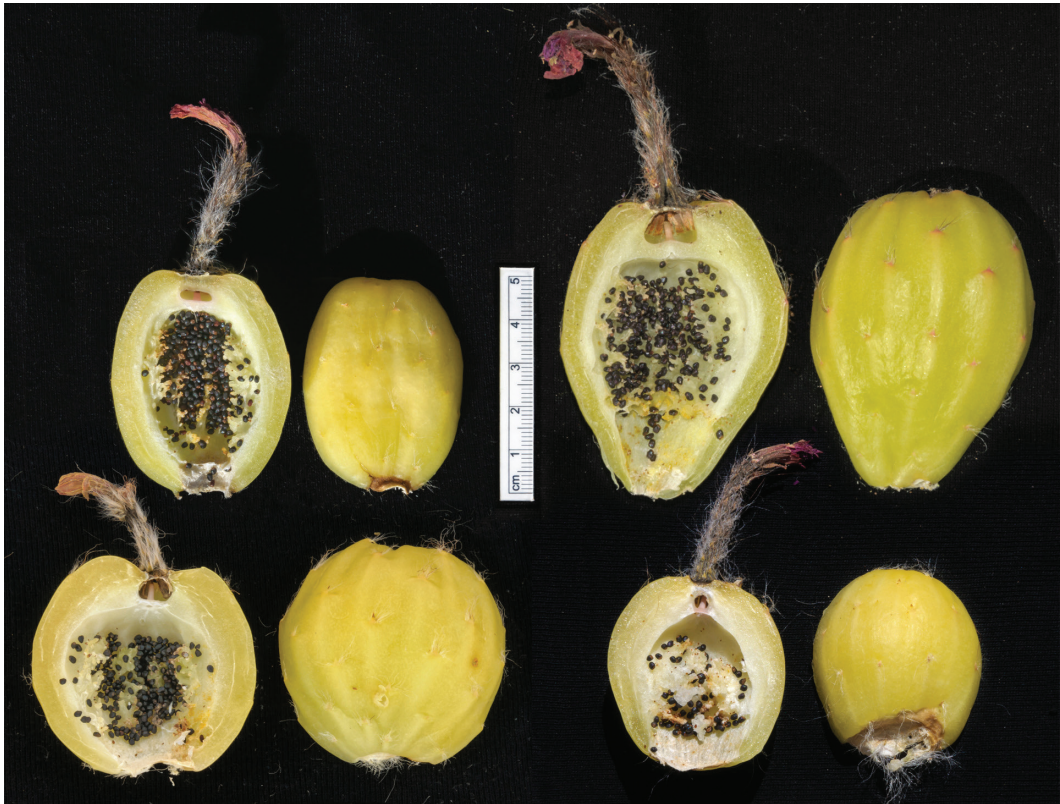


Figure 12. Fruits of *Oreocereus leucotrichus* are quite variable as to size and shape, but always show the characteristic diagnostic pore at the base (top left Guatín, 3033 m amsl, 11. Nov. 2018; bottom left Guatín, 2951 m amsl, 23. Nov. 2017; top right Guatín, 2931 m amsl, 20. Nov. 2013; bottom right Guatín, 2937 m amsl, 21. Nov. 2015).

able to insects, and this may explain why the seemingly ornithophilous flowers are attractive to nectar-seeking flies.

Different pollinators over an extended geographical range of a species have also been observed in two other Chilean cactus species: the flowers of *Echinopsis chiloensis* (Ossa Gómez and Medel 2011, Walter 2010) are pollinated by hawkmoths (as expected from the flower morphology) in the S part of its range, but by solitary bees at the N end of its range where the hawkmoths appear to be absent. The flowers of *Browningia candelaris* (Humaña et al. 2021) are visited by bats (as expected from the flower morphology) in the N of its range, but by hummingbirds and solitary bees at the S end of its range.

Conclusions

Oreocereus leucotrichus at the southern margin of its geographical range in the Andes of N Chile and S Peru presents an obvious discrepancy between the pollinator expected (hummingbirds) on the base of the ornithophilous flower syndrome, and the observed main flower visitors, two species of solitary bees. Despite incompatibility of the flower syn-

drome with the observed pollinators, *O. leucotrichus* achieves modest fruiting success, ensuring maintenance and continuation of its population in the study area. Our study is based on a large population at the southern margin of the geographical range of the species. Whether the predicted pollinator (hummingbird) visits its flowers in the more northern parts of the species' range in spring during its migration to the south is an intriguing question, especially since the food resources exploited by the Giant Hummingbird on its southward migration remain largely unknown (Williamson et al. 2024).

Author Contributions

Urs Eggl: Conceptualization, Writing – Original Draft, Writing – Review & Editing. Mario Giorgetta: Conceptualization, Investigation, Data Analysis, Formal Analysis, Visualization, Writing – Original Draft.

Conflict of Interest

None.

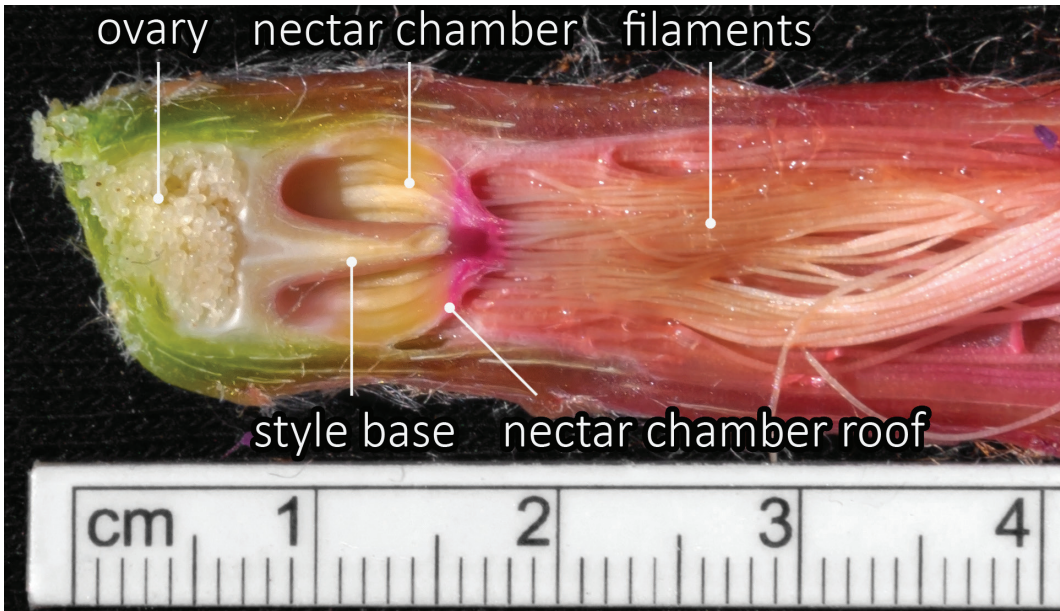


Figure 13. Sectioned flower of *Oreocereus leucotrichus* to show the partially closed nectar chamber; the nectar droplets on the filaments are an artefact caused by sectioning the flower (Guatin, 3032 m amsl, 7. Nov. 2018).

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