

# FLOWERING PHENOLOGY AND OBSERVATIONS ON THE POLLINATION BIOLOGY OF SOUTH AMERICAN CACTI. 1. *DENMOZA RHODACANTHA*

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**Summary:** Pollination biology is an especially important component of the overall ecological setting of a plant species since it has direct implications on reproductive success. Over time, a typological approach to classifying flower–pollinator interactions in the form of “floral syndromes” has been developed, and considerable predictive power is traditionally ascribed to these syndromes. Recent studies have increasingly questioned both the predictive value of the syndrome concept, as well as the underlying notion of increasing specialization amongst flower–pollinator interactions. The casual discovery that the seemingly ornithophilous flowers of the globose to shortly columnar South American cactus *Denmoza rhodacantha* (Cactaceae: Cactoideae: Cereeae: Trichocereinae) are visited by solitary pollen-collecting halictid bees, rather than the expected hummingbirds, adds another example to the growing body of mismatches between floral syndrome and observed pollinator.

**Zusammenfassung:** Die Bestäubungsbiologie ist eine besonders wichtige Komponente der Ökologie einer Pflanzenart, da sie direkte Auswirkungen auf den Fortpflanzungserfolg hat. Im Laufe der Zeit wurde ein typologischer Ansatz zur Klassifikation der Interaktionen zwischen Blüten und Bestäubern in Form von “Blütensyndromen” entwickelt. Traditionell werden diese Syndrome auch zur Vorhersage solcher Beziehungen verwendet. Neuere Studien haben sowohl den Vorhersagewert des Syndromkonzepts, wie auch die zugrundeliegende Annahme einer zunehmenden Spezialisierung der Blüte-Bestäuber-Interaktion in Frage gestellt. Die zufällige Beobachtung, dass die auf den ersten Blick ornithophil erscheinenden Blüten der kugelförmigen bis kurzsäuligen südamerikanischen Kakteenart *Denmoza rhodacantha* (Cactaceae: Cactoideae: Cereeae: Trichocereinae) von solitären Pollen sammelnden Bienen der Halictidae besucht werden, und nicht von den erwarteten Kolibris, fügt der wachsenden Zahl von Beobachtungen ein weiteres Beispiel einer fehlenden Kongruenz zwischen Blütensyndrom und beobachtetem Bestäuber zu.

**Resumen:** La biología de polinización es un elemento de gran importancia para la ecología de una especie vegetal pues influye directamente en el éxito de su reproducción. Con el andar del tiempo se estableció un enfoque tipológico para clasificar la interacción entre flores y polinizadores en forma de “síndromes florales”. Habitualmente, tales síndromes se usan también para la predicción de dichas interacciones. Estudios recientes ponen en cuestión tanto el valor pronóstico del concepto de síndrome como también la suposición de una creciente especialización en la interacción entre flores y polinizadores. La observación casual, que las flores aparentemente ornitófilas de la especie de cactácea sudamericana *Denmoza rhodacantha* (Cactaceae: Cactoideae: Cereeae: Trichocereinae) con forma esférica hasta columnar, fuesen visitadas por abejas solitarias de la familia de halictidos buscando polen, en vez de que por los supuestos colibríes, aumenta la creciente cantidad de observaciones con respecto a la ausente congruencia entre síndrome floral y polinizador observado.

**Key words:** Cactaceae, *Denmoza*, South America, Argentina, pollination ecology

## INTRODUCTION

Studies of pollination biology are an important component towards elucidating the natural settings in which a plant taxon is embedded because such studies investigate the interrelationships that allow successful reproduction, which is a prerequisite for the temporal persistence of the plant taxon at a given locality beyond the lifespan of the individuals.

Over time, a fascinating array of interrelationships between plants and their floral visitors and pollinators have 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).

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**Figure 1.** Adult columnar individual (as seen from the bristly spination) of *Denmoza rhodacantha* (individual 9C, photographed 12. Jan. 2013 after 9 years of drought terminated by 3 short rains at the beginning of January).



**Figure 2.** Juvenile flowering individual (as seen from the coarse spination) of *Denmoza rhodacantha* (individual 5S, photographed 18. Feb. 2013, with a flowering *Talinum polygaloides* in the foreground).

Cacti are important and often conspicuous landscape-dominating community members of the vegetation in arid and semiarid North and South America. The majority of cacti are outcrossing (Anderson 2001: 33, Boyle 2003, Mandujano et al. 2010), i.e. 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.

Already early studies found that certain characteristics of the flowers were linked to the types of pollinators that are attracted by them, and soon a concept of “pollination syndromes” was developed, culminating in the comprehensive overview by Faegri & van der Pijl (1979) (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). Since the study of aspects of pollination biology is a time-consuming undertaking, the syndromes previously defined were rapidly ascribed with a high predictive power. Interpretations of the (easily observable) syndromes were therefore widely used as a substitute for (time-consuming and therefore costly) direct observations (for cacti e.g. Porsch 1938, 1939, Rowley 1980). In recent years, evidence is accumulating, however, that in many cases, other than the pollinators predicted by the syndrome are in effect, either in addition to, or instead of the expected ones. This has opened the door to a general criticism of the value of pollination syndromes, especially as analysis of flower characteristics showed that almost no flowers fit the pre-defined syndromes precisely (Ollerton et al. 2009, see also Schlumpberger & Raguso 2008 and Schlumpberger et al. 2009 for detailed studies on the lability of the expression of pollination syndromes at a population-level context of cacti). Also, there is a rapidly increasing body of investigations that found “multi-purpose flowers”, i.e. flowers that are serviced by more than one pollinator group, and such flowers are not as rare as generally assumed (e.g. Schlumpberger 2012: 302 and Lendel et al. (in prep.) for cacti).

A second problem associated with the study of pollination biology is the difficulty to differentiate between mere flower visitors, and effective pollinators. Diligent reciprocal exclusion experiments are needed to establish effective pollinators and identify mere vis-

itors (including nectar robbers and flori-vores). 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.

In recent years, there has been a slow accumulation of pollination biology studies of cacti (see Schlumpberger 2012 for an overview), and a couple of examples have uncovered apparent mismatches between syndrome (= expected pollinators) and real pollinators, or more than the expected pollinator taxa have been observed. Such a deviation from the conceptually favoured 1:1 or “key-and-lock”-relationships (= extreme specialization) is indeed predicted in vegetations with pronounced year-to-year variability in climate, especially rainfall, and concomitant variability of presence/absence of pollinator groups (Johnson & 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 North American columnar cacti (Valiente-Banuet et al. 2004 and references there cited). In addition, some taxa have been found to differ as to pollination ecology over their range, e.g. *Echinopsis chiloensis* (Colla) H. Friedrich & G. D. Rowley, whose flowers are visited by hawkmoths at the south end of its range (Walter 2010), but by solitary bees at the north end of its range (Ossa & Medel 2011). For *Echinopsis atacamenensis* ssp. *pasacana* (F. A. C. Weber) G. Navarro with flowers seemingly adapted to nocturnal pollinators (as witnessed by the predominantly nocturnal nectar production, Viana et al. 2001), a mismatch between expected and observed pollinators is also documented, and flowers are known to be visited by several species of solitary bees (especially *Xylocopa ordinaria*), a social wasp (*Polybia ruficeps*), and occasionally by the giant hummingbird *Patagona gigas*, as well as the hawkmoth *Manduca diffusa* (Schlumpberger & Badano 2005, Viana et al. 2001).

Also, pollination syndromes exhibited by certain cactus taxa have been found to be “incomplete”, and sometimes incredibly labile, such as in *Echinopsis ancistrophora* Spegazzini, where different populations show a complete array of different flower morphs bridging apparent sphingophily and melittophily (Schlumpberger & Raguso 2008).

Individual (C = columnar, S = spherical)	Growth form	Height (cm)	Diameter (cm)
1C	columnar	40	19
2C	columnar, 2-headed	85 46	25 25
3S	globose	25	25
4S	globose, 2-headed	24 24	24 24
5S	globose	23	23
6S	globose	24	18
7C	columnar	90 (+c. 80 cm underground)	26
8C	columnar	120	24
9C	columnar	130	27

**Table 1:** The studied individuals and their form and size.

Because full-scale detailed pollination biology studies will probably remain comparatively few in relation to total species numbers as a result of time and resource constraints (see e.g. Chacoff et al. 2012 for a time estimate to recover a complete plant-pollinator network), observations (including casual observations) of visitors are a good and simple proxy, and when unexpected visitors appear, or expected visitors are absent, ideas for future research of interesting study systems can be generated. In the series of short communications that we are starting here, we will report on exactly such cases, based on recent field observations for a number of South American cactus species.

## MATERIAL AND METHODS

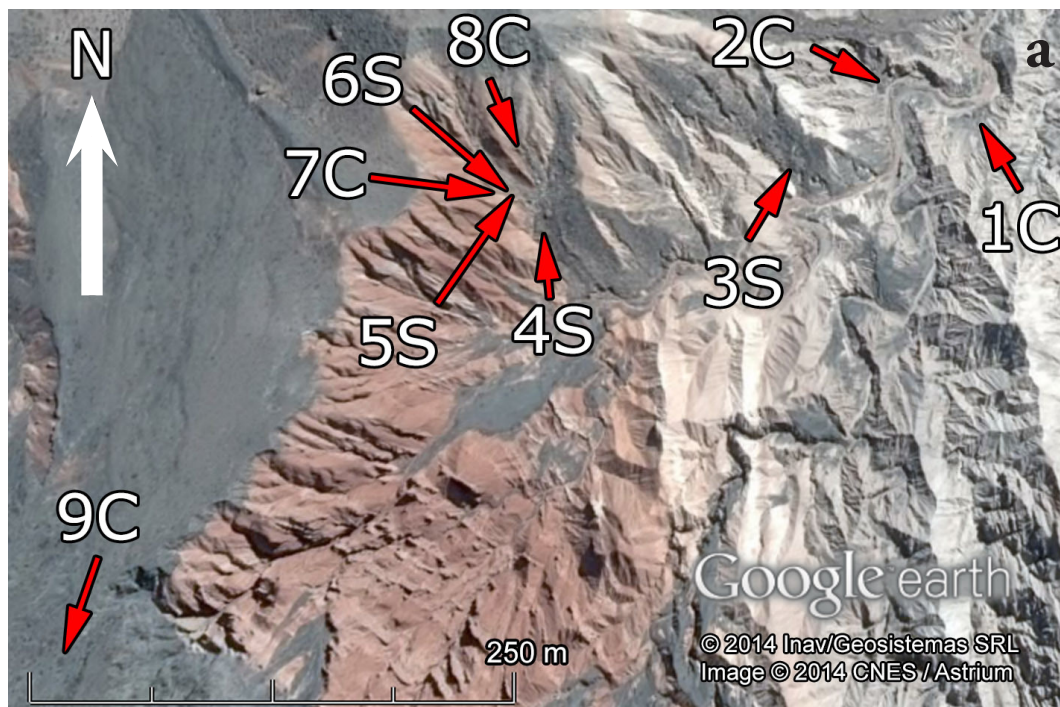
The study organism: *Denmoza* Britton & Rose is a monotypic genus of tribe Cereeae, subtribe Trichocereinae (Nyffeler & Eggli 2010). Its only species, *D. rhodacantha* (Salm-Dyck) Britton & Rose has a fairly wide distribution on the east Andean slopes and foothills in Argentina, spanning a range from central Mendoza province to the extreme north parts of Argentina (Jujuy and Salta provinces), and occurring from 1000 to 2500 masl, usually in “Monte” vegetation and variations of this unit (Leuenberger 1993, Charles 2004 (“to over 3000 m”), Kiesling & Ferrari 2005). The species is notable for the large size it attains (to over 4 m, Charles 2004), for the extreme spination dimorphism between juvenile and adult specimens (accompanied by a gradual increase in rib number), and for the fact that seemingly juvenile specimens are flowering regularly (illustrated, e.g., by Charles 2004 and Laney 2007) (figs. 1, 2). The plants presumably reach a great age, probably well over 100 years, based on the slow growth, even in cultivation under optimal conditions, but detailed demographic studies have not been conducted so far. Fruit set in general appears to be low throughout the range, although - judging from spent dried-up flowers - most plants flower regularly each season (pers. obs.).

The red, tubular flowers with their often somewhat untidy-looking bunch of exerted stamens and style/stigmas conform to the ornithophilous syndrome, i.e. their appearance suggests pollination by hummingbirds. This is also given as plain fact by Anderson (2001: 217, repeated in the German edition [Anderson 2011]) or Charles (2004), probably all going back to Porsch (1938: 70-71, 77). However, we are unaware of any published information based on field observations.

Natural hybridization with the sympatric *Echinopsis atacamensis* was reported by Font & Picca (2001), and the hybrid was formally described as  $\times$ *Trichomoza roseiflora* F. Font & Picca (=  $\times$ *Echinomoza roseiflora* (F. Font & Picca) G. D. Rowley). Font & Picca (2001) report that only a single solitary and apparently sterile individual in a large sympatric population of the two presumed parents in Salta was ever found, and interpreted it as first-generation hybrid. They ascribed the apparent rarity to reproductive isolation resulting from different pollination syndromes, although no direct observations of any pollinator was communicated, and only the syndromes were identified on the basis of Rowley (1994) (Font 2004). Laroze (2013) also found only a single individual of the hybrid (likely the same as originally found), and repeated the statement on hummingbird pollination for *Denmoza*, again without citing evidence. Laroze (l.c.) also found a dried fruit on the plant with a single seed that was subsequently germinated in cultivation. The hybrid is thus at least partly fertile.

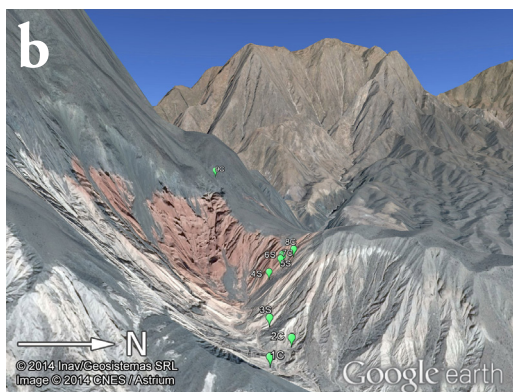
In the list of known intergeneric cactus hybrids from South America, Eggli & Giorgetta (2013) also noted the combination *Cleistocactus*  $\times$  *Denmoza*, obtained in cultivation in Holland (Pullen 2002, without full parentage reported), and Backeberg (1959: 991) reports the combination *Seticereus*  $\times$  *Denmoza*, again without complete parentage reported. In addition, László (2014) recently reported the combination *Denmoza*  $\times$  *Haageocereus*. Nothing is known whether these hybrids were fertile or sterile.





**Methods:** Numerous casual observations at localities between central Mendoza and northern Jujuy and Salta were made by Eggli during several trips in the period 1994 - 2003, and by Giorgetta during numerous trips to the region of the Valles Calchaquies (Salta province) in the past almost 30 years. Detailed observations were then conducted by Giorgetta during 17 days in the period 7 Jan. 2013 – 23 Feb. 2013, and during 21 days in the period 21 Dec. 2013 – 20 Feb. 2014, totalling about 100 observation hours. The studied plants, their flowering phenology, and flower and fruit visitors were documented by means of photographs and videos.

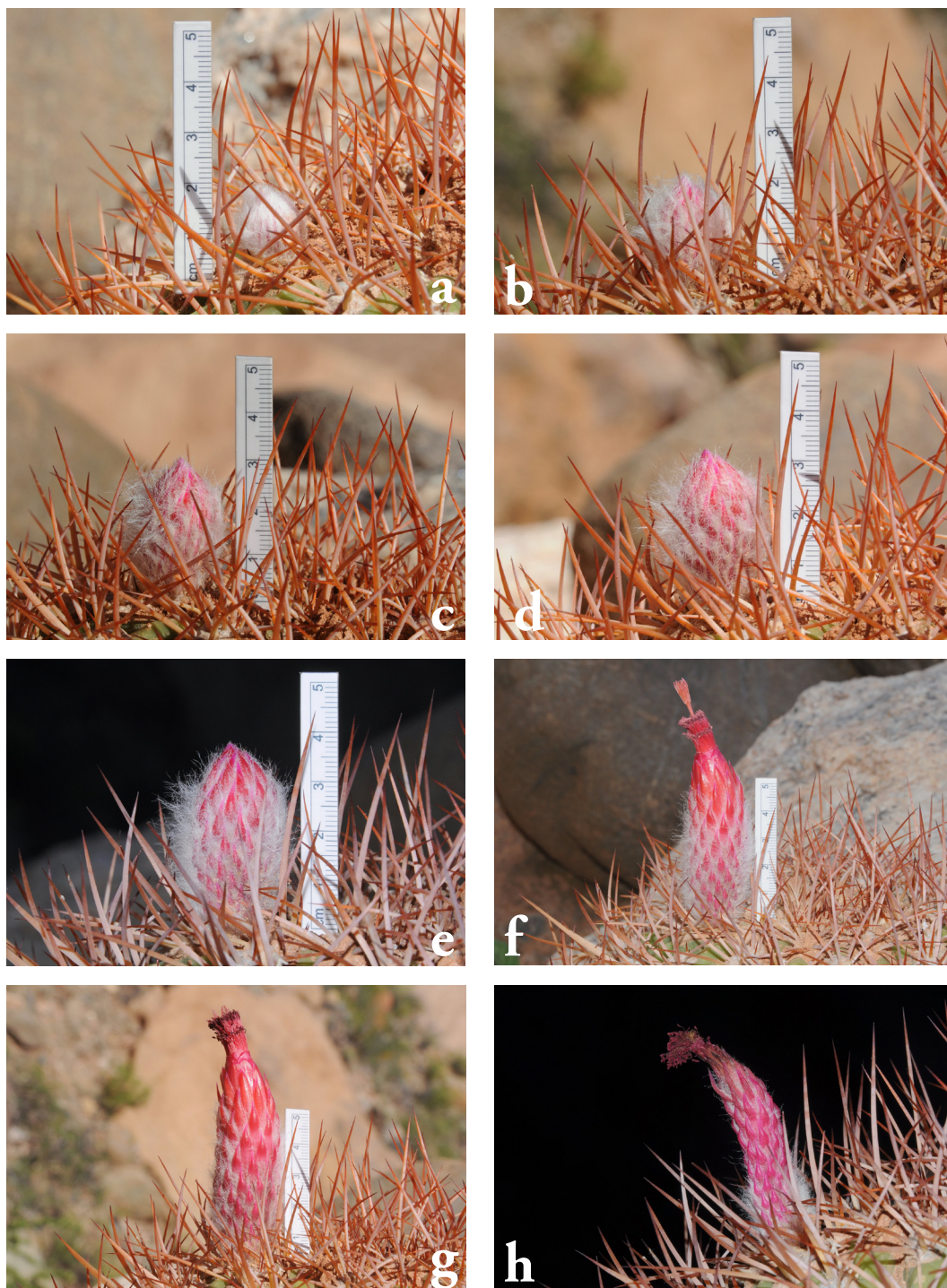
**Study site:** The study population is situated in the Valles Calchaquies near Angastaco, Dept. San Carlos, Prov. Salta, Argentina. The study locality is at Los Colorados on the ascent to the Cerro Negro, c. 3 km S of the village of Angastaco, at an average altitude of 2100 masl, and thus high above the valley bottom of the Río Angastaco. The population numbers about 30 individuals, in total, scattered over an area of c. 800 × 400 m. It comprises small globose juveniles to large shortly columnar adults, the largest measuring c. 170 cm in height. Nine individuals (4 globose, 5 columnar) were selected for the detailed study in the 2013/14 period (see table 1, fig. 3) on the basis of their accessibility. Associated cacti within a 400 m radius were *Opuntia sulphurea* Gillies ex Salm-Dyck, *Tephrocactus weberi* (Spegazzini) Backeberg, *T. molinensis* (Spegazzini) Backeberg, *Tunilla soehrensii* (Britton & Rose) D. R. Hunt & Iliff agg., *Acanthocalycium thionanthum* (Spegazzini) Backeberg, *Echinopsis atacamensis* (Philippi) H. Friedrich & G. D. Rowley, *Gymnocalycium saglionis* (Cels) Britton & Rose, *G. spegazzinii* Britton & Rose, *Parodia aureicentra* Backeberg and *P. microperma*



**Figure 3.** Localization of the studied plants in the field: a) map; b) 3D-view. Views generated on the base of Google Earth data; data sources: Inav/Geosystems SRL; CNES/Astrum.

(F. A. C. Weber) Spegazzini. *Cereus aethiops* Haworth is also found at c. 800 m distance. Associated other flora with hummingbird-syndrome flowers in the 400 m radius flowering simultaneously with *Denmoza* included *Tecoma fulva* ssp. *garrocha* (Hieronymus) J. R. I. Wood (Bignoniaceae) (confirmed as hummingbird-pollinated by Curti & Ortega-Baes 2011) and *Justicia xylosteoides* Grisebach (Acanthaceae) (pollination ecology not known to have been studied). Another common hummingbird-pollinated taxon is *Deuterocohnia haumannii* A. Castellanos (Bromeliaceae), but this flowers only later in the season when the flowering period of *Denmoza* is terminated. *Denmoza* is by far the least numerous cactus at the site. The closest known population of *Denmoza* is located at a place with similar topography and soil conditions at c. 4 km distance.





**Figure 4.** Flower development of *Denmoza rhodacantha* from bud to full anthesis: a) 8. Feb. 2013 - small bud; b) 13. Feb. 2013; c) 14. Feb. 2013; d) 15. Feb. 2013; e) 16. Feb. 2013; f) 18. Feb. 2013 - first day of anthesis; g) 19. Feb. 2013 - second day of anthesis; h) 23. Feb. 2013 - withering flower.

## RESULTS

**Flowering phenology:** Buds of *Denmoza* develop within c. 10 days from the first visible bud stage to open flowers (fig. 4a-h). The start of anthesis is

marked by the appearance of the closed stigma and the rapidly increasing degree of exertion of the style from the bud when the perianth segments are still tightly pressed together. The start of anthesis can be



**Figure 5.** Opening of the flower bud of *Denmoza rhodacantha* starts around noon, and within 8 hours, the stigma lobes start to spread (left photograph taken 12:45, right photograph 20:23).

at any time during the morning or afternoon. Soon after style emergence, the perianth segments start to unfold at their extreme tips, and the dense bunch of stamens appears in the throat and the anthers dehisce to release violet-coloured pollen (a typical trait for ornithophilous cactus flowers according to Rose & Barthlott 1994), soon followed by the beginning of the spreading of the stigma lobes. The flowers thus show a short protandrous phase. No changes in flower development occur during the night, and open flowers do not close (fig. 5, left). The receptive phase starts usually on day 2, when the stamens become more exerted, and when the stigma lobes spread out (fig. 5, right). Nectar is usually abundantly present at this time. On day 3, stamens and style/stigma rapidly wilt, and the flower is contracting in length. Unfertilized flowers dry up and abscise within 2–3 days. No floral scent has been noted during the whole period of anthesis, neither during the day nor during the early night hours (observation periods extended to 22:00).

**Diurnal flower visitors: Hummingbirds:** No hummingbirds were recorded on *Denmoza* flowers, either during the detailed observation periods in 2013 and 2013/14 or during the numerous visits to other populations of *Denmoza* throughout its range in the past almost 30 years. Hummingbirds of the two species *Chlorostilbon lucidus* (fig. 6, left) and *Sappho sparganura* (fig. 6, right) are common in the study area, and they were present during all study visits, but did not pay any attention to the available *Denmoza* flowers – instead, they regularly visited the flowers of *Tecoma fulva* ssp. *garrocha*. A third species of hummingbird, *Patagona gigas*, which has been recorded as flower visitor of *Oreocereus celsianus* (Lemaire ex Salm-Dyck) Riccobono (Eggl & Giorgetta 2013, for Bolivia), is more rarely seen in the area. A single *Patagona* was sighted near a flowering *Denmoza* individual only once, approaching the flowers, hovering for a brief period in front of it (fig. 7, only 1 of 3 flowers visible), and then rapidly disappearing.

**Insects:** Individuals of an iridescent, 3–4 mm long, presumably solitary, halictid bee, possibly a species of the genus *Dialictus* (A. Roig Alsina, pers. comm. July 2014), were rarely but regularly seen on open *Denmoza* flowers and were also visiting other



**Figure 6.** Hummingbirds visiting *Tecoma fulva* ssp. *garrocha* (Quebrada Los Sayar near Angastaco, 15. Feb. 2013): left *Chlorostilbon lucidus*; right *Sappho sparganura*.



**Figure 7.** The hummingbird *Patagona gigas* was observed only once approaching a flowering *Denmoza rhodacantha*, but it did not visit the flowers. Note that the photograph is misleading as to the length of the bird's bill, which is at a different angle than the flower whose base is moreover partly hidden by the plant body.

mostly red-flowering cacti, such as the locally red-flowering *Tephrocactus weberi* and *Tunilla soehrensii* agg., but also the yellow-flowering *Acanthocalycium thionanthum*. The bees collected pollen on the hind legs as well as on the ventral surface of the abdomen, and individuals visiting *Denmoza* repeatedly crawled over the bunch of exerted stamens as well as over the spreading stigma lobes. The bee did not attempt to crawl into the flower to get access to the abundant nectar, but confined its activities to collecting pollen (figs. 8, 9, 10). At least in one case (5<sup>th</sup> Jan. 2014, globose individual 3S), an incoming bee was observed that was already heavily loaded with the typical violet-coloured pollen of *Denmoza*, probably from the columnar study individual 9C with 3 open flowers at 460 m distance. This would indicate that the bees are actively searching for the *Denmoza* flowers as a pollen resource.

In addition to the halictid bee, unidentified small flying beetles and small-bodied ants were also observed on open *Denmoza* flowers. Both are able to crawl into the flower along the filaments to reach the nectar. It appears unlikely that they come into regular contact with the stigma lobes, and their contribution to pollination is likely nil.

**Nocturnal flower visitors:** Although observation periods ended before night-fall, flowering plants were briefly visited on the way back to the village,





**Figure 8.** *Denmoza rhodacantha* flower at full anthesis with visiting pollen-collecting solitary bee.



**Figure 9.** An individual of the solitary halictid bee actively collecting pollen from a single anther. The pollen grains collected on the abdomen and the hind legs are easily visible.



**Figure 10.** Size comparison between the common introduced *Apis mellifera* (right) and the *Denmoza*-pollinating solitary halictid bee (left) on a flower of *Acanthocalycium thionanthum*.



**Figure 11.** Buds, flowers and ripening fruits of all stages are commonly present simultaneously on *Denmoza rhodacantha* plants.



**Figure 12.** Almost ripe fruit of *Denmoza rhodacantha*, 45 days after flowering.



**Figure 13.** Ripe fruits of *Denmoza rhodacantha* dehisce by an irregular semi-circumscissile split.

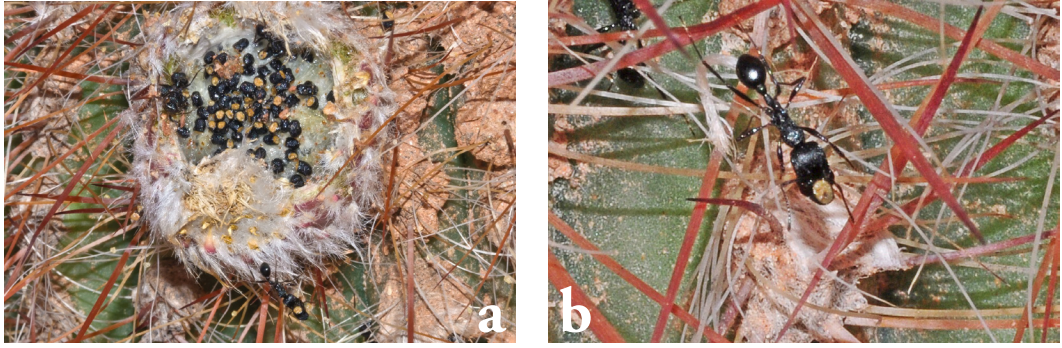
and no insects were ever observed near flowering *Denmoza* individuals. Hawkmoths of several sizes were observed around flowering specimens of *Cereus aethiops* in or near the overall study region, and they would have been noticed if they had been present in the vicinity of the study plants of *Denmoza*.

**Fruiting phenology:** The ripening time of the fruits is in the order of two months - fruits from flowers that opened around 21. Dec. 2013 opened only in the afternoon of 20. Feb. 2014. During fruit ripening, further buds and flowers were produced, and it is common to find all stages from early buds to ripe fruits concurrently on *Denmoza* individuals (fig. 11). Ripe fruits develop a dark red colour (fig. 12), and finally open by an irregular semi-circumscissile split (fig. 13). The seeds are densely packed and

there is only scant pulp. A single fruit counted contained about 1500 seeds. Dehiscing fruits were rapidly visited by several unidentified species of ants of different sizes. The smaller ants appeared to harvest the scant pulp, while the larger ants carried away individual seeds cleaning them from adhering pulp first (Fig. 14).

Fruit set has been observed to be poor during many trips to numerous populations throughout the range of *Denmoza*. A very low fruit set (22.4%) was observed in the study period 2013/2014, i.e. only 19 out of a total of 85 observed flowers developed into fruit. Interestingly, fruit set is higher (28.6%, 63 flowers, 18 fruits) for the columnar individuals studied, compared with almost nil (4.5%, 22 flowers, 1 fruit) for the globose juvenile individuals. The





**Figure 14.** a) Seeds of *Denmoza rhodacantha* are rapidly carried away by ants, as can be seen at the lower edge of the picture. b) Ant carrying a seed.

low fruit set of *Denmoza* is in marked contrast to the almost 100% fruit set rates of the sympatric cactus species at the study site.

## DISCUSSION

*Denmoza* is yet 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 pollinator is not observed. Two species of hummingbirds were observed to be common and regularly present at the study site, but they showed no interest at all in the *Denmoza* flowers, but rather visited nearby *Tecoma fulva* ssp. *garrocha* (flowers 3–4 cm long) and *Justicia xysteoides*, despite the fact that *Denmoza* flowers contain abundant nectar (with >30% sugar content [B. Schlumpberger, pers. comm., based on cultivated plant], which is typical for hummingbird flowers). Instead, a small species of solitary halictid bee, probably of the genus *Dialictus*, is found with regularity throughout the season, although in small numbers, suggesting that the flowers are recognized by these bees as a reliable source of pollen (the main reward which they are searching for), even though the flowers could be considered to be “ill adapted” to these visitors. It should be kept in mind, however, that adaptations do not have to be perfect, as long as they work sufficiently well (Niklas & Spatz 2012). Halictid bees are generally opportunist generalists (B. Schlumpberger, pers. comm.), and indeed visit many of the sympatric simultaneously flowering cacti (with a bias to red-flowered plants). The observation that an incoming bee was heavily loaded with *Denmoza* pollen, identifiable by its violet colour (in contrast to the yellow pollen of the sympatric cacti), shows that the bees actively locate and visit *Denmoza* flowers when available.

On the other hand, the single observation that an individual of *Patagona gigas* approached a *Denmoza* flower but did not visit it, appears significant. A closer examination of the flower proportions relative to the size of the hummingbird species of the study region show that hummingbirds are unlikely to be the main targets of the flowers - the birds would need a bill 4.5–5 cm long to exploit the nectar, but *Chlorostilbon lucidus*, *Sappho sparganura* and *Patagona gigas* all have much shorter bills (1.6 cm, 1.75 cm

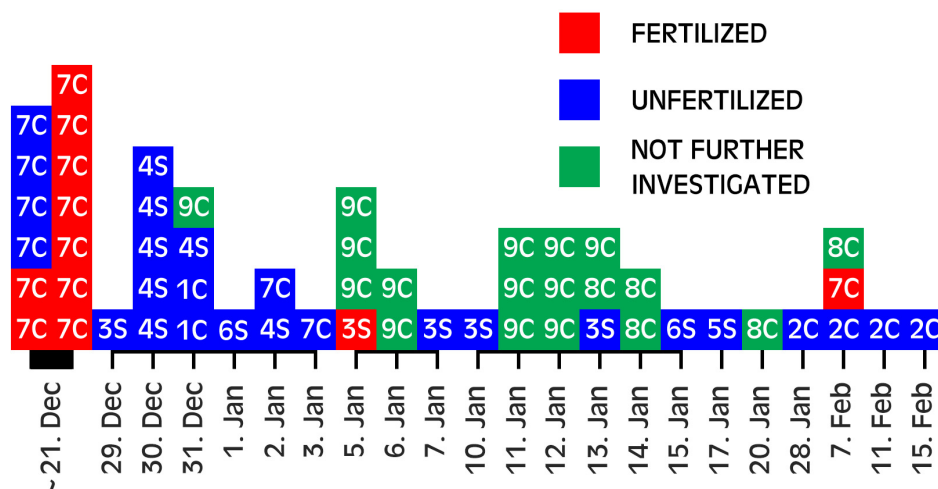
and 3.8 cm, respectively; data from Nattero & Cocucci 2007). Because of the flower structure and size, the birds have no possibility to land on the flower, or at least “hug” it in a similar way as observed for *Oreocereus celsianus* (Eggl & Giorgetta 2013: 38). In addition, the flower are often hardly longer than the surrounding spination, and this probably further deterred the hummingbirds.

The low fruit set observed could be taken as evidence that the small solitary halictid bee regularly observed does not represent the main pollinator, which therefore would have been absent from the study site during the study periods 2013/2014. It is more likely that the asynchronous flowering of the small number of individuals making up the study population is responsible, together with a short period of receptivity of only a single day. Since *Denmoza* is self-sterile (observed in the study area as well as in cultivation), at least two synchronously flowering individuals are necessary to allow successful pollination. The flowering chronogram (Fig. 15) shows that conditions for successful pollination were relatively rare; the abundant fruit set of individual 7C flowering around 21 Dec. 2013 must be due to pollen from an unstudied individual of the population that flowered at that time.

The evolutionary history that produced the observed situation is not known, and any interpretations must remain speculative. The apparent lack of hummingbird interest in *Denmoza* flowers is likely due to the mismatch between bird and especially bill size and the *Denmoza* flower construction, which makes nectar extraction almost impossible, and thus costly in terms of time and energy involved. It could, however, also be the result of competition with simultaneously produced flowers of other species in the local plant communities that offer better or more easily gathered rewards. Routinely exploiting the *Denmoza* resource might simply be uneconomical for the pollinator. Because the flowers exhibit all the attributes (size, shape, colour, consistency, nectar) associated with ornithophily in the syndrome concept, avoidance of it by the hummingbirds probably involves some degree of learning.

Interestingly, casual observations of numerous *Denmoza* stands over many years and localities show that the modest reproductive output observed in

*Denmoza rhodacantha* - flowering chronogram



**Figure 15.** Flowering chronogram of the studied population in the period of 21 Dec. 2013 to 15 Feb. 2014. The flowers of individuals 8C and 9C were not further studied due to difficult access to the plants.

this study is the rule rather than the exception - usually few fruits are present and many plants have no fruits at all, although the number of withered flower remains suggests that they have flowered profusely. Poor pollen transfer (frequency and/or quality of transfer and deposition) is the likely reason for this, and it is well possible that the observed bees, while visiting the *Denmoza* flowers regularly, are inefficient pollinators.

The likely evolutionary pathway that led to the observed pollination biology remains obscure. In the recent molecular phylogeny of the *Echinopsis* clade by Schlumberger & Renner (2012), *Denmoza* is shown as basal sister to *Acanthocalycium* + *Echinopsis leucantha*, and this clade in turn is sister to *Echinopsis mirabilis*. *Denmoza* and *Acanthocalycium* have diurnal flowers, while the two *Echinopsis* species have nocturnal flowers and conform to the sphingophilous syndrome. No attempt has been made to deduce the ancestral state of flower characteristics, but it is evident that switches between flower characteristics that influence pollination must have occurred repeatedly in this clade. The *Denmoza* flower is completely unique within the small *Denmoza* clade of Schlumberger & Renner (2012), and we have no idea what driver could be responsible for its evolution.

## CONCLUSIONS

*Denmoza rhodacantha* presents an obvious discrepancy between the pollinator expected on the base of the ornithophilous flower syndrome, and the observed flower visitors, halictid solitary bees. We do not have an explanation for this apparent mismatch. Whether the low fruit/seed set is linked to the pollinator mismatch is unknown, and it could also be the result of the small population size and the asynchronous flowering behaviour. On the other hand,

poor fruiting has also been casually observed in *Denmoza* populations with numerous individuals. Since morphologically juvenile plants are usually present in *Denmoza* populations, reproduction at the population level does not seem to be of concern. Also, it should be stressed that our flower visitor studies were conducted in a very narrow portion of the geographical range of the species, and conditions could be different elsewhere.

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