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THE ADAPTIVE ROLE OF NECTARIAL APPENDAGES IN COLCHICUM

By

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The adaptive role of nectarial appendages in *Colchicum*

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Running head – The adaptive role of nectarial appendages in *Colchicum*

Abstract

A few species within the genus *Colchicum* of the Colchicaceae family, a small group of species native to the transitional belt of the Mediterranean and the Middle East deserts, are characterized by unique morphological traits: nectarial appendages that occur at the base of the perianth segments and consist of two lamellae with teeth. The morphology of the nectarial appendages was measured in three species and in a new population with similar traits to this group for the first time. Nectarial appendages and nectar standing crop are larger for the inner whorl of perianth segments in all species, although the perianth segments are themselves usually smaller. Intact flowers received more ant visits in outer than in inner whorl perianth nectaries. Removal of the nectarial appendages resulted in an opposite trend, implying that these organs prevent ant access to nectaries. Ant access to flowers reduced nectar standing crop, which could reduce the fitness of the species assuming that ants do not pollinate. The role of nectarial appendages as nectar-theft deterrents is reinforced in light of the group's harsh habitat and flowering season.
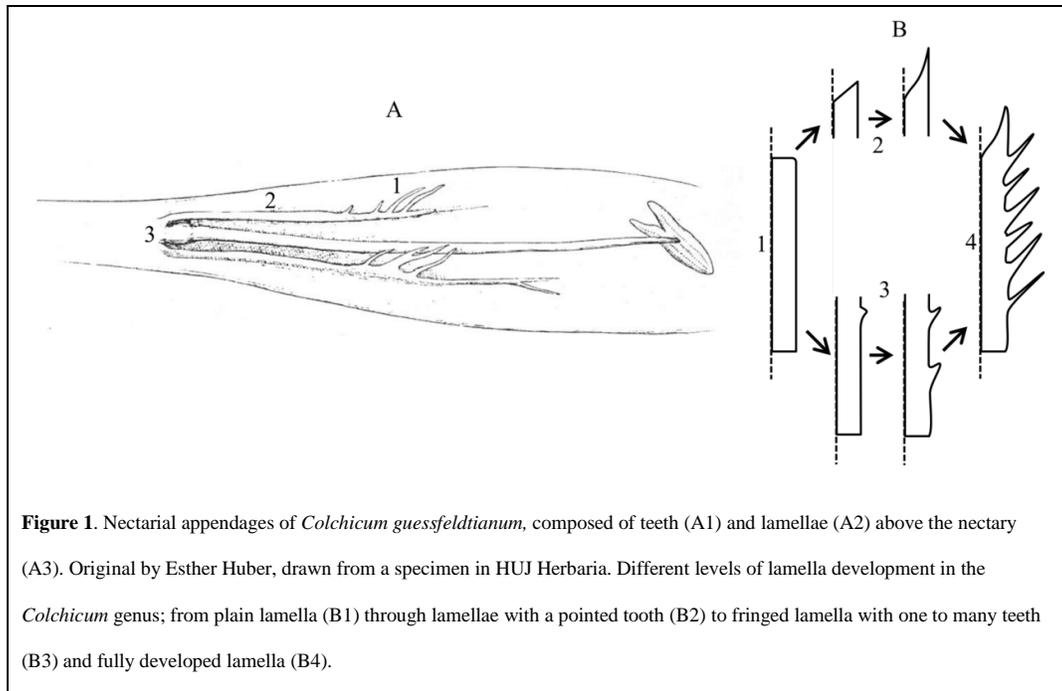
Introduction

Peculiar morphological traits have long been carefully observed and described in systematics in an attempt to distinguish one species from another (Stebbins 1970). In several cases, the unique traits of certain species have triggered the imagination and research of evolutionary biologists and ecologists in an attempt to find reasons for these phenomena (Kaplan 2001). An adaptive advantage to a certain feature may improve our understanding of the adaptive radiation of the species involved. *Colchicum* belongs to the Colchicaceae family which comprises two genera - *Colchicum* and *Androcymbium* (Dahlgren, Clifford & Yeo 1985). The genus *Colchicum* is distributed mainly in the Mediterranean and Irano-Turanian regions and extends to the Saharo-Arabian region. Some species extend to central and western Europe and the mountains of Pakistan and Central Asia (Persson 2007). Four species - *C. ritchii*, *C. guessfeldtianum*, *C. tuviae* and *C. deserti-syriaci* - were grouped and documented as having "fimbriated or toothed lamellae" (Feinbrun 1953). This phenomenon comprises two elongated parallel ridges (i.e., lamellae), fimbriated or not, which form a small submerged nectar-accumulating cup at the base of the filament between the filament and the perianth segment (Fig. 1A).

Figure 1. Nectarial appendages of *Colchicum guessfeldtianum,* composed of teeth (A1) and lamellae (A2) above the nectary (A3). Original by Esther Huber, drawn from a specimen in HUJ Herbaria. Different levels of lamella development in the *Colchicum* genus; from plain lamella (B1) through lamellae with a pointed tooth (B2) to fringed lamella with one to many teeth (B3) and fully developed lamella (B4).

 Geophytes, plants with subterranean bulb organs, are typical to the Mediterranean biseasonal climate and are common in the Mediterranean basin and south-west Asia (Blondel & Aronson 2010, Shmida 1981, Shmida & Burgess 1988, Fragman & Shmida 1996). Leafless autumnal flowering geophytes is a special perennial subgroup of geophytes which dominates within the flowering market of the Mediterranean autumn; they usually bloom near the ground and their center of distribution is in the East Mediterranean (Dafni et al. 1981, Shmida & Polak 1987, Dafni & Shmida 1990). Among the autumnal geophytes *Colchicum* is the largest and most common taxa; it comprises 91 species, most of which bloom in autumn or early winter (Fienbrun 1953, Persson 1992, Persson 1999, Persson 2007, Dafni & Shmida 2002, Shmida & Dafni 1990).

While only a minority of species from the genus are restricted to desert and semi-desert climates, most members of the above fimbriated group are distributed within the Levant Mediterranean and semi-deserts. In accordance with the rest of the Levant

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Colchicum species, the species of this group flower in autumn and early winter. The seasonal and geographical distribution of these species entails high variability and unpredictability in precipitation and frequent extreme weather conditions (Shmida, Evenari & Noy-Meir, 1986) as well as a possible low synchronization with pollinators (Wolf et al. 1986).

While some systematic descriptions of the nectarial appendages have been made in the past, quantitative measurements were never conducted and no attempt to find the adaptive advantage to this unique morphological trait was made.

In this study we suggest an adaptive advantage to the fimbriated floral appendages and hypothesize on the ecological circumstances that arid-land *Colchicum* species are exposed to, which may have supported the evolution of these organs.

Material and Methods

Organ description and definition

Flowers have six perianth segments arranged in an inner and an outer whorl. Each of the six segments has an individual stamen and nectary at its base. Three styles with small pointed stigmas, which originate in the subterranean ovary, protrude from the perianth tube. The filament of the stamen stems from the base of the perianth segment. Nectar-producing tissue, similar in color to the anther (either yellow or brown), is located at the base of the filament. The color of the perianth is homogeneous and consistent within the flowers of each individual and is usually typical on a species level (Feinbrun 1953), but anther and nectar tissue color may vary within a population. Anthers and nectar tissues have a yellow or brownish color which can be noticed from outside. These colors are a typical diagnostic character in

some *Colchicum* species (Feinbrun 1953, Persson 2007) but are polymorphic in others: it is consistently brown in *C. tiviae* but it varies within populations in *C.ritchii*.

In some species of *Colchicum* the nectar tissue at the base of the filament is crowned by 2 lamellae/ridges, with or without teeth, on each side. The lamella is connected to the perianth segment on one side and to the segment base on the other.

In some *Colchicum* species it is possible to distinguish a lamella, with or without one miniature tooth, within part of the population (e.g., *C. antilebanoticum*), while in other species there is no lamella at all.

There are different ways of describing the above-mentioned morphological organs in the systematics literature. Stefanoff (1926) described them as "calycis lacinales basi bicritatae" and included them in *C. bulbodicodiae*, Feinbrun (1953) described them as "fimbriate or toothed lamellae at the base of the perigorium segments," and Persson (2011) described the nectarial appendages as two separate traits within the list of characters used for phylogenetic analysis of the genus : trait 16 – teeth at the limb segment base, and trait 17 - filament channels that could include lamellae with or without teeth. Our experience with *Colchicum* species is that a lot of variation and transition exists between the two traits mentioned by Persson (2011). In other words, there is gradation from plain lamellae through lamellae with a pointed tooth to fringed lamellae with one to many teeth (Fig. 1B).

Feinbrun (1953) emphasized the important difference in the nectarial appendages between the outer and inner segments. We measured the elements of the nectarial appendages separately in the inner and outer perianth segments and found them to be important and applicable features to distinguish between species of *Colchicum*. Since Persson did not distinguish between the inner and outer features of the nectarial appendages (e.g., the difference between *C. tuviae* and the other species), we could

not follow the systematic treatment of Persson (2007, 2011) and we based our

research on Feinbrun (1953, 1958).

Study species and sites

Our study focused on three of the fimbriated species – *C. ritchii*, *C. tuviae*, and *C. guessfeldtianum*. We also analyzed a population that was recently found to have similar characteristics and it is potentially a new species since it has consistently only one style. It will hereafter be referred to as *C. "ramonensis."* Access to *C. deserti-syriaci*, which was described as having poorly fimbriated appendages (Feinbrun 1953), was not possible. Research site details are described in Table 1.

Table 1. Study site details for research populations

	C. tuviae	*C. tuviae*	*C. ritchii*	*C. guessfeldtianum*	*C. "ramonensis"*
Name of site	Keidar, Judean desert	Ma'on, Judean desert	Tel Arad, Negev desert	Saint Katherine, protectorate, Sinai desert	Mt. Ramon, Negev desert highlands
Coordinates	35.30041 E, 31.74694 N	35.16452 E, 31.41809 N	35.12545 E, 31.27524 N	33.91579-33.95297 E, 28.53448-28.62495 N	34.60862 E, 30.51469 N
Altitude (m)	520	785	530	1,418-2,221	960
Average rainfall (mm)	332	315	183.3	35.9	78
Average temperature (Jan, Aug) (C)	9.4,22.6	8.4, 24.6	9.8, 26	9, 15	7.7, 22.6
Sampling dates	6.11.08-15.12.08 27.11.09-27.12.09	20.12.09	27.2.09-4.3.09 26.11.08-15.12.08	17.11.09-19.11.09	26.12.09

Data for sites were taken from the GIS database and data for Saint Katherine relates to the documented rainfall for the years 1970-1994 and 2001-2009 from the town of Saint Katherine in the center of the relevant area. Ant behavior was recorded on days with clear skies, max temperatures of 18-20 C, and low wind.

Floral features and nectar properties

Specimens (N~20) from one population each of *C. tuviae*, *C. ritchii*, and *C.*

"ramonensis" were examined. For *C. guessfeldtianum* a larger sample (N=29) from different populations was taken because of flower scarcity in the Saint Katherine protectorate. One flower in peak flowering was measured per specimen. Morphological traits were examined for each specimen on both inner and outer perianth segments. One perianth segment was randomly chosen and examined for inner and for outer segments. Similarly, one of the two appendages was randomly chosen and measured in each perianth segment. Perianth, lamella, and tooth sizes were all measured with a clear plastic ruler. For tooth-counting purposes, all segments protruding from the lamella exceeding 0.2 mm were included. Average tooth length is calculated as the mean of all teeth within each specimen.

Nectar standing crop was taken with 1 µl pipettes for all six nectaries. Average standing crop per nectary in the inner and the outer whorl is the mean of the three relevant nectaries. Samples greater than ~0.15 µl were measured for sugar concentration with a Bellingham-Stanley handheld refractometer modified for low volumes. Due to low nectar production, all measurements were taken before pollinator activity began and should be treated as nectar standing crop.

Presence of ants in perianth segments and its effects on nectar

Ant presence in inner and outer perianth segments was observed for *C. tuviae* and *C. ritchii*. The presence of ants was scored when an ant's head was in contact with a nectary for longer than 1 sec. A total of 100 untreated flowers were documented several times while observing all perianth segments once an hour in Keidar for *C. tuviae* over two days ($N_1=5$, $N_2=5$) and in Tel Arad for *C. ritchii* over two days ($N_1=3$, $N_2=3$). Specimens of ants present in perianth segments were collected in the field,

preserved in 70% alcohol, and identified with species level when possible by Jacob Ofer of the Kibbutz Seminary.

C. tuviae is sub-synanthous with 1(2) flowers per specimen; *C. ritchii* is synanthous and larger with 3(4-5) flowers per specimen. As described in Table 1, *C. ritchii* perianth segments are larger than those in *C. tuviae* flowers. These morphological differences restricted our ability to perform all the tests on both species.

In order to evaluate changes in ant access to inner and outer perianth segments, a total of eighty flowers of *C. tuviae* in peak flowering from the Keidar (N_1=64) and Ma'on (N_2=16) populations were cut below ground level and divided into 8 flower groups. Nectarial appendages were removed from inner and outer perianth segments of 4 randomly chosen flowers in each group. Untreated flowers were cut on the edge of one of the perianth segments to control for effects of volatile substances secreted by floral cuts. Flowers were placed as "bouquets" in Eppendorf tubes filled with water to prevent flower dehydration, and "planted" in the ground to prevent ant access to the water. The "re-planting" procedure was possible only for *C. tuviae,* as it is sub-synanthous and usually single-flowered. Flowers in each bouquet were positioned in equal proximity to ant nests or ant trails and treated and un-treated flowers were positioned alternately. Ant entrances to control and treated flowers were recorded for three to five cycles of 10 minutes at 30-minute intervals.

Testing the effect of fimbriation removal on nectar standing crop and concentration involved specimens of *C. ritchii* in Tel Arad (over two days (N_1=10, N_2=11). Two flowers in peak flowering and of similar sizes were marked on each plant. The nectarial appendages of one of the flowers (randomly chosen) were removed and nectar concentration was determined in samples exceeding ~0.15 µl. Only in *C. ritchii* could we find a significant number of specimens with more than one flower in peak

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flowering on the same plant. This design was chosen due to high variance between flowers' nectar crop which is mainly due to differences between plants. Plants were covered with fine netting to prevent visits from airborne insects and ants. After 3.5 hours, flowers were harvested and nectar standing crops and concentrations were measured.

Determination of the effect of ant access on nectar standing crop entailed 30 pairs of *C. ritchii* individuals that were 0.4-0.6m away from each other and recorded in Tel Arad over three days ($N_1=12$, $N_2=11$, $N_3=7$). *C. ritchii* was chosen for this experiment due to higher ant activity and its larger nectar volumes compared to *C. tuviae*. Each individual plant had 4-5 flowers in peak flowering. Before ant activity began, one of the two plants was randomly chosen and surrounded by a plastic ring (diameter 10.5 cm) covered with Vaseline to prevent ant access. Flowers of similar sizes and similar flowering stages were chosen and marked on each of the plants. The flowers were harvested after 4 hours, and nectar standing crop and concentration were measured. Intensive grazing by local goat herds did not allow plant marking that would allow us to evaluate fruit production as a measure of pollination success.

Data analysis

Paried *t*-tests comparing inner and outer traits were conducted for the 31 trait sets and P-values were obtained. Need for familywise error control resulted in two corrections – the conservative Bonferroni correction and the False Discovery Rate (FDR) control (Benjamini & Hochberg 1995). Both thresholds are displayed; we chose to follow the results from the FDR control.

For the remaining trait comparisons paired *t*-tests were performed using SPSS 20.

Results

Floral features and nectar properties

Outer perianth segments were bigger (length and width) for the three species and the ramon taxa. Lamella size (length and width), number of teeth, and nectar standing crop were bigger for inner perianth segments in all species. No trend was found for tooth size and nectar concentration throughout the different species (Figure 2).
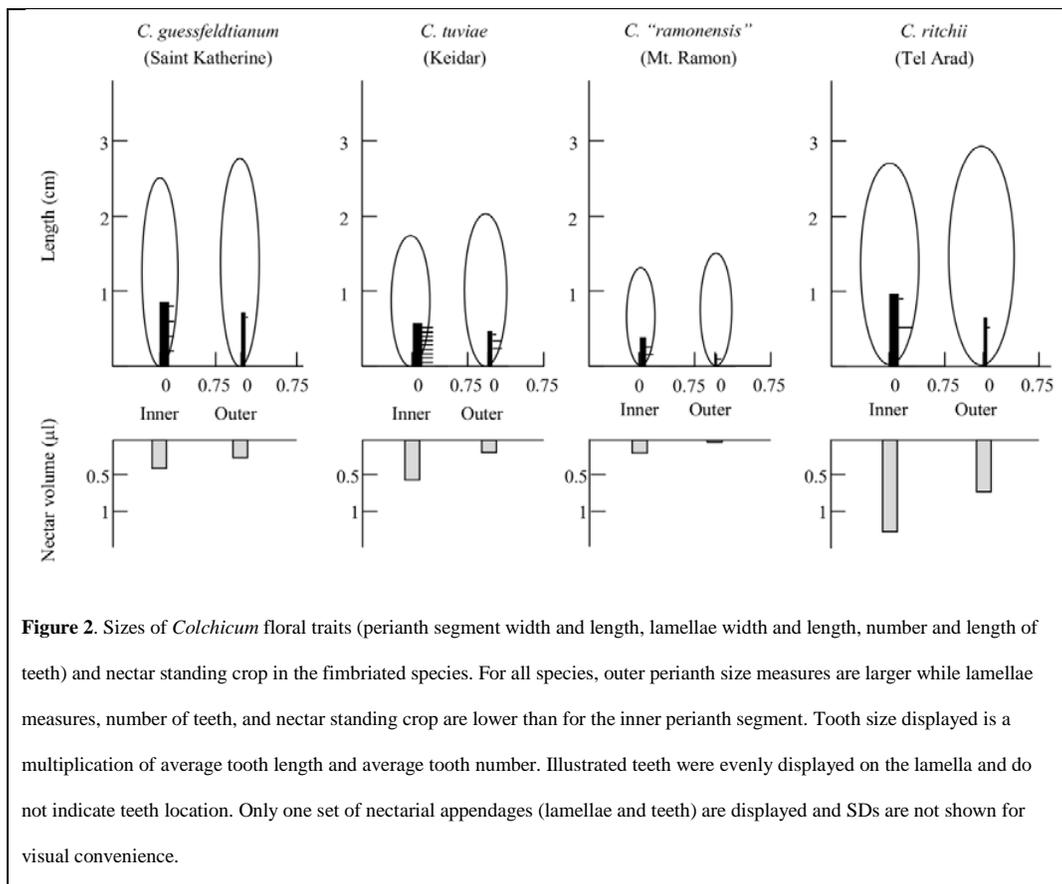
Figure 2. Sizes of *Colchicum* floral traits (perianth segment width and length, lamellae width and length, number and length of teeth) and nectar standing crop in the fimbriated species. For all species, outer perianth size measures are larger while lamellae measures, number of teeth, and nectar standing crop are lower than for the inner perianth segment. Tooth size displayed is a multiplication of average tooth length and average tooth number. Illustrated teeth were evenly displayed on the lamella and do not indicate teeth location. Only one set of nectarial appendages (lamellae and teeth) are displayed and SDs are not shown for visual convenience.

Controlling familywise error rate with an original P-value of 0.05 resulting via the Bonferroni correction generated a critical P-value of 0.0016. Using False Discovery Rate (FDR) control generated a critical P-value of 0.043. Statistical significance of the tests according to both criteria is presented in Table 2.

Table 2. *t*-test results for floral measurements between inner and outer perianth segments
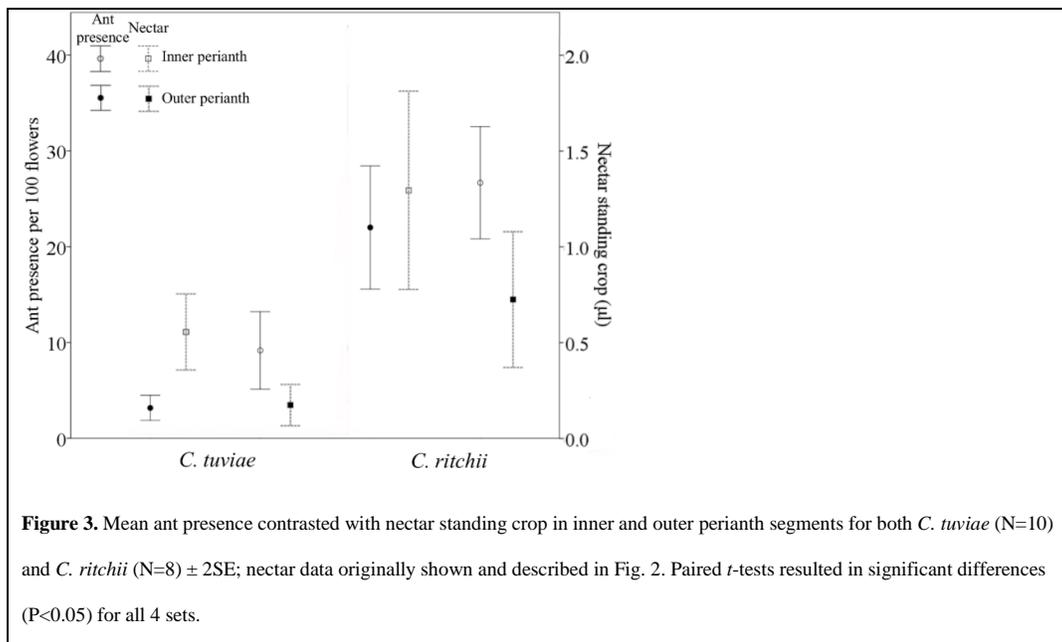
	C. guessfeldtianum			*C. tuviae*			*C. ritchii*			*C. "ramonensis"/*		
	N	t	P	N	t	P	N	t	P	N	t	P
Perianth length (cm)	27	-6.43	<.001	21	-14.07	<.001	20	-13.91	<.001	20	-0.06	<.001
Perianth width (cm)	29	-3.44	.002*	21	-5.39	<.001	20	-4.77	<.001	20	-5.6	<.001
Lamellae length (cm)	29	2.86	.008*	21	2.38	.027*	20	3.61	.002*	20	5.49	<.001
Lamellae width (cm)	29	16.26	<.001	21	5.41	<.001	20	10.66	<.001	20	9.27	<.001
Number of teeth	29	9.67	<.001	21	9.91	<.001	20	2.77	.012*	20	4.18	<.001
Average tooth length (cm)	10	.81	.435**	21	.56	.579**	5	.192	.857**	9	.37	.719**
Nectar crop (µl)	29	3.03	.005*	21	4.89	<.001	20	3.94	.001	20	3.13	.005*
Nectar concentration (%)	10	3.23	.010*	10	-1.9	.089**	12	-.5	.626†*	0	-	-

* Non-significant result according to α=0.05 with Bonferroni correction

** Non-significant result according to α=0.05 with FDR control (BH) and Bonferroni correction

Ant presence in perianth segments

Ants were more abundant in outer perianth segments than in inner ones for *C. tuviae* $(t_{(9)} = -6.815, P < 0.001)$ and for *C. ritchii* $(t_{(5)} = -4.889, P = 0.005)$. These trends are contrasted in Fig. 3 to nectar standing crop trends between inner and outer perianth segments for *C. tuviae* $(t_{(21)} = 4/89, P < 0.001)$ and for *C. ritchii* $(t_{(20)} = 3.94, P = 0.001)$ which were presented in Fig. 2.

Figure 3. Mean ant presence contrasted with nectar standing crop in inner and outer perianth segments for both *C. tuviae* (N=10) and *C. ritchii* (N=8) ± 2SE; nectar data originally shown and described in Fig. 2. Paired *t*-tests resulted in significant differences (P<0.05) for all 4 sets.
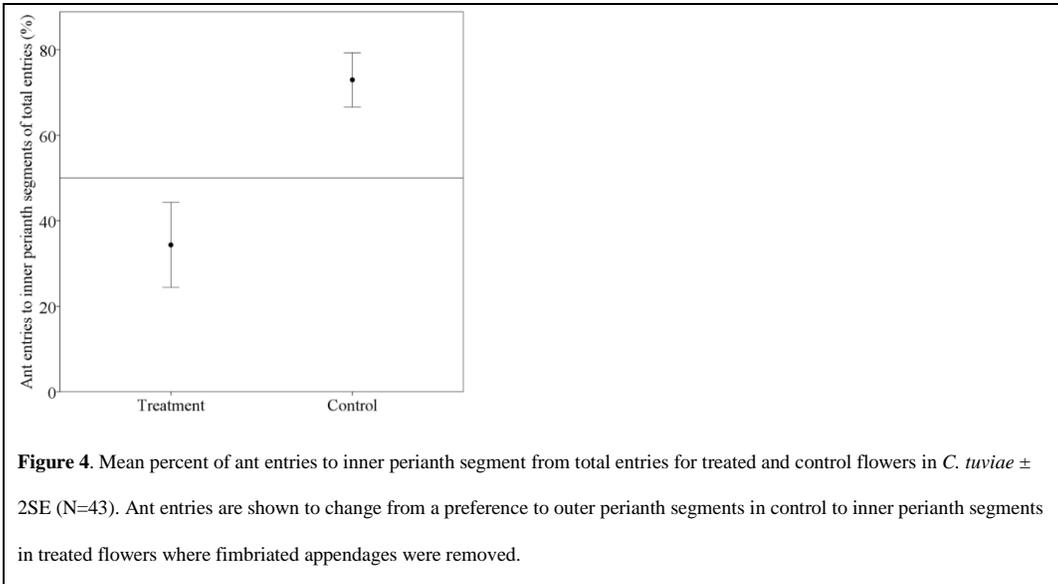
Identified ant species are displayed in Table 3. For *Camponotus,* only genus level
identification was achieved due to bad preservation of samples. Total body length for
all species is ~3mm excluding *Camponotus* at ~8mm.

Table 3. Ant species in different habitats. Systematic treatment follows Vonshak & Ionescu-Hirsch 2009
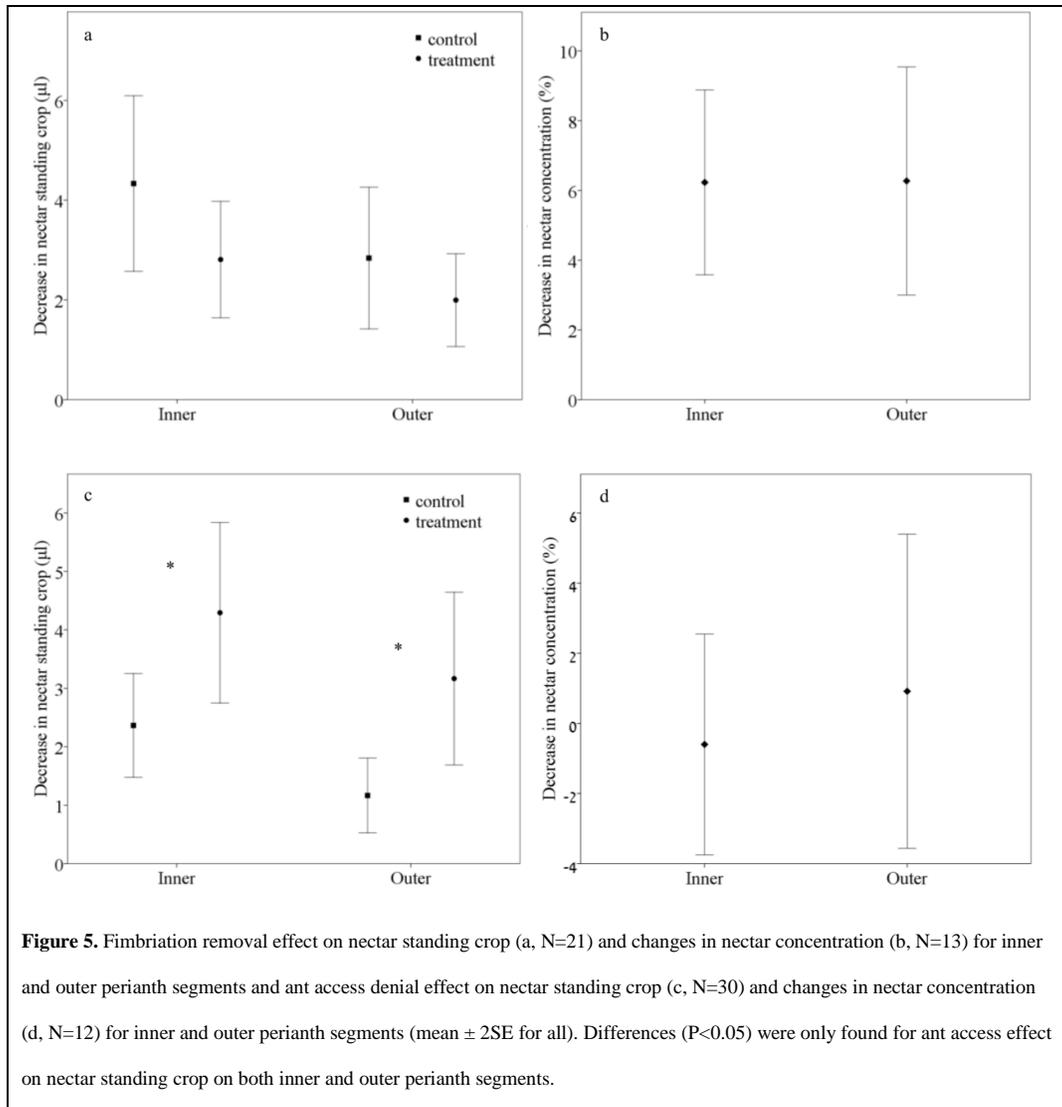
Keidar	Ma'on	Tel Arad	Family
Tapinoma simrothi phoeniceum Emery, 1925	*Tapinoma simrothi phoeniceum* Emery, 1925		*Dolichoderinae*
Lepisiota opaciventris (Finzi, 1936)			*Formicinae*
	Lepisiota bipartita (Smith, F., 1861)	*Lepisiota bipartita* (Smith F., 1861)	*Formicinae*
		Camponotus May, 1861	*Formicinae*
Monomorium sahlbergi Emery, 1898			*Myrmicinae*
		Monomorium dentigerum (Roger, 1862)	*Myrmicinae*
		Monomorium pallidum Donisthorpe, 1918	*Myrmicinae*
Cardiocondyla mauritanica Forel, 1890			*Myrmicinae*
		Cardiocondyla emeryi Forel, 1881	*Myrmicinae*
		Cardiocondyla elegans Emery, 1869	*Myrmicinae*

Floral groups with no entries to either treated or control flowers were removed from
analysis. One sample *t*-test for an uneven ant entry preference to inner perianth
segments showed that while ant entries to inner segments were low in control flowers
($32.54\%, t_{(42)} = -3.14, P = 0.003$), treated flowers showed higher entries to inner
segments ($72.96\%, t_{(42)} = 7.241, P < 0.001$) (Figure 4). Paired *t*-tests for changes
in ant preference in the different groups suggest a significant change ($t_{(42)} = -7.11, P < 0.001$).

Figure 4. Mean percent of ant entries to inner perianth segment from total entries for treated and control flowers in *C. tuviae* ± 2SE (N=43). Ant entries are shown to change from a preference to outer perianth segments in control to inner perianth segments in treated flowers where fimbriated appendages were removed.

Fimbriation removal and the effect of ant entries on nectar

Paired sample *t*-tests for removal of fimbriation did not show a significant difference in nectar standing crop for *C. ritchii* in either inner ($t_{(20)} = 1.49, P = 0.152$) or outer ($t_{(20)} = 1.085, P = 0.291$) perianth segments (Fig. 5a). Similar tests performed on nectar concentration for pairs where both samples exceeded ~0.15 µl showed a decrease in nectar concentration for both inner ($t_{(12)} = 4.699, P = 0.001$) and outer ($t_{(10)} = 3.836, P = 0.003$) perianth segments, although independent *t*-tests showed no difference between inner and outer perianth segments for these decreases ($t_{(22)} = -0.20, P = 0.984$) (Fig. 5b).

Figure 5. Fimbriation removal effect on nectar standing crop (a, N=21) and changes in nectar concentration (b, N=13) for inner and outer perianth segments and ant access denial effect on nectar standing crop (c, N=30) and changes in nectar concentration (d, N=12) for inner and outer perianth segments (mean ± 2SE for all). Differences (P<0.05) were only found for ant access effect on nectar standing crop on both inner and outer perianth segments.

Paired sample *t*-tests for ant access effect on nectar standing crop showed a decrease in manipulated *C. ritchii* flowers in both inner ($t_{(29)} = 2.64, P = 0.014$) and outer ($t_{(29)} = 3.097, P = 0.004$) perianth segments (Fig. 5c). Similar tests performed on the change in nectar concentration for pairs, where both samples exceeded 1/6µl, showed no effect of the manipulation on nectar concentration for both inner ($t_{(19)} = -0.381, P = 0.707$) and outer ($t_{(11)} = 0.409, P = 0.690$) .

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Discussion

Colchicum species show typical autumn flower traits (Shmida & Dafni 1989) – they flower close to the ground surface and provide easy access to nectar and pollen for unspecialized pollinators. These features facilitate nectar theft by land-dwelling animals, especially ants (Herrera, Herrera & Espadaler 1984). Ants are rarely regarded as effective pollinators (Willmer 2011: 299) and have been shown to damage floral structure (Irwin et al. 2010), reduce pollen viability (Beattie et al. 1984, Galen & Butchart 2003), deter pollinators (Ness 2006), and inhibit pollination by reducing available nectar rewards (Irwin et al. 2010, Irwin 2003).

Floral physical traits of the group studied here show different trends within and between species. Species with larger displays (e.g., *C. ritchii*) seem to have more rewards than species with smaller displays (e.g. *C. "ramonensis"*).

The unique floral organs of this group of species that are all native to desert and semi-desert habitats, along with the observation of unexpected ant nectar foraging, led us to suspect that there might be an adaptive role to these organs.

Several different strategies of nectar robbery reduction without deterring pollinators were documented across flowering plants (Irwin, Adler &Brody 2004) and were connected to high investment in nectar (Ballantyne &Willmer 2012).One of these strategies is the development of mechanical restrictions on nectar access that were shown to decrease nectar theft by opportunistic ants for different species in different habitats (Herrera, Herrera & Espadaler 1984, Wootton & Sun 1990, Junker et al. 2011) and were suggested in Israeli desert plants (Eisikowitch 1986) for *Calotropis procera*. Similar suggestions regarding ant access prevention were made for inner floral hairs in *Stephanotis* (Willmer 2011: 547).

The quantitative morphological differences between inner and outer perianth segments in *Colchicum* allowed us to manipulate and examine the effects of these organs. We managed to establish the negative effect they have on ant access to nectaries in *C. tuviae*. We further established the negative effect ant access has on nectar standing crop for *C. ritchii*. While we found that fimbriation removal for *C. ritchii* does not affect nectar standing crop, this procedure does lower nectar concentration in both inner and outer perianth segments. This finding could result from fluid secretion from the dissected areas complemented by a reduction in nectar production. However, since these findings were shown to affect the concentration in inner and outer perianth segments equally, we do not expect this change to alter ant preferences between perianth segments.

Our findings suggest that the evolution of nectarial appendages confers an adaptive advantage by creating a *"thicket"* surrounding the nectary. This added layer protects the flower's nectar storage from consumption by ants, whose mandibles are not suitable for nectar extraction through the thicket. Insects with a long proboscis, on the other hand, are able to penetrate and consume the nectar. Increased nectar reward in flowers where ant entrance was denied stresses the advantages in terms of the relationship between the fimbriated *Colchicum* species and their pollinators.

Ant-foraging pressure on nectar in desert and semi-desert habitats is predicted to be higher for nectar consuming ants as a result of water scarcity (Whitford, Kay & Schumacher 1975); at the same time harsh conditions are expected to enhance the importance of nectar reward to pollinators (Eisikowitch, Ivri & Dafni 1986). This problem culminates in the autumn and early winter when the low food reserves are almost depleted. In light of the impoverished autumn-pollinating market (Shmida & Dafni 1989) it is not likely that nectar theft would cause pollinators to avoid

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Colchicum flowers (Cohen & Shmida 1993) due to limited alternatives. However, a long-term decrease in nectar reward by ants could reduce pollinator resources which would then reduce "legitimate" pollinator visits in *Colchicum*. Under these conditions, the evolutionary pressure on these species could explain why fimbriation has evolved in species native to these regions.

Not all desert *Colchicum* species have developed this strategy (e.g., *C. tunicatum*). While a few other species of the genus have some level of fimbriated appendages (all of a smaller size than the species described above), only one (*C. sanguicolle*), which was recently described (Persson 1999), is not found in a desert or semi-desert habitat. Ant pollination has been proposed in this group due to the sheer numbers of ant visits as well as the harsh abiotic environment leading to low specialized pollinating systems (Gomez et al. 1996). In our view, this is improbable. Floral structure – comprising three stamens usually protruding from the perianth surface – allows for low chances of contact between visiting ants and female reproductive organs owing to ant size.

While justification for the evolution of ant repellence was formerly connected to high investment in nectar (Ballantyne &Willmer 2012), here we found that nectar theft is prevented in flowers with low nectar rewards. It is likely that plant investment should be a relative measure with regards to the plant environment and pollinating regime. According to our findings, it is advantageous to have densely fimbriated appendages since they protect the nectar reward. This finding would presumably predict maximum fimbriation on all perianth segments. Why differentiate between whorls? Variability in fimbriation levels could be explained with a typical bimodal strategy (Manning & Goldblatt 2005). While large nectarial appendages would allow insects with a long proboscis (e.g., butterflies and large bees) to obtain nectar from the inner

perianth segments, pollinating insects with a shorter proboscis (e.g., flies and smaller bees) would be prevented from visiting these nectaries. The gain of pollinators with a short proboscis by allocating fewer fimbriated lamellae in the outer whorl segments is accompanied by an increased chance of nectar theft.

Nectar standing crops have been determined in several other *Colchicum* species that do not have nectarial appendages (e.g., *C. tunicatum*, *C. hierosolymitanum*, and *C. stevenii*). Nectaries from inner and outer whorls provided similar rewards in these species (Dafni A & Shmida A unpublished data, Shmida A unpublished data, Keshet 1997). The uneven nectar-partitioning in our desert species stresses the uniqueness of the phenomenon. This situation would decrease the groups' potential pollinator pool and could affect its reproductive success. Possibly, the vulnerability of the outer whorl would select for smaller floral investment in it, which again helps to explain lower nectar production for outer perianth segments.

It was shown that the possible adaptive goal of the fimbriated appendages is an ant anti-theft deterrent, which is highly important in *Colchicum* which grows close to the ground, and distributes in semi-deserts where ant communities are very active in autumn.

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