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Extrafloral nectaries in cacti

Many plants produce nectar that encourages bees, humming-birds, and other animals to visit the flowers, then carry pollen from flower to flower as they search for more nectar. This pollination is more effective if the animals rummage around within the flower, and in fact floral nectaries are often located deep inside flowers. During nectar-based pollination, both partners benefit: Animals obtain food while plants obtain the transport of their pollen. Therefore, this relationship is a mutualism.

A second type of mutualism involves **extrafloral nectaries** (abbreviated **EFNs** here), glands that produce sugary water but which are located on some part of the plant other than within a flower. You may have already noticed small yellow, orange or red glands on plants of *Ferocactus* and *Coryphantha* (Fig. 1). Several studies indicate that EFNs provide plants with various benefits. For example, they encourage ants and other insects to not only visit a plant but also to patrol it, clean it, and even protect it from various harmful organisms ranging from fungi to insects (Chamberlain and Holland, 2008; Ness, 2006; Ruffner and Clark, 1986). Ants attracted by EFNs may increase soil nutrients near the cactus because the ants may nest near the plant and thus bring nutrients to it as they bring food back from foraging expeditions; and another possibility is that the presence of ants attracted by EFNs indirectly increases genetic diversity because only flying pollinators can visit the flowers of cacti guarded by ant colonies. Very little is known about EFNs in cacti, and our objectives here are to review some of the published details, add a few points, and encourage further study.

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1. An ant visiting four extrafloral nectaries on *Ferocactus emoryi*. No droplets of nectar are visible because ants harvest them as quickly as the glands secrete them. Ordinary non-secretory spines are at the bottom of the image, and an aborted flower bud is at the top.

2. Each areole at this shoot apex of *Cylindropuntia cholla* has numerous EFNs but few have emerged above the abundant areole hairs; each ring of hairs surrounds an EFN. Several green leaves are present, as well as long ordinary spines.

Genus	species	Genus	species
Coryphantha	*clavata*	*Ferocactus*	all species?[1]
Coryphantha	*echinoidea*	*Sclerocactus*	*erectocentrus*
Coryphantha	*erecta*	*Sclerocactus*	*glaucus*
Coryphantha	*georgii*	*Sclerocactus*	*papyracanthus*
Coryphantha	*glanduligera*	*Sclerocactus*	*scheeri*
Coryphantha	*glassii*	*Sclerocactus*	*uncinatus*
Coryphantha	*jalapensis*	*Sclerocactus*	*unguispinus*
Coryphantha	*maiz-tablasensis*	*Sclerocactus*	*whipplei*
Coryphantha	*nickelsiae*	*Stenocactus*	*coptonogonus*
Coryphantha	*octacantha*	*Stenocereus*	*thurberi*
Coryphantha	*ottonis*	*Thelocactus*	*bicolor*
Coryphantha	*poselgeriana*	*Thelocactus*	*bicolor* subsp. *heterochromus*
Coryphantha	*potosiana*	*Thelocactus*	*conothelos*
Coryphantha	*pseudoechinus*	*Thelocactus*	*hastifer*
Coryphantha	*pseudonickelsieae*	*Thelocactus*	*hexaedrophorus*
Coryphantha	*pulleineana*	*Thelocactus*	*lauseri*
Coryphantha	*robustispina*	*Thelocactus*	*leucanthus*
Coryphantha	*vaupeliana*	*Thelocactus*	*macdowellii*
Coryphantha	*vogtherriana*	*Thelocactus*	*rinconensis*
Coryphantha	*wohlschlageri*	*Thelocactus*	*setispinus*
		Thelocactus	*tulensis*

[1] *The New Cactus Lexicon* describes secretory glands in the genus treatment of *Ferocactus* but not in the treatment of individual species of *Ferocactus*.

**Table 1.** Extrafloral nectaries mentioned in *The New Cactus Lexicon* (Hunt, 2006).

The first point is that cacti have at least four morphologically different types of glands that all qualify as extrafloral nectaries:

1. Highly modified spines that are short, broad and blunt. These occur in several closely-related genera (*Coryphantha*, *Echinocactus*, *Ferocactus*, *Sclerocactus*, *Thelocactus*; Table 1) as well as several opuntioids, *Cylindropuntia cholla* and *C. imbricata,* that are not closely related to the *Coryphantha/Ferocactus* group (Figs. 1, 2).

2. Nectaries that resemble ordinary spines and which have no readily apparent modifications. Examples occur in *Brasiliopuntia brasiliensis*, *Calymmanthium substerile*, *Harrisia pomanensis*, *Opuntia pycnantha*, *Pereskiopsis*, and *Quiabentia* (Fig. 3).

3. The small foliage leaves that occur just below an areole. *Acanthocereus tetragonus*, *Leptocereus paniculatus*, *L. weingartianus*, *Myrtillocactus geometrizans*, *Pachycereus schottii*, *Stenocereus thurberi* and others (Figs. 4, 5). In many cacti, the foliage leaves of flowering branches are large and scale like (Mauseth, 2016), and in several species, nectar is secreted from a region on their underside (the outward facing side) just below the leaf tip.

4. Regions of epidermis and cortex just below an areole. These are known from only *Armatocereus procerus*, *A. rauhii*, *Leptocereus weingartianus*, and
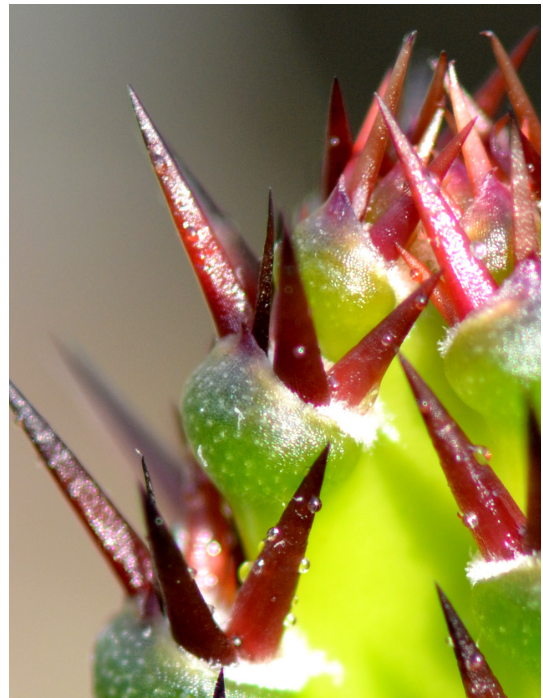
3. Each young, growing spine at the shoot tip of this *Harrisia pomanensis* is exuding several tiny drops of sticky liquid, presumably nectar.

Pachycereus (*Lophocereus*) *gatesii* and *P. (L.) schottii* (Figs. 5, 6).

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4. Although typically called a flower, this is actually a flowering branch covered in leaves and areoles (the true flower parts are inside). A drop of nectar has been secreted from tissue at the base of most leaves. *Leptocereus weingartianus*.

6. The drop of nectar on this *Pachycereus (Lophocereus) schottii* was produced about 1 mm below the edge of the areole, so it is unlikely that it was secreted by a foliage leaf (we would expect the foliage leaf to be hidden among the areole hairs).

5. Several drops of nectar are present on vegetative shoots of this *Leptocereus weingartianus* (the same plant as Fig. 4). One drop (liquid, at center of image) is at the very base of an areole as if secreted by a tiny foliage leaf. A second drop (crystallized, just below of image center) is separated from any areole as if secreted by stem tissue. The branch was growing horizontally, so it is unlikely that drops of nectar had dripped away from whatever gland had produced them.

7. Areoles on flowering branches of *Acanthocereus tetragonus* secrete nectar, but areoles on vegetative branches do not (at least not that we have noticed).

In cacti, the location of EFNs is also important because of a peculiarity of cactus flowers. The true flowers of all cacti (except for a few species of *Pereskia*), are embedded completely within a flowering branch; that is the reason so many cactus "flowers" have spines, glochids and leaves on their outer surface (Mauseth, 2016). Various terms have been used to refer to the branch tissues, the two most common being "pericarpel" and "floral tube." Here we use the term "flowering branch." We mention this because many cactus EFNs seem to occur only on flowering branches whereas others occur only on vegetative shoots (the main body) of the plant. For example, many species of *Coryphantha* and *Ferocactus* have EFNs on the tubercles of their vegetative shoots but have none on their flowering branches. In contrast, we have seen EFNs on the flowering branches of *Acanthocereus tetragonus* but not on their vegetative shoots (Fig. 7).

Extrafloral nectaries were mentioned in 1894 by the great cactus biologist W. F. Ganong, and other early observations were made by F. E. Lloyd and C. S. Ridgway (1912), W. Weingart (1924, 1932) and W. Leinfellner (1937). In 1930, E. Daumann expressed the hypothesis that the bottle-shaped EFNs in *Opuntia monacantha* were modified glochids. A wonderfully detailed review of cactus morphology by Franz Buxbaum (1950) summarized earlier work on EFNs but added no new details. Norman Boke studied the EFNs of *Toumeya* (now *Sclerocactus*) *papyracantha* (1957), *Coryphantha clava* and *C. erecta* (now *C. octacantha*) (1961). James Mauseth (1982) investigated those of *Ancistrocactus* (now *Sclerocactus) scheeri*. The beautifully illustrated and encyclopedic *The New Cactus Lexicon* (Hunt, 2006) mentions every species in the tribe Cacteae known to have large EFNs that are modified spines. We used *The New Cactus Lexicon* as the source material for preparing Table 1 (we also follow the scientific names presented in *The New Cactus Lexicon*). Several recent studies have focused on the ecology of EFNs, investigating the species of ants that are attracted to the cacti, the benefits the cacti obtain, and the seasonality of secretion (Alma et al., 2015; Chamberlain and Holland, 2008; Holland, Chamberlain and Horn, 2010; Ness, 2006; Pickett and Clark, 1979; Ruffner and Clark, 1986).

Below, we describe the various types of cactus EFNs known to us based on published reports and on our own casual observations. In Table 2, we list cacti with EFNs that we three authors have observed personally but which seem to have never been studied or reported.

Genus	species
Acanthocereus	*quadricostatus*
Armatocereus	*matucanensis*
Armatocereus	*procerus*
Armatocereus	*rauhi*
Brasiliopuntia	*brasiliensis*
Calymmanthium	*substerile*
Cylindropuntia	*cholla*
Cylindropuntia	*imbricata*
Echinocactus	*grusonii*
Harrisia	*martinii*
Harrisia	*pomanensis*
Hylocereus	*escuintlensis*
Hylocereus	*undatus*
Leptocereus	*paniculatus*
Leptocereus	*weingartianus*
Myrtillocactus	*geometrizans*
Neobuxbaumia	*euphorbioides*
Neoraimondia	*arequipensis*
Opuntia	*monacantha*
Opuntia	*pycnantha*
Pachycereus (*Lophocereus*)	*gatesii*
Pachycereus (*Lophocereus*)	*schottii*
Peniocereus	*fosterianus*
Pereskiopsis	sp.
Pilosocereus	*arrabidae*
Pilosocereus	*gounellei*
Quiabentia	sp.
Stenocereus (*Rathbunia*)	*alamosensis*
Stenocereus	*gummosus*
Stenocereus	*thurberi*
Stenocereus	*littoralis*
Tephrocactus	*articulatus* (*strobilformis*)

Table 2. Taxa other than those mentioned in *The New Cactus Lexicon*.

EFNs that are short, blunt, obviously modified spines.

Cactus spines typically are needle-like and consist of numerous elongate, slender fiber cells with extremely thick walls and with no obvious intercellular spaces and no vascular tissues; the mass of fibers is covered by an epidermis that lacks stomata (Boke, 1944; Buxbaum, 1950; Mauseth, 1977; Schill, Barthlott, and Ehler, 1973). The location, shape and internal structure of EFNs of *Coryphantha*, *Ferocactus* and their relatives (Table 1) are similar to those of spines, except that the EFNs are short and blunt (Figs. 1, 8, 9, 10). These EFNs are up to 1.3 mm in diameter and 1-4.0 mm long. The glands of *Ferocactus* resemble short, stubby, blunt spines, having parallel sides for most of their length. At least in *F. glaucescens* and *F. emoryi* var.

8. This plant of *Ferocactus peninsulae* is aberrant, producing many more glandular spines than is typical, and it also produces them all around the non-glandular spines, rather than only in the area between the non-glandular spines and the flower bud.

9. Enlarged view of several areoles in Fig. 8. Tiny drops of nectar emerge from the very center of the top of each gland.

10. Scanning electron micrograph of a secretory spine in *Ferocactus emoryi* var. *rectispinus*. The epidermis has neither stomata nor trichomes, and it has broken open at the top, revealing that the interior is composed of long, slender fiber-like cells. We do not know if the epidermis broke open due to the pressure of accumulating nectar or if ants chewed it away. The epidermis is still intact on a younger gland in the background.

11. "Distal" and "proximal" are important terms, and they refer to the distance of something from the site where the root and shoot meet. Imagine drawing a line up the rib of this *Thelocactus schwarzii*. The pen would first touch the spine at the bottom of the areole: That spine is proximal to all other parts of the areole. As the line continues up, it would leave the areole through the farthest white hairs: Those hairs are distal to the rest of the areole. Later, a flower bud will emerge from the distal portion of the areole. The EFNs in Fig. 1 are distal to the ordinary spines, proximal to the flower bud.

rectispinus the glands are elevated on a short (0.1 mm long) base of shoot tissue that produces an abundance of trichomes. Glands of *Coryphantha* and *Sclerocactus* are similar but seem to have a more slender base and a broader secretory apex; they were described as being capitate by Boke (1957) and Zimmerman (1985).

Boke's micrographs of *Toumeya* (now *Sclerocactus*) *papyracantha* (1957), *Coryphantha clava*, and *C. erecta* (1961) show each EFN as having a broad secretory head supported by a more slender stalk. Secretory cells are small and densely cytoplasmic whereas stalk cells are elongate and vacuolate. The stalk has hairs on its surface and is vascularized, but the secretory head lacks stomata, hairs and vascular tissues. Consequently, the secretory head strongly resembles a spine whereas the stalk appears to be an upward growth of shoot tissue. The tissue structure of EFNs in *S. scheeri* also

resembles that of immature spines, consisting only of an epidermis overlying a mass of fiber-like cells (Mauseth, 1982). The epidermis lacks stomata and hairs. The interior consists of slightly elongate cells with somewhat thickened walls and noticeable intercellular spaces. The stalk of EFNs in *S. scheeri* contains vascular bundles.

Coryphantha, *Ferocactus*, and their relatives are unusual cacti in that as the tissues underlying their areoles enlarge into tubercles or ribs, the axillary buds and areoles also elongate rather than remaining circular or oval as is typical of most cacti (Figs. 1, 2, 11; Boke, 1952). Furthermore, the elongate axillary bud is located in a groove on the upper surface of the tubercle; the bud extends from the tip of the tubercle to about half way to its base. All spines are located near the tip of the tubercle (developmentally, at the proximal end of the elongate areole), and the meristematic tissue that will produce any flower or vegetative branch is located at the other, distal end of the groove closer to the shoot axis. EFNs are located in the groove between the two extreme ends, none are located among the ordinary non-secretory spines. Boke (1957) reported that EFNs can encircle the dormant shoot meristem in *Sclerocactus* (*Toumeya*) *papyracanthus* (similar to the unusual *Ferocactus peninsulae* in Fig. 9). In *S.* (*Ancistrocactus*) *scheeri*, numerous nectary primordia occur in the groove where they are hidden below numerous trichomes that also fill the groove (Mauseth, 1982). Periodically a primordium is stimulated to become active and enlarge, its tip emerges out of the groove, and the gland becomes easy to observe. After secreting, the gland collapses and its remnants are hidden within the tubercle groove. Consequently, if a plant is examined at a time when no EFN is secreting, it will appear as if the plant lacks EFNs. Boke pointed out that EFNs of *S. papyracanthus* would not be visible on either dried herbarium specimens or on plants collected during drought. To be certain whether a species has or does not have EFNs, it is necessary to carefully dissect areoles from a plant several years old, then examine the tissues with a dissecting microscope.

Areoles of *Ferocactus* are oval, and the large non-secretory spines emerge from the proximal side (Fig. 1). The distal end of the oval areole usually contains either a dormant bud or the circular abscission scar of a flowering branch. EFNs seem to only occur close to the spines, on the distal side of them (the side nearer the bud or scar). EFNs seem to never be mixed among the ordinary spines, nor to be on the proximal side of them (between the spines and the small

12. Each of these two areoles of *Echinocactus grusonii* has a yellow EFN.

foliage leaf; personal observation, with the exception of the plant in Fig. 9). In *Ferocactus*, EFNs are most readily apparent in areoles near the top of the vegetative shoot, near the region where flowering branches are present. However, prominent, healthy EFNs are sometimes present on much older areoles; it seems likely that *Ferocactus* axillary buds may produce many EFN primordia, at least some of which remain dormant for years before becoming active. At least in *F. glaucescens*, more distal EFN primordia (those closer to the flower bud) develop first whereas more proximal ones (those closest to ordinary spines) develop later. On several species of *Ferocactus* cultivated in a garden in Austin, EFNs become active weeks before flower buds are visible.

As far as we know, EFNs do not occur on flowering branches of any *Coryphantha*, *Echinocactus*, *Ferocactus*, *Sclerocactus* or *Thelocactus*.

Although several reports state that EFNs do not occur in the areoles of *Echinocactus*, one of us (JDM) has observed broad, short, blunt yellow spines that resemble EFNs in many large (28 cm diameter) cultivated plants of *E. grusonii* (cultivated at The Desert Botanical Garden, Phoenix; The Huntington Botanical Gardens, San Marino; and The University of Texas, Austin; Fig. 12). We have not seen them on younger, smaller plants. We have not known of these long enough to observe whether they actually secrete nectar.

In *Cylindropuntia cholla* and *C. imbricata*, EFNs are short (about 2.0 mm), wide (1.0 mm) blunt modified spines that occur distal to the ordinary non-secretory
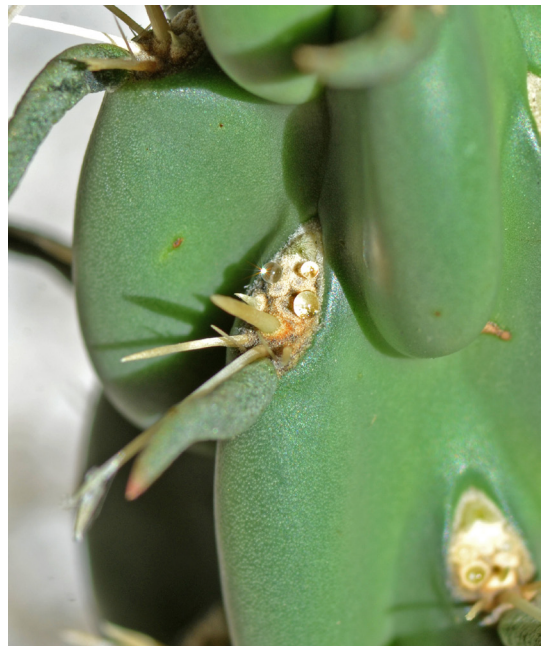
13. Three EFNs are secreting simultaneously in this areole on a vegetative branch of *Cylindropuntia imbricata;* several immature EFNs have not enlarged enough to be visible.

spines, similar to the position of EFNs in *Ferocactus* (Figs. 2, 13). Despite their similarity in appearance and position, the EFNs of *C. cholla* and *C. imbricata* and those of *Ferocactus* must have originated independently of each other because these two genera are so distantly related; these EFNs are not homologous

14. Nectar on areoles of *Tephrocactus articulatus*.

15. Multiple large drops of nectar on every areole of young branches of *Calymmanthium substerile*.

16. This areole of *Calymmanthium substerile* has at least 6 lumps of crystallized nectar. The bumpy surface of each lump results from a spine secreting fresh nectar after old nectar had crystallized.

to each other but rather are the product of convergent evolution. The EFNs of *C. cholla* and *C. imbricata* occur in areoles on both the flowering and vegetative branches. On a large plant of *C. imbricata* cultivated outdoors in Austin by Jeff Pavlat, no EFNs were visible anywhere as the plant produced flower buds. But once many of the flowers had opened and numerous vegetative branches began to grow, EFNs became easily visible in many areoles on the flowering branches and in all areoles of the vegetative branches except for the basal-most first four or five areoles. Most areoles on the vegetative branches had at least one EFN visible and secreting, several had 2 or 3 EFNs active simultaneously within individual areoles. Consequently, this plant had hundreds of EFNs present in the two or three week long period when many of its flowers were open; but the great majority of the EFNs were located on new, growing vegetative branches that would not produce flowers until the following year. No EFNs were noticed on old, persistent fruits or on vegetative shoots more than one year old. *Cylindropuntia imbricata* is a widespread species and is common in cultivation; it would be easy for someone to study these EFNs and their mutualism with ants.

Another species of Opuntioideae, *Tephrocactus articulatus* (also known as *T. strobiliformis*), was observed with large drops of nectar on its areoles, but

17. This areole of *Calymmanthium substerile* had large lumps of crystallized sugar on it, but they were washed away, and the areole observed. These new secretions formed about one day later.

the plant was not available for study (Fig. 14).

Extrafloral nectaries that resemble ordinary spines.

In several cacti, young spines in areoles located at the growing shoot tip will have tiny drops of liquid here and there on their surface (Fig. 3). The liquid is sticky when touched, so it probably is sugary water – nectar. In our experience, these droplets are so small and sparse that one must look for them carefully. In nature, the nectar probably does not accumulate because it is washed away by rain or dew or is collected by ants. In general, nectar is rarely visible on the EFNs of any cacti if ants have access to the plants: ants harvest the nectar too rapidly for it to form a large drop.

The most vigorous, productive EFNs of this type that we know of occur in *Calymmanthium substerile*. On plants cultivated in a greenhouse at UT Austin, large drops of nectar accumulate. As water evaporates, the sugar crystallizes into lumps that encase the secreting spine (Figs. 15, 16). The sugar can be washed away easily with water to reveal a single small spine located within each lump. Each secretory spine must be active for many days, because periodically a dry lump of sugar will have a fresh droplet or two of nectar on its surface. One young shoot had 27 mature areoles, all of which had active EFNs, and on average,

18. Flowering branches of *Calymmanthium substerile* have EFNs that appear similar to those on the vegetative branches.

19. Lumps of crystallized sugar on EFNs of *Brasiliopuntia brasiliensis,* cultivated in a greenhouse in Austin.

there were 5.3 secretory spines per areole (personal observations). All sugar was washed off this branch, and within one week, several spines had fresh, new droplets of nectar even though the shoot had been detached from the plant and kept in a laboratory (Fig. 17). Secretory spines were located on the periphery of the spine cluster, not mixed among the larger, thicker non-secretory spines. EFNs occur on the flowering branches of *C. substerile* as well as the vegetative shoots (Fig. 18).

The accumulated nectar on protected plants of *C. substerile* is strikingly obvious, but none is readily visible on plants that have been watered from overhead or that were cultivated outdoors where they were exposed to rain and ants. During observations of *C. substerile* in habitat on March 6, 1997 in Balsas, Peru by Dr. Carlos Ostolaza and JDM, extrafloral nectar was not noticed, nor is it apparent in photographs taken at that time. Considering that the secretory spines of *C. substerile* look just like ordinary spines and that nectar does not accumulate enough to be readily visible under normal conditions, it seems possible that many other cacti may have this type of EFN. Young spines on growing shoot tips of *Harrisia martini* and *H. pomanensis* (Fig. 3) also exude droplets of nectar (personal observation), and Boke (1961) reported secretion by ordinary-looking spines in *Quiabentia* and *Pereskiopsis*. Just recently, we discovered spine-like EFNs on plants of *Brasiliopuntia brasiliensis* cultivated

20. These EFNs of *Brasiliopuntia brasiliensis* cultivated in Rio de Janeiro are not hidden by crystallized sugar: They are spines with a more or less ordinary appearance.

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21. Drops of nectar at the bases of leaves of a young vegetative bud of *Hylocereus undatus*.

22. Nectar is present on the lower edge of each areole of this growing shoot of a cultivated plant of *Armatocereus rauhii*. Lower areoles on the previous year's growth have brown areas where nectar had been.

in The Rio de Janeiro Botanical Garden, then subsequently noticed them on a plant at UT Austin (Figs. 19, 20). Also, areoles on pads of *Opuntia pycnantha* in Baja California Sur had small white spines with nectar drops that were being collected by ants. None of these species has been studied yet, but *B. brasiliensis* can be obtained and cultivated easily. *Calymmanthium substerile* is less easily obtained, and it requires considerable greenhouse space, but its EFNs are very active and should be good candidates for research.

Foliage leaves as extrafloral nectaries.

All cacti still produce foliage leaves (Mauseth, 2007). Cactus spines are the modified bud scales of the bud located in the axil (the region immediately above a leaf) of each foliage leaf. In most species, the foliage leaf stops developing while still extremely tiny — often while still microscopic — and consequently they are almost never noticed. Cactus foliage leaves are easily visible in *Pereskia*, *Maihuenia* and all

opuntioids. In almost all cacti, foliage leaves on flowering branches are much larger and more easily visible than those on vegetative shoots (Mauseth, 2016).

A well-documented case of secretion by foliage leaves of flowering branches occurs in *Pachycereus* (*Lophocereus*) *schottii* (Chamberlain and Holland, 2008; Holland, Chamberlain, and Horn, 2010). We have also observed secretions by flowering branch leaves in *Acanthocereus tetragonus* (Fig. 7), *Leptocereus paniculatus* and *L. weingartianus* (Fig. 4). Flowering branches of *Neoraimondia arequipensis* also bear EFNs (personal communication from Sydney Novoa). Foliage leaves with secreted drops of nectar also occur on vegetative shoots of *Hylocereus undatus* (Fig. 21) and *Leptocereus weingartianus* (Fig. 5). The anatomy of these secretory leaves has not yet been studied.

23. Close view of crystallized nectar on *Armatocereus rauhii*. Each areole has nectar touching the proximal side of the areole as if secretion is due to the foliage leaf, but several small droplets are independent, as if secreted by stem tissue instead.

24. Fresh, uncrystallized nectar near areoles of *Armatocereus rauhii*. One large drop touches the areole but others appear independent. Notice the purple coloration proximal to the areole proper.

25. This shoot tip of *Armatocereus rauhii* is secreting nectar from all young areoles. Because the ribs are nearly horizontal at this stage of development, drops are unlikely to have dripped or rolled away from the point at which they were secreted. Each areole here is definitely secreting from several points within a region just proximal to each areole; the foliage leaf of each areole could also be secretory.

26. This is one of the older areoles of *Armatocereus rauhii* in Fig. 23. The nectar was washed off, then later new secretion began from two sites just outside the tan-colored area.

Regions of epidermis and cortex proximal to an areole.

We know of no reports about these, and we have not examined them in detail ourselves. We have seen these EFNs on just a few plants. In plants of *Armatocereus procerus* and *A. rauhii* cultivated in a greenhouse in Austin, nectar accumulates just below the foliage leaf of the areole (Figs. 22, 23). It may be that the foliage leaf itself is the nectary, and some nectar simply runs downward over the shoot surface. But a small patch of tissue just below the leaf differs from surrounding shoot tissue by being slightly raised and having a darker color. Each patch is about 0.5 mm wide and 2.0 mm long. Occasionally very tiny droplets are visible on this patch and are not in contact with the foliage leaf of the areole (Figs. 24, 25). The nectar was intentionally washed off all areoles of one rib of a plant of *A. rauhii*, and after one month of observation, new nectar was produced by those EFNs (Fig. 26).

27. Bump-shaped EFN just proximal to areole of *Pachycereus schottii*, similar to the one in Fig. 6 but with no nectar present when photographed.
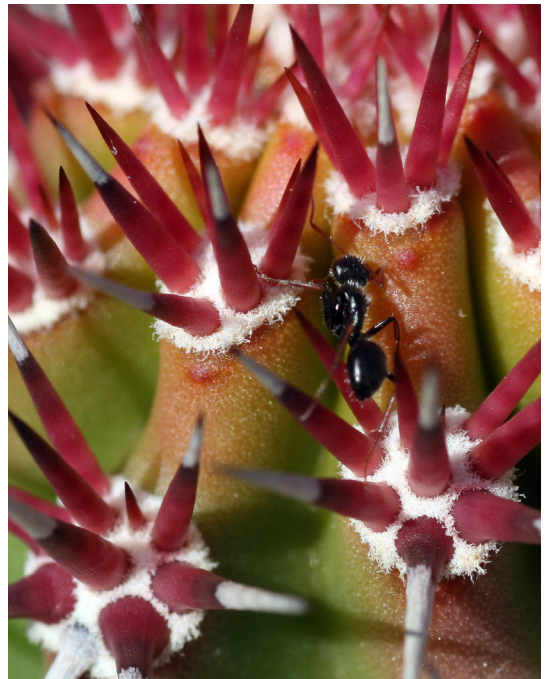
28. Bump-shaped EFNs on *Pachycereus gatesii*.

29. Areoles with small, inconspicuous EFNs in *Pilosocereus arrabidae*.

30. Ants visiting EFN on the flowering branches of *Pilosocereus gounellei* before the flower opens. There are no ants on the nearby developing fruits.

Similar areas are present on the young shoot tips of *Pachycereus* (*Lophocereus*) *schottii* and *Pachycereus* (*Lophocereus*) *gatesii* growing in habitat in Baja California, and also in cultivated plants at The Desert Botanical Garden in Phoenix. The regions in *P. schottii* and *P. gatesii* each have a tiny but pronounced "bump" (Figs. 6, 27, 28) somewhat like the chin of a *Gymnocalycium*. The bump resembles a residual, partly developed foliage leaf, but it seems to be located too far (about 1.0 mm) from the areole to be a leaf, and we have not had the chance to dissect an areole to examine it more closely.

We offer several suggestions for further study:

1. More accurate and extensive knowledge of which taxa actually have EFNs. So many of the species mentioned here have few or no obvious morphological characters to distinguish them from ordinary non-secretory spines or non-secretory foliage leaves (Figs. 29, 30, 31). It is necessary to check plants carefully, and best to examine ant-free plants that have been protected from rain or overhead watering

(however, the presence of ants patrolling a cactus while ignoring other plants is an excellent clue that EFNs may be present).

Even in taxa with easily recognizable EFNs, such as *Coryphantha* and *Thelocactus*, EFNs may not be visible if examined in a season when they are inactive or have deteriorated, thus many of these taxa – even well-known, familiar taxa – should be re-examined carefully. *Echinocactus grusonii* is a good example: Their EFNs are large and easily recognizable if one searches for them on an old plant, but they are otherwise easily overlooked.

2. The anatomy and morphology of EFNs. Many details are still unknown about even the most obvious, most highly modified glands in *Coryphantha*, *Ferocactus* and others. The presence, structure, and especially the function of secretory foliage leaves in cacti, particularly in subfamilies Cactoideae and Opuntioideae, are almost completely unexplored. The fact that some foliage leaves secrete extrafloral nectar opens the possibility that foliage leaves in cacti may play much more significant roles than previously realized.

31. The presence of ants on this flowering branch of *Stenocereus gummosus* is the only clue in this photograph that EFNs are present. It is rare for nectar to accumulate on the surface of plants growing outdoors.

The presence of droplets on young spines of growing shoots indicates that some spines may have a complex structure rather than being just a hard mass of dead fibers.

3. The timing, amount and location of secretion. Except for one or two species, we know almost nothing about the timing of secretion: time of day; time of year; relation to period of flowering or vegetative growth; duration of secretion from each gland; duration of secretion from all glands. We do not know the amount of secretion per gland or per plant; the location of the secretion (flowering branches; vegetative shoots; only young areoles of vegetative shoots or older areoles also). Attention should be given to both the amount of water and of sugar secreted. In desert habitats, water itself could be a powerful reward to insects, and the EFNs of leaves on flowering branches resemble hydathodes (water-secreting glands present on leaves in many plant families). Holland, Chamberlain and Horn (2010) provide a good introduction to these concepts in *Pachycereus schottii*.
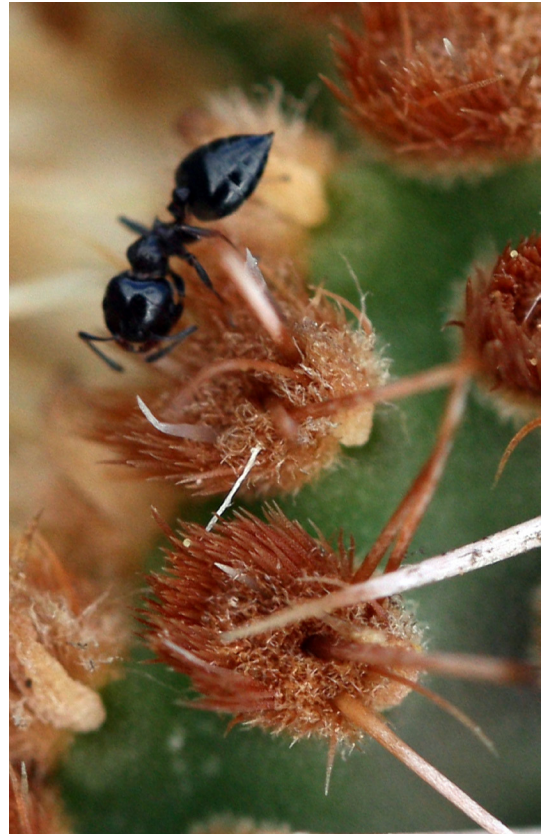
32. The small white spines of this *Opuntia pycnantha* are EFNs; ants have already harvested the nectar drops that were on them before the photo was taken.

4. The biology of the mutualism, including the animals. Chamberlain and Holland (2008) documented not only a dozen ant species that visited the EFNs of *Pachycereus schottii*, but also flies, beetles and parasitoids. Although ants may protect cacti from pests, if ants enter flowers searching for floral nectar, they may scare away bees or other pollinators. Ness (2006) discovered that the petals of *Ferocactus wislizeni* flowers can actually deter the ants that are attracted by EFNs on the vegetative shoot, thus keeping them out of the flowers. Particularly intriguing is a report that bees visit vegetative pads of a cultivated plant of *Opuntia bergeriana*, where they suck on sticky places ("saugt an klebrige Stellen"; personal communication from Kiki Schmidt).
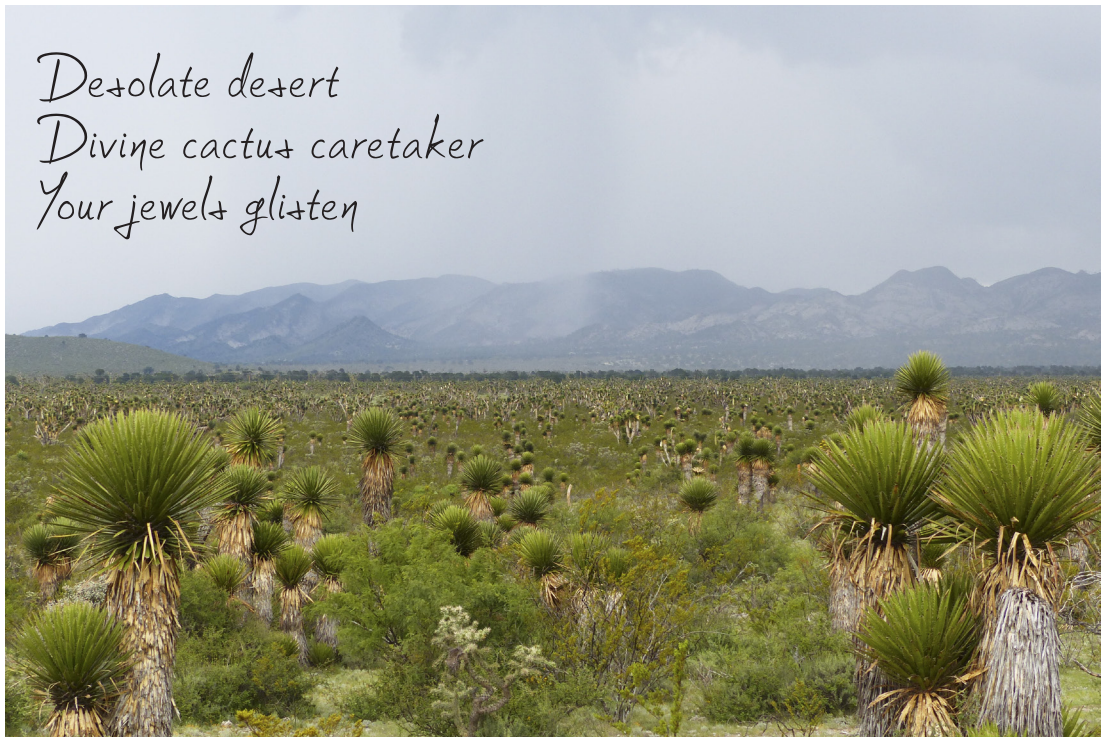
The interactions between plants and animals in mutualistic relationships are often complex. An extremely rich aspect of cactus biology awaits exploration.

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Acknowledgements

We thank Barbara de Ha Said for help with field work and photography in Brazil, and Jeff Pavlat, Bob Barth, and Sydney Novoa for advice and donation of specimens.

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A forest of *Yucca carnerosana*, with *Y. filifera* in the background, being soaked by a sudden rainstorm in the Chihuahuan desert. Haiku by Louise Stack, photo by Jeff Chemnick.