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FRONT COVER: *Tillandsia kautskyi* a native of Brazil, see the article on page 8 in this issue. Grown and photo by Eric Gouda.



BACK COVER: A form of *Tillandsia chapeuensis* another Brazil native, closely allied to *T. gardneri*. Grown since 1996 and photo by Andrew Flower.

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The poorly known genus *Greigia* Regel (Bromelioideae) and its mysterious pollinators

Nayeli Gomez-Escamilla¹, Bruno Tellez-Baños² & Thorsten Krömer²

Bromeliads fascinate with their spectacular inflorescences, colorful bracts, and beautiful flowers, and increase their charm even more when we observe that they are visited by a hummingbird, bat, or an insect (Aguilar-Rodríguez et al., 2019; Kessler et al., 2020). However, there is a genus of the subfamily Bromelioideae that is somewhat shy because it is hardly possible to observe its hidden flowers with the naked eye as their inflorescences are not present on a conspicuous peduncle but located at the base of the leaves. The identity of its pollinators is also still a mystery and basically nothing is known about the sexual reproductive biology of this genus.

We refer to *Greigia* Regel, whose large members have leaves arranged in a rosette pattern, more or less caulescent, of terrestrial and/or rupicolous habit, leaves with marginal spines, the flowers tubular, purple or white and borne in flattened inflorescences that are deeply arranged in the axils of the leaves (Espejo Serna & López-Ferrari, 1998). The inflorescences are usually covered by accumulated organic matter (e.g., leaf litter), so their presence is hardly visible. This is why its 36 unspectacular species, distributed mainly in humid montane forests from Mexico to Chile (Gouda et al., cont. updated; Will et al., 2009) have gone largely unnoticed by botanists, resulting in few collections and a low number of herbarium specimens.

This genus has been little studied in terms of its interactions with animals; so far it is known that individuals of the Andean bear, *Tremarctos ornatus* (F. Cuvier, 1825) feed on the leaves of various *Greigia* species in Colombia (Cáceres-Martínez et al., 2015, 2020) and Ecuador (Troya et al., 2004). This relationship was also reported from *G. macbrideana* L. B. Sm. in Peru (Figueroa, 2013), from *G. kessleri* H. Luther in Bolivia (Paisley, 2001) and *G. columbiana* L. B. Sm. in Venezuela (Goldstein Aizman, 1990). In addition, *G. landbeckii* (Lechl. ex Phil.) Phil. is part of the diet of the wild boar, *Sus scrofa* Linnaeus, 1758, an exotic wild pig introduced to Chile (Hernández et al., 2017).

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Figure 1. Location of the study area in the municipality of Xico, Veracruz, Mexico. Both *Greigia* populations occur at the limit between humid montane and pine-oak forest. Map by N. Gomez-Escamilla

Amphibians such as the frog species *Diasporus ventrimaculatus* Chaves *et al.*, 2009 have also been observed among the leaves of *Greigia sylvicola* Standl. in Costa Rica (Chaves et al., 2009), and specimens of the salamander *Chiropterotriton ceronorum* Parra-Olea *et al.*, 2020, in *G. vanhyningii* L. B. Sm. in Mexico (Aguilar et al., 2022).

So far, only Darwin's fox or Chiloé fox, *Lycalopex fulvipes* (Martin, 1837) has been documented as a disperser of the fleshy fruits of *Greigia* in Chile (Elgueta et al., 2007; Jiménez, 2007), and a small rodent, *Thomasomys kalinowskii* (Thomas, 1894), for a *Greigia* species in Peru (Sahley et al., 2015, 2016).

Some human groups use the fleshy fruits of several species of *Greigia* as food. In Mexico, those of *G. oaxacana* L. B. Sm. are consumed by the Chinantecos in Oaxaca and those of *G. van-hyningii* by some rural communities in Veracruz, which refer to these fruits as "*Piña de monte*" or "*Piña cimarrona*" (Espejo-Serna et al., 2005; Rendón-Aguilar et al., 2022), while in Peru the fruits of *G. macbrideana* L. B. Sm., also known as "*Ucush-piña*", "*Jirka-piña*", and "*Muntipiña*", are consumed by farmer communities (Pancorbo-Olivera et al., 2020). In Chile, the Mapuche people consume the fruits of *G. sphacelata* (Ruiz & Pav.) Regel, known as "*Chupón*", which are used for medicinal purposes (Gusinde, 1936) and to make flour (Smith-Ramírez, 1995). In addition, fibers are extracted from the leaves of *G. landbeckii* and *G. sphacelata* in Chile to make basketry and textiles (Carrasco & Cisterna, 2019; Wilhelm de Mösbach, 1992).

Although there is some information about their interactions with animals, currently we know nothing about the pollination biology of *Greigia*. Regarding their floral visitors and possible pollinators, there is no related work in studies of bromeliad floral ecology (Kessler & Krömer, 2000; Krömer et al., 2006) as no species of this genus have been included. However, some authors suggest hummingbird pollination (i.e., trochilophily) as floral syndrome for *G. berteroi*, *G. landbeckii*, *G. pearcei*, and *G. sphacelata* (Abrahamczyk & Renner, 2015; Bernardello et al., 2001) and recently insect pollination (i.e., entomophily) has been proposed (Gonzalez et al., 2019). Considering the latter, there is only one publication that we know of related to arthropod association with the rosette of *G. juareziana* L. B. Sm. conducted in Los Tuxtlas, Veracruz, Mexico (Hernández-Baz et al., 2011).

Three endemic species, *Greigia juareziana*, *G. oaxacana*, and *G. vanhyningii*, inhabit Mexico. These grow mainly on steep slopes of 45° and in the understory of humid montane and pine-oak forests in the states of Chiapas, Oaxaca, and Veracruz (Espejo-Serna & López-Ferrari, 2018). In Veracruz we made a first attempt to discover the mysterious pollination protagonists of the genus *Greigia*. Our study area was the Salvaterra private reserve, located in the municipality of Xico (19.47 N – 97.05 W), at an elevation of 2,000 m. in humid montane forest (Fig. 1). At this site, populations of two morphospecies (white vs. lilac) of the genus were found, material was collected for later identification, and there is a possibility that they corresponded to one or two undescribed species. This material was placed in the Mexican herbaria of CITRO, UAMIZ, and XAL (Thiers, updated continuously), and we are currently working on the correct determination and/or description of these so far unknown species (Gomez-Escamilla et al., 2022).

For both species, observations of their floral visitors (n = three individuals per species) were made in two different years (Fig. 2), on September 27 and 28, 2021, from 12:30 to 16:00 h and from 9:30 to 12:30 h, respectively, and on February 22 and 23, 2023, from 20:00 to 23:00 h each.



Figure 2. A) Individual of *Greigia* sp. 2 (lilac flowers) and B) individual of G. sp. 1 (white flowers) in Xico, Veracruz, Mexico. Photo by B. Tellez-Baños.



Figure 3. A) White flower of *Greigia* sp. 1 (12:30-16:00, 27/Sep/2021) and B) same flower without stamens and gynoecium, the detached conduplicate-spiral stigma and style are located on the leaf surface (09:30-12:30, 28/Sep/2021). Photos by N. Gomez-Escamilla.

During direct diurnal observations, in the population of *Greigia* sp. 1 (white flowers, remains of the reproductive whorls, androecium, and gynoecium, were found on the leaf of the observed inflorescence, indicating possible florivory (Figs. 3A and 3B). In the *Greigia* sp. 2 (lilac flowers) population, a *Drosophila* fly was observed perching on the petals of a flower (Fig. 4). During nocturnal sampling, one coleopteran species was recorded, which made three visits to the flowers of *Greigia* sp. 1 and two visits to the flowers of *Greigia* sp. 2; for the latter, a photographic record of one of the visits was obtained (Figs. 5A and 5B). Finally, two individuals of the coleopteran species were collected for further taxonomic determination.

Moreover, indirect observations were made on an individual of *Greigia* sp. 2, with the help of a NIKON D800 camera, equipped with a lens for macrophotography (Tokina 100 mm, with f 2.8) and two flashes with light diffusers. The camera was set to take pictures automatically every 10 minutes, from 13:12 h on September 26 until 13:35 h on September 28, 2021. The digital photographs obtained were processed with the help of the Adobe Lightroom Classic program and the *time-lapse* technique was applied using the LR Time lapse v. 5. Thereby it was possible to record the moment of floral opening, which occurred around midday (Fig. 6A), and part of floral senescence, which began 48 h after anthesis (Fig. 6B), as well as the visit of the coleopteran species *Platynus variabilis* (Chaudoir, 1837) (Carabidae family) at four different times between 16:00 and 24:00 h (Figs. 7-9).

The photographs showed that after the coleopteran visits to the flowers, the pollen remained adhered to its body mainly on the elytra and legs and the stigma was bearing pollen (Figs. 7B, 8B, and 9B), which suggests possible pollination by this insect (Figs. 5B and 9A). Floral scent unpleasant to humans was detected that could be attracting both flies and beetles.

We report the first observation of floral visitors for the genus *Greigia* in Mexico, one of which turned out to be a potential pollinator; however, a greater investigative effort will be required to verify the pollination capacity of this coleopteran, in addition to study the floral and reproductive biology of this bromeliad. We consider that due to the difficulty of direct observation the *time-lapse* technique is ideal to expand the record of visitors or potential pollinators, in addition to enable the recording of the different stages of anthesis.



Figure 4. *Drosophila* fly visiting flowers of *Greigia* sp. 2 (16:00, 27/Sep/2021). Photo by B. Tellez-Baños.



Figure 5. Visit of the coleopteran species *Platynus variabilis* (Carabidae family) to *Greigia* sp. 2 A) Coleopteran entering the flower (21:50, 22/Feb/2023) and B) coleopteran leaving the flower, with pollen adhering to its body mainly on the elytra and legs (21:52, 22/Feb/2023). Photos by B. Tellez-Baños.



Figure 6. Photographic sequence of *Greigia* sp. 2 A) Floral opening (13:12, 26/Sep/2021) and B) senescence (13:35, 28/Sep/2021). Photos by B. Tellez-Baños.



Figure 7. Photographic sequence of *Greigia* sp. 2 A) First coleopteran visit to *Greigia* sp. 2 (19:48, 26/Sep/2021) and B) flower with pollen on stigma after coleopteran visit (19:58, 27/Sep/ 2021). Photos by B. Tellez-Baños.



Figure 8. Photographic sequence of *Greigia* sp. 2 A) Second coleopteran visit to *Greigia* sp. 2 (16:18, 27/Sep/2021) and B) flower with pollen on stigma after coleopteran visit (16:28, 27/sep/2021). Photos by B. Tellez-Baños.



Figure 9. Photographic sequence of *Greigia* sp. 2 A) Third coleopteran visit to *Greigia* sp. 2 (23:58, 28/Sep/2021) and B) flower with pollen on stigma after the visit, the tip of the petals turned brown (00:14, 28/Sep/2021). Photos by B. Tellez-Baños.

There are still information gaps on aspects related to the diversity and distribution of the genus *Greigia* in Mexico, so we believe that it is important to continue exploring the humid montane and pine-oak forests to obtain more collections. It seems that some *Greigia* species occur in the same geographic locations and therefore it is probable that other new species will be discovered in montane areas of the Neotropics. In addition, this genus apparently has one of the most unusual pollination and seed dispersal syndromes among the Bromeliaceae (Benzing, 2000), so more effort is needed to elucidate its mysterious pollinators and seed dispersers.

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