

Flowering Phenology and Pollination of *Cobaea aschersoniana* (Polemoniaceae)¹

Key words: bat-pollination; *Cobaea*; Costa Rica; polemoniaceae; pollination; phenology.

COBAEA ARE VINES AND LIANAS THAT OCCUR IN MONTANE AND UPLAND FORESTS from Mexico through Central America to Venezuela and in the Andes from Colombia to northern Chile (Grant 1959). *Cobaea aschersoniana* Brand is a rare member of the genus with only five known populations, all in Costa Rica (Luis Diego Gomez, pers. comm.). The purpose of our study was to describe the floral phenology of *C. aschersoniana* and to determine the mechanism of pollination in a population occurring at Cerro de la Muerte, San Jose Province, Costa Rica.

Cobaea aschersoniana is included in section *Rosenbergia* (Prather, in press). The pendant flowers of the species of section *Rosenbergia* have a less developed throat relative to other sections in the genus, are greenish-yellow, have very long ribbon-like corolla lobes, and the anthers and stigmas mature simultaneously (Fig. 1; Prather, in press). *Cobaea penduliflora*, a member of section *Rosenbergia*, has a floral cup 2.5 cm deep and 1 cm wide and is hawk moth pollinated (Ernst 1880; Fig. 2). Hawk moths (Sphingidae) pick up sticky, yellow pollen on their wings as they hover to take nectar and pollen is transferred to stigmas on flowers subsequently visited (Ernst 1880). All flowers observed by Ernst that were visited by moths set fruit while flowers that were inaccessible to moths did not set fruit. Bats are unlikely visitors because the small floral cup would restrict access to the nectar reward. Ernst (1880) concluded that *C. penduliflora* is self-incompatible by self-pollinating 12 flowers on one plant of which only one set fruit while all nine flowers cross-pollinated by hand set fruit. In contrast, *C. lutea* and *C. rotundiflora*, other known members of section *Rosenbergia*, are self-compatible and strongly autogamous (Prather, in press).

Species of *Cobaea* section *Cobaea* are similar in floral form and phenology. At the onset of anthesis, flowers of *C. scandens* (section *Cobaea*; Fig. 2) are greenish-yellow with a cabbage-like odor but turn muddy purple and lose their odor as the anthers dehisce throughout the first day (Grant & Grant 1965). After 3 or 4 days, the filaments retract into the corolla while the style elongates and stigma lobes open and become receptive; thus, the flowers are protandrous. The floral cup is 3 cm deep and the entrance is 2–3 cm wide. Grant and Grant (1965) simulated visits to *C. scandens* using preserved specimens of the nectivorous glossophagine bat *Leptonycteris nivalis*. Pollen adhered to fur on the breast and chin, and the breast and chin contacted receptive stigmas (Grant & Grant 1965). Flowers of *C. trianaei* (section *Cobaea*) are similar in shape and slightly smaller than *C. scandens* are greenish-yellow with violet veins, have a pungent odor and are protandrous. Vogel (1958) inferred that claw marks on outer lateral walls of corolla throats of *C. trianaei* were made by nectivorous bats and concluded that *C. trianaei* is bat-pollinated.

Solitary flowers of *C. aschersoniana* are borne sequentially along the vine on long peduncles, up to 40 cm, with the youngest floral bud most terminal on a branch. As buds mature, flowers move from a nodding position to an upright pendant position and most extend above tree and bush foliage. Flowers are visually apparent from the ground and easily accessible by floral visitors. As flowers senesce, the peduncles curl down and the developing fruit hangs inside the foliage. The floral phenology and pollination of *C. aschersoniana* are uncertain and although the flowers are structurally similar to other members of section *Rosenbergia*, the flowers are similar in size to bat-pollinated species of *Cobaea* section *Cobaea*.

To determine floral phenology and pollinators of *Cobaea aschersoniana*, we studied plants growing at Cuereci Biological Station, Cerro de la Muerte, San Jose Province, Costa Rica. The site is located at 2700 m and consists of secondary growth dominated by *Quercus* and *Alnus*, with Oak-Bamboo primary forest on steep slopes and ridge tops. Although several hundred flowers could be seen in the canopy, the number and sizes of vines could not be assessed. We marked 25 flowers on five vines accessible from ground level and observed the flowers at 6 h intervals from 1730 h on 25 February to 0700 h 28 February 1994. We recorded six floral characters: position of flower relative to vine, position of pistil

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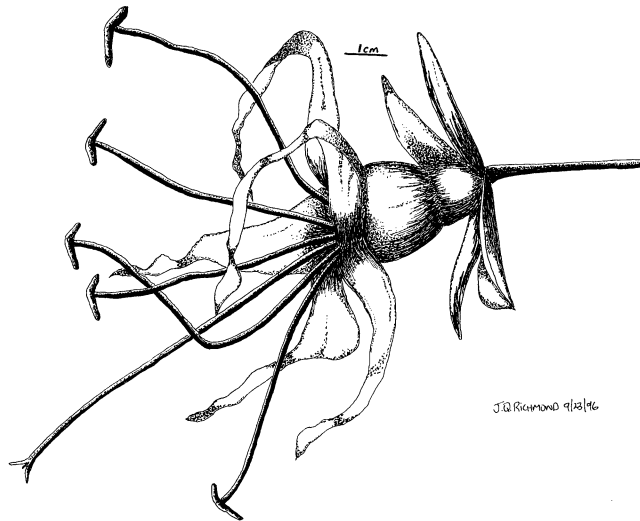


FIGURE 1. Flower of *Cobaea aschersoniana*, anthers are dehiscent and the three-lobed stigma is receptive.

and anthers relative to corolla, stigma condition, anther dehiscence, odor production, and nectar presence. We bagged seven flowers before anthesis and collected nectar samples from each with microcapillary tubules. A Fisher handheld refractometer was used to determine nectar sugar concentration. We made observations of floral visitors at each 6-h interval and additional observations during the day and night. Moonlight was sufficient for night observations because the moon was nearly full during the observation period. Mist and hand nets were used to capture potential pollinators. We removed pollen from captured animals using forceps or cellophane tape and transferred the pollen directly to dry glass slides for im-

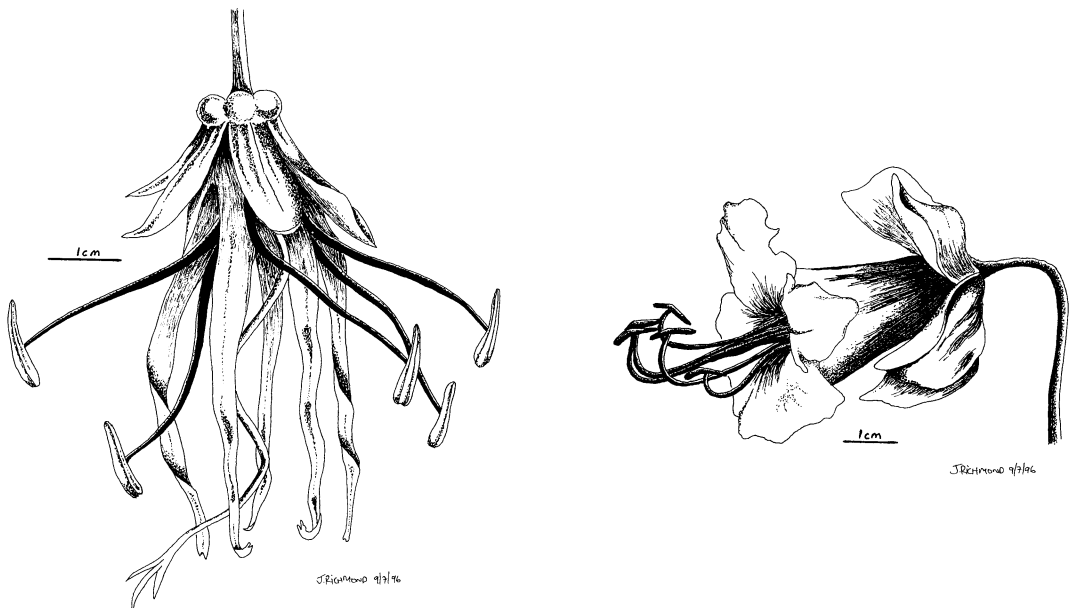


FIGURE 2. *Cobaea penduliflora* (section *Rosenbergia*) on left and, *C. scandens* (section *Cobaea*) on right (redrawn from Grant and Grant 1965).

mediate observation. We compared morphology of pollen collected from pollinators with hand-collected pollen from *C. aschersoniana* using a compound light microscope.

Thirteen of 25 marked flowers were in floral phases that revealed information on sequence and timing of stigma receptivity and anther dehiscence. For 61.5 percent of flowers (8/13) opening of the trilobed stigma and anther dehiscence occurred simultaneously or within hours of each other between 1800–2300 h. The stigmas appeared moist and pollen masses were bright yellow and sticky. For a few of these flowers, one or two anthers did not dehisce until a few hours after the others. For 38.5 percent of flowers (5/13), the trilobed stigma opened and appeared moist during one night approximately 12–24 h before the anthers dehisced suggesting protogyny of some flowers or plants. For all flowers, as filaments uncoiled, anthers were exerted and dehisced at dusk between 1700–1800 h. As for other members of the genus (Erdtman 1952, Grant 1959), the yellow pollen grains were large relative to the rest of the family, 211 ± 21.2 microns in diameter ($x \pm 1$ SE, $N = 7$ grains). *Cobaea* pollen grains were polyporate with a reticulate sexine (outer sculpted part of the exine) (Erdtman 1952); the distinct pattern resembled a soccer ball. Simultaneous with anther dehiscence, a slightly sweet musty odor and 100–150 μ l of nectar were produced. However, because the nectary and nectar reservoir were covered by a mat of hair, we were unable to extract the total amount of nectar produced. Standing crop nectar collected between 2000 h and 0800 h had a mean sugar concentration of $17.5 \% \pm 4.1$ (wt./vol.; $x \pm 1$ SE, $N = 7$ flowers). After anther dehiscence, the style remained exerted with the stigma lobes open 6 to 24 h, before the style wilted. Six to 18 hours after the style wilted, the exerted filaments gradually curled back into the bell-shaped corolla. We estimated that 60–80 percent of the pollen had been removed from the anthers at this time. The corolla wilted and was abscised as the peduncle curled downward.

We examined 22 mature fruits on five vines of which 21 (95.5%) had viable seeds. Several of the fruit with viable seeds were collected within thickets that were inaccessible to any animal visitors suggesting *C. aschersoniana* may be self-compatible, similar to other members of section *Rosenbergia* (Prather, personal communication).

We observed one species of hummingbird, the gray-tailed mountain-gem (*Lampornis cinereicauda*), and a bee (*Bombus* spp.) visiting *Cobaea aschersoniana*. Gray-tailed mountain-gems visited throughout the day, approaching flowers from the side and raiding nectar from holes and tears on the lateral walls of the floral cup. The holes were similar in size and shape to those made by slaty flowerpiercers (*Diglossa plumbea*) which were commonly seen at this site. Eighteen of 22 flowers (81.8%) examined had holes on the lateral walls of the floral cup. We did not see any *Lampornis cinereicauda* approach flowers or take nectar from the front of the flowers. We did not find pollen from *C. aschersoniana* on two gray-tailed mountain-gems captured at the site. Bees visited flowers only from 0900–1600 h, presumably to take residual nectar, but we did not observe any bee visits earlier than 0900 h. Bees did not contact dehisced anthers or receptive stigmas. Although we found seven discernible types of pollen on two bees captured after visiting *C. aschersoniana* flowers, they did not carry pollen of *C. aschersoniana*.

We set up mist nets from dusk until dawn parallel with two of our marked vines. Two species of bat were netted at the site: the little brown bat (*Myotis nigricans*, Vespertilionidae) and Geoffroy's long-nosed bat (*Anoura geoffroyi*, Phyllostomidae, Glossophaginae). *Myotis nigricans* are insectivorous and were not found with pollen of any type, and are not considered potential pollinators. All members of the subfamily Glossophaginae take floral nectar (Emmons & Feer 1990), although stomach content analysis of *Anoura geoffroyi* has shown them to be highly insectivorous as well (Garner 1977). Similar to other members of the subfamily, *A. geoffroyi* have elongated snouts and highly extensible brush-tipped tongues (Nowak 1991; personal observation). Two of three *A. geoffroyi* netted at the site carried the distinctive pollen of *C. aschersoniana* on their chests, throats, snouts, and foreheads, albeit in small amounts (< 50 grains per bat).

In conclusion, the floral characteristics of *C. aschersoniana* (nocturnal anthesis, exerted pendent flowers, light green color, strong sweet-musty odor, large floral cup, and copious amounts of nectar) are consistent with other bat-pollinated flowers (Fægri & van der Pijl 1979). Since *C. aschersoniana* is similar in morphology to *C. penduliflora*, hawk moths may also contribute to the fertilization of *C. aschersoniana* (Ernst 1880), although we did not observe any hawk moth visitation or hawk moth activity in the area. Geoffroy's long-nosed bats are the only potential floral visitor we observed that are considered capable of effecting pollination.

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