

WING POLLINATION BY BEES IN *MEXACANTHUS* (ACANTHACEAE)?

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ABSTRACT

The monotypic genus *Mexacanthus* in the Acanthaceae is endemic to west central Mexico where the species *M. mcvaughii* T.F. Daniel grows. The flower structure is unusual with anthers and stigma positioned laterally, and a nectar barrier opened by force. A pollination study showed that the flowers are mainly visited by fork-tailed emerald *Chlorostilbon canivetii* (Lesson) and Mexican carpenter bee *Xylocopa mexicanorum* (Cockerell). Both species manage the nectar barrier and behave as pollinators. The hummingbird transferred pollen by its auricular area. The bee transferred pollen by its wings, which carried numerous pollen grains. Wing pollination is earlier known only from butterfly pollination.

Key words: Acanthaceae, Apidae, Hymenoptera, *Mexacanthus mcvaughii*, wing pollination, *Xylocopa mexicanorum*.

RESUMEN

El género monotípico *Mexacanthus* de la familia Acanthaceae es endémico del centro occidente de México, donde está representado por la especie *M. mcvaughii* T.F. Daniel. La estructura de la flor es poco usual, con las anteras y el estigma en posición lateral y una barrera de néctar que no se abre sin el ejercicio de fuerza. El estudio de la polinización muestra que las flores son visitadas principalmente por el colibrí tijereta esmeralda *Chlorostilbon canivetii* (Lesson) y por el abejorro *Xylocopa mexicanorum* (Cockerell). Ambas especies abren sin problemas la barrera de néctar y se comportan como polinizadores. Los colibríes transfieren el polen en su área auricular; la abeja lo hace en sus alas, en las cuales lleva numerosos granos. La polinización por alas anteriormente se conocía sólo de lo registrado en representantes del grupo de las mariposas.

Palabras clave: Acanthaceae, Apidae, Hymenoptera, *Mexacanthus mcvaughii*, polinización por alas, *Xylocopa mexicanorum*.

When an insect visits a flower, pollen is generally deposited onto either its hairy head, proboscis, thorax or abdomen. More rarely, floral adaptations may result in pollen being deposited onto the wings (pterotriby; L. Anders Nilsson, pers. com.), with subsequent pollination of the flower. This has been reported in *Gloriosa superba* L. (Hingston, 1930) and *Caesalpinia pulcherrima* (L.) Sw. (Cruden & Hermann-Parker, 1979), both pollinated by butterflies. Hitherto, wing pollination is known only from butterflies (Lepidoptera). However, in a preliminary study of the pollination biology of *Mexacanthus mcvaughii* T.F. Daniel (Acanthaceae), indications of wing pollination by a carpenter bee, *Xylocopa mexicanorum* (Cockerell), were found.

Mexacanthus (Acanthaceae) is a monotypic genus (Daniel, 1981) from Colima and Jalisco in west-central Mexico, where the only species *M. mcvaughii* grows on slopes and along washes in dry forest. Many of its floral features are peculiar in comparison to closely related genera, e.g., *Anisacanthus*. The species of *Anisacanthus* all have reddish, long-tubed corollas (Fig. 1A) typical of bird-pollinated flowers (Faegri & van der Pijl, 1979), but *M. mcvaughii* (Fig. 1B) has a corolla with traits suggesting a more generalized pollination system that also involves insects (cf. Johnson & Steiner, 2000). The sympetalous and zygomorphic corolla in *Mexacanthus* is mainly yellow. Only the narrow, reflexed upper lip is dull red. The corolla tube is fairly short (3.5-5.0 mm) relative to the lips (13-19 mm). The strongly reflexed lower lip is apically split into lobes, but the base of the lip is undivided and may serve as a landing platform (Fig. 1C). The stamens protrude to each side forming an angle of approximately 60 degrees. The filaments are partly fused with the corolla wall. However, they are not fastened inside the corolla tube, which is common in Acanthaceae, but onto the lower, outer corolla lobes. The style is slightly longer than the stamens, and is directed more or less parallel to either one of the filaments, but slightly below. A unique feature in *Mexacanthus* compared to related genera is the pollen being two-aperturate rather than three-aperturate. A transverse nectar barrier is located at the mouth of the tube (Holmqvist, 2000). The style may be pushed downwards into a slit in the barrier, leaving a circular opening to the nectar chamber. A homologous barrier has been found in *Anisacanthus* (Manktelow, 1998, Holmqvist, 2000), where it is believed to be an adaptation to bird pollination by excluding other visitors from the nectar. The bird presumably has to push the style from the top to the bottom of the barrier with its beak to reach the nectar (Mariette Manktelow & Per-Henrik Holmqvist pers. obs.).

Hummingbirds have been observed as frequent visitors of *M. mcvaughii* (Thomas F. Daniel, pers. obs.), as may be predicted by some characters of the species, including the protruding anthers, the placement of the flowers along leafless flexible branches, the lack of odor, the nectar barrier, and the red and yellow color of the corolla (cf. Grant & Grant, 1968; Faegri & van der Pijl, 1979; Endress, 1994).

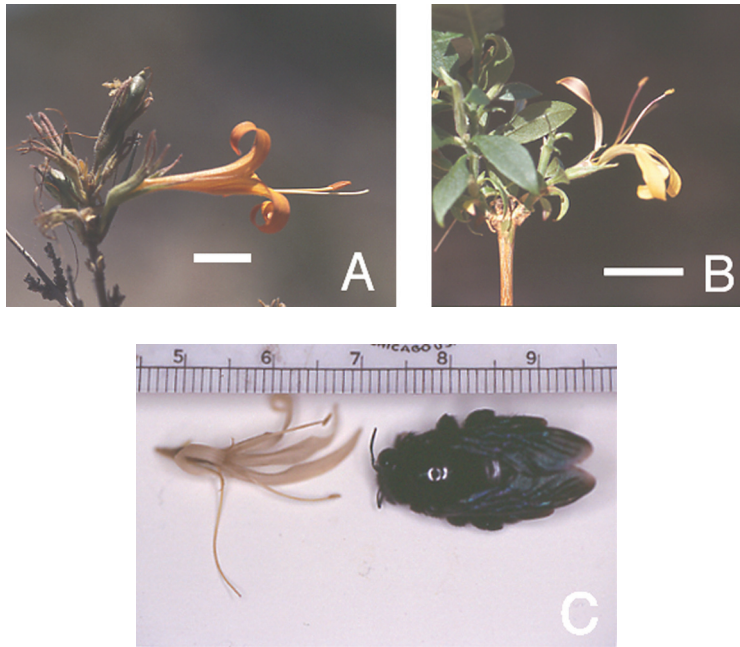


Fig. 1. Comparison of the flowers of (A) *Anisacanthus thurberi* and (B) *Mexacanthus mcvaughii* (bar in both figures 1 cm); (C) Picture of *Xylocopa mexicanorum* with a pickled flower of *Mexacanthus mcvaughii*. Photographs by Mariette Manktelow (A), Stephen Manktelow (B) and Per-Henrik Holmqvist (C).

However, the yellow corolla parts, the landing platform and the short tube suggest involvement of a nectar-feeding insect pollinator. Such a pollinator must: 1) be able to get through the nectar barrier, and 2) have contact with the anthers and stigma such that deposition of pollen may take place.

The field studies were carried out from March 22 to March 25, 1999, near the end of the dry season in Arroyo de Colorado, near Chamela, Jalisco, Mexico (19°30'57" N; 105°02'33" W; 20 m elev.). A total of seven shrubs were included in the study, one of which was observed during the visitor frequency study. Eight species of floral visitors were observed during daylight hours, and no visitors were detected at night. A visitor frequency study was carried out for eight daylight hours at different times during the day.

Five visitors were infrequent and behaved as nectar thieves or robbers (sensu Inouye, 1980): the butterflies *Eurema boisduvaliana* (Felder & Felder), *Heliopetes* sp., *Pontia protodice* (Boisduval & LeConte), the stingless bee *Trigona fluiventris* Guérin, and a bombylid fly of the subfamily Exoprosopinae. Three visitors were

frequent: *Apis mellifera* L. (common honeybee), which acted as a pollen thief and did not contribute to the pollination, *Chlorostilbon canivetii* (Lesson) (fork-tailed emerald) and *Xylocopa mexicanorum* (Mexican carpenter bee), which both behaved as legitimate visitors and potential pollinators.

Chlorostilbon canivetii visited each flower for one to two seconds, and inserted its beak into the corolla tube while hovering. It thereby touched the anthers and stigma with its auricular area (the sides of its head). To reach the nectar it seemed to push the style downwards with its beak. The bird made 2.4 visits/hour/shrub, and visited several flowers of the same shrub in a period of one to two minutes. A total of 19 visits to all shrubs by the hummingbird were recorded during the field study.

Xylocopa mexicanorum landed on the platform of the lower lip after a short time of hovering in front of the flower. The bee landed on the style and inserted its proboscis into the nectar chamber above the style. It took nectar for approximately one second. The only part of the bee in contact with the anthers and stigma were the lateral parts including the wings. *Xylocopa mexicanorum* made 3.3 visits/hour/shrub, and visited around 20 (i.e., almost all) flowers on the observed shrub systematically during a period of two to five minutes. A total of 32 visits to the shrubs by *X. mexicanorum* were noted during the field study. All carpenter bees behaved in the same way.

A preliminary phenology study of ten flowers distributed on five shrubs of *M. mcvaughii* showed that 50 percent of the flowers opened around sunrise, and the rest at different times between 10.00 and 14.00. Most corollas remained on the plant less than 24 hours, before dehiscing. The number of simultaneously open flowers was low, resulting in a prolonged flowering period for each individual shrub as well as for each branch. Analyses of nectar sugar composition in two flowers of a cultivated individual of *M. mcvaughii* (Daniel 2107gh) have revealed sucrose-dominated nectars with sucrose/hexose ratios of 4.7 and 2.4 (ave. = 3.55; Thomas F. Daniel & C. Edward Freeman, pers. obs.). Greenhouse studies have revealed that *M. mcvaughii* is self-compatible but not autogamous (Thomas F. Daniel, pers. obs.).

Pollination by both the hummingbird *C. canivetii* and the carpenter bee *X. mexicanorum* in *M. mcvaughii* is congruent with the flowers opening mainly in the morning (when these two animals were active, and exclusive visitors), the prolonged flowering period of each individual shrub (Janzen 1971), the nectar barrier opened by force alone (van der Pijl, 1954; Hedström & Thulin, 1986; Westerkamp, 1993; Endress, 1994; Mariette Manktelow & Per-Henrik Holmqvist pers. obs.), and the high proportion of sucrose relative to hexose sugars in the nectar. The latter is typical of hummingbird-flowers (Baker & Baker, 1983; Freeman et al., 1984; Stiles & Freeman, 1993), but occurs also in species adapted to pollination by *Xylocopa*, e.g.,

Brillantaisia spp. (Acanthaceae) (Troll, 1951; Kullenberg, 1955; Schwerdtfeger, 1996; Manktelow, 2000).

Xylocopa mexicanorum fulfills the above criteria for a nectar-taking insect pollinator in *M. mcvaughii*. The weight of the bee when landing upon the style should be enough to open the nectar barrier (i.e., to push the style downwards into the slit in the nectar barrier). No destruction of the barrier, suggesting piercing by the bee, was seen on the flowers after a visit. The morphological match between *X. mexicanorum* and the *Mexacanthus* flower predicted pollen deposition on the lateral parts of the insect (Fig. 1C). The maximum width of the captured bee was 12 mm, while the average distance between the anthers was 15 mm. A bee that had visited half of the flowers in sequence (around 10) on one shrub was captured and examined.

Numerous pollen grains of *M. mcvaughii* were found predominantly on the surfaces of the wings (Fig. 2), as well as within the “curled” hamuli (hook-like hairs keeping the two sidewings together during flight) of each hind wing, but not on other parts of its body. As the wings are unhooked by a circular movement at landing, they apparently also brush the sexual parts of *M. mcvaughii*.

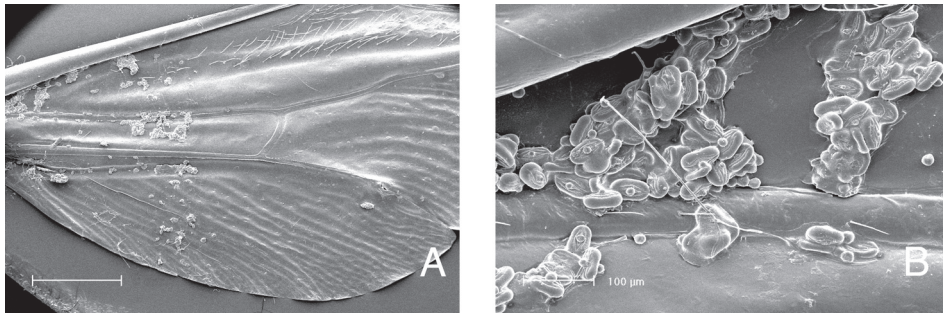


Fig. 2. Pollen from *Mexacanthus mcvaughii* on the wings of *Xylocopa mexicanorum*. (A) lower surface of hindwing with pollen; (B) detail of wing showing pollen of *Mexacanthus mcvaughii*. SEM Photograph by Gary Wife.

We conclude that wing pollination by bees may occur in *Mexacanthus*. This needs to be confirmed by subsequent studies. These should include prolonged visitor frequency and behaviour studies, a detailed study of the capture and stigma deposition of pollen by the wings, and an evaluation of the relative effectiveness of *Xylocopa* pollination.

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