

## An ancient pollinator of a contemporary plant (*Cyclamen persicum*): When pollination syndromes break down

Racheli Schwartz-Tzachor<sup>a</sup>, Amotz Dafni<sup>b,\*</sup>, Simon G. Potts<sup>b</sup>, Dan Eisikowitch<sup>a</sup>

<sup>a</sup>Department of Plant Sciences, Tel Aviv University, Tel Aviv, Israel

<sup>b</sup>Laboratory of Pollination Ecology, Institute of Evolution, Haifa University, Haifa 31905, Israel

Received 15 March 2005; accepted 25 July 2005

Dedicated to Prof. Dr. Stefan Vogel on the occasion of his 80th birthday

### Abstract

Pollination of *Cyclamen persicum* (Primulaceae) was studied in two wild populations in Israel. Buzz-pollination proved to be extremely rare, and performed by a large *Anthophora* bee only. The most frequent pollinators were various unspecialized species of thrips (Thysanoptera) and hoverflies (Syrphidae). In the Winter-flowering populations the commonest visitor was a small primitive moth, *Micropteris elegans* (Micropterigidae, Lepidoptera). These moths feed on pollen, copulate and oviposit within the flowers. From the rarity of buzz-pollination it is concluded that the genus *Cyclamen* co-evolved with large bees capable of buzz-pollination, but lost its original pollinators for unknown historical reasons. The vacant niche was then open to various unspecialized pollen consumers such as thrips, hoverflies and small solitary bees. While these insects are not specific to *C. persicum* and seem to play a minor role only, the moth strictly relies upon *Cyclamen* and seems to be the most efficient pollinator.

© 2006 Elsevier GmbH. All rights reserved.

**Keywords:** *Micropteris elegans*; Buzz-pollination; Pollinator specificity

### Introduction

In 1862, Charles Darwin predicted that the long spurred (15 in) orchid *Angraecum sesquipedale* is pollinated by a suitable moth: "... in Madagascar there must be moths with proboscides capable of extension to a length of between 10 and 11 in" (Darwin, 1862, p. 163). A possible candidate, the hawkmoth *Xanthopon morgani praedicta*, was proposed by Rothchild and Jordan (1903) and it was finally verified in 1996 by L.T. Wasserthal, who also described the pollination mechanism. As

Darwin predicted, the floral morphology closely matched the pollinator's proboscis.

Darwin's prediction was inferred from the flower's structure, color and the spur length. This classical case beautifully illustrates the concept of "pollination syndromes", which premises that a given set of floral suits matches the characteristics of a certain class of pollinators (Faegri and Van der Pijl, 1979). Most of the described zoophilic flower types across families and orders can be classified quite objectively (based on their morphology, color, scent, etc.) into clear syndromes such as fly-pollinated (Myophily), bee-pollinated (Melitophily), beetle-pollinated (Cantharophily) flowers (Faegri and Van der Pijl, 1979; Proctor et al., 1996).

\*Corresponding author. Fax: +972 8240 312.

E-mail address: [adafni@research.haifa.ac.il](mailto:adafni@research.haifa.ac.il) (A. Dafni).

While many excellent works have examined interactional evolution between animals and flowering plants (e.g. Nilsson, 1989; Herrera, 1996), the concept of syndromes has been recently challenged by several authors (Wasserthal, 1996; Johnson and Steiner, 2000). Here we present a striking example of where the collapse of a mutualism has not lead to the extinction of a flowering plant as the original pollinator has been substituted with, on what seems on first appearances, a very unlikely replacement.

## Study, results and discussion

*Cyclamen persicum* (Primulaceae) is a common eastern Mediterranean geophyte. In Israel two phenological ecotypes are found: a hysteranthous form in which flowering occurs prior to leaf development and with blooming during October–December and a synanthous form which flowers with leaves and blooms from December to March. The plant bears large (2–3 cm) pink–violet showy and fragrant flowers which contain a lot of pollen but no nectar. The *Cyclamen* flowers are pendant, radially symmetrical with reflexed petals and with anthers that are introrsely dehiscent and poricidal (Affre et al., 1995). These are typical features characteristic of buzz-pollinated flowers (Buchmann, 1983) and so flower visitors would be expected to be capable of this function.

Intensive observations, throughout the Mediterranean, on the floral biology of the genus *Cyclamen* have revealed a rarity of pollinators (Affre and Thompson, 1997; Affre et al., 1995; and our data). Affre et al. (1995) expected buzz-pollination in *C. balearicum* but found no insect visitors. In a later study Affre and Thompson (unpublished) observed buzz-pollination by bumblebees only in *C. repandum*, and pollination by syrphid flies and bumblebees in *C. hererifolia* with visitation rates for both species that were very low (J.D. Thompson, pers. comm.). These observations regarding the rarity of pollinators are in stark contrast to expectations for several common *Cyclamen* species found flowering in large populations during the Autumn and Winter when many other co-occurring plants are not flowering, such that an abundance of visitors would be predicted based upon such a temporally and spatially concentrated resource. For example, members of the genus *Dodecatheon* (Primulaceae) have floral structures very similar to that of *Cyclamen*, and these species are regularly visited and pollinated by a variety of buzz-pollinators (Harder and Barclay, 1994; Macior, 1964). Our study showed buzz-pollination of *C. persicum* to be extremely rare, and performed by a large solitary bee *Anthophora* sp. only (pers. obs.). The most frequent pollinators were various unspecialized species of thrips (Thysanoptera)

and hoverfly (Syrphidae). In the Winter-flowering populations we found that the commonest visitor was a small primitive moth *Micropteris elegans* (Micropterigidae, Lepidoptera, Fig. 1). These moths feed on pollen, copulate and oviposit within the flowers. The hairy moths were observed loaded with pollen of *C. persicum* (Fig. 2). The moths were observed with the aid of a close-up video-tape, eating pollen for a period of up to 60 min and as they were also observed scratching the stigma for several seconds with their pollen-loaded mandibles, probably pollinating the flowers.

Though *C. persicum* is a self-incompatible species, it still requires a mediator to carry out pollination because of the spatial separation of the stigma and anthers (Schwartz-Tzachor, 1999; Thompson, unpublished data). In controlled experimental cages it was shown by using fluorescent dyes that these moths moved among flowers and so presumably facilitate outcrossing. We never observed the moths on any other co-blooming plant species.

The micropterigid moths represent an ancient family that has a fossil record from the Eocene Baltic and Early Cretaceous Lebanese ambers (Thien et al., 1985; Whalley, 1977). They are scattered throughout the world with a concentration of species in the southwest Pacific (Gibbs, 1983). Micropterigidae are the pollinators of the primitive angiosperm *Zygogynum Baillonii* in New Caledonia, where *Sabatinea* sp. live, eat and copulate in the flowers (Thien et al., 1985). *Micropteris* spp. are also common visitors of several genera of the Ranunculaceae, e.g. *Caltha* spp. and *Ranunculus* spp. (Proctor et al., 1996); these species have simple flowers and are regarded as less advanced genera in the family.

Thus, it was surprising to find the primitive moth *M. berytella* as a pollinator of *Cyclamen* species. Our data on the phenology of the moth and *C. persicum* show a close association between the plant and the



Fig. 1. Primitive moth *Micropteris elegans* (Micropterigidae, Lepidoptera) on the outer sepal of *Cyclamen persicum*.

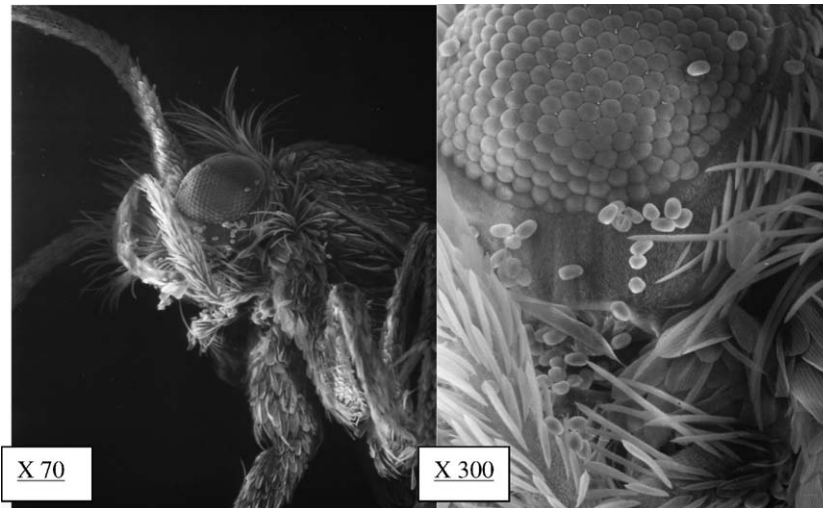


Fig. 2. SEM micrograph of *Micropterix elegans*; note pollen of *Cyclamen persicum* on its head and mouthparts.

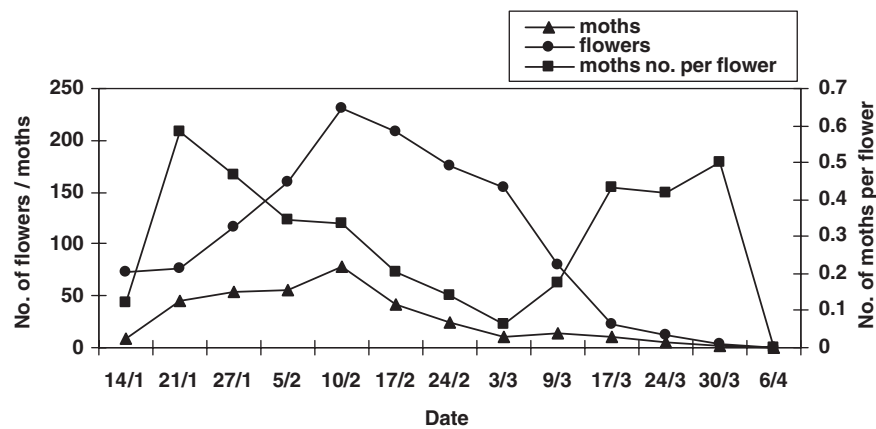


Fig. 3. Moth and flower abundance from field census of the Winter 1997 population of *Cyclamen persicum* and its pollinator *Micropterix elegans*.

moth (Fig. 3). Both have similar peaks of abundance, with beginning and end of the season having the highest relative frequency of the moths per flower. This suggests that their contribution to pollination may be more important at the start and the termination of the *Cyclamen* flowering season.

The lack of buzz-pollination in other Mediterranean *Cyclamen* brought Affre et al. (1995) to conclude that “to what extent the floral phenotype of this relic endemic species represents an adaptation to historical selection, remains unknown.” Along the same line we speculate, based on the floral morphology and the data on the pollination of *Dodecatheon* spp., that the genus *Cyclamen* was co-evolved with large bees capable of buzz-pollination. However, for unknown historical reasons (e.g. climate changes, glaciations, tectonic movements) the original pollinators of several species of the genus *Cyclamen* have disappeared and/or lost their attraction to the flowers. The vacant niche was then open to invasion by various unspecialized pollen consumers such

as thrips, hoverflies and small solitary bees, none of which are capable to perform buzz-pollination. All these agents have been found feeding on several other plant species and are not specific to *C. persicum* and therefore may play only a minor role in its pollination. The *Micropterix* described here, on the other hand, strictly relies upon *Cyclamen*. *Micropterix* survived in this underexploited rich food source which also might confer a shelter from adverse weather conditions which are typical to the Mediterranean Winter. All this assemblage of non-related pollinators resulted in a low efficiency pollination system that may be compensated by the long-lived corm, long stigma receptivity (up to 16 days) and prolonged pollen longevity (20 days).

### Acknowledgment

The authors thank J.D. Thompson for his thoughtful comments on the draft of this paper.

## References

- Affre, L., Thompson, J.D., Debussche, M., 1995. The reproductive biology of the Mediterranean endemic *Cyclamen balearicum* Willk. (Primulaceae). *Bot. J. Linn. Soc.* 118, 309–330.
- Affre, L., Thompson, J.D., Debussche, M., 1997. Variation in the population genetics structure of two *Cyclamen* species on the island of Corsica. *Heredity* 78, 205–214.
- Buchmann, S.L., 1983. Buzz pollination in angiosperms. In: Jones, C.E., Little, R.J. (Eds.), *Handbook of Experimental Pollination Biology*. Van Nostrand Reinhold, New York, pp. 73–113.
- Darwin, C., 1862. On the various contrivances by which British and foreign orchids are fertilised by insects. Murray, London.
- Faegri, K., Van der Pijl, L., 1979. *The Principles of Pollination Ecology*. Pergamon Press, Oxford.
- Gibbs, G.W., 1983. Evolution of Micropterigidae (Lepidoptera) in SW Pacific. *Geo Journal* 7, 505–510.
- Harder, L.D., Barclay, M.R., 1994. The functional significance of anthers and buzz pollination: controlled pollen removal from *Dodecatheon*. *Funct. Ecol.* 8, 509–517.
- Herrera, C.M., 1996. Floral traits and plant adaptation to insect pollinator: a devil's advocate approach. In: Lloyd, D.G., Barrett, S.C.H. (Eds.), *Floral Biology*. Chapman and Hill, New York, pp. 65–87.
- Johnson, S., Steiner, K.E., 2000. Generalization vs. specialization in plant-pollination systems. *Trends. Ecol. Evol.* 15, 140–143.
- Macior, L.W., 1964. An experimental study of the floral ecology of *Dodecatheon media*. *Am. J. Bot.* 51, 98–108.
- Nilsson, L.A., 1989. Deep flowers for long Tongues. *Trend Ecol. Evol.* 13, 259–260.
- Proctor, M., Yeo, P., Lack, A., 1996. *The Natural History of Pollination*, second ed. Harper & Collins Publ., London.
- Rothchild, L.W., Jordan, K., 1903. A revision of the lepidopterous family Sphingidae. *Nov. Zool.* 9 (Suppl.), 1–972.
- Schwartz-Tzachor, R., 1999. Pollination and seed production in two populations of *Cyclamen persicum*. M.Sc. Thesis, Department of Plant Sciences, Tel Aviv University.
- Thien, L.B., Bernhardt, P., Gibbs, G.W., Pellmyr, O., Bergstrom, G., McPherson, G., 1985. The pollination of *Zygogynum* (Winteraceae) by a moth *Sabatinca* (Micropterigidae): an ancient association? *Science* 227, 540–543.
- Wasserthal, L.T., 1996. Of hawkmoth species with long “tongues.” Report DFG 1/96, pp. 22–25.
- Whalley, P., 1977. Lower cretaceous lepidoptera. *Nature* 266, 526.