

Multiple occurrences of mutualism in the yucca moth lineage

(coevolution/mutualism/pollination)

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ABSTRACT The complex mutualism between yuccas and the moths that pollinate their flowers is regarded as one of the most obvious cases of coevolution. Studies of related genera show that at least two of the critical behavioral and life history traits suggested to have resulted from coevolved mutualism in yucca moths are plesiomorphic to the family. Another trait, oviposition into flowers, has evolved repeatedly within the family. One species with these traits, *Greya politella*, feeds on and pollinates plants of a different family, but pollination occurs through a different component of the oviposition behavior than in the yucca moths. Major differences compared with yucca moths and their hosts are that *G. politella* only passively pollinates its host and that copollinators often contribute to pollination. This analysis suggests that evolution of mutualism between yuccas and yucca moths may have required few behavioral and life history changes in the moths. The truly coevolved features of this interaction appear to be the evolution of active pollination by the moths, the associated morphological structures in the moths for carrying pollen, and the exclusion of copollinators by yuccas.

Many mutualisms between species are thought to have arisen over evolutionary time from antagonistic interactions (1, 2). Among the most striking mutualisms suggesting antagonistic origins are the coevolved interactions between plants and insects that are both pollinators as adults and seed parasites as larvae. These include yuccas and yucca moths, figs and fig wasps, and globeflowers and globeflower flies (3–11). These associations are often cited as the classic textbook cases of mutualism (1, 12, 13), but the phylogenetic origins of all of these interactions have been unknown. Recent work, however, on the systematics and ecology of the Prodoxidae—the family including the yucca moths—allows for the first time an evaluation of which traits in the moths may be novel to the coevolved obligate mutualism between yucca moths and their hosts. Here we present evidence for *Greya politella* (Walsingham) (Lepidoptera: Prodoxidae), a close relative of the yucca moths, indicating that pollination mutualism has evolved more than once via seed parasitism in this moth family. Moreover, several of the behavioral and life history traits found in ovipositing and pollinating yucca moths suggested to be novel are likely not to be the direct result of coevolution with yuccas.

A female yucca moth (*Tegeticula*) oviposits into the ovary of a *Yucca* flower and immediately afterward actively pollinates the flower, at least if it has not been pollinated before (4). Pollination secures seeds for her developing offspring to feed upon, but the destruction of seeds is sufficiently limited that, on balance, the interaction is also beneficial to the plant (3–6). The sequence of behaviors followed by *Tegeticula* females during oviposition and pollination is generally con-

sidered to be the result of long-term coevolution between the moths and their yucca hosts (1, 12–15).

The 16 recognized species of *Greya*, which are endemic to western North America (16), are the sister group of five small genera that include the yucca moths (Fig. 1; 17–19). *Greya* species are highly host-specific on members of the families Saxifragaceae and Umbelliferae, whereas yucca moths and allies feed exclusively on the Agavaceae. The Agavaceae feeders include seed parasites, some of which also pollinate their hosts, as well as stem borers and leaf miners (5, 19). Similarly, *Greya* species include seed parasites, stem borers, and leaf feeders (16, 20), and as we demonstrate here, at least one seed-parasitic species is a major pollinator of its host.

Greya politella feeds almost exclusively on *Lithophragma* spp. (Saxifragaceae), the only exception being utilization of the closely related *Heuchera grossulariifolia* along the Clearwater River in Idaho (16). All life stages are strongly associated with the host plant: the adults appear only during the flowering period of the host, take nectar from flowers, and usually mate on the host. Eggs are deposited inside the ovary. Larvae feed initially on developing seeds and, after diapause, on vegetative parts. Pupation occurs in a cocoon on the host.

At least seven of the nine species of *Lithophragma* (21) are utilized as hosts by *G. politella* in different parts of its geographic range, but local populations are usually limited to one host (16). In southeastern Washington, the exclusive host is *Lithophragma parviflorum* (Fig. 2). Pollination by *G. politella* can potentially occur during either nectaring or oviposition. Both sexes take nectar by extending the proboscis past the anthers and stigmas down to the nectary atop the ovary. During oviposition, which is always preceded by nectaring ($n = 130$ ovipositions), a female struggles to push her abdomen down the narrow floral tube, extending a membranous eighth segment that normally rests inside the long seventh segment, to cut into the ovary and to deposit one to nine (mode 2–3; median 3; n flowers = 36) eggs. In the process, the abdomen touches both the anthers and the stigma (Fig. 2), and the eighth segment of the abdomen is often completely coated with pollen.

Efficacy of nectaring and oviposition in causing pollination was tested by measuring the seed production resulting from single moth visits. Seeds of *L. parviflorum* collected from numerous ramets in the experimental population near Granite Point in southeastern Washington (Whitman Co: T13N R46E S24; see ref. 22 for site description) in 1989 were stratified in early January 1990 in troughs, and individual seedlings were transplanted to tree tubes as soon as size permitted. The plants were grown at ambient temperature in Pullman, WA, without artificial lighting. When field and greenhouse plants were at the peak of flowering (March 28–April 4), greenhouse plants were brought to the source population. Individual plants were set out one at a time within the natural population and were observed until a moth alighted on a flower. Each plant was then transferred with its moth to a 1-m³ mesh cage containing about 20 additional plants. The moth is extremely tolerant of disturbance while on *Lithophragma* flowers and

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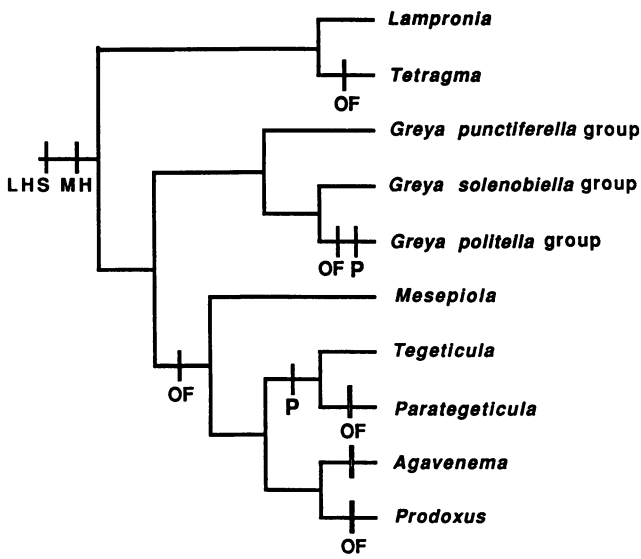


FIG. 1. Partially collapsed cladogram of Prodoxidae, indicating sites of evolution of life history traits critical to the evolution of pollination based on oviposition and of pollination itself. LHS, local host specificity; MH, mating on host; OF, oviposition in flower; P, pollinator. All genera from *Mesepiola* on feed on Agavaceae. The filled bars indicate gain, open bars indicate loss, and the mixed bar indicates both states present within the genus. Data are missing for one genus (*Tridentiforma*) and three *Greya* species. They have been excluded in this figure. Phylogeny is based on information in refs. 16–19, and life history traits are based on refs. 16, 17, 19, and unpublished data.

can be moved without any effects. After a single nectaring or oviposition in the flower, the moth was allowed to alight on its choice of flower on any other plant in the cage. Visited flowers were then marked and denied further visits. Experi-

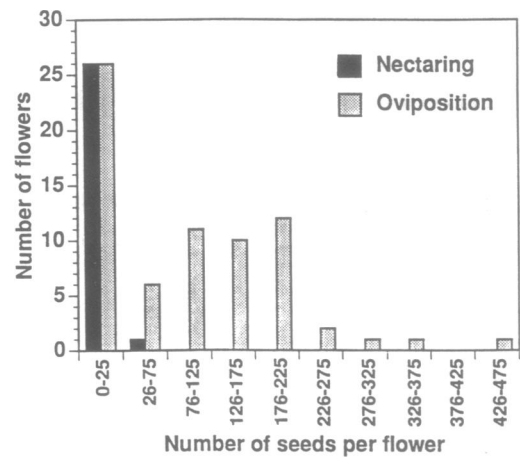


FIG. 3. Seed number in *Lithophragma parviflorum* resulting from a single bout of nectaring or oviposition by *Greya politella*. Filled bars, nectaring only ($n = 27$); stippled bars, oviposition ($n = 70$).

mental plants were returned to the greenhouse, and the flowers were dissected 9 days later. At that time, developing and nondeveloping ovules were readily separated, but moth larvae had not yet hatched from the eggs. Nonpollinated flowers abort shortly after anthesis, and 4 of 70 experimental flowers in the oviposition trials aborted before they could be examined for eggs. The results (Fig. 3) showed that nectaring alone contributed very little to seed set, causing no seeds at all in 59% of all cases, 10 or fewer in 85%, and never more than 27 seeds in any observation (median and mode = 0 seeds; $n = 27$ flowers). Individual flowers contained 276 ± 78 ovules (mean \pm SD; $n = 187$). Consequently, nectaring resulted in a rare single case in 10% seed set and, predominantly, none at all. In contrast, oviposition resulted in 28–453 seeds (median = 93) in 63% of the visited flowers and failed

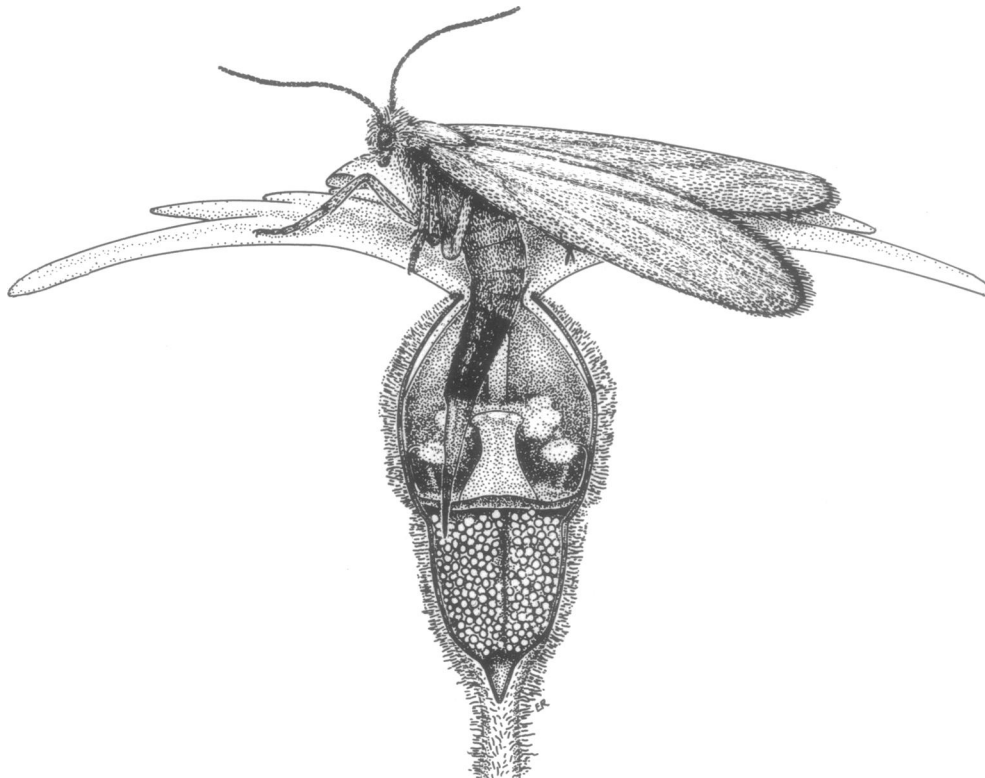


FIG. 2. *Greya politella* ovipositing into flower of *L. parviflorum* (flower shown in cross-section; composite from photographs). The flower is genetically self-incompatible (21). The actual corolla diameter is ca. 15–18 mm, and the forewing length of the moth is ca. 9–10 mm.

to result in seed production in only 37% ($n = 70$). Considering the exceedingly low efficiency of nectaring behavior in pollination, in effect only ovipositing females were potentially mutualistic in these interactions; that is, the interaction was mutualistic only when it was simultaneously antagonistic.

The cost of oviposition to the plant was generally small, averaging 10–14 seeds per larva in a separate sample ($n = 27$). With two or three larvae per flower, most developing seeds remain intact. Moreover, moths often failed or opted not to oviposit in a flower; 30 of 66 experimental flowers lacked eggs, thus further reducing the cost of the interaction to the plant.

The interaction between *G. politella* and *L. parviflorum* shares many of the features characterizing the obligate mutualism involving yucca moths: the moths display extreme local host specificity, mate on their host, and oviposit within the flower. The first two traits are ubiquitous among the prodoxids, while the latter condition is present in at least five genera, only some of which are pollinators of their host (Fig. 1). In *Greya*, it is confined to one group nested within the genus. Hence, even though these life history traits are necessary prerequisites for the evolution of pollination associated with oviposition, their presence in plesiomorphic antagonists suggests that these traits in yucca moths are not necessarily the result of long-term coevolution in mutualism with their yucca hosts as is commonly assumed.

The two major differences between the *Greya*–*Litho-phragma* and the yucca–yucca moth interactions are (i) the evolution of active pollination (and associated morphological structures) by yucca moths and (ii) the presence of copollinators in *L. parviflorum*. Floral morphology links pollination directly to oviposition in the case of *Greya* on *Litho-phragma*, whereas in the larger, more open flowers of yuccas this is not so. If a yucca moth fails to pollinate the flower where she oviposits, her progeny face certain starvation (3–6). By contrast, in most populations of *L. parviflorum*, other insects serve as efficient copollinators. At Granite Point, several species of bee-flies (Diptera: Bombyliidae) and solitary bees (Hymenoptera: especially Megachilidae) were effective pollinators and visited flowers at a higher rate than did the moths; among the most frequent visitors, single visits by *Bombylius major* caused a mean of 130 seeds (range 0–530, $n = 155$); *Bombylius* n.sp., 110 seeds (range 0–443, $n = 37$); *B. albicapillus*, 94 seeds (range 0–371, $n = 50$); and the bees *Osmia californica* and *O. bakeri* (not distinguishable in the field), 64 seeds (range 0–125, $n = 8$). Recording of all flower visits within three designated grids for 78 hr during 1990 and 1991 showed that 97.7–99.5% of all visits ($n = 5524$) were performed by insects other than *Greya politella*.

When the copollinators are abundant, moth larvae seldom face starvation even if their mother is a poor pollinator. Studies of marked plants at Granite Point over 3 years indicated that 80.3% of *L. parviflorum* flowers set some seed ($n = 451$ flowers), and the mean seed set ranged between 49% and 54%. Under these circumstances, selection would not necessarily favor active pollination by *Greya* females.

The other consequence of copollinators is that, unlike the interaction between yuccas and yucca moths, the interaction between *G. politella* and *L. parviflorum* is at least sometimes not mutualistic. Unlike the copollinators, *Greya* destroys

some of the seeds as larvae, and this damage may outweigh its contribution to pollination when copollinators are abundant. The fluctuating availability of copollinators will mean that the interaction between *G. politella* and *L. parviflorum* varies between antagonism and mutualism. Consequently, selection for an obligate mutualism similar to that between yucca moths and yuccas may be unlikely (23, 24).

Overall, the results indicate that several traits found in the yucca moths that are essential for the evolution of mutualism are present also in more primitive taxa, most of which are antagonists of their hosts. Hence, they are not necessarily special adaptations evolved for interactions with *Yucca*. Pollination mutualism has evolved through different behavioral pathways in *Greya* and yucca moths. This analysis also suggests that the traits requiring special analysis in understanding coevolution of yucca moths and yuccas are the evolution of active pollination by ovipositing females and the exclusion of copollinators by yuccas. This type of analysis, combining phylogenetic and ecological studies, should be useful in other studies of coevolution, where it is important to determine which traits are actually involved in the process of coevolutionary change.

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