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## The reproductive biology of *Vincetoxicum nigrum* (L.) Moench (Asclepiadaceae), a Mediterranean weed in New York State<sup>1</sup>

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LUMER, C. (Department of Biology, College of New Rochelle, New Rochelle, NY 10805) and S. E. YOST (Biology Department, Manhattanville College, Purchase, NY 10577). The reproductive biology of *Vincetoxicum nigrum* (L.) Moench (Asclepiadaceae), a Mediterranean weed in New York State. Bull. Torrey Bot. Club 122: 15–23, 1995.—The reproductive biology of *Vincetoxicum nigrum* was investigated in Dutchess County, New York. The small, dark purple flowers open in the morning and remain open for approximately 7 days. Although a heavy, fruity, unpleasant scent is emitted throughout the day and night, it is strongest during the day. The first flowers appear in mid-May, but peak flowering occurs in mid- to late-June, tapering off in early July. The flowers are autogamous, with 4.2% of 167 bagged flowers setting fruits with viable seeds, as compared to 11.1% of 72 unbagged flowers. In addition, the plants are clonal, with deep roots and rhizomes. Of 50 seeds tested in September (without a period of dormancy) 14 germinated, versus 20 of 50 that had overwintered. Of seeds from unbagged flowers, 49% germinated versus 40% of those produced by autogamy. Although more than 14 species of flies visited the flowers of *V. nigrum*, only six species, representing four families, carried *V. nigrum* pollinia. Flies pick up pollinia on their proboscises as they probe for nectar. A large territorial fly, *Sarcophaga* sp., defends flowers from visits by other flies.

Key words: Asclepiadaceae, fly pollination, pollinia, *Vincetoxicum*.

The morphology and pollination mechanisms of the Asclepiadaceae have long fascinated biologists (Brown 1883; Müller 1883; Robertson 1887a, 1887b). This interest has continued during recent years with extensive studies of several North American species of *Asclepias* (Bookman 1981, 1984; Broyles and Wyatt 1993; Kephart 1981, 1983; Kephart and Heiser 1980; Morse 1982, 1987; Morse and Fritz 1983; Shannon and Wyatt 1986; Willson and Price 1976, 1980; and Wyatt 1982). With the exception of Drapalik (1969), who incorporated pollination into his studies of the North American species of *Matelea*, and Sundell (1981), who studied tropical and subtropical species of *Cynanchum* subgenus *Mellichampia*, recent studies of the pollination mechanisms and breeding systems of other North American genera, both native and non-native, are lacking.

In this paper we report the results of our investigation of the reproductive biology of *Vincetoxicum nigrum* (L.) Moench (= *Cynanchum nigrum* (L.) Pers.), a non-native weedy member of the Asclepiadaceae in New York State. In 1883, Müller described the differences in floral morphology between those asclepiads whose pollinators pick up pollinia on their legs and those whose pollinators pick up pollinia on their mouthparts. We confirm and illustrate these differences with reference to *V. nigrum* and discuss their importance and relationship to pollination systems within the family. In addition, we explore the natural history of *V. nigrum* with regard to its establishment and reproductive success in New York.

**Materials and Methods.** SPECIES DESCRIPTION. *Vincetoxicum nigrum* (black swallowwort), a native of southwestern Europe (Markgraf 1972; Polunin 1969), is considered a garden escape in the northeastern United States (Gleason and Cronquist 1991), where it grows along roadsides and in other open, disturbed areas. It is a perennial herbaceous vine, which climbs to heights of 1–2 meters each season. The plants are clonal, from deep rhizomes. The tiny flowers form unbelliform clusters in the leaf axils of all but the lowest 3–4 nodes of the twining stems and mature in an irregular centripetal fashion.

<sup>1</sup> We thank S. Pagan for help with seed germination and L. N. Sorkin for fly identification. The flies have been deposited at the American Museum of Natural History, and voucher specimens of *V. nigrum* have been deposited at the New York Botanical Garden.

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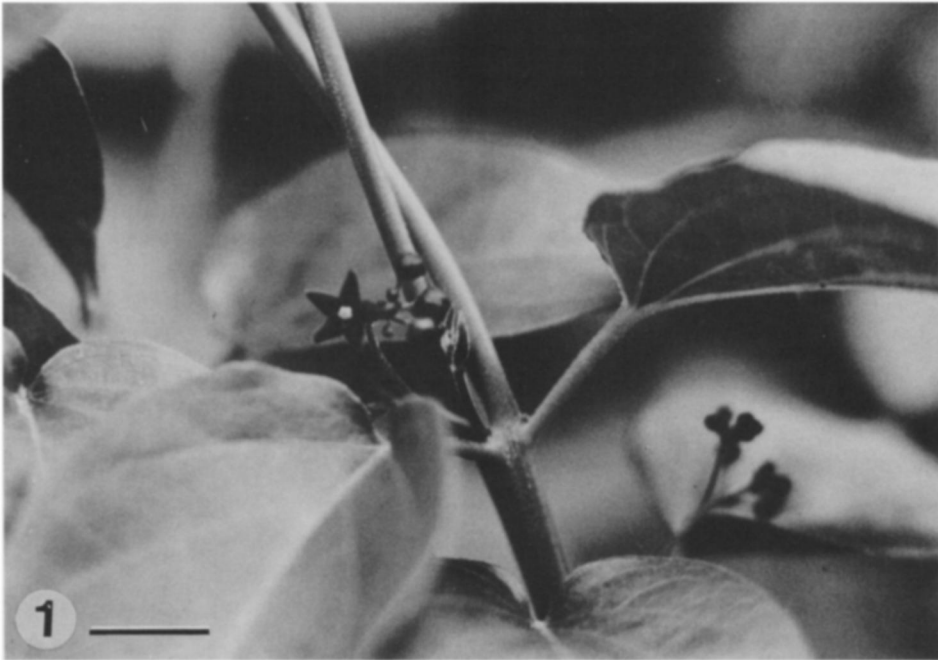


Fig. 1. Flower of *Vincetoxicum nigrum*, illustrating its small size and open dish shape. Bar scale = 10 mm.

The floral display is enhanced when several stems twine around each other, as commonly occurs. The flowers are small (6–8 mm across), open, and dish-shaped (Fig. 1). The corolla and corona are dark purple, succulent, and hairy, and the gynostegium is green. Typical of the family, there are 5 pairs of pollinia (each approximately 0.21 mm long). The fruit is a slender follicle (4–6 cm long), although twin follicles are not uncommon, and the comose seeds are wind dispersed.

**STUDY SITE.** The main study site was in Hudson Highland State Park, off Route 9D, 3.2 km south of Beacon, Dutchess County, New York. In disturbed sunny areas, which had been repeatedly cut over, *V. nigrum* formed dense clumps, twining about itself, as well as other weedy plants, such as *Toxicodendron radicans* L., *Euphorbia cyparissias* (L.) Kuntze, and *Solidago* spp. Additional observations were made of populations growing along Route 9D, on Slocum Road in Beacon, and at Iona Island and Piermont Marsh, approximately 21 km south of Beacon.

**PHENOLOGY.** The length of the growing season, as well as the flowering and fruiting seasons, was recorded in 1985 and in 1986. To determine floral phenology, 31 buds were tagged and observed daily as they opened, closed, and abscised.

**FLORAL MORPHOLOGY.** Specimens were observed and photographed using a JEOL T-20 scanning electron microscope (SEM). Flowers were prepared for SEM by fixation in 3% glutaraldehyde in phosphate buffer, dehydration in an acetone series, critical-point-drying in a Polaron model E3000 critical-point-drying apparatus using CO<sub>2</sub> as a transitional fluid, and gold coating in an ISI model PS-2 sputter-coater. Pollinia, and flies with pollinia, were air-dried, and then gold coated in the same manner as the flowers.

**FLORAL VISITORS.** Flowers were observed on 38 different days, for a total of 60 hr between dawn and midnight. At these times we noted all insects visiting the flowers and their behavior. In addition, we timed the visits of 30 flies to individual flowers.

Floral visitors were collected in 1985 and 1986. They were inspected under a dissecting microscope for number and location of *V. nigrum* pollinia. Selected individuals were then inspected under SEM.

**BREEDING SYSTEMS.** The possibility of autogamy was tested by enclosing 167 flower buds on seven stems in fine mesh nylon bags and counting mature fruits at the end of the growing season. These were compared to 72 tagged, but un-

bagged, flowers that were observed weekly from the day the flowers first opened until mature fruits formed. The flowers were too small for us to determine the numbers of pollinia inserted, to pollinate by hand, or to allow extraction of nectar with capillary tubes.

The possibility of clonal growth was studied in May 1985. Several plants were dug up and their belowground roots and stems examined for signs of vegetative reproduction.

**SEED GERMINATION.** To determine whether seeds produced by autogamy were viable, and, if so, to compare their germination rate with that of seeds from open-pollinated flowers, seeds from fruits produced by autogamy (15 seeds from bagged fruits) and seeds from open-pollinated fruits (65 seeds from unbagged fruits) were collected at the study site on 9 February 1986. Germination tests were begun 3 weeks later. The data were analyzed using the Z statistic to compare the difference between population proportions (Zar 1984).

In addition, seeds were tested for dormancy requirements. Fifty fresh seeds were collected from newly opened pods on 7 September 1986, and germination tests were initiated 2 days later. Seeds were germinated by placing them in 100 mm diameter glass petri dishes on moistened filter paper. The petri dishes were closed, but not sealed, and kept on the laboratory bench in indirect light at room temperature (approximately 22°C). The filter paper was kept moist by adding water as needed. A maximum of 25 seeds was placed in each petri dish.

**Results. FLOWERING SEASON.** In 1985 and 1986, in Hudson Highland State Park, flowering began in late May, peaked in mid-June, and ended in mid-July. At other locations slight variations were noted. Flowering began 2 weeks earlier at the more southerly locations of Piermont Marsh and Iona Island (the first flowers were seen in mid-May), and in the shadier site along Slocum Road, *V. nigrum* bloomed through mid-August.

**PHENOLOGY.** Flowers began to open just after sunrise, between 5:30 and 6:30 a.m., and took 20–30 min to open. The petals opened one at a time, so slowly that the movement was almost imperceptible. Individual flowers remained open 6 to 8 days, and flowers often remained on the plant 1 to 2 days after closing.

Although we were unable to test for nectar due to the small size of the flowers, we could see a glistening wetness in the areas probed by the floral visitors. We assumed this to be nectar. This “nectar” became visible soon after the flowers opened and appeared to be present during the life of the flower. The flowers have a heavy, nauseatingly sweet scent, reminiscent of rotting fruit. Although the odor was present at night, as well as during the day, it became noticeably stronger during mid-day when the sun was strongest. On hot humid days, the smell was often overwhelming.

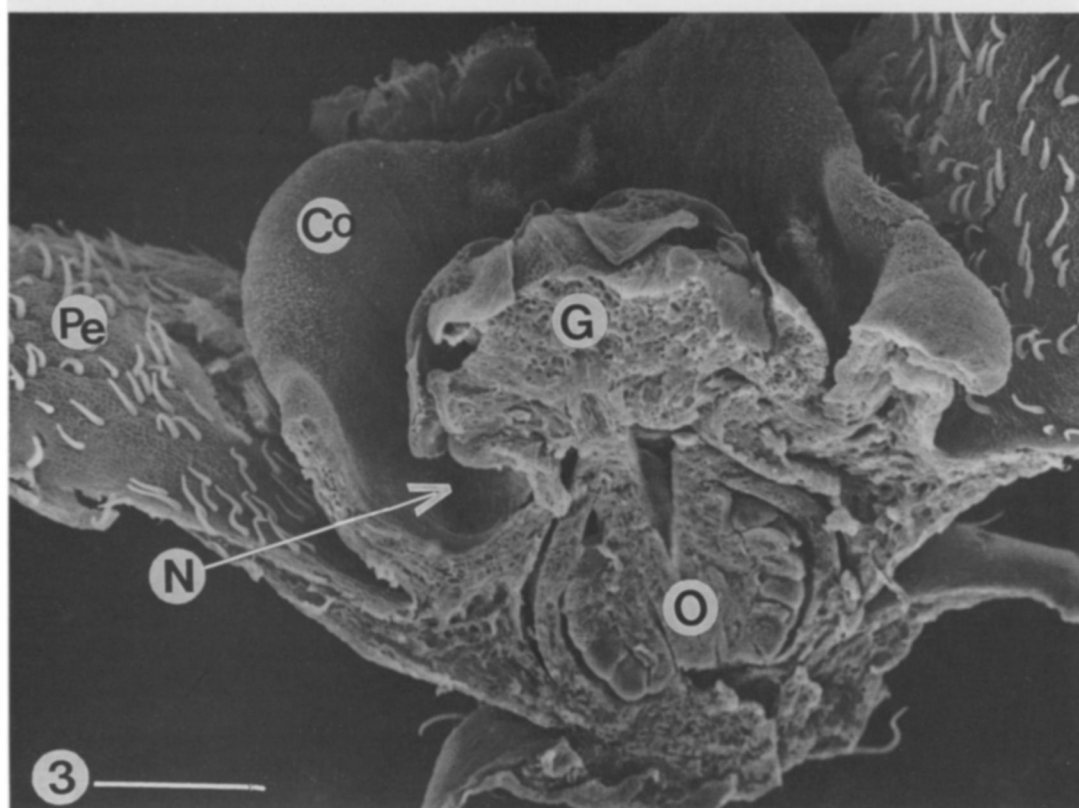
The first fruits began to dehisce and release seeds in mid-August. Later-developing pods reached maturity and released seeds through early October.

**FLORAL MORPHOLOGY.** Nectar areas are located opposite the corpuscula (Fig. 2) and are angled under the gynostegium (Fig. 3). The pollinium of *Asclepias syriaca* is approximately 6 times larger than that of *V. nigrum* (Fig. 4).

**FLORAL VISITORS.** Flies were the principal floral visitors and the only possible pollinators of *V. nigrum* during the period of this study. During our hours of observation, at least fourteen species of flies, representing six families, were observed and collected. Of these, six species, representing four families, carried from 1 to 10 pollinia (Table 1). The most important dipteran visitors were the blowflies *Pollenia rudis* and *Phaenicia sericata* (Calliphoridae) and the flesh flies *Sarcophaga* spp. (Sarcophagidae). Unidentified members of the Anthomyiidae and Tachinidae also carried pollinia of *V. nigrum*. Flies that did not carry pollinia included *Lucilia illustris* and two unidentified members of the Calliphoridae, *Poecilographa decora* of the Sciomyzidae, one unidentified species of Sarcophagidae, one member each of the Anthomyiidae and Tachinidae, and *Rivellia* spp. of the Platystomatidae (Table 2). In addition, seven gall gnats (Cecidomyiidae) were found dead, having been trapped by the flowers.

Fly visits lasted 3–120 sec, with most visits taking 10 to 40 sec before a fly moved to another flower. Flies inserted their proboscises into each of the five nectar areas in turn, while standing on the petals of the same or adjacent flowers.

Most of the pollinia were found on the pollinators' mouthparts (Figs. 5 and 6). Only one fly had pollinia on its abdominal hairs, and another had pollinia on one leg. The flies did not carry foreign pollen, or strings of pollinia and corpus-



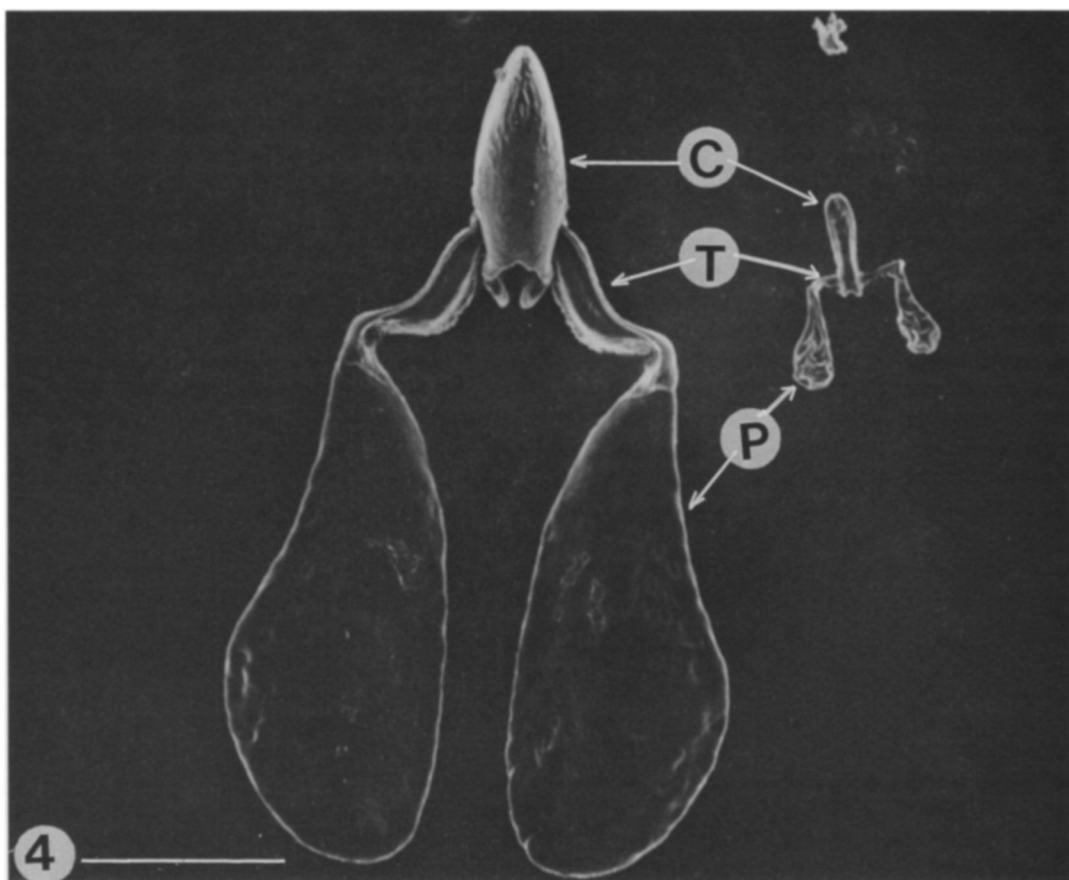


Fig. 4. SEM of a pollinarium of *Vincetoxicum nigrum* (right) and a pollinarium of *Asclepias syriaca* (left), illustrating the difference in size. Bar scale = 0.5 mm. Corpusculum (C), pollinium (P), translator arm (T).

cula, as has been described for floral visitors to species of *Asclepias* (Morse 1981; Robertson 1887a; Volovnik 1982).

Territoriality was displayed by an unidentified species of *Sarcophaga*. These flies actively defended an area against all other flies. An individual would sit on a leaf in the midst of *V. nigrum* flowers, and when other flies landed on flowers in the area it would fly directly at them, while making loud buzzing sounds. This caused the other flies to leave. When we removed one of these defenders, another individual of the same species soon took its place.

**BREEDING SYSTEMS.** Mature fruits with viable seeds were produced by 4.2% of the bagged flowers and by 11.1% of the unbagged open-pollinated flowers. (Of 72 unbagged flowers, 24 (33.3%) initiated fruits, but most of these aborted before reaching maturity, so that only 8 (11.1%) produced mature fruits.)

We found that what appeared to be several plants were often one, connected by horizontal underground stems. Roots and rhizomes grew at a depth of about 50 cm.

**SEED GERMINATION.** Seeds produced by autogamy were viable, and their germination rate

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←  
Figs. 2–3. SEM of flowers of *Vincetoxicum nigrum*. Bar scales = 0.5 mm. — 2. Surface view showing the placement of a nectar area (N) opposite a corpusculum (C). Corona (CO), gynostegium (G), petal (Pe), stigmatic slit (S). — 3. Longitudinal section, showing base of nectar area (N) angled under gynostegium (G). Corona (Co), ovary (O), petal (Pe).

Table 1. Dipteran visitors carrying pollinia of *Vincetoxicum nigrum*.

	Number caught	Placement of pollinia	Number of pollinia/fly
<b>Calliphoridae</b>			
<i>Pollenia rudis</i> Fabricius	5	proboscis, 1 on abdomen	2, 2, 2, 4, 5
<i>Pollenia</i> , prob. <i>rudis</i>	3	proboscis, 1 left front leg	2, 6, 10
<i>Phaenicia sericata</i> Meigen	3	proboscis	1, 2, 5
<b>Sarcophagidae</b>			
<i>Sarcophaga</i> spp.	5	proboscis	1, 1, 2, 2, 4
Unidentified #1	1	proboscis	1
<b>Anthomyiidae</b>			
Unidentified #2	2	proboscis	2, 4
<b>Tachinidae</b>			
Unidentified #3	1	proboscis	4

(40%) was not significantly different from that of seeds produced by unbagged open-pollinated flowers (49%) ( $Z = 0.64531$ ;  $P = 0.51873$ ). Of the seeds collected and germinated in September 1986, 28% germinated, whereas seeds that overwintered had 49% germination.

**Discussion.** This study indicates that, in New York, *V. nigrum* is pollinated by small, unspecialized flies with short tongues. The flies are apparently attracted to the flowers by their fetid odor of rotting fruit and dark purple color.

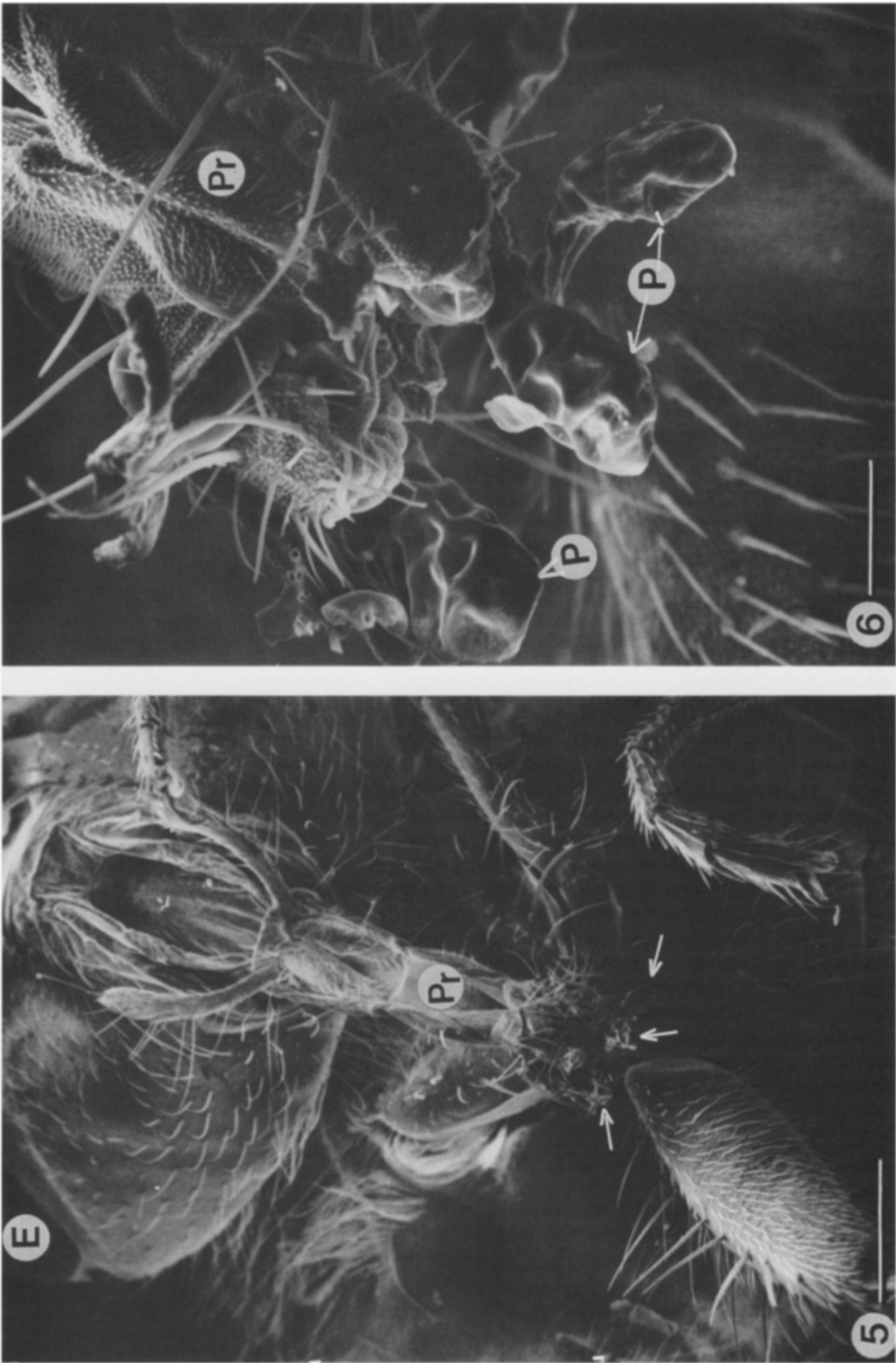
Flies are a large and important group of pollinators, ranging from the highly specialized syrphid flies (Syrphidae) and the long-tongued *Bombylius* (Bombyliidae), to unspecialized small flies with short tongues (Faegri and van der Pijl 1979; Müller 1883; Proctor and Yeo 1972). Small, un-

specialized flies are important floral visitors in diverse habitats worldwide, and to many plant families, including the Asclepiadaceae (Faegri and van der Pijl 1979; Proctor and Yeo 1972). Flowers pollinated by unspecialized flies normally belong to one of two pollination syndromes: sapromyophily or myophily (Faegri and van der Pijl 1979; van der Pijl 1961). Sapromyophilous flowers release fetid odors, are dark brown-purple, or have dark brown-purple splotches, often form traps, and lack nectar. Carrion and dung flies visit these flowers and are often deceived by the floral odor, color, and texture of the petals, into laying their eggs and thereby pollinating the flowers. *Stapelia*, for example, has foul-smelling, dark red or flesh colored flowers, in which flies lay eggs and effect pollination, and the trap flowers of *Ceropegia* use scent to attract flies interested in egg laying (Faegri and van der Pijl 1979; Proctor and Yeo 1972). Myophilous flowers, on the other hand, are regular, lack a three-dimensional depth effect, have light or dull colors, little odor, and easily accessible nectar. However, it appears that some species combine elements of both syndromes. For example, *Vincetoxicum officinale*, the most common asclepiad in Europe, is pollinated by flesh flies (Sarcophagidae). The flowers are greenish-white and have nectar, characteristic of myophilous flowers, but they have a disagreeable odor (Proctor and Yeo 1972), which is more characteristic of sapromyophily.

The situation with *V. nigrum* appears to be even more complex. The regular flowers lack depth effect and have easily accessible nectar, both features of myophily, but the dark purple color and fetid odor are more characteristic of sapromyophily. In New York, flies visit the flowers for nectar. During the two years of our study,

Table 2. Dipteran visitors not carrying pollinia of *Vincetoxicum nigrum*.

	Number caught
<b>Calliphoridae</b>	
<i>Lucilia illustris</i>	5
Unidentified #4	1
Unidentified #5	1
<b>Sarcophagidae</b>	
Unidentified #6	2
<b>Sciomyzidae</b>	
<i>Poecilographa decora</i>	1
<b>Anthomyiidae</b>	
Unidentified #7	1
<b>Tachinidae</b>	
Unidentified #8	1
<b>Platystomatidae</b>	
<i>Rivelia</i> spp.	4



Figs. 5-6. Bar scales: Fig. 5 = 0.5 mm; Fig. 6 = 0.1 mm. — 5. SEM of a number of *Vincetoxicum nigrum* pollinia (arrows) on the proboscis (Pr) of the fly *Pollenia rudis*. Eye (E). — 6. Close-up of pollinia (P) from Fig. 5. Proboscis (Pr).



we found no evidence of flies laying eggs on *V. nigrum* flowers.

On the other hand, we did observe definite displays of territorial defense by *Sarcophaga* sp. These flies were large, compared to the other dipteran visitors, and consistently chased away other floral visitors by flying directly at them, while making a buzzing sound. Because these flies did not lay their eggs on the flowers, and visited the flowers for nectar only, we believe that *V. nigrum* flowers are a high quality nectar source for flies.

Müller (1883) described an association within the Asclepiadaceae between the location of nectar in the flower and placement of pollinia on an insect. In species where the nectar alternates with the corpusculum (*Asclepias*, *Hoya*), pollinia are picked up on the legs of the insects, whereas in species where the nectar is opposite the corpusculum (*Vincetoxicum*, *Cynanchum*, and *Stapelia*), insects pick up pollinia on their mouthparts. This has also been confirmed by Drapalik (1969) for *Matelea*, and Kunze (1991) for several species, including *Vincetoxicum officinale*. In *V. nigrum*, flies sit on a flower, or an adjacent flower, and probe for nectar. The chance that their proboscises will pick up and/or insert pollinia is enhanced by the fact that the nectar area lies partially under the gynostegium. The flies' proboscises exit the nectar at an angle and, guided by the stigmatic slit, catch on the corpusculum, thus picking up a pollinarium.

When small insects visit larger asclepiads (e.g., *Asclepias*), they are often caught by a proboscis or leg. If they are unable to free themselves, they die. This has been recorded many times (Faegri and van der Pijl 1979; Frost 1965; Morse and Fritz 1983; Robertson 1887a; Volovnik 1982). Although *V. nigrum* flowers are very small, they do trap small gall gnats.

In many of its reproductive traits, *V. nigrum* is a typical weed (Baker 1974). The plants reproduce vegetatively through extensive underground rhizomes. Any stand of aboveground stems is probably composed of only one, or perhaps 2 or 3 different genets. Moreover, *V. nigrum* can set fruits with viable seeds without a pollen vector. Fertilization probably occurs by germination of the pollen tubes directly into the gynostegium. Woodson (1941) noted that pollen tube germination within pollinia is common in *Asclepias*, and germinated pollen tubes can easily be seen on herbarium specimens. Kunze (1991) reports autogamy as a result of in situ pollen tube germination in *Tylophora*. He also notes that

Chaturvedi and Pant reported that *T. hirsuta* is reliant on self-pollination. Autogamy may be an important alternative for plants dependent upon small, unspecialized flies as pollinators. Small flies are not always dependable pollinators, because they do not normally travel far and are therefore dependent upon food sources that are near their breeding places (Faegri and van der Pijl 1979).

Fruit-set in *V. nigrum* is enhanced by long-lived flowers. The flowers are open for approximately one week, which is longer than most temperate or tropical plants (Wyatt 1981), but comparable to other asclepiads (Drapalik 1969; Morse 1987; Willson et al. 1978; Wyatt 1981). Long-lived flowers are also common in the Orchidaceae and may be related to the fact that the pollen grains move together as a unit within pollinia, rather than as separate grains. The pollination mechanism in both the Asclepiadaceae and the Orchidaceae requires a complex interaction between vector and plant, and long-lived flowers increase the possibility that pollinia will be removed and inserted.

Given the clonal growth habit of *V. nigrum*, it is questionable whether pollen moves between different genets with any regularity. Plants in our study areas were clumped, and each clump (or clone) was a minimum of 4 m away from the next nearest clump, so that gene flow between different genets appears to be restricted.

Pollination of *V. nigrum* in the New York area may be enhanced by the presence of the fly, *Pollenia rudis*. This fly is of European origin and considered an important pollinator in Europe (Proctor and Yeo 1972). It is possible that *P. rudis* is a pollinator of *V. nigrum* over at least some of its European range, but that information is not presently available.

The flexible breeding system is also enhanced by seeds that do not require either dormancy or stratification to germinate, which probably reflects the southern Mediterranean origin of *V. nigrum* (Polunin 1969). Mediterranean winters are mild and wet and the summers are hot and dry (Walter 1985), so that seeds germinating in the late fall become established in the mild, wet winter (Cox and Moore 1993). Therefore, in New York, seeds from early-maturing fruits of *V. nigrum* may germinate and become established before the first frost, whereas seeds from late-maturing fruits overwinter and germinate in the spring.

Roots and rhizomes which penetrate deeply into the soil are also adaptive in Mediterranean

climates, as plants with deep roots are able to obtain water during periods of summer drought (Walter 1985). Kerner (1886) noted that *Cynanchum vincetoxicum* has roots that draw the stems down with them as they grow. In our study area, the deep roots permitted *V. nigrum* to resprout in one area, after the soil was removed to a depth of more than 40 cm.

*Vincetoxicum nigrum* may be more widespread than is presently thought, since the tiny flowers make it easy to overlook. Characteristics such as autogamy and seeds that do not have to overwinter, coupled with the ability to spread through underground rhizomes, help make *V. nigrum* a successful colonizer of disturbed areas in southern New York.

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