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FLORAL BIOLOGY OF PROBOSCIDEA LOUISIANICA (MARTYNIACEAE)

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In July 1973, while on the faculty of the University of Oklahoma Biological Station, I studied the floral biology of the unicorn plant, *Proboscidea louisianica* (Miller) Thellung. A few additional observations were made in August, 1974, in Salt Lake City, Utah, on plants of this species in a home garden. Results of my study are reported in this paper. Previously I had sought in vain for published information on most aspects of this subject. Bracketed data below refer only to Utah plants; otherwise, the account is based on Oklahoma plants although almost all data apply to western *Proboscidea* as well.

The ten individual Oklahoma plants observed were in a sandy grazed field overlooking Lake Texoma, 1 mile west of Willis and 2 miles west of the Biological Station, Marshall County. In addition to the unicorn plants, prominent forbs in the field were *Cnidoscolus texanus*, *Monarda punctata*, *Helenium amarum*, and *Verbesina encelioides*. Grasses included *Axonopus affinis*, *Cenchrus pauciflorus*, *Cynodon dactylon*, *Eragrostis sessilis*, and *Tridens albescens*. Observations were begun on 1 July and were concluded on 21 July. During the first three days (not successive), I watched the flowers for a half-hour period every four hours throughout the day. Because no insect or other visitors to the flowers were noted at night, I thereafter confined my observations mostly to daylight hours.

Thirty-five flowers — at least three from each of the 10 plants — were tagged and numbered for study of time and pattern of opening, duration of anthesis, and early stages of fruit development. Every time I observed these flowers I examined the stigmas for the presence of pollen. Additional data collected from tagged and also from untagged flowers included flower color and odor, kinds of insect visitors, and duration and pattern of their visits. Insects were caught in a 1-inch-wide killing vial placed over the throat of the corolla; the vial was quickly capped as the insect backed into it from the corolla tube.

FLOWERS

A “face” view and a side view of a unicorn plant flower are shown in Figure 1. The flowers of *Proboscidea louisianica*, each bracteate at the base of its pedicel and bibracteolate at the base of its calyx, are in several-flowered, terminal, erect racemes. The bracts are deciduous at or even before the beginning of anthesis. [In the Utah plants they persisted longer — until the fruits were 3-6 cm long.] A single raceme may show floral development from unopened buds distally to full-sized fruits proximally. The axis of the raceme elongates as the fruits mature.

The synsepalous, somewhat zygomorphic calyx is five-lobed and is split to the base between the two lowermost lobes. It is deciduous soon after anthesis. [In Utah plants, many calices persisted until the fruits were nearly full sized.] The corolla tube is narrowly cylindrical at its base but rather abruptly widens at about the level of the top of the ovary; from there it is narrowly campanulate. The corolla limb is five-lobed, the two upper lobes erect, the two lateral lobes spreading to reflexed, and the lower lobe projecting forward in the plane of the tube. The upper lobes of the corolla are external in bud and overlap each other and the lateral lobes. The laterals overlap the lower lobe, which is completely internal. Just prior to anthesis, the corolla in bud is very pale whitish yellow, sometimes

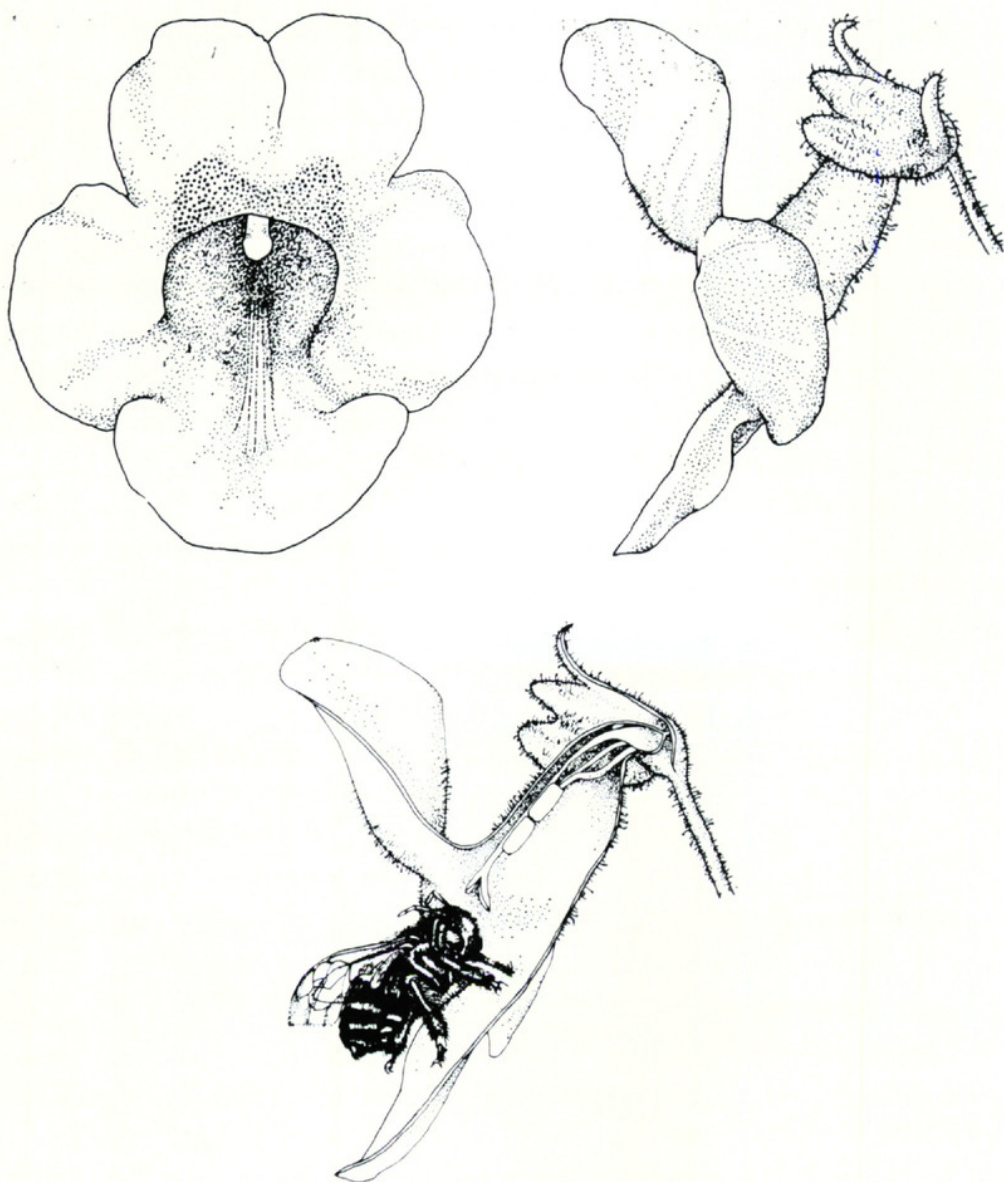


Fig. 1. Flower of *Proboscidea louisianica*. Upper left: "face" view. Upper right: side view. Lower: cutaway view, showing *Melissodes communis* alighting on lower lip.

tinged with green. As the corolla opens, the yellow and green disappear. At full anthesis the corolla is white with a pink tinge that increases with age. Orange guidelines arise centrally on the lower lobe and extend back along the lower side of the tube to between the bases of the lower pair of stamens. Minuscule purplish dots sprinkle the

inside of the tube and spill over onto the corolla throat and onto the bases of the two upper lobes; those on the lobes are larger than the others.

The four stamens are didynamous and epipetalous. In bud the anthers are free from each other and each is bent into a broad "V." As the flower develops, the filaments lengthen and the anthers straighten. The anthers of each pair become connate side to side; tips of the anthers of one pair of stamens become connate to adjacent tips of the anthers of the other pair. By anthesis, the "anther box" (as I call the structure composed of the connate anthers) is positioned midway on the upper surface of the corolla tube behind the stigma and the distal portion of the style. Opening of the anthers occurs by longitudinal dehiscence of the anther walls on the side facing the axis of the tube. A mass of pollen is thus precisely in place for some of it to be picked up by the hairs on the backs of pollinating insects ascending the tube. Stages in the development of the anther box are shown in Figure 2.

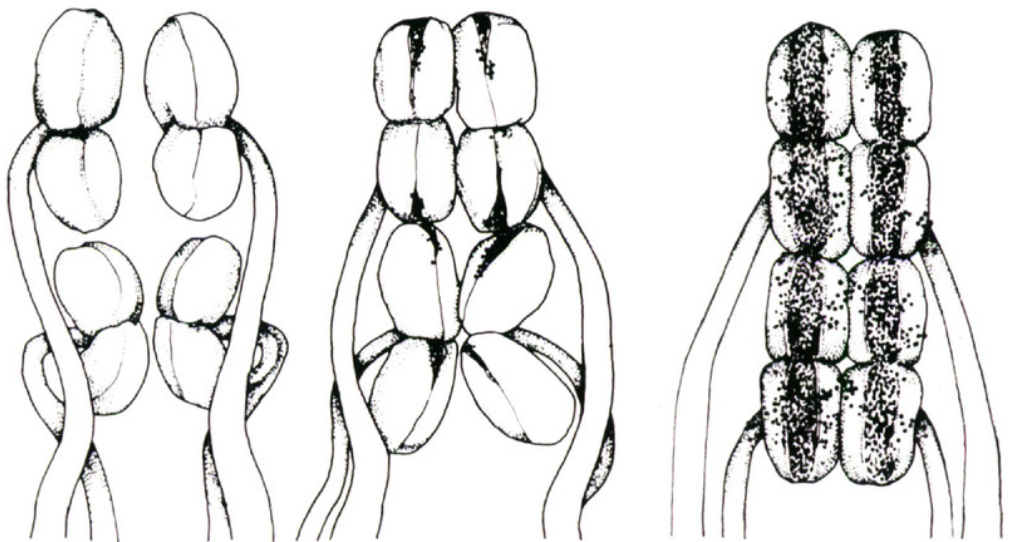


Fig. 2. Stages in the development of the anther box of *Proboscidea louisianica*. Left: young stage, the anthers not yet in contact and not yet dehiscent. Center: somewhat older stage, anther contact and dehiscence beginning. Right: at beginning of anthesis, anthers in contact and fully dehiscent.

In every flower I examined, a staminode (a fleshy protuberance about 1.5-3 mm long) occupied the place of the fifth stamen. That the staminode may sometimes be lacking is suggested by some descriptions of *Proboscidea* flowers that fail to mention it, although I prefer to think this results from faulty observation of floral morphology.

The ovary is bicarpellate and unilocular; each of its two placentae is intruded and expanded into a broad lamella. The slender style is about thrice as long as the ovary. The stigma, positioned well in front of the anther box, is sensitive to even the slightest touch, its two flat lips, with their receptive inner surfaces, closing together rapidly (within about 2 seconds). After about 5 minutes (in the first of a series of touches) the lips will have spread apart again. Opening and closing of the lips occur mainly because of movement of the lower lip. When the lips are open, the lower one is in position to "scoop" pollen from the back of an insect passing beneath it. Immediately after so doing, it closes against the upper one, trapping the pollen between them and thus preventing its possible dislodging as the insect leaves the flower. The closing of the lips also may prevent or significantly reduce transfer of pollen of a flower to the stigma of that flower by the exiting insect — the receptive surfaces of the stigma are simply not exposed. When the lips are well covered with pollen, they do not reopen.

In a series of touches, the time required for closing of the lips increases hardly at all, but the time for their spreading apart again increases considerably, resulting in the phenomenon of stigmatic "fatigue." In four flowers, each on a different plant, I observed stigma response to eight successive touches, each touch (after the first) being made after the lips had returned to the fully open position. The average times required for this return were: Touch I — 5 minutes; II — 8 minutes; III — 15 minutes; IV — 18 minutes; V — 18 minutes; VI — 20 minutes; VII — 25 minutes; and VIII — 25 minutes. Observation of "fatigue"

in the stigma was halted after eight touches because of fatigue on the part of the observer.

Glandular hairs, producing a copious, viscous, and sweet secretion, are abundant on the bases of the filaments and on the area of the corolla tube between the bases of the filaments. No secretion was noted elsewhere in the flower. It is presumably this secretion that pollinators seek, although I was unable to demonstrate this (stomach analysis of pollinators of the unicorn plant should be carried out).

At full anthesis the pedicel is ascending, forming a 35° - 45° angle with the vertical (i.e., the axis of the raceme). The calyx is nearly 90° from the vertical. The corolla, however, is sharply declined, its tube and lower lobe being at about 135° , so that visiting insects must move upward into the tube. In a single raceme I saw no more than three flowers in anthesis at one time; usually there was only one, infrequently two.

The flowers typically begin to open in the afternoon, mostly at about 6:00 PM but occasionally as early as 1:00 PM or as late as 11:00 PM. As opening proceeds, the upper lobes of the corolla become directed forward, exposing the lateral lobes. The laterals then become directed forward, exposing the lower lobe. Finally the lower lobe, too, assumes the forward position, which it retains. The upper lobes become gradually erect as the laterals spread or become somewhat reflexed. The opening process lasts from 3 to 6 hours.

The anthers have dehisced by the time the flower is half open. The lips of the stigma, however, do not part until the flower opens fully.

The odor of the flowers is difficult to describe. Somewhat unpleasant, rather penetrating, it was characterized by an Oklahoma colleague as "aminoid." I cannot improve upon this description. The secretion from the glandular hairs covering the stem and leaves imparts to hands that handle the plant an odor similar to that of the flowers.

Once a flower is open it stays so for the duration of anthesis. Most flowers last about 40 hours, the corolla

dropping suddenly — usually at about noon to 3:00 PM of the third day. Flowers on some plants, however, may last only 30-36 hours. Within 24 hours after corolla fall, the pedicel moves to about 90° from the vertical. Within another day it becomes reflexed to about 135° , the position it retains during fruit development.

Flowers on individual plants behave similarly with respect to opening time, time required for the flowers to open fully, and duration of anthesis. This suggests that these may be genetically-controlled features.

INSECT VISITORS

Visitors to the flowers were infrequent and all were bees (Hymenoptera, Apoidea); many flowers appeared not to be visited at all, as evidenced by the lack of pollen on their stigmas. Pollinators were the following:

Family Anthophoridae

Anthophora occidentalis Cresson

Centris subhyalina Fox

Mellisodes communis Cresson

Family Halictidae

Augochlorella striata (Provancher)

[In the Utah plants the only pollinator taken was *Bombus fervidus* (Fabricius), of the family Apidae.]

These fast flying bees behaved similarly during visits to the flowers. Landing on the lower lip (see Figure 1), they quickly ascended the corolla tube, first brushing against the stigma, the lips of which then closed, and then against the anther box. Several (5-8) seconds later, they backed out of the tube and resumed flight, usually, but not always, going to another *Proboscidea* flower on the same or on a different plant. The amount of pollen deposited on the stigma as the result of a single visit of a bee varied from many grains (55, in one count) to almost none, depending on how much pollen the insect was carrying. The bees taken as specimens showed most pollen adhering to the hairs on top of the thorax but also some on those of the

face, abdomen, and legs. The pollen baskets (corbiculae) on some of the specimens were full of *Proboscidea* pollen — and, in some instances, of other, unidentified kinds as well.

Several small bees of the genus *Lasioglossum* (family Halictidae) visited *Proboscidea* flowers but were not pollinators. They landed on the lower or lateral lobes and walked immediately to the anther box, from which they took pollen and packed it into their pollen baskets. At no time did they contact the stigma or even the style.

Unicorn plants are markedly viscid pubescent on the stems and leaves. The glandular hairs entrap many minute insects (including thrips, fairyflies and other Hymenoptera, *Drosophila* and other Diptera, aphids, Hemiptera, and weevils and other Coleoptera).

POLLINATION EXPERIMENTS

An exclusion experiment was set up by erecting a crude "tent" of cheesecloth around a large *Proboscidea* plant. The tent effectively excluded the bees that, by that time, I had recognized as pollinators. During the 14 days of the experiment, eight flowers on the enclosed plant came into and passed anthesis. One of these I pollinated by hand with pollen from a flower in a neighboring raceme on the same plant; it did not set fruit. Another one I pollinated by hand with pollen from another plant; it set fruit. The six other flowers, unpollinated, dropped soon after anthesis.

In an additional mini-experiment I pollinated, with its own pollen, a flower on each of three plants and then bagged each flower to exclude all other pollen. These flowers produced no fruits.

[In Utah, I pollinated four newly-opened and previously-unpollinated *Proboscidea* flowers on one plant: flower 1, with its own pollen; flower 2, with pollen from another flower on the same plant; and flowers 3 and 4, with pollen from another plant. The flowers were then bagged to exclude insects. Flowers 1 and 2 set no fruit; flowers 3 and 4 had developed fruits 6 cm long by the time my observations of them were concluded.]

The results of these limited experiments suggest (1) that *Proboscidea louisianica* fruits do not develop in the absence of pollination and (2) that pollination of a flower of this species with its own pollen or with pollen from another flower on the same plant is fruitless. Further such studies, however, are obviously necessary to reach definite conclusions.

FRUITS

Twenty-three of the tagged flowers produced no fruits. Instead, they dropped, pedicel and all, within 3 days after the corollas fell. On the stigmas of these flowers I had observed no pollen or but a few grains.

Fruit development in the other tagged flowers, each of which had been well pollinated by bees, was rapid, at least in the early stages observed by me. Three days after corolla fall, the fruits begin to protrude from the calyx. Three days later, they were as much as 6 cm long, and the calyx had dropped. At this point my observations of developing fruits were halted — my teaching assignment at the Biological Station was over. However, seemingly nearly mature fruits were carried to my home laboratory in the hope that, as they dried out, they would behave as if they were *in situ* at Lake Texoma. I believe that they did just this. Additionally, many last year's fruits were collected from the ground for study.

At maturity — but before drying and dehiscence — the fruits have a body 6 - 10 cm long and 2 - 3 cm thick and an arcuately-upcurved, slender beak 1.5 - 3 times as long as the body. During drying of the fruit, the exocarp, starting along the upper suture, sloughs off in two valves, revealing the stony, sculptured endocarp and the intricate crest (see Figure 3). The beak splits longitudinally into two sharp-pointed, hooked "horns." With further drying, these "horns" become oriented in such a way that they are reminiscent of mammoth tusks with their tips pointing toward each other or, when extremely dry, even overlapping.



Fig. 3. Fruits of *Proboscidea louisianica*. Upper left: fruit not yet shed from plant, splitting of exocarp beginning to reveal crest. Lower left: fruit shed, lying on ground, exocarp sloughing off, fruit beak and body splitting longitudinally. Right: fruit with exocarp gone and longitudinal splitting completed.

The shape and center of gravity of the dehisced fruits are such that these fruits usually lie with the distal or median portion of the lower surface of the body in contact with the ground, with the proximal portion somewhat elevated, and with the "horns" pointing upward (see Figure 3). This position is the one in which the fruit is most likely to hook onto the feet or ankles of animals, including students of floral biology. Many times I have had to remove *Proboscidea* fruits that had hooked onto my stockings. One of my students at the Biological Station, mentioning that an Oklahoma name for *Proboscidea* is "cow catcher," told me that one of her minor chores, as a child on a farm, was periodically to gather and remove from the barn floor the unicorn plant fruits that stock had brought in. Presumably — although I did not personally observe this — seeds are scattered from the fruits as animals carry them about. The seeds, large and black, are 7-10 mm long. The number of seeds per fruit, in the 10 fruits whose seeds I counted, ranged from 15 to 67.

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