

THE MARTYNIACEAE IN THE SOUTHEASTERN  
UNITED STATES <sup>1</sup>

JOHN W. THIERET

MARTYNIACEAE Stapf in Engler & Prantl,  
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(UNICORN-PLANT FAMILY)

Strong-scented annual herbs [or perennials, sometimes with tuberous roots], pubescent with both glandular and nonglandular hairs. Leaves exstipulate, simple, long-petioled, opposite to alternate, entire to sinuate [dentate or lobed], cordate at base, sometimes inequilaterally so. Inflorescence racemose, terminal. Flowers perfect, zygomorphic, hypogynous, pediceled, each axillary to a bract. Calyx of 5 sepals, zygomorphic, bibracteolate at base, either synsepalous and spathaceous, more or less unequally 5-lobed, split abaxially to base [or of free sepals]. Corolla sympetalous, the tube cylindrical at base, this cylindrical portion about equaling [or much longer than] the calyx, the throat campanulate [or infundibular], the limb 5-lobed, somewhat 2-lipped, aestivation imbricate, the upper lobes external. Androecium of 4 [2] didynamous, fertile, alternate stamens and usually 1 [3] staminode, all inserted on the corolla near junction of tube and throat, included in throat; anthers dorsifixed, becoming more or less connate, with placentoids, 4-sporangiate, bilocular at maturity, locules dehiscent longitudinally and introrsely; pollen

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The length of the paper and the number of references are quite out of proportion to the representation of Martyniaceae in our flora, especially considering that *Proboscidea louisianica* cannot with certainty even be called a native of the area. I hope that the greater than usual biological interest of the family and the bringing together of much of a widely scattered literature will justify the extra pages.

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spheroidal, reticulate, apparently nonaperturate. Gynoecium syncarpous, carpels 2; stigma 2-lipped, the lips thin, broad and flat, sensitive to touch; style elongate, included in or slightly exerted from the throat; ovary unilocular, with 2 parietal intruded placentae, each placenta expanded into a broad lamella, T-shaped in cross-section; ovules many [few], unitegmic, tenuinucellar, anatropous; embryo sac development normal (*Polygonum* type); endosperm *ab initio* cellular, with haustoria. Fruit a 2-valved drupe, imperfectly 5- [4-] locular, terminated by an upcurved beak developed from proximal portion of the style and longer [or shorter] than the fruit body; exocarp thick, fleshy, deciduous in 2 valves; endocarp woody, sculptured [or echinate], crested along the adaxial [and sometimes abaxial] suture, dehiscing along both sutures [sometimes only distally, then more or less indehiscent proximally], the beak splitting into two elongate [or short], sharp-pointed "horns"; seeds numerous [few], relatively large, rugose-tuberculate; endosperm thin, membranaceous; embryo straight, oily, with fleshy, epigeal cotyledons. TYPE GENUS: *Martynia* L.

The Martyniaceae comprise about 20 species. Van Eseltine, the most recent monographer of the family, recognized five genera; his treatment has since been followed by most workers, although a few (e.g., Chittenden) include, in an enlarged (and more than a century old) concept of *Martynia*, the genera *Ibicella* (Stapf) Van Eseltine, *Proboscidea* Schmidel, and *Martynia* L. sensu stricto (= *M. annua* L.). Two genera (one native and one introduced) occur in the conterminous United States. One species of *Proboscidea* represents the family in the southeastern United States.<sup>2</sup> The family is indigenous to tropical and warm temperate areas of the New World from southern (southwestern?) United States to Uruguay and northern Argentina; a few species have been introduced as weeds into the Old World.

As with many "Personatae," the taxonomic status of the Martyniaceae is debatable. The family has been included in Bignoniaceae (Jussieu, Kunth), Gesneriaceae (Baillon), and Pedaliaceae (Bentham & Hooker, Decaisne, Hutchinson [1926], and, more recently, Backer, Heine, and Humbert). A close relationship between Martyniaceae and Gesneriaceae has been re-emphasized, mainly on anatomical grounds, by Cortesi. The Martyniaceae now are most commonly considered to be a separate family, the New World counterpart of the Pedaliaceae, from which they differ in their unilocular ovary and parietal placentae.

A characteristic vegetative feature of Martyniaceae is their glandular

<sup>2</sup> *Ibicella*, a South American genus of three species, has been collected as a waif in the southeastern United States, e.g., on "ballast" in Alabama (Van Eseltine). I find, however, no evidence that the genus has become established in our area, although it is naturalized in parts of California. It can be distinguished from *Proboscidea* as follows:

Calyx synsepalous and spathaceous, 5-lobed, split to the base abaxially; fertile stamens 4; endocarp body sculptured. . . . . *Proboscidea*.  
 Calyx of 5 free sepals; fertile stamens 2; endocarp body echinate. . . . . *Ibicella*.

hairs, which consist of a one- to several-celled uniseriate stalk and a several-celled head. The copious, sticky secretion of the hairs gives the plants a distinctive aminoid odor and clammy feel. That many small insects are trapped by the secretion on the leaves and stems has been noted by various authors and can be seen on both living plants and herbarium specimens. The function of the hairs and their secretion is unknown. Insectivory immediately comes to mind, and this indeed has been strongly affirmed for *Martynia* [i.e., *Ibicella*] *lutea* by Mameli, who reported a proteolytic enzyme in the secretion and stated unequivocally that the plant "è una pianta insettivora." Earlier, Fermi & Buscaglioni got negative results in a search for such an enzyme in *Martynia*. Manganaro suggested that the secretion of *Ibicella lutea* "se trate de un aparato capturado de la humedad atmosférico, dado que la planta . . . es seguramente xerófila."

The fruits of Martyniaceae are certainly the family's outstanding characteristic. As these fruits mature, the endocarp becomes woody, the exocarp fleshy. An upwardly-curved beak (longer than the fruit body in our genus and in *Ibicella*, shorter than it in *Craniolaria* and *Martynia*) develops from the proximal portion of the style, and it is the long beak of some Martyniaceae that evidently suggested the name "unicorn plant." At fruit maturity, in an unsurpassed example of vegetable ecdysis, the exocarp sloughs off in two valves, splitting along the abaxial and adaxial sutures. Concurrently, the endocarp, crested along one or both sutures and sculptured, echinate, or ribbed, begins to dehisce distally along the sutures. The beak splits into two sharp-pointed, hooked, and (in ours) elongate horns.

The fruits are adapted for dispersal through attachment to mammals by means of the hooked horns: the literature records sheep, mules, horses, cattle, bison, and panthers (!) as vectors but surely there are others. Aided by the styler horns, the fruits cling to fetlock, tail, mane, or body fur. In our genus, seeds presumably drop out as the fruits are carried about. In *Martynia*, the seeds seem to be freed only by crushing or rotting of the endocarp.

Nomenclature for the fruit type of the Martyniaceae is problematical. The fruit has been called, *inter alia*, a "capsule with fleshy deciduous exocarp and woody endocarp," a "woody many-seeded capsule," a "capsule with deciduous pericarp" (!), a "ligneous drupe," a "drupaceous capsule," a "subdrupaceous capsule," a "drupaceous follicle," and a "pod." Authors unwilling to commit themselves use simply "fruit." I have seen only one paper on fruit classification that mentions Martyniaceae: Gusuleac included *Martynia* among "Steinfrüchten" in his category "Eusynkarpe Früchte." I call the fruit of Martyniaceae a drupe even if the choice does not fit into the classical definition of a drupe, which emphasizes a fleshy or pulpy, indehiscent exocarp (the exocarp plus mesocarp of some authors), a hard or bony, indehiscent endocarp, and a single carpel and seed. Fruits of *Prunus* best exemplify this concept. In practice, however, the term "drupe" is used for many fruits not fitting this definition.

Characteristics making martyniaceae fruits aberrant as drupes can be seen in other drupaceous fruits, although, so far as I am aware, not all in the same one. The fleshy exocarp of the Martyniaceae separates in two valves to reveal the endocarp or "stone" (Nafday calls it a "pyrene"), and a similarly dehiscent exocarp is found in the almond (*Prunus amygdalus*) and in *Bursera Simaruba* (three valves). The endocarp of Martyniaceae dehisces along two sutures (at this point in its development the endocarp is a remarkable mimic of a "typical" capsule); dehiscent endocarps seem to be rare among drupes but can be seen occasionally in *Prunus*. The drupes of Martyniaceae are bicarpellate, and those of *Rhamnus*, *Melia*, *Ilex*, *Empetrum*, *Elaeis*, and certain other genera also consist of more than one carpel. The "stones" of Martyniaceae contain many or as few as four seeds, or even sometimes two in *Martynia* (Nafday); "stones" with more than one seed occur also in other drupes, e.g., *Borassus* (three), *Orbigyna* (three to eight), *Melia* (six), and even *Prunus* (sometimes two). There appears, then, to be no way to avoid calling the fruits of Martyniaceae drupes, although they are unlike that fruit type as generally typified by *Prunus*. Such a situation emphasizes the need, as far as classification and nomenclature of fruits are concerned, of a thorough review and revision.

Gametic and somatic chromosome numbers (mostly undocumented) reported for Martyniaceae indicate diploid numbers of  $2n = 30$  (Martini, Perry) or  $2n = 32$  (Covas & Schnack) for *Ibicella (Proboscidea) lutea*;  $2n = 32$  for *Martynia annua* (Srinivasan); and  $2n = 30$  for *Proboscidea fragrans* (Perry, Sugiura) and *P. louisianica* (Gaiser, Martini, Perry, Snow).

Several Martyniaceae are grown in gardens for their showy flowers and curious fruits. A few are widely distributed weeds that, in some regions, are considered noxious. Some species are used in folk medicine, and some produce edible roots, young fruits, and seeds.

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1. *Proboscidea* Schmidel, Icones Plantarum (Keller ed.) 49. tab. 12, 13. 1763.

Erect to decumbent, glandular-pubescent, strong-scented annual herbs [or tuberous-rooted perennials]. Leaves simple, long petioled, opposite to alternate, entire to sinuate [or palmately or pinnately lobed], cordate and sometimes inequilateral at base. Racemes usually exceeding leaves, few- to many-flowered, the axis lengthening in fruit, as do the pedicels. Calyx

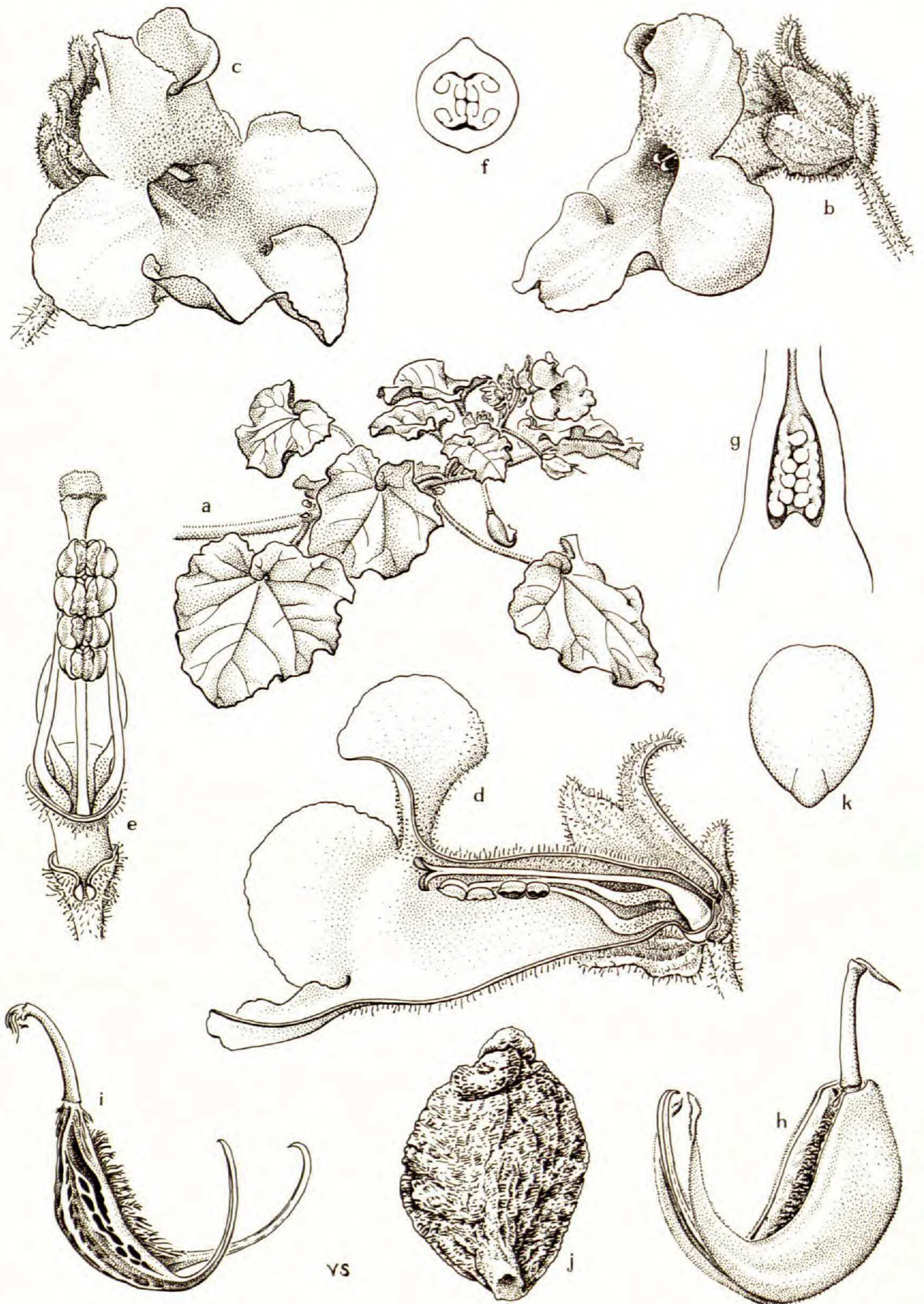


FIGURE 1. *Proboscidea*. *P. louisianica*: a, branch with flower and young fruit,  $\times \frac{1}{4}$ ; b, lateral view of flower to show calyx, bractlets, and expanded stigma,  $\times 1$ ; c, flower with stigmatic lobes nearly closed together after stimulation,  $\times 1$ ; d, flower in partial longitudinal section to show position of style and stamens,  $\times 1\frac{1}{2}$ ; e, flower with calyx and most of corolla removed to show stamens and style from below,  $\times 2$ ; f, cross section of ovary oriented as in flower to show parietal placentation,  $\times 8$ ; g, ovary in vertical section, cut between the two placentae, showing one placenta and its ovules,  $\times 8$ ; h, mature

bibracteolate at base, synsepalous, spathaceous, more or less unequally 5-lobed, split to base on abaxial side, eventually deciduous. Corolla tube cylindrical at base, this cylindrical portion about equalling calyx, the throat campanulate [or infundibular], the limb somewhat 2-lipped, 5-lobed, the lobes rounded. Androecium of 4 fertile stamens and one short staminode, included in throat, the abaxial pair of fertile stamens the longer; anthers of each pair becoming connate side by side, and the proximal tips of anthers of the longer stamens becoming connate to distal tips of anthers of the shorter. Gynoecium somewhat exceeding [or about as long as] stamens; style about three times as long as ovary; stigma lips sensitive, obovate [obovate-ob lanceolate], included in or slightly exerted from the throat. Drupe with thick, dehiscent exocarp, terminated by an upcurved beak  $1\frac{1}{2}$ -3 [ $1\frac{1}{4}$ - $3\frac{1}{2}$ ] times as long as the body; endocarp woody, sculptured, crested adaxially [sometimes also abaxially], dehiscent along both sutures, the beak splitting into two elongate, sharp-pointed "horns"; seeds several to many, black [rarely white], rugose-tuberculate; endosperm thin, delicate, papery, whitish. TYPE SPECIES: *P. louisianica* (Miller) Thellung. (*Martynia louisianica* Miller). (Name from Greek, *proboskis*, in allusion to the long-beaked fruit.) — UNICORN PLANT.

A genus of 14 species (9 recognized by Van Eseltine, 5 described since) native from the southern (southwestern?) United States south to Peru. Our species, *P. louisianica* (*Martynia Proboscidea* Gloxin),  $2n = 30$ , is widespread in the southern United States, but whether it is indigenous to the southeastern United States is uncertain. Occurring in meadows, fallow fields, waste places, and garbage dumps, along roadsides, and as a garden weed, it has spread to the Old World where in some areas (e.g., Australia) it is considered noxious.

The flowers are protandrous and, according to published accounts, pollinated by bees. The insects seek nectar produced by glandular hairs on the filament bases and on the area of the corolla tube between these bases; they may also take pollen. The pollination mechanism of *P. louisianica* is noteworthy (Thieret). The sensitive stigma is distal to the connate anthers along the median line of the upper surface of the corolla tube; its two lips, with their receptive inner surfaces, close together rapidly after even the slightest touch. An insect ascending the tube first contacts the stigma; pollen on its back is "scooped" off by the lower lip, which then closes against the upper lip, trapping the pollen between them and preventing its dislodging as the insect leaves the flower. Next, the insect rubs against the connate introrse anthers and is re-dusted with pollen. As the insect exits, the closed stigma lips may prevent or significantly reduce transfer of pollen of a flower to the stigma of that flower, simply because the receptive surfaces of the stigma are not exposed.

In a series of touches, the time required for closing of the stigma lips

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fruit, the fleshy exocarp dehiscent and beginning to fall away from endocarp,  $\times \frac{1}{2}$ ; i, endocarp after drying,  $\times \frac{1}{2}$ ; j, seed with tough seed coat,  $\times 4$ ; k, embryo, oriented as in seed,  $\times 4$ .

increases hardly at all, but the time for their spreading apart again increases considerably (from 5 minutes after the first touch to 25 minutes after the eighth) — the phenomenon of “stigmatic fatigue.”

After sloughing off of the exocarp, the beak of the fruit of *P. louisianica* splits into two sharp-pointed, hooked, elongate horns that, with further drying, become oriented in a way reminiscent of the tusks of a mammoth, with their tips pointing toward each other or even overlapping. After dropping from the plant, the endocarps usually lie with their horns pointing upward, the position in which they are most likely to hook onto animals and thus be dispersed. The common names “mule-grab” and “cow-catcher” for *P. louisianica* attest to the effectiveness of this adaptation for dispersal.

In sheep-raising areas (e.g., Arizona, Australia), the endocarps, with their long, hooked horns, get tangled in the wool of sheep (as do those of *Ibicella lutea*) and interfere with shearing. The horns have been known to work into eye sockets of grazing animals, and stock are recorded as having starved to death when a *Proboscidea* or *Ibicella* endocarp has clamped their jaws together (Gardner). Froggatt reported that “men employed in cutting [*Martynia (Ibicella) lutea* for weed control] become extremely dizzy in the head after working on it for any length of time.” It would be interesting to know the physiological basis of this and whether the same reaction would occur with *P. louisianica*.

Young fruits of *P. louisianica* (and probably other species of *Proboscidea*) can be made into pickles (Harrington) and have even been grown commercially for this purpose (Van Eseltine). They pose no gastronomic threat, however, to *Cucumis sativus*. The dried dehisced endocarps are made into “floral” decorations. Cultivation of *P. louisianica* for its oil-rich seeds (60% fat in the embryo) has been suggested (Bailey & Long, 1915a, 1915b). Strips split from mature *Proboscidea* endocarps are woven, as dark designs, into baskets by certain southwestern Amerindians; Hevly (1970a) mentions “semicultivated strains” of *P. parviflora* being so used. *Proboscidea louisianica* is an attractive, easily grown garden ornamental. Its fetid aroma and its tendency to become somewhat weedy are its main drawbacks. Its seeds germinate slowly and irregularly, but if Heit’s method of removing the outer, dark coat and the delicate, whitish endosperm layer before the seeds are planted is followed, germination will usually occur within 10 days.

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DEPARTMENT OF BIOLOGICAL SCIENCES  
NORTHERN KENTUCKY UNIVERSITY  
HIGHLAND HEIGHTS, KENTUCKY 41076