THE TRIMORPHISM AND INSECT VISITORS OF PONTEDERIA

By Tracy E. Hazen

Barnard College, Columbia University

(with plates 14 and 15)

The family Pontederiaceae is notable as containing the only known heterostyled species among monocotyledonous plants (with one possible exception*) and is further remarkable among heterostyled plants as furnishing the only recorded examples of distinctly zygomorphic or irregular flowers in such plants.

Fritz Müller,† writing in 1869 from Santa Catharina in southern Brazil, described a *Pontederia* which had for several years been introduced as an ornamental plant in the colony of Blumenau, and which increased with incredible rapidity by asexual propagation; the species he thought to be *P. crassipes*, and from the fact that the flowers showed the same relative positions of long and short stamens and style found in the mid-length-style form of the well-known *Lythrum Salicaria*, he was convinced that he was dealing with a trimorphic species of which only the mid-styled form had been introduced. He found another species growing wild on the banks of the Itajahý-mirim, which presented long- and short-styled flowers, but no mid-styled form could be found there. From the finely toothed petal segments shown in Müller's figures of this second species (*loc. cit. f. 1–3*) it almost immediately occurred to me that it was the plant which I have regularly seen labelled *Piaropus azureus* (Sw.) Raf., growing with the more famous water-hyacinth at the New York Botanical Garden, and later I discovered that it is so identified by Müller himself (as

* It is stated by Kerner (Pflanzenleben 2: 369. 1891; Eng. Ed. 2: 374) that flowers of *Colchicum autumnale* present three style lengths, but his brief description does not indicate any corresponding difference in stamen lengths such as always accompanies truly trimorphic species.

† Müller, F. Ueber den Trimorphismus der Pontederien. Jen. Zeitsch. Naturwiss. 6: 74–78. 1871.

Eichhornia azurea) in a paper published eleven years after his first report.* In this paper the first-mentioned species is positively identified as *Eichhornia crassipes* [=*Piaropus crassipes* (Mart.) Britton], the water-hyacinth, which has so conspicuously exhibited the same habit of rapid vegetative propagation in the St. John River in Florida, and Müller reports that during 1881–2 he found long-styled plants of this species, hitherto known only in the mid-styled form. These long-styled plants he thought could have appeared in the Blumenau region only as the illegitimate offspring of mid-styled parents.

In the English edition of Hermann Müller's classic handbook on flower pollination† published in the same year as this last paper, *Pontederia* (*Eichornia*) *crassipes* [sic] is described as existing in the colony of Blumenau "in long-, mid-, and short-styled individuals." This statement is doubtless an error on the part of the translator and editor, for it would seem improbable that Hermann Müller should have had such information from his brother Fritz at that time. This error appears to be transferred to the other species in the Engler-Prantl treatment of the Pontederiaceae, for there‡ it is stated that *Eichhornia azurea* has trimorphic flowers, while of *E. crassipes* only a long- and a mid-styled form is known. Our view of the misapplied character of these last two reports finds confirmation in the carefully edited handbook on flower pollination by Knuth§, where no later original work on these species is indicated than Fritz Müller's second paper, and where any such almost certainly would have been mentioned if it had been published. Further examination of the water-hyacinths would be of considerable interest.

---

* Müller, F. Einige Eigenthümlichkeiten der *Eichhornia crassipes*. Kosmos 13: 297–300. 1883.

† Müller, H. The fertilisation of flowers through insects, 561. 1883. (Translated by D'Arcy W. Thompson.)

‡ Schönland, S. Pontederiaceae. Engler & Prantl, Nat. Pflanzenfam. 2^4: 73. 1888.

§ Knuth, Paul. Handbuch der Blütenbiologie. 3^2: 113, 114. 1904. It is perhaps worth while to call attention to the fact that the English translation of this work, issued in three large volumes, covers only the first two volumes of the original; the third German volume (posthumous) devoted to extra-European plants, and therefore most useful for American students, contains several references to American literature which nearly escaped the attention of the present writer, owing to the failure of the translator and editor to mention the abridged character of the English edition.

Darwin* in his book on heterostyled plants, published in July, 1877, reports a "third species of *Pontederia*" recently discovered by Fritz Müller, which had all three flower forms growing together in the interior of Brazil. I was at first inclined to suppose that this was another species of *Piaropus*, for it seems strange that so acute an observer as Darwin should have been so bound by the conservative English conception of these plants current at that time, as to fail to distinguish between the large-flowered, many-seeded forms then beginning to be segregated on the continent as *Eichhornia*,† and the small-flowered, one-seeded *Pontederia;* but that this third species was a true *Pontederia* is attested by Fritz Müller himself six years later (*op. cit.* 297) when he also states that it was collected near Curitibanos in the highlands. This species may have been *Pontederia rotundifolia* L., or one of the imperfectly known allied forms; details of Darwin's description indicate that it could not have been our *P. cordata* L., or *P. montevideensis* Hort. (see note, p. 466) although the former is reported to grow as far south as Argentina, and the name of the latter suggests for it a South American origin.

The first mention of heterostylism in our native pickerel-weed, *Pontederia cordata*, is found in a brief note by Mr. William H. Leggett‡ a prominent early member of the Torrey Club, and probably first communicated in a meeting of the Club. In November, 1875, he reported having noted during a previous season an appearance of di- or trimorphism in this plant, but his somewhat inaccurate description, based upon examination of dried flowers, led Darwin to express doubt whether the species is really heterostyled. In August, 1877, the month following the publica-

* Darwin, Charles. The different forms of flowers on plants of the same species, 183–187. 1887.

† The very natural genus *Piaropus* (thick feet) was established by Rafinesque in 1837 on *Pontederia azurea* and *P. crassipes* (Flora Telluriana 2: 81, 82); nevertheless these two species continued to be treated under the generic name *Pontederia* in most of the literature for about four decades thereafter. If the principle of priority is ever to be maintained, there can be no justification for such provincialism in science as that practised by the Brussels Congress in ordering Rafinesque's well-founded name for a small strictly American genus published in Philadelphia to be rejected in favor of the Teutonic *Eichhornia* Kunth (Enum. Plant. 4: 129. 1843) published six years later, even though Kunth's name was latterly attaining some degree of currency among continental writers.

‡ Leggett, W. H. *Pontederia cordata.* Bull. Torrey Club 6: 62, 63. 1875.

tion of Darwin's book, Mr. Leggett reported* that he found on examination of growing plants that *Pontederia cordata* "is as truly trimorphic as *Lythrum Salicaria*, or even more so." His brief account appears to have received little notice in this country, for only one of our manuals mentions the trimorphism, and to answer some of the questions raised by Mr. Leggett as to the insect visitors, the relative fertility of the three forms, and the function of the peculiar glands which beset the flowers, was the purpose of the investigations now to be reported.

Early in July, 1916, while searching for another plant seen during a previous season at Arcola, a trolley station about midway between Hackensack and Paterson in Bergen County, New Jersey, I was attracted by the opportunity to secure a good photograph in natural surroundings of our pickerel-weed—a plant which does not seem to grow extensively in the immediate vicinity of New York. Here at Arcola it was abundant in two long ditches in a pasture, and presently the attempt to obtain a photographic record of its numerous insect visitors became a fascinating pursuit. I made many visits to the station during the remainder of July, August, and September, always laden with cameras and butterfly-net and killing-bottle. Flowering spikes were generally brought back from the field for laboratory study, and though all the flowers opening on any one morning begin to fade often by mid-afternoon if the day is sunny, later if it is cloudy or humid, nevertheless when brought to the greenhouse, the spikes would be furnished with freshly opened flowers for several successive mornings. The flowering proceeds in general from below upwards, but as not more than one of the three or four flowers of a single spikelet or sessile cluster of buds is open at one time, the main portion of the spike may be well clothed with new flowers for some days. In this way the biological advantages of conspicuousness of the whole inflorescence and economy in condensation of the axis and spacing of the open flowers are maintained at the maximum degree of efficiency.

As Mr. Leggett discovered, the species consists of three kinds of plants, each kind bearing a flower of somewhat different form. At one time I thought the different plants might be recognized by

* *Loc. cit.* 6: 170, 171. 1877.

differing shades of color in the flowers, as described by Fritz Müller for *Eichhornia azurea*, in which he found the short-styled flowers regularly of a deeper blue, and the long-styled flowers of a paler, more violet tint; but on another day all of the spikes were indistinguishable in this respect. By a little observation of the position of the anthers, however, one may easily recognize the three forms without having recourse to dissection of the flowers (PLATE 14).

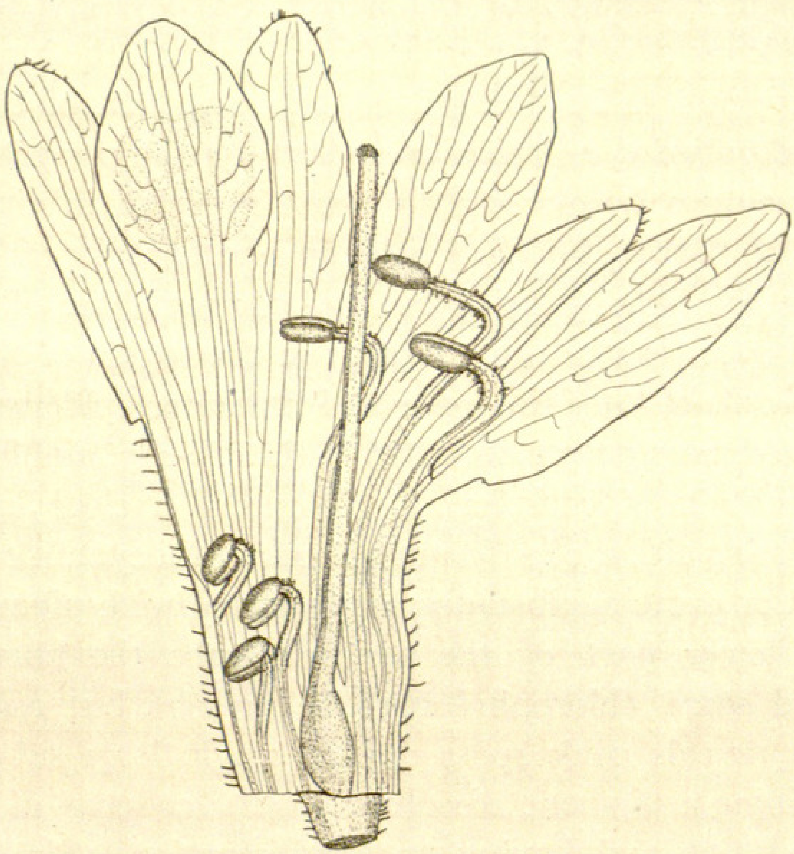


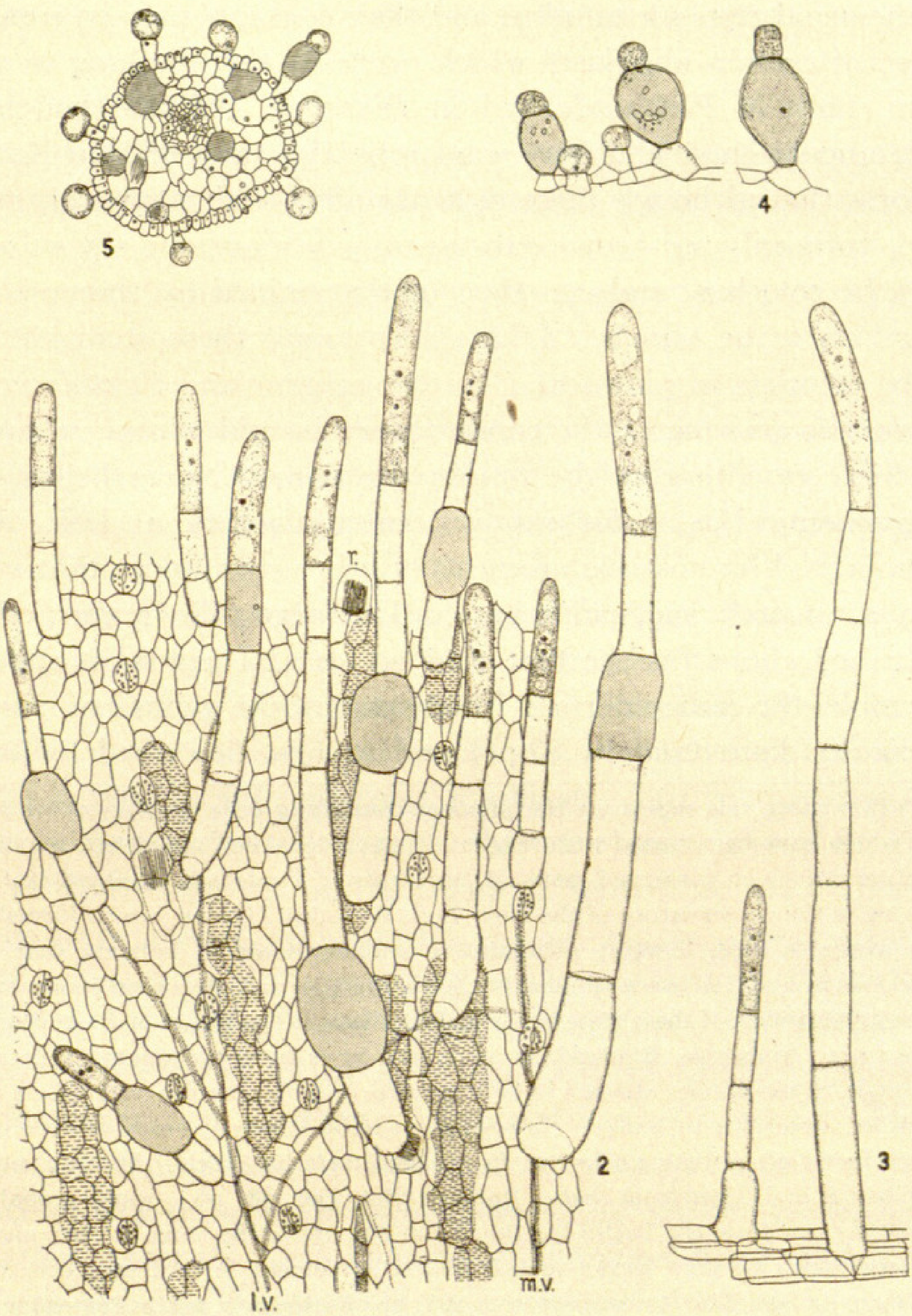
FIG. 1. *Pontederia cordata* L.; flower of the long-styled form with the perianth tube cut lengthwise and laid open to show the typical position and relative height of all the stamens ($\times$ 5).

In all of the three flower forms the three narrower sepal-segments and the three ovate petal-segments are united into a tube about seven or eight millimeters in length, which, however, often has four narrow slits in its lower part between the segments on the anterior or lower side of the flower, so that it would seem to be less efficient as a nectar receptacle than many tubular flowers. These clefts are so inconspicuous that they do not appear in any of my sketches made from fresh flowers, but are evident in material preserved in formalin (FIG. 1) and in pressed specimens, from which one might suspect that they are formed in part at least by shrinkage. Similar clefts are found in *Piaropus.* The three spreading segments of the lower lip form a convenient landing platform for smaller insects. The three segments of the upper lip are rather erect and form a sort of standard with a conspicuous mark on the posterior petal-segment which has been regarded as a nectar-guide for insects, a large double blotch of bright yellow—rarely two separate spots as often described, at least in plants from several regions examined by the writer. The yellow pigment is located in a layer of cells immediately underneath the inner epidermis, and appears to be diffused in the cytoplasm of these cells; they extend outward in irregular scallops on the periphery of the spot, producing a border slightly more greenish in tint, hardly perceptible to the eye, but noticeable in photographs made with a color-screen too light to bring out the correct value of the main part of the spot (PLATE 14). Except in the region of this yellow blotch, the cells of both the inner and the outer epidermis show a rather violet-blue pigment dissolved in the cell-sap, and in addition each cell contains a conspicuous globule of a clear indigo-blue color, consisting either of solid amorphous anthocyanin or possibly of a tannin or protein substance impregnated with pigment.*

In the lower part of the perianth tube the blue color is lacking and some chlorophyl may be present, but examination with a lens reveals pink spots due to single large subepidermal cells containing a pigment dissolved in the cell-sap, of a slightly purplish-red tint and having an acid reaction. Similar hypodermal cells are found throughout the pistils, where they also contain red pigment at least in the short-styled form (FIG. 8). In the middle and upper regions of the perianth, where the epidermal cells are blue, much larger scattered hypodermal cells occur in abundance (FIG. 2) but when dissected out, these are found to be colorless; to assume, however, that anthocyanin is absent from

* When the cells are treated with hydrochloric acid and osmic acid (employed as a tannin test) this deep blue globule turns to a wine-red color, and the dissolved anthocyanin may be precipitated in small globules of the same color. If copper acetate is used, the globule turns to an emerald green color and the precipitated anthocyanin shows the same tint. Such a combination of dissolved and solid anthocyanin was first described and figured in *Gilia* by Hildebrand in 1863, but has been little mentioned since until 1906, when Gertz in his important work *Studier öfver Anthocyan* reported the wide occurrence of such a condition; summarized in Miss Wheldale's book, The Anthocyanin Pigments of Plants 32–35. 1916.

them is unsafe, since Willstätter finds that in *Centaurea* and some other plants purple, red, or blue anthocyanin may readily change to a colorless isomer. These large cells were first noticed in ma-



FIGS. 2–5. 2. Outer surface of sepal-segment: showing stomata in the epidermal layer; large subepidermal idioblasts shaded with broken lines, and three raphide-sacs (*r.*) in the same layer; the mid-vein (*m.v.*) and a lateral vein (*l.v.*) lying underneath; on the surface, hairs of two forms (× 105). 3. Typical simple glandular hairs on the lower part of the perianth tube (× 105). 4. Hairs near tip of filament of mid-length stamen (× 113). 5. Cross section of filament from a bud 3 mm. long; showing a raphide-sac, and several of the elongated hypodermal idioblasts shaded (× 113).

terial preserved in formalin and in alcohol, by both of which their contents are turned to a reddish-amber color.*

Both the red-pigmented and colorless cells respond to several of the usual tests for tannins, and their contents may be similar to those of certain idioblasts which occur in the diaphragms of the stem, both in *Pontederia* and in *Piaropus*. Olive† thought the substance in these idioblasts was probably a fatty oil, but Rothert‡ reports that although these cells are filled with a strongly refractive, ordinarily red-brown substance, yet in autumn the substance may be colorless, and can then be determined by the customary reactions to be tannin. I have also found these stem idioblasts to be colorless in plants of *Piaropus azureus* and *Pontederia montevideensis* growing in the conservatory in mid-winter, when they likewise seem to give the tannin reactions. Nevertheless, these microchemical tests for tannins, unsatisfactory at best, are so complicated by possible mixtures of other substances that we feel they are merely suggestive here. The large cells of the perianth, described above for the first time so far as I can find, appear to resemble the subepidermal idioblasts in the petals of *Fumaria officinalis* discovered by Zopf§ and at first described by him as

* In writing this report on the pigment-containing cells, and on other peculiar cells which have been tested with reagents, I have depended somewhat, for checking up observations on preserved material, on plants of *Pontederia montevideensis* Hort. growing in the conservatory of the New York Botanical Garden, which furnished the only available fresh flowers; comparative studies, however, indicate that all the structures in question are so similar in the two species as to leave no room for doubt of the applicability of these statements to *P. cordata*. The plants of *P. montevideensis* came from Cambridge, England, in 1901, and have been propagated vegetatively; the origin of the species appears to be unknown, and its botanical characters are undescribed, according to Bailey. In vegetative habit it closely resembles the narrow-leaved forms often distinguished as *P. cordata lancifolia* (Muhl.) Morong, but I am confident it is distinct from that. Rothert (Bot. Zeit. **58**: 96. 1900) probably had the same plant from the Berlin Botanical Garden, under the name *Eichhornia montevidensis*, which he says shows such complete agreement in leaf structure with *P. cordata* as to lead him to suspect that it is no *Eichhornia*, but a *Pontederia*. The spelling *montevideensis* has been adopted from Index Kewensis Suppl. **4**: 188. 1913, and is in harmony with the French practise in forming the name of the inhabitants of Montevideo, though *montevidensis* is said to be more in accord with Latin usage.

† Olive, E. W. Contributions to the histology of the Pontederiaceae. Bot. Gaz. **19**: 183. *pl. 17. f. 5, 6.* 1894.

‡ Rothert, W. Die Krystallzellen der Pontederiaceen. Bot. Zeit. **58**: 78. 1900.

§ Zopf, W. Ueber die Gerbstoff- und Anthocyanbehälter der Fumariaceen. Bibl. Bot. **1**^{2}: 20. 1886. For more literature on this subject see Solereder's Syst. Anat. of Dicotyledons (Eng. Ed.) **1**: 57. 1908.

containing a blood-red tannin; later it transpired that Zopf had confounded true anthocyanin receptacles with "sac-cells" occurring throughout the vegetative structures of Fumariaceae, which he finally considered to be alkaloid-receptacles, though Heinricher, who gave the name "sac-cells," states that their contents are a mixture of substances, including a fatty oil.

The rôle of these peculiar perianth cells in *Pontederia* (and in *Piaropus*) can only be surmised at present, whatever the nature of their contents. In fixed and stained sections they often behave much like mucilaginous or gummy substances, and if of such a nature might possibly function in protecting the perianth from danger of desiccation until after anthesis, when the upper part promptly rolls up and soon dries, though the tube persists as an increasingly fleshy envelope around the ovary until the seed is mature. Even in the open flower, some of these large hypodermal cells are often found with their thin protoplasmic layer collapsed, and the contents apparently discharged; half of such a cell is shown at the bottom of FIG. 2. It is interesting to note that the stamen filaments in both *Pontederia* and *Piaropus*, which have blue anthocyanin in their epidermal cells, are well supplied with these long, mostly subepidermal idioblasts; but in the case of *Pontederia montevideensis*, though they are conspicuous in filaments of flowers grown out of doors in September, they appear to be entirely absent in filaments of mid-winter, conservatory-grown flowers, while still persisting in the perianth of the latter. In April, after two or three weeks of sunshine, the flowers of the same conservatory plant have the cells sparingly developed in the filaments and showing a pink anthocyanin color. That a temporary suppression of such structures should occur in consequence of lack of need for them is rather incredible; the suggestion, rather, presents itself, that the contents of these idioblasts, as perhaps also the numerous raphide-sacs which are early found in a similar position in perianth, pistils, filaments, and most abundantly in the anthers, are after all only in the nature of by-products of metabolism.

The outer surface of the perianth is clothed with spreading glandular hairs (FIG. 2); their elongated terminal cell, rich in protoplasmic contents and sometimes binucleate, is not infrequently smeared with a secretion which behaves under reagents much like certain globules visible inside the cell; the other cells show very scant cytoplasmic contents. Many of the hairs, however, particularly toward the tip of the perianth segments, have one cell notably distinguished from the others, often by its swollen ellipsoid form, but always by its strongly refractive, colorless contents contained in the vacuole which practically fills the cell. To anticipate a possible suspicion that these hairs are abnormal, it may be remarked that they also occur on the perianth of *Pontederia montevideensis* and of *Piaropus azureus*. On the upper part of the stamen filaments are hairs of apparently similar character, though consisting of only three cells, a basal cell set in the epidermis, a terminal globular secreting cell, and between them a barrel-shaped cell with colorless refractive contents (FIGS. 1, 4). This cell is perhaps slightly more resistant to reagents than the swollen cell of the perianth hairs, but in both the presence of tannins is indicated, though probably not associated with exactly the same other substances that may be found in the hypodermal idioblasts. These peculiar stamen hairs are developed early (FIG. 5) and in buds only three millimeters long the barrel-shaped cell occasions difficulty in sectioning, much more than the hypodermal cells. More thickly sprinkled over the upper part of the filaments, and also the upper part of the long- and mid-length styles (FIGS. 9, 10) are simpler hairs, consisting only of the globular secreting cell and a basal cell. LeMaout and Decaisne* figure the short-styled pistil as fringed on one side with numerous spreading hairs, but I have always found it almost entirely devoid of such structures.

Growing plants of the form known as *Pontederia cordata lancifolia*, collected 23 March 1918 near Tampa, Florida, by Professor and Mrs. R. A. Harper, arrived in New York in good condition a week later, with only the flowers withered. These somewhat dried flowers, when soaked out in water, showed a blue color in the idioblasts of the hairs on both filaments and perianth; the subepidermal idioblasts in the upper part of the perianth also showed a fine deep prussian blue color, though all the anthocyanin had disappeared from the epidermal cells, except for the solid

* LeMaout et Decaisne. Traité général de Botanique. 607. 1868.

globule. This same change of the colorless idioblasts to blue has also been observed in fading flowers of *P. montevideensis* treated in a similar fashion, while the pink idioblasts remain unchanged in appearance.

It would be a matter of much interest to be able to determine the function of these three sorts of hairs. Kerner and Stahl* would doubtless regard the perianth hairs as a protection against undesirable creeping insect visitors and snails. If this were their function, here it might have been more easily secured if the hairs had been developed on the large spathe-like bract just below the flowers. Goebeler† regards the glandular and tannin-bearing hairs abundantly present on young fern shoots as serving in a much higher degree as a protection against desiccation, by diminishing transpiration, and by absorbing and storing water or conducting it back to young tissues. *Pontederia* shows a strong tendency to dry up on the slightest provocation, and the hoary glandular covering so conspicuous all over the young buds and even over the stem down to the point of insertion of the bract, may well furnish a protection against excessive transpiration. Along this line, it is also suggestive, that the hairs on the stamens and styles are chiefly found on the parts exposed when the flower is opened, and that they are almost entirely absent from the short-styled pistil, which is so completely enveloped by the perianth tube as to need no other protection. The longer stamen hairs do also, in some cases at least, catch the pollen from the anthers and hold it in the most advantageous position in relation to insect visitors, but it can hardly be supposed that so specialized a form was evolved for such a purpose. Knuth‡ found that the flowers of *Sicyos angulata* L. acted upon a photographic plate much more strongly than their inconspicuous greenish-white color would lead one to expect, and suggested that this may be due to the numerous glands covering the flowers which possibly "act as so many mirrors or lenses receiving and reflecting light, so that their glitter strongly

---

* Stahl, E. Pflanzen und Schnecken. Jen. Zeitsch. Naturwiss. **22**: 557–684. 1888.

† Goebeler, E. Die Schutzvorrichtungen am Stammscheitel der Farne. Flora **69**: 483–497. 1886. See also Gardiner, E., & Ito, T. On the structure of the mucilage-secreting cells of *Blechnum* and *Osmunda*. Ann. Bot. **1**: 30. 1887.

‡ Knuth, P. Handbook of Flower Pollination. **1**: 87. 1906.

affects gelatine sensitized by silver bromide, and also the optic nerves of insects." If such a theory has any basis in fact, it might be applied to the hairs of the stamens, and possibly also of the styles of *Pontederia*.

There can be no doubt that the numerous insect visitors of the pickerel-weed seek it for the nectar it affords. It was at first supposed that this was secreted by the basal region of the perianth, but on examination of sections I found that the fleshy character of the tube is due chiefly to the presence of numerous air chambers separated by diaphragms much as in the stem structures, and that nothing like nectar-secreting cells can be detected there. In sections of the ovary, however, are found conspicuous epidermal cells lining the three slit-like cavities left by the incomplete fusion of the carpels (FIGS. 6, 8); these and one or two layers of cells beneath them stain deeply because of their rich protoplasmic contents and large nuclei, and there can be no doubt that they secrete nectar which flows freely from the open lower end of the narrow cavities to form an accumulation in the perianth tube. These secreting cells were indicated in the figures of *Pontederia* given by LeMaout and Decaisne* and by Wilson Smith,† but their significance was not discussed. Similar septal nectaries were discovered in 1854 by Brongniart‡ in several genera; their histological development was more exactly studied by Saunders§; and their variety of form and phylogenetic development in many genera of the Liliales, Scitaminales, and Bromeliaceae have been more elaborately set forth by Schniewind-Thies.||

Ovary sections of *Pontederia* show also several groups of cells whose large nuclei and abundant protoplasmic contents present practically the same appearance as those of the septal nectaries; these groups of cells are found imbedded in the tissue of the anterior carpel, and in the solid portion of the two anterior septa lying above the septal nectaries, which do not reach higher than

* LeMaout et Decaisne. *Loc. cit.*

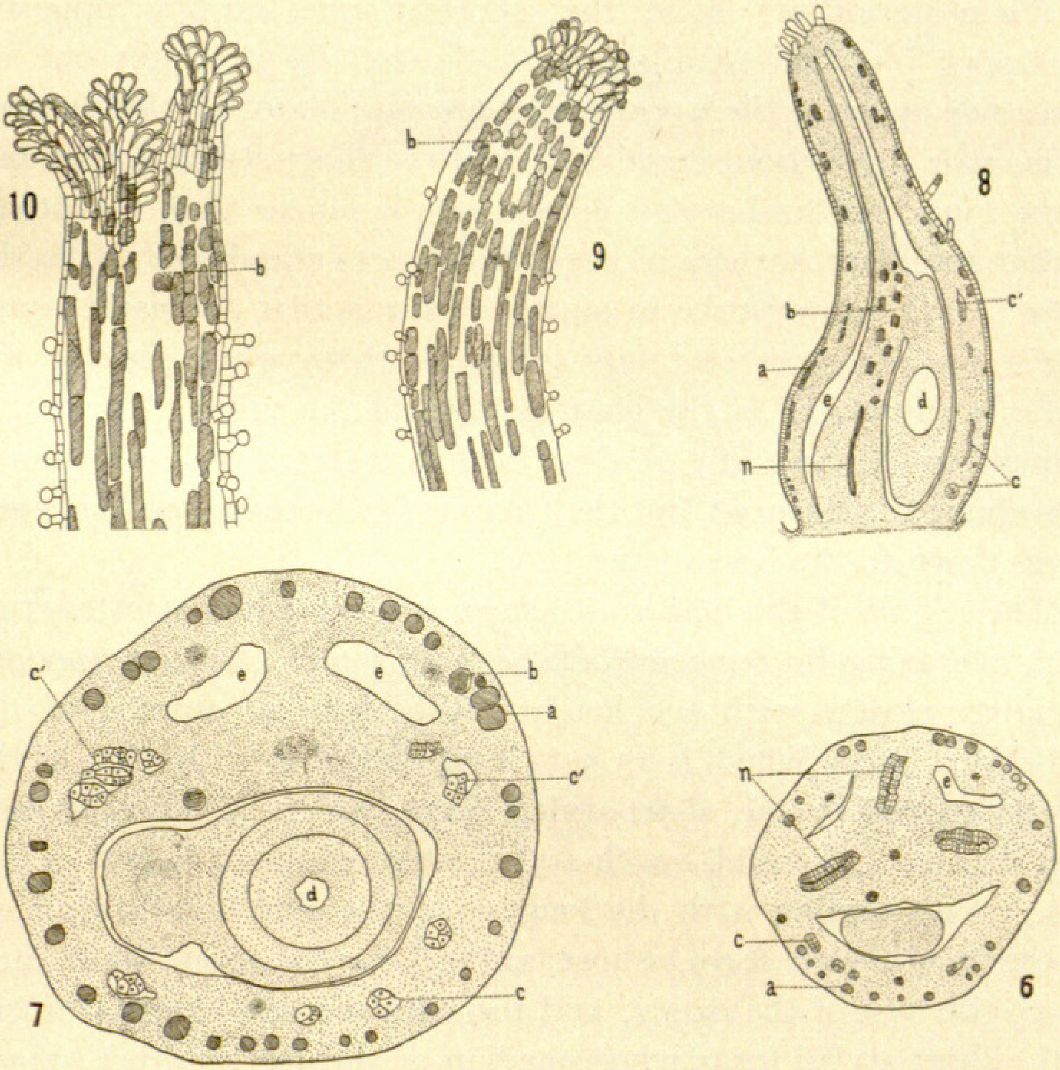
† Smith, R. Wilson. A contribution to the life history of the Pontederiaceae. Bot. Gaz. 25: 324–337. *pl. 20. f. 54.* 1898.

‡ Brongniart, A. Mémoire sur les glandes nectariféres de l'ovaire dans diverses familles de plantes monocotylédones. Ann. Sci. Nat. Bot. IV. 2: 5–23. 1854.

§ Saunders, E. R. On the structure and function of the septal glands in *Kniphofia*. Ann. Bot. 5: 11–25. 1890.

|| Schniewind-Thies, J. Beiträge zur Kentniss der Septalnectarien. 1897.

the middle of the ovary (FIGS. 7, 8). Often even in a young ovary these cells abut on small schizogenous cavities, as at c' in FIG. 7, and in older sections of *Pontederia montevideensis*, where they are more extensively developed, the cavities may form elongated



FIGS. 6–10. 6. Section through lower half of ovary, short-styled form ($\times$ 57). 7. Section through central part of same ovary ($\times$ 100). 8. Longitudinal diagram of similar ovary, constructed from threee sections ($\times$ 35); from buds 3 mm. long. 9. Curved style-tip of mid-styled flower with small and mid-size pollen grains germinating on the stigma ($\times$ 35). 10. Six-parted stigma of long-styled flower, three of its divisions lying behind those shown; epidermal cells indicated only at the top; below the elongated subepidermal idioblasts, shaded ($\times$ 37). *a*, anthocyanin idioblasts, shaded, mostly subepidermal; *b*, bundles of raphides; *c*, groups of secretory cells, at c' abutting on small schizogenous cavities; *d*, embryosac; *e*, empty loculi; *n*, septal nectaries.

canals lined with secretory cells. The fact that these cells appear to be functional long after these of the septal nectaries cease to show any trace of secretion indicates that they may belong to a quite different category.

The stamens are always in two sets; a longer set of three on the anterior side of the flower, consisting of a pair opposite the lateral petal-segments, with a median one slightly longer, opposite the lowest or anterior sepal-segment· the three short stamens of the posterior set· have the shortest one always opposite the upper blotched petal-segment, flanked by a longer one on either side opposite the lateral sepal-segments (FIG. 1); the stamens of this pair show about equal length in the short-styled flower, but in the long- and mid-styled flowers one is longer than the other, so that the three anthers of the shortest sets stand one above the other in the narrow tube in such a position that an insect's proboscis would almost certainly graze all three when seeking the nectar accumulated in the basal portion of the tube. The longer stamens would generally be described as inserted on the perianth tube about at the throat, but they may easily be traced as thickened ridges down to the base of the tube.

The stigma of the long-styled form reaches a height of 12–13.5 mm., averaging (in ten flowers) about 12.5 mm., and corresponding fairly closely with the height of the longest stamen of the mid-styled form, which is 13.5–15 mm., and also with that of the longest stamen in the short-styled form, which is 13–14.5 mm. The stigma of the mid-length-styled form reaches a height of 7–8 mm., corresponding with the longest of the mid-length stamens of the long-styled form, whose anther stands about 9–10 mm. above the base of the ovary, and also with the mid-length stamens of the short-styled form, whose median or shortest another stands 6.5–8 mm. above the base of the ovary. The stigma of the short-styled form is only 2.7–3 mm. above the base of the ovary, and the shortest stamen of the long-styled form has the tip of its anther 3–3.5 mm. above the base of the ovary, while the anther tip of the shortest stamen in the mid-styled form measures 2.6–3 mm. above the base of the ovary. Measurements of all three stamens of the mid-length sets would show a closer correspondence with the mid-length style, but it may be noted that the stamens of the shortest sets are all generally taller than the shortest styles.

The ratio of the average height of the long pistils to that of the mid-length pistils is approximately as 100 to 60; and the average height of the long pistils to that of the short ones is as 100 to 22.

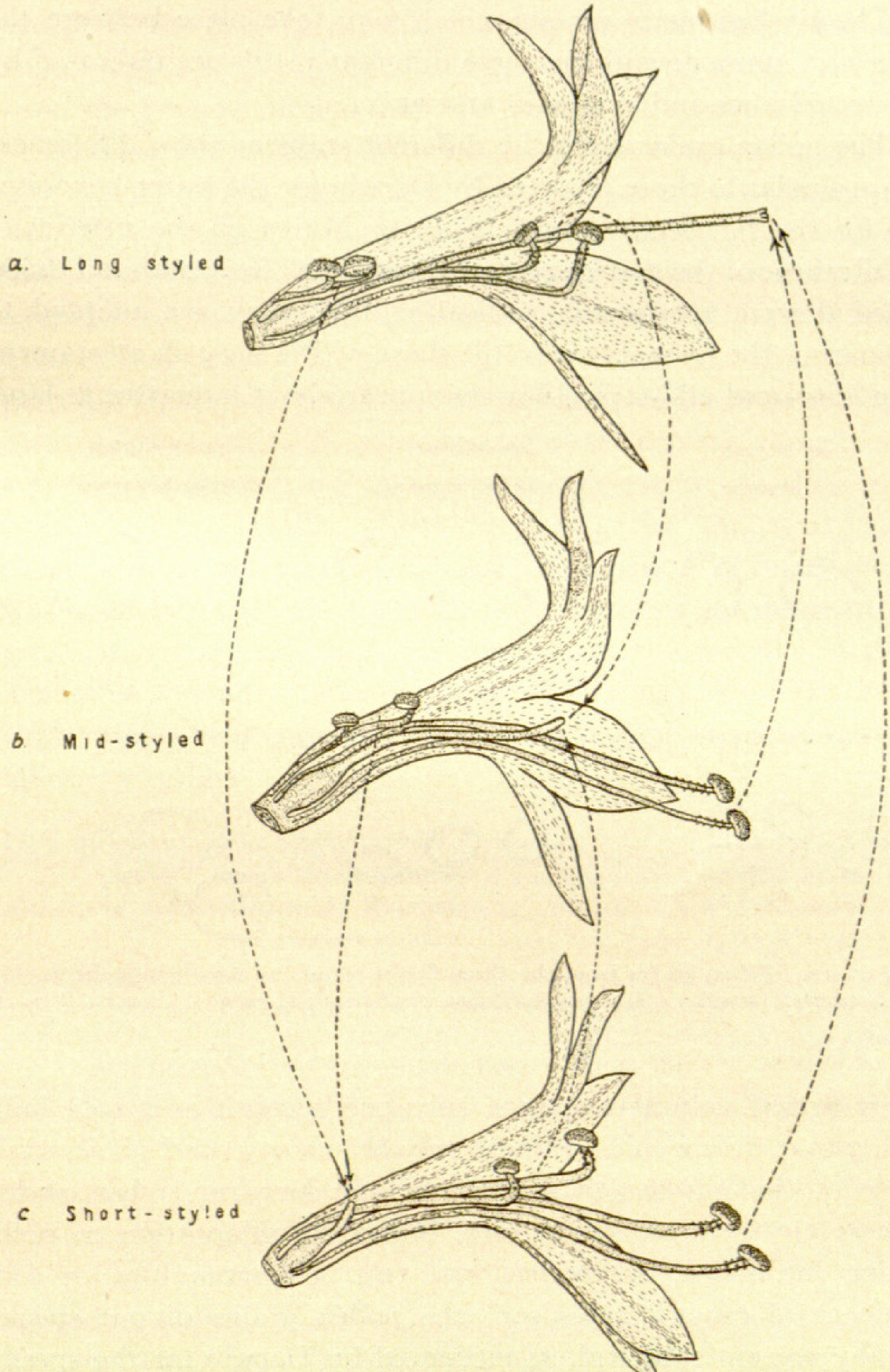


FIG. 11. *Pontederia cordata;* flowers of the three forms in approximately natural position (× 4). The dotted lines with arrows indicate the six legitimate pollinations. From each flower the left lateral petal-segment with its stamen, and half of the left sepal-segment and its stamen have been cut away, in order to show the position of the short stamens with their inverted anthers and the short pistil. Drawn 28 August 1916.

The six legitimate crosses which may take place between the six sets of stamens and the three different pistils are indicated by the dotted lines and arrows in FIGURE 11.

The pollen grains from the different stamens show differences in size similar to those reported by Darwin for the water-hyacinths and for the *Pontederia* found by Fritz Müller in the interior of Brazil; those of the two longest sets of stamens from mid-and short-styled flowers are largest, indicating that they are adapted to pollinating the long-styled pistil; those of the very short stamens from long- and mid-styled flowers appear about a quarter as large

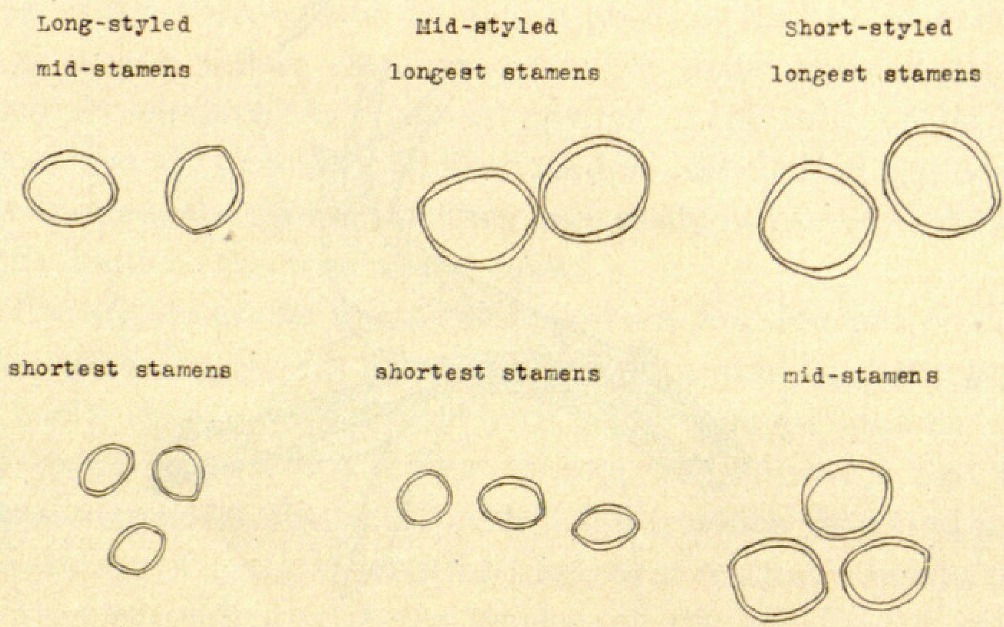


FIG. 12. Pollen grains from the three flower forms, to show comparative size, and similarity of those taken from stamens of similar length in the different forms (× 200).

(their actual volume averages only one seventh as great) indicating that they would pollinate only the short-styled pistil; while those of the mid-length stamens of the long- and short-styled flowers are intermediate in size, indicating adaptation to pollinating the mid-styled flower (FIG. 12). Unfortunately for convenience of exact comparison, the pollen grains of our species usually are not spherical, as intimated by Darwin for the species studied by him, but they are here rather ellipsoidal or lemon-shaped; in only ten out of three hundred measured have I found isodiametric grains.

In order to obtain as definite a record as possible, five flowers of each form were selected, each flower from a different spike, except in the case of the short-styled form, of which only three spikes had been preserved, and from each flower five pollen grains from the longest stamen and five from the shortest were selected at random and measured by means of the eyepiece micrometer. The twenty-five measurements from each of the six stamen types were then averaged. Some weeks later a duplicate set of twenty-five measurements was made in the same manner, and while they averaged uniformly slightly greater than those of the first set, the difference was only such as might be expected because of the personal equation, though in each of the three forms of the second set it was noticeable that one or two of the flowers were especially vigorous, as shown by a considerable increase in size of all grains, both larger and smaller, above the average for similar anthers in other flowers. Nevertheless, when the second set of measurements was combined with the first, the ratios between the different sized grains diverged from those obtained from the first set by only a negligible amount, indicating the substantial reliability of the work. The fifty measurements of each type of pollen give the following result:

Long styled form,	from median mid-length stamens	37.44 × 33.79	microns
" " "	from shortest stamens	23.94 × 21.69	"
Mid-styled form,	from longest stamens	46.33 × 41.61	"
" " "	from shortest stamens	23.95 × 20.95	"
Short-styled form,	from longest stamens	45.84 × 41.32	"
" " "	from median mid-length stamens	36.94 × 33.01	"

It will be seen that the pollen grains from the two sets of longest and shortest stamens correspond most closely, the mean diameters of the shortest sets differing by less than half a micron, but even the divergence between the mean diameters of the two mid-length sets amounted to only seven tenths of a micron. There is a much closer correspondence here than in the smaller number of measurements made by Francis Darwin for his father on the Brazilian plant. It does not appear whether Darwin selected pollen grains from more than one anther of each type, and there is considerable variation in different plants. The extremes found in *Pontederia cordata* may be of interest. The grains from the median (i. e., longest) mid-length stamen of the long-styled flowers showed such averages in different flowers as 35.4 × 34.2, 39.3 × 36, and 36.6 × 33 microns; the similar grains from the median (i. e., shortest) mid-length stamen of the short-styled flower showed such averages as 34.8 × 32.7, and 38.1 × 33.6 microns. The average for a single flower of grains from the longest stamen in the mid-styled form ranged from 42.3 × 37.2 to 49.5 × 42.3 microns; while the small grains from the shortest stamen of a single long-styled flower furnished such averages as 22.8 × 23.1, 24 × 21, and 25.8 × 23.1 microns. The proportions of the grains are by no means constant, and in examining many grains one gains the impression that the two (or really three) diameters balance each other even more than is indicated in these sample averages, that is, that when one diameter increases beyond the average, the other decreases correspondingly so as to keep the volume average more constant than appears. It should be remarked that the above measurements were all based on material preserved for a year in formalin, and that they uniformly average less than a small number of measurements made in August 1916, of grains taken from fresh flowers and mounted in water. These few measurements of fresh grains, considered not enough to be reliable, in general approach more nearly the dimensions of a series made by Halsted* whose report came to my notice only after my own had been completed. As indicated by Halsted, dry pollen from fresh anthers is so contracted as to make its measurement of little significance. It might be expected, however, that though the amount of swelling of the grains would be greater when mounted in water than when fixed in formalin, nevertheless it would be proportional in similar grains, whatever the medium used; and as a matter of fact the ratio between my large- and mid-size grains is almost exactly the same in fresh and preserved material; a greater difference between the size of large and smallest grains mounted in water as compared with similar grains in formalin, I assume to be chargeable to the small number of measurements of fresh grains.

In order to obtain a comparison between our ellipsoid pollen-grains and those reported by Darwin as spherical, the measure-

* Halsted, B. D. Pickerel weed pollen. Bot. Gaz. 14: 255–57. 1889. In this brief article, no indication of the number of measurements is to be found; with the mere statement that "only three prevailing dimensions" occur, and indications of faulty calculations, it seems worth while to detail my own definite results.

ments of each of the two similar sets of grains given above were combined, and the mean of the three diameters of the average grain of each kind was then taken; this makes the mean diameter for all the large grains 43.3 microns, for all the mid-size grains 34.66 microns, and for all the small grains 22.16 microns. On this basis the ratio of all the large to all the mid-size grains is as 100 to 80, and the ratio of the large to all the small grains is as 100 to 51, which is a slightly greater difference than that reported by Halsted, who pointed out the fact that *Pontederia cordata* shows the greatest range of pollen size yet recorded for any flower. This method of averaging, however, is not accurate, and in any case comparison of volumes would seem to be more significant. Computing the volume of spheroids with diameters represented by the measurements detailed above, or, more simply, calculating the ratios only by use of logarithmic tables, it is found that the volume average of the two sets of large grains is to that of the mid-sized grains as 100 is to 53, and the ratio of the volume of the large to that of the small is approximately as 100 to 14. It will be seen that these ratios present a much better basis for comparison with the ratios of style length than the ratios of the diameters. Darwin's comparison, however, was based on the extremes of size in single sets of pollen grains. In our plant the largest and smallest sets of grains are found in the mid-styled form, where the ratio of mean diameters is as 100 to 50, and the volume ratio about as 100 to 13. In our species, as in Darwin's Brazilian plant, the pollen grains of both sets of stamens in the short-styled flower are slightly smaller than those of the stamens of corresponding length in the other flower forms.

The significance of these differences in pollen size is a point of much interest. Delpino regarded the difference in size as a direct adaptation to the style length, supposing the larger grains could produce a pollen-tube long enough to penetrate the length of the long style, and that the tube of the smallest grains would readily grow only the length of the short style. This view Fritz Müller considered confirmed by his experimental work with *Eichhornia crassipes** where he found that long- and mid-styled pistils

* Müller found, for example, that flowers on a long-styled spike legitimately fertilized by pollen from the long stamens of mid-styled flowers produced 141.7

pollinated with grains from the smallest anthers were less fruitful than in the case of other illegitimate crosses.

An additional suggestion may be gathered from Halsted's experiments made to determine whether the small pollen grains were fertile, since doubt on this point had been expressed by more than one previous writer. He found all the grains equally capable of germination if sufficient time was given, but that the largest grains germinated much more promptly. In *Pontederia* such promptness of germination of the large grains would be of great importance for the long- and mid-styled plants, inasmuch as the style withers so early that the pollen-tube of a slow-germinating grain might be unable to reach the ovule. I have found that large- and mid-size pollen-grains of *P. montevideensis* both germinate very quickly in weak sugar solutions; the only apparent difference is that the pollen-tube from the mid-size grains has a diameter about three fourths as great as that of the large grains. I had no flowers containing small grains for comparison. But this is a point which can hardly be settled by study of one small group of species.

In *Lythrum* and other heterostyled flowers it has been noted that the stigma of the long-styled form is larger than those of the mid- and short-styled flowers, and it has been considered that the longer stigmatic papillae are adapted to receive the large pollen-grains. In *Pontederia cordata* there is very little difference in the length of the papillae in the different stigmas (FIGS. 8–10) but the stigma of the long-styled flower is frequently, though not uniformly, six-parted, and this spreading stigma may be regarded as directly correlated with its exserted position, for such a stigma would have a distinctly better chance of being dusted with pollen by the insect visitor. In the case of the mid- and short-styled pistils, however, there is no need for such a spreading stigma, since the perianth-tube would almost certainly guide the pollen-smeared proboscis of an insect in such a manner as to brush even a narrow stigma.

Observation of the manner in which the flowers are placed on

seeds per capsule; other flowers fertilized by pollen from the mid-length stamens of the same spike produced 121.3 seeds; while still other flowers fertilized by pollen from the short stamens of mid-styled flowers produced 113.3 seeds. Kosmos 13: 298. 1883.

the axis of the spike in a nearly horizontal, though slightly ascending position, indicates that automatic self-pollination is regularly precluded (FIG. 11 and PL. 14). In the long-styled flower the stigma stands out stiffly too far to be reached by pollen from its own anthers, and these are so nearly included in the perianth-tube that pollen from them would be very unlikely even to fall on stigmas lower down on the same spike; in the short-styled form it would be impossible for the pollen to drop down the long, narrow tube to the low stigma. Only in the mid-styled form does it appear that pollen from the long-exserted anthers might possibly fall on the stigma of a lower flower, and here again in all ordinary cases the erect upper lip of the perianth would protect the lower stigma, which furthermore hardly projects from its tube far enough to catch pollen from above.

Among the insect visitors of the pickerel-weed ten species of Lepidoptera, distributed among five families, and showing nearly all possible range in size were collected during several excursions in July and August, 1916, and all of these but two or three were photographed as they sipped nectar from the flowers, several species many times. The list includes the least skipper, *Ancyloxypha numitor* Fabr.; the yellow-spotted skipper, *Polites peckius* Kirby; the silver-spotted skipper, *Epargyreus tityrus* Fabr.; the variegated fritillary, *Euptoieta claudia* Cramer; the clouded sulphur, *Colias philodice* Godart; the white cabbage butterfly, *Pieris rapae* L.; the viceroy, *Basilarchia archippus* Cramer; the tiger swallow-tail, *Papilio turnus* L.; the black swallowtail, *Papilio polyxenes* Fabr.; and the humming-bird moth, *Hemaris thysbe* Fabr. It is strange that the monarch butterfly, *Anosia plexippus* L., which was frequently seen on neighboring plants of Joe-Pye weed, never visited the *Pontederia*, and the so-called mimic, the viceroy, made only one fleeting visit; they evidently prefer the large flat-topped flower clusters of *Eupatorium* and milk-weed, or the nectar found there; or is it possible that blue flowers do not attract them? Another curious case was that of the pearl crescent butterfly, *Phycioides tharos* Kirby, which was the commonest visitor of the vervain, *Verbena hastata* L., growing close to the pickerel-weed ditch, but never came to the *Pontederia*, though the latter possesses much the same blue color and has a similar flower structure. Perhaps a parallel case is that of the honey-bee, which was the most abundant visitor of the vervain, and is generally regarded as catholic in its tastes, but which was not taken on the pickerel-weed. These cases may have a bearing on the view held by some entomologists, that insects have less color sense than has been supposed, but are much more keenly attracted by odors of particular plants, which may not always be perceptible to man.

Of the Hymenoptera, the following species were taken from the middle to the last of August: the bumble-bees, *Bombus fervidus* Fabr., *B. impatiens* Cress., *B. pennsylvanicus* DeGeer; and a smaller Anthophorid bee, *Xenoglossa pruinosa* Say (?) perhaps only gathering pollen. Of Diptera, one specimen of a large "horse-fly," *Tabanus giganteus* DeGeer, was perhaps only a casual caller.* An aggressive large blue-black bee, observed several times, but always eluding the pursuing reflex-camera as well as the net, was probably one of the carpenter-bees of the genus *Xylocopa*. Schneck† has reported that *Xylocopa virginica* regularly slits the lower end of the corolla tube to reach the nectary in *Pontederia* and in other plants. In the present case, however, I feel sure that the bee was sucking nectar from one flower after another in legitimate fashion.

Lovell‡ reports as visitors to *Pontederia* at Waldoboro, Maine, July 21 to August 10, 1898, two species of bumble-bees, two species of small cliff-dwelling bees, one collecting pollen, and four species of Diptera, all feeding on pollen; butterflies, he states, were comparatively rare, and only *Colias*, *Pieris*, and *Argynnis cybele* Fabr. are mentioned. During one warm but cloudy afternoon in August, at the New York Botanical Garden, I saw no butterflies visiting *Pontederia*, but only bumble-bees. Similarly, during August, 1917, abundant colonies of pickerel-weed growing in the open border of Lake Cossayuna in Washington County, New York,

* For the identification of these insects I am indebted to Dr. Frank E. Lutz, of the American Museum of Natural History, whose Field Book of Insects published in January, 1918, will be a handy guide for the student of floral biology. The Lepidoptera, identified by myself, were all compared with specimens at the American Museum.

† Schneck, J. Further notes on the mutilation of flowers by insects. Bot. Gaz. **16**: 313. 1891.

‡ Lovell, J. H. Three fluvial flowers and their visitors. Asa Gray Bull. **6**: 63–65. 1898.

were watched from a boat, and no butterflies, but numerous bees were seen visiting the plants, though one of the photographs taken there shows clearly a humming-bird moth with extended proboscis poised before a flower. Knuth would doubtless place this plant having a perianth tube of seven or eight millimeters in length among his groups of bee- or humble-bee-flowers, but the record at Arcola shows clearly that such a classification cannot be rigidly adhered to in this case, for there certainly the Lepidoptera surpassed the bees as visitors of this plant both in number of species and individuals. This I think was the case throughout the whole of July and August, though constant pursuit with the camera and net prevented making an exact record of the number of visits of any particular species.

Unquestionably the least skipper, *Ancyloxypha*, was the most frequent visitor, two or three individuals often being present on one spike, and often one of them flitted to several flowers on the same spike in succession; this was always an attractive little butterfly as the golden-brown scales on the lower surface of the folded wings caught and reflected the sun. These smaller butterflies, using the alighting platform furnished by the spreading lower lip of the flower, get the under side of their thorax or abdomen well dusted with pollen from the longest stamens (PLATE 15) and then carrying it to a long-styled flower rub off some of it on the protruding stigma; at the same visit they may dust the head with pollen from the mid-length stamens, or thrusting the proboscis into the tube on the upper side of the flower where there is a wider space between the perianth and the pistil than on the lower side, on withdrawing it after sucking the nectar, they drag it through the row of three inverted anthers of the shortest stamens (FIG. 1) to carry the pollen away to other flowers with appropriate length of style. Larger butterflies, like the silver-spotted skipper, often stand out farther from the flowers so that only the legs and proboscis tip become dusted with pollen, though one photograph of the black swallow-tail shows it grasping the spike with the abdomen tightly pressed against the flowers. The persistent visits of these large butterflies furnish the strongest reason for doubting the rigid applicability of Knuth's classification in the case of this plant. Standing at the south end of a ditch filled, like a garden border, with the bright-flowered plants, I would see a black swallow-tail alight at the north end and flit, sipping restlessly, the whole length of the bed to the point where the camera was focussed on the nearest spike; then he would fly without stopping straight back to the north end, and repeat the performance, until, after three or four exposures in the same place, he was captured. Query, why did he always proceed in the same direction, never reversing? Perhaps for some reason he prefers to sip while flitting toward the sun.

It appears, then, that the pickerel-weed is well supplied with a varied and constant procession of visitors, which must serve it effectively while supplying themselves with food. Although illegitimate pollinations may be frequent, at least some kind of cross-fertilization is undoubtedly the rule after these visits. Self-pollination, however, is probably possible; the little skippers might easily thrust some pollen from protruding anthers down to the stigma of the same flower, or might carry it from one flower to another of the same spike. But the question arises, would such pollination be effective, or are the plants self-sterile? And which of the legitimate crosses are most fruitful? For the purpose of obtaining some light on these points, plants were brought from the field and kept in pots placed in tubs of water in the greenhouse. Numerous crosses and self-pollinations were made, and many of the pistils so treated apparently set seed, but owing to various accidents not so many were brought to maturity. It can only be reported at present that a few mid-styled flowers matured apparently good seed when pollinated from their own long stamens, and also when pollinated from long stamens of other flowers on the same spike; owing to further accidents, no seeds were germinated. More definite results will be looked for from future experimental work.

It is interesting to note that in his second paper* Fritz Müller reported having found himself mistaken in his early assumption that *Eichhornia crassipes* is unfruitful with its own pollen, for although only one plant was introduced in his region, his nephews discovered seeds and young seedlings, and the barrenness had been due merely to the lack of proper insect visitors.

* Kosmos 13: 297. 1883.

In the field one is often inclined to think that one of the three forms of the species predominates in a particular locality. This might occur quite as readily as a result of vegetative propagation by rapid growth of the rhizomes as by greater fruitfulness of one form. But the pickerel-weed stem regularly becomes geniculate after flowering, usually just below the insertion of the spathe-like floral bract (the 'knee' is already indicated in PLATE 15) and bending downward, the inflorescence is lowered into the water for maturing the fruits, and they are most apt to fall to the bottom in the near vicinity of the parent plant; in this way also extensive patches of one plant form may be established. Müller reported in 1883 (*op. cit.* 299) that all the Pontederiaceae known to him, including *Heteranthera reniformis* and *H. zosteraefolia*, the two species of *Eichhornia*, and the *Pontederia* from Curitibanos, have this habit of bending the flower-stalk down to the marshy ground or water in which they grow. In 1912 Hauman-Merck* reported, as a peculiarity which he thought had escaped previous observers, this habit of maturing the fruit under water in *Pontederia rotundifolia*, and stated that *P. cordata* growing in abundance in the same places in pools of the banks of the Rio de la Plata matures its fruits out of the water. This statement is rather surprising, since our plants are so fixed in this habit of bending down after flowering that plants kept in the greenhouse with little water develop in a manner precisely similar to those left in the field. *Pontederia montevideensis* shows practically no such tendency when grown here and it would appear possible that Hauman-Merck was really dealing with this species rather than with *P. cordata*.

The final judgment reached at the Arcola station was that all three forms of the plant were about equally numerous there. During the dry August (in the region of New York) of 1917, one visit to the station revealed such a desolate and discouraging group of plants that no attempt was made to do anything further during that season. Perhaps clumps of the plant growing in the borders of the Hackensack River, if they could have been reached, might have proved more rewarding in such a season, for, contrary to the usual statement that this family comprises only fresh water

---

* Hauman-Merck, Lucien. Sur un cas de géotropisme hydrocarpique chez *Pontederia rotundifolia* L. Rec. Inst. Bot. Léo Errera **9**: 28–32. 1912.

forms, here plants of *Pontederia* are daily bathed, or even flooded, by tide water.

EXPLANATION OF PLATES 14 AND 15

PLATE 14. *Pontederia cordata:* at the left, a short-styled spike, longest and mid-length stamens protruding from the perianth tube; in the center, mid-styled spike, long stamens only exserted, style-tip barely protruding from tube; at the right, long-styled spike, mid-length stamens only slightly protruding in throat of tube, styles exserted and about as long as the perianth segments. Photographed 10 Aug. 1916, about three fourths natural size.

PLATE 15. Spike of the mid-styled form visited by the least skipper, *Ancyloxypha numitor;* photographed at Arcola, N. J., 15 Aug. 1916.

The drawings for all the text figures were made with the aid of the camera lucida, figures 1–4, 9, 10, and 12 from material preserved in formalin, figure 11 from fresh flowers.