Small Butterwort (*Pinguicula pumila*) in its natural habitat

John Bradford • Jensen Beach • Florida • USA
George Rogers • Horticulture Department • Palm Beach State College • 3160 PGA Blvd. • Palm Beach Gardens • Florida 33410 • USA • rogersg515@gmail.com

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Abstract: Two wild populations of Small Butterwort (*Pinguicula pumila*, Lentibulariaceae) were studied during its 2019/2020 late autumn–spring flowering season in Palm Beach County, Florida. The rare yellow-flowered form known primarily from Southwest Florida turned up in East Florida. Except possibly for 19th century literature we were unable to examine, stigmatic curling in response to touch is first reported for *Pinguicula*. Diverse Dipteran and Hymenopteran floral visitors were observed. Previous indications that spontaneous self-pollination is rare to none in this and related species, especially with reference to cultivated plants, were consistent with our results using insect exclosures on wild plants, whereas open-pollinated flowers made fruits and seeds abundantly. In our area the known populations are all spotty and small, in wet-then-dry disturbed habitats.

Introduction

South Florida is a great place for native carnivorous plants, with sterile soils, extensive wetlands, and insects aplenty year-round. Here live several species of *Drosera*, *Pinguicula*, *Utricularia*, and, marginally, *Sarracenia*. The tank bromeliad *Catopsis berteroniana* hosts bacterial symbionts as digestive aids. The present study is a profile of one of the prettiest and most curious local insectivores, Small Butterwort, *Pinguicula pumila* Michx.

Distribution and Habitats

Butterworts, comprising the genus *Pinguicula,* number debatably around 75 species from Canada to Chile, and around much of the globe mostly in North Temperate regions (Legendre 2000). Six live in Florida, comprising a single clade (Shimai *et al*. 2007). *Pinguicula pumila* resembles the other Florida species by having a nearly round floral tube that closes and nods at night, although the plants are distinctively tiny. The basal rosettes are often around 2-3 cm across, with the taller floral stalks rising to about 7-12 cm bearing flowers with the petals spread to about a cm.

The overall range of *Pinguicula pumila* is the Southeastern Coastal Plain from the Bahamas to Texas, including most of Florida. In South Florida, *P. pumila* blooms winter through early spring on seasonally inundated and later drying, sunny to lightly shaded, muddy, sandy, or marly habitats. Although specific pH data are mostly lacking, herbarium label data suggest broad tolerances in that regard.

The wet-then-dry habitats are varied, including pine woods, ditches, and shores. Moist pathways, roadsides, and power lines dominate specimen labels in the University of South Florida Herbarium. This preponderance of disturbed rights-of-way begs the question of management practices, especially the relationship of Small Butterwort with glyphosate-based weed control, prescribed burning, roto-chopping, and feral hogs. Disturbance appears to favor the species.

Figure 1: Habitat of *Pinguicula pumila*. Cypress Creek site near Jupiter, Florida.

The two populations we studied late autumn through spring 2019/2020 are in and adjacent to semi-neglected dirt roads in low wet slash pine woods in Palm Beach County on the Florida south-eastern coast. One patch is in the Pine Glades Natural Area west of Jupiter, Florida, the other a few miles farther east, occupies similar habitat in the Cypress Creek Natural Area (Fig. 1), and was the site of most of our efforts. We are aware of three additional nearby patches, two in and adjacent to disturbed dirt roads through low pine woods. The third occupies nearly bare sandy soil upturned by feral hogs.

In our area, Small Butterwort is usually mixed with other moisture-loving insectivores, *Drosera capillaris* and *Utricularia subulata*. Locally present also, if not in the immediate company of *P. pumila*, are *Pinguicula caerulea* and *P. lutea*, both larger in all dimensions.

Prey Capture

Most prey are tiny, rapidly degraded, and hidden under the curling leaves. We have observed small Dipterans, springtails, what appear to be minute beetles, and ants. Curiously common on the sticky leaves are planthoppers, *Delphacodes puella*, a widespread herbivorous species. These, perhaps due to size and strength, frequently evade capture by leaping away upon disturbance. It is unclear if their presence is random, or perhaps due to some form of attraction. Mary Treat (1876) suspected slash pine pollen to help feed the foliage.

Flower Colors

The most salient feature of *P. pumila* is the mix of its floral colors intermixed in any given patch. In our experience, white and violet are almost always together, sometimes on the same rosette. The

Figure 2: **A:** Yellow *Pinguicula pumila* flower. **B:** *P. pumila* palate in violet flower.

patch on the soil upturned by hogs is completely white-flowered although we are not suggesting any connection between the hogs and flower color. The flowers usually have yellow throats and reddish nectar guides leading into the spur. Gluch (2005) listed color variations. Flowers of many plant species change color, presumably to signal pollination status to pollinators. A prominent Florida example is Jamaica-Caper (*Quadrella jamaicensis*) where the corollas transform from white to violet. In *P. pumila* marked and monitored uncultivated flowers likewise sometimes change from white to violet. The violet coloration grades from barely perceptible to deep and rich. Many flowers remain white through their entire life.

A rare bright yellow variant (Fig. 2A) is best documented in southwestern Florida. We found bright yellow, white, and violet blossoms all together at the Pine Glades site. The yellow variant has been recognized previously as *P. pumila* var. *buswellii* Moldenke. Given its mingling among the white- and violet-flowered individuals, there is no basis for taxonomic recognition except arguably as a "forma," which we regard as pointless. Other botanists, for example Wunderlin *et al*. (2020) have placed var. *buswellii* in synonymy where it belongs.

Fleischmann (2016) suggested that, because *Pinguicula* offers false pollen on the fuzzy yellow palate (Fig. 2B), pollinators may learn to avoid flower colors associated with false promises while remaining willing to try other colors on the same species, as a frustrated gambler may try different slot machines in the same casino. We wonder alternatively if the different-colored flowers "suggest" the diverse colors of different nearby rewarding species. There are similar-sized, white (e.g., *Viola lanceolata*, *Mecardonia acuminata*), violet (e.g., *Lindernia grandiflora*, *Sisyrinchium angustifolium*), and yellow (e.g., *Utricularia subulata*, *Xyris elliottii*) flowers around to share visitors. We mention the analogous flowers as general examples of plausibility, not to suggest one-on-one mimicry.

Some species of *Pinguicula,* perhaps all, offer true rewards. Lustofin *et al*. (2019) documented nectary hairs in *Pinguicula* floral spurs, although they did not check *P. pumila*. A tiny insect visitor we photographed in a yellow *P. pumila* flower was eating or nuzzling knob-tipped hairs in the floral tube at the time of our photo. Knob-tipped hairs from *P. pumila* are illustrated in Wood & Godfrey (1957).

Floral Structure and Function

The flowers rise singly on one to several delicate scapes a few cm above the rosette (Fig. 3). The maturation time for a scape and its flower is several days, and the mature flower likewise persists several days. The tubes are usually, but not necessarily, upright at times of visitation. We find most flowers to open 10-11 AM EST and to close and nod late afternoon well before dark, not opening or closing in unison. Weather makes a difference. In other Florida *Pinguicula* species, Molano-Flores *et al*. (2016) found unpollinated flowers to last longer than pollinated ones.

The flowers are tubular and provided with a spur. The corolla tube has on its "floor" a pronounced outgrowth, the palate which is a hairy yellow ridge sloping down and inward toward the stigma and partly blocking entrance to the tube.

Wood & Godfrey (1957) regarded the palate as a "foothold" for pollinators. It presumably has an "advertising" function, given its bright yellow coloration. False-anthers and yellow floral decorations are common in the plant world. Additionally, the palate may block unauthorized insect visitors (see footage suggestive of this in the video link provided below), may help guide welcome visitors inward, and may participate in the physical dynamics of floral shape during insect visitation.

In a flower opened on its side with the pedicel at the "top" and the palate at the "bottom," the palate is visible lengthwise, with the pistil and stamens deeper in the flower. The globose ovary is sessile where the pedicel joins the tube. From the ovary a short style holds the large flat stigma as a ramp having its top (toward the pedicel) deeper in the tube than its base on the floor of the tube behind the palate (Fig. 4).

Looking into the mouth, the palate greets the eye end-on (Fig. 4 righthand views, Fig. 2). Behind it the tilted stigma blocks most of the tube. The top of the stigma (2nd lobe) almost matches in shape the opening around and above it. At the floor of the tube behind the palate the stigma covers the two anthers (Fig. 5A) and prevents access to the spur.

Figure 3: White *Pinguicula pumila* flower on scape.

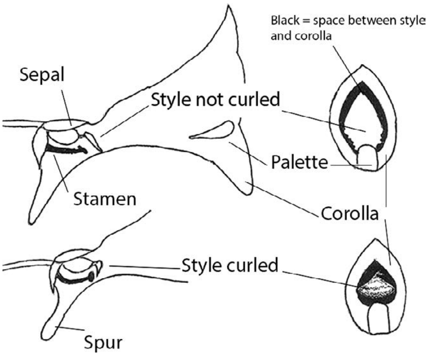

Figure 4: *Pinguicula pumila* flower diagram (cross-section from side) showing uncurled and curled condition of stigma.

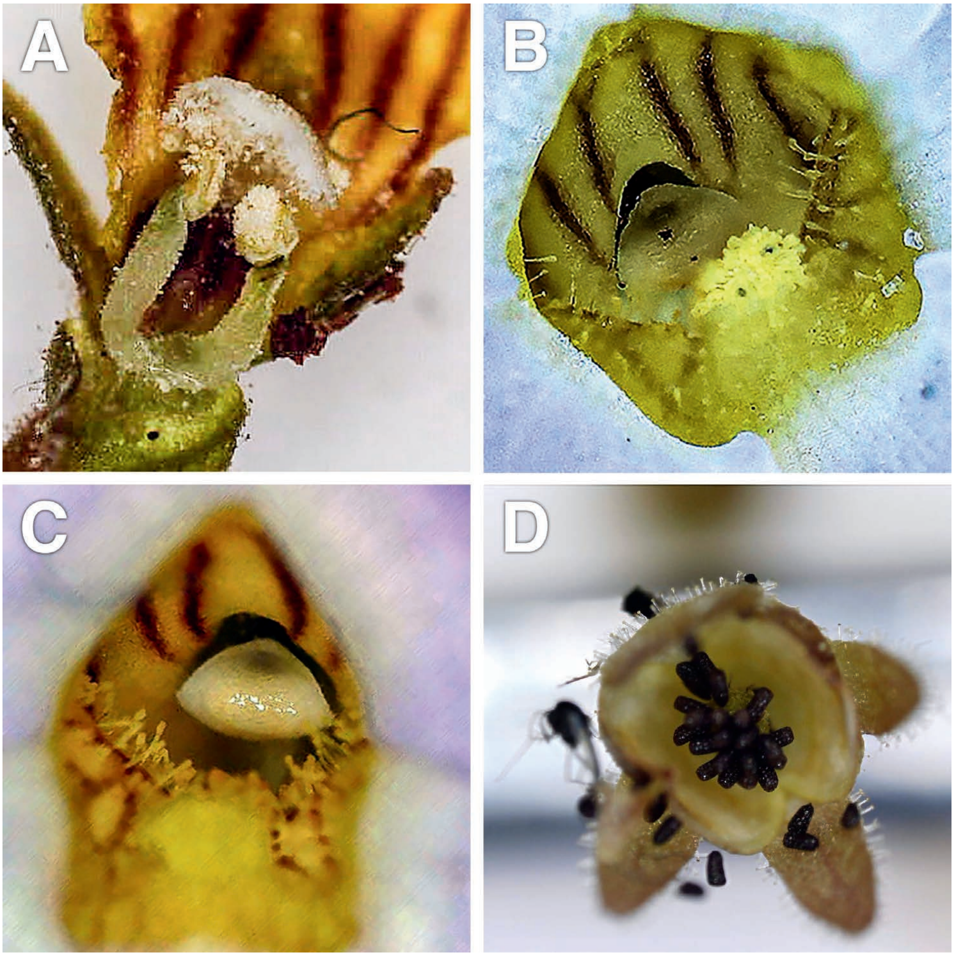

Figure 5: **A:** View of *Pinguicula pumila* stamens from beneath (lower corolla lip removed); **B:** stigma not curled; **C:** stigma curled; **D:** fruit (cut open) with seeds.

Stigmatic Curling

In related *Utricularia*, the stigma curls upon physical stimulation. Newcombe (1924) looked for similar sensitivity in *Pinguicula* but failed to find it in species he examined, not including *P. pumila*. We have found the stigma sensitive in *P. pumila*. Probing the flower with a false proboscis, for instance a tiny stem, causes the stigma base to curl back and inward, opening the door to the spur and exposing the anthers to insect contact. The movement happens within seconds of contact, or repeated contacts, and the movement lasts about 1 or 2 seconds. The uncurled and curled stigmatic positions appear in Figures 5B-C. Wild plants examined undisturbed commonly have curled stigmas, while many others have the stigmas uncurled. If and when or under what circumstance they may uncurl is not established.

Floral Visitors

Wood & Godfrey (1957) and Molano-Flores *et al*. (2018) determined other Florida *Pinguicula* species to be pollinated mostly by Hymenopterans. Using video cameras, in *P. pumila* we recorded numerous floral visits where insects entered the floral tube in addition to several non-penetrating "inspections" or perhaps would-be visits thwarted by the palate. Visitors witnessed entering the flowers are diverse, including wasps and Syrphid flies. Visitation is displayed at https://vimeo.com/399208537. An odd floral guest was the tiny Hymenopteran mentioned above in connection with the corolla hairs. Under natural conditions the plants regularly produce abundant capsules and seeds (Fig. 5D), although many flowers end up seedless, and many rosettes of this delicate species decline before reproductive success.

Self-Pollination

The stigma curling toward the anthers, even if the receptive surface does not contact anthers directly, hints at potential for self-pollination. Merilaun (1895) with reference to other *Pinguicula* species described stigma curling as a response to age, and suggested the movement to assure pollination. Citing multiple 19th Century authors reporting curled *Pinguicula* stigmas, Willis & Burkill (1903) reported seeing pollen tubes from the anthers entering the curled stigma in sectioned material of *P. vulgaris*. If age-related (or otherwise induced) curling leads to selfing as Marilaun and Willis & Burkill perceived over a century ago, stigma curling as a result of insect visitation could conceivably cause selfing in *P. pumila*, although that notion has complexities:

Wood & Godfrey referring to all the Southeastern Pinguiculas, and later Fleischmann (2016) determined *Pinguicula pumila* to be self-compatible, and the latter author found *P. pumila* not to self-pollinate spontaneously in cultivation. We have seen the same failure to form capsules on two flowering cultivated rosettes. Similarly, Molano-Flores *et al*. determined *Pinguicula ionantha*, *P. planifolia*, and *P. lutea* (see also Primer 2016a) to be self-compatible yet free of spontaneous self-pollination or very nearly so. Primer (2016b) speculated that an insect-visitor might cause selfing along with whatever outside pollen it delivers in the species she studied, not *P. pumila*. This would make sense, given the massive numbers of seeds produced requiring enormous numbers of pollen grains, debatably more than floral visitors are likely to deliver.

Our results echo our predecessors that spontaneous self-pollination is minimal at best. At the Cypress Creek site, we excluded flying visitors for 4-6 weeks from 16 marked rosettes under small screen tents affixed to the ground with nails. None of the rosettes had open flowers, post-opening flowers, or maturing capsules at the time of covering. The rosettes were allowed to flower under the tents, most rosettes producing numerous blossoms during the study period. The tents were placed on different days within the first two weeks of February and monitored until the time of this writing in late March. Of these, one flower produced a dehisced seed-bearing capsule. A single instance could be caused oddly, perhaps even by insects crawling under the tent, although crawlers would have to run the gauntlet of the sticky leaves and scape.

Wondering if probing the flowers in the fashion found to trigger stigmatic curling might boost self-pollination, pre-anthesis plants were allowed to flower under seven screen tents with each flower probed upon opening. This crude simulation of insect visitation resulted in one flower producing seeds, not a discernable boost. It is impossible to know if the ostensibly probe-induced self-pollination resulted from stigmatic curling, or from self-pollen clinging to the probe, or otherwise.

In short, spontaneous self-pollination is probably unimportant as a back-up means of reproductive assurance, given its reluctance to occur, and given that in open-pollinated flowers insect visitations are common, as are fruit and seed production. A possible consequence of self-pollination in general is the conferred ability of lone plants to found new populations. The scarcity of selfing in *P. pumila* might coincide with the scarcity of isolated patches in seemingly suitable habitats.

Dispersal

In our area the patches are spotty, small, and widely scattered relative to what seems to the inadequate human eye to be suitable habitat, perhaps the outcomes of individual seed releases, although unknown ecological constraints probably matter too. The dust-sized seeds undoubtedly disperse sometimes by wind and on creatures. Locally the plants favor rough dirt roads traversed by maintenance crews, hikers, hunters, equestrians, and abundant hooved wildlife, all suspected agents of seed dispersal.

Water movements certainly relocate seeds in this immersion-prone species. The patch borders reflect the boundaries of large seasonal puddles. During the 2019/2020 winter and early spring the Cypress Creek patch borders morphed like an amoeba as the wet-dry and sun-shade patterns changed, older rosettes faded out while replacements popped up outside the original patch footprint. As conditions became seasonally hotter and drier, the largest and most robust individuals were in shade with violet-colored flowers more abundant than elsewhere. We were unable to detect any form of vegetative propagation and dispersal.

Summary

Pinguicula pumila has largely fallen between the academic cracks. Within the scope of our study it forms small patches in disturbed sites prone to seasonal immersion followed by drying, the rosettes tolerating both extremes. Among the prey, planthoppers visit the leaves, frequently able to leap free. White and violet flowers are almost always together, even on the same rosette, and some white flowers become violet. The yellow-flowered variant occurs freely mixed with rosettes bearing white or violet flowers. The flowers are complex. The stigma hides access to the floral spur and to the anthers until physical contact triggers curling. Consistent with prior reports, the species is self-compatible yet disinclined toward spontaneous self-pollination. Our encounters with curling stigmas are more consistent with *Utricularia* and with 19th Century reports on *Pinguicula* than with contemporary research on the other Florida species. Floral visitors are varied, including Dipterans and Hymenopterans. Capsules and seeds are plentiful under open pollination in natural habitats. A one-season study raises more questions than it answers, some of them beyond our technical equipment and ability. Suggested further research includes broadened data on the relative importance of self-pollination and factors influencing it including insect visits, stigmatic status before and after visitation, stigmatic dynamics in this and related species, pollen loads on visiting insects, population genetics and gene flow, and demography of the small isolated patches.

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