

LONGITUDINAL ALLOMETRY OF INFERIOR LAMINA SUBSTRUCTURES IN  
*SARRACENIA* (SARRACENIACEAE)

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Abstract: While *Sarracenia* petioles, phyllodia, leaf plasticity, and seasonal pitcher cohorts are common subjects of discussion, these features have not yet been clearly delimited or described. Longitudinal allometry disclosed new substructures of the *Sarracenia* pitcher leaf on the first and climax leaf cohorts of several taxa with upright leaves. Petioles, previously thought to comprise the entire solid proximal portion of leaves, are found to be different from pitcher phyllodes, the two being adjacent but independently plastic substructures. Leaf cohort heterophylly is characterized by different substructure proportions and their constituent plastic properties. A locus at the transition point of internal pitcher chamber Zones 3 and 4 separates the inferior from superior lamina and dampens the influence of plastic substructures in derived indices, including the inferior lamina to whole leaf longitudinal allometric index. This index helps distinguish cohorts within taxa and taxa from each other as its degree of relative variability is exceptionally low and consistent. The inferior lamina index and its core locus provide modular solidarity to the methodology, facilitating comparative analysis of substructures, the inferior and superior lamina, leaf cohorts, and taxa by means of allometric indices and their relative variability. Inferior lamina substructures facilitate known conditional responses in upright *Sarracenia*, with critical differences between taxa bearing implications for systematics.

Introduction and background

Morphological species concepts guide *Sarracenia* taxonomy (McDaniel 1986), with much attention devoted to their peculiar and highly characteristic pitcher leaves. Taxonomists have analyzed *Sarracenia* leaves in diverse and interesting ways for well over a century (Macfarlane 1889, 1893, 1908; Wherry 1929; Bell 1949, 1952; Bell & Case 1956; McDaniel 1971; Case & Case 1975, 1976; Krider & Schnell 1976; Schnell 1977, 1979, 1980, 2002; Naczi *et al.* 1999; Mellichamp 2008; Mellichamp & Case 2009; Rice 2018; good summaries in Lloyd 1942 and Juniper *et al.* 1989). Yet there remains no reliable method for analyzing *Sarracenia* foliage. The unusual morphology and plasticity of *Sarracenia* leaves make it challenging and controversial to categorize, and recent taxonomy has not produced or resulted from a wholly articulated leaf model or systematic methodology. Over the past hundred years, morphologically-centered *Sarracenia* taxonomy has revolved around a small set of characteristics, some of which, though wielded strongly in important taxonomic decisions, remain unclearly defined.

*Sarracenia* pitcher leaves have been described as being comprised of homologous parts, including a lid, peristome, ala (adaxial wing), petiole, leaf base, and a pitcher chamber whose internal surface micromorphologies facilitate carnivory (Macfarlane 1908; Lloyd 1942). Phyllodia and scale leaves (squamulae) are the non-carnivorous foliage of *Sarracenia* (Macfarlane 1908; McDaniel 1971). Foliage of different types may be produced in discrete cohorts at different times of the growing season. Pitchers of separate cohorts within the same year are thought to differ in most taxa, but how they do is not always clear (Macfarlane 1908; Lloyd 1942; McDaniel 1971; Case & Case 1975, 1976; Schnell 1977, 1980; Mellichamp & Case 2009).

The above model of the *Sarracenia* leaf originates in Macfarlane's preparatory studies for the first modern treatment of the genus (1889, 1893, 1908). While *Sarracenia* is regularly taxonomically revised (Mellichamp 1978), the basic layout of the pitcher leaf has not been revisited since the time of Macfarlane, even for generic treatments (e.g., McDaniel 1971). More recent decisions in the genus have not systematically integrated new findings that could explain differences between similar, often at-issue taxa. New findings challenging Macfarlane's model have indeed inspired taxonomic revision (Case & Case 1975, 1976), but some critics discourage this, declaiming unclear systematic value (Schnell 1977; McPherson & Schnell 2011). It seems however that *Sarracenia* morphology related to prey niche may be important for comparative biology of the genus (Gibson 1983). This has implications for *Sarracenia* taxonomy, which canonically revolves around morphologic criteria. Implications for classifying and valuing leaf morphology are considerable (e.g., Naczi *et al.* 1999).

Macfarlane's leaf model does not clearly locate sources of plasticity in pitcher leaves, and to date, plastic regions of the leaf have not been delimited (but see Lloyd 1942 re. internal surfaces). Plasticity radically transforms the pitcher in development (Lloyd 1942; Case & Case 1976), making affected leaves bewildering for determinations and stymying attempts to systematize *Sarracenia* (Wherry 1933; Weakley pers. comms. 2023). Some have noted that, as in the upper portions of the pitcher leaf, lower halves of pitchers show temporal plasticity in some instances, with some work suggesting an ecological relationship (see Brewer 2019, Ellison *et al.* 2004, Lloyd 1942).

This study is inspired in part by observations of hybrid *Sarracenia*. Hybrids are useful for exploring distinguishing characters as they contrast parent morphology, growth, and behavior in living plants, and inspire critical comparisons of taxa (Russell 1919; Bell 1952; Bell & Case 1956; Case & Case 1975; Mellichamp 2008a, 2008b; Trexler 2023). *Sarracenia* hybrid leaf structures are intermediate between parents down to internal surface micromorphology (Russell 1919), structural proportions, and non-structural properties, including phenology, circannual growth patterns, tissue life span, the presence of phyllodia, colors and markings, volatile properties of the flowers, etc. (Macfarlane 1907; Russell 1919; Bell 1952; Bell & Case 1956; McDaniel 1971; Case & Case 1975; Mellichamp 2008a, 2008b; Trexler 2023). This is well-known amongst cultivators, especially those specializing in hybrids (e.g., Mellichamp & Gardner 1998). Such characters are useful for making correlative determinations in hybrids because they demonstrate the predictably intermediate homologous modularity of pitcher leaf parts derived from parents. Assuming *Sarracenia* foliage is comprised of homologous parts, a unified way to model and analyze the leaves is possible.

#### Preliminary observations

This study investigates substructures of the *Sarracenia* leaf. It builds upon past works by referencing established knowledge while suspending some older concepts. The internal Zones of the

pitcher chamber and general physiology of the leaves (Macfarlane 1889, 1893, 1908; Arber 1941) guide exploration for boundaries between new parts and any dynamic properties.

Before formal research commenced, in all studied taxa it was noticed that the point of transition between internal Zones 3 and 4 (Fig. 1) divided pitcher leaves into the same two suites of consolidated structures, that this point of transition occurred in consistent proportional locations within leaves, and that the proportional location seemed to differ between taxa. It was also noticed that the location of this feature appeared to characterize leaf cohorts of taxa, that taxa differed in its location along leaf length per leaf cohort, and that the internal Zone 3-4 transition (hereon, “iZ3-4”) in hybrids was allometrically intermediate relative to the parents. The iZ3-4 roughly corresponds to an external “hip”.

Sources of plasticity and leaf substructures were not clear when patterns involving the iZ3-4 were noticed, but it was clear that first and climax leaf cohorts were differentiated by the ability to convert various degrees of the proximal end of the pitcher chamber to a solid alate structure which appeared to correlate strongly with length of independent phyllodia. The phenomenon in this ambiguously defined part of the leaf suggested pitcher leaves are both internally and externally plastic.

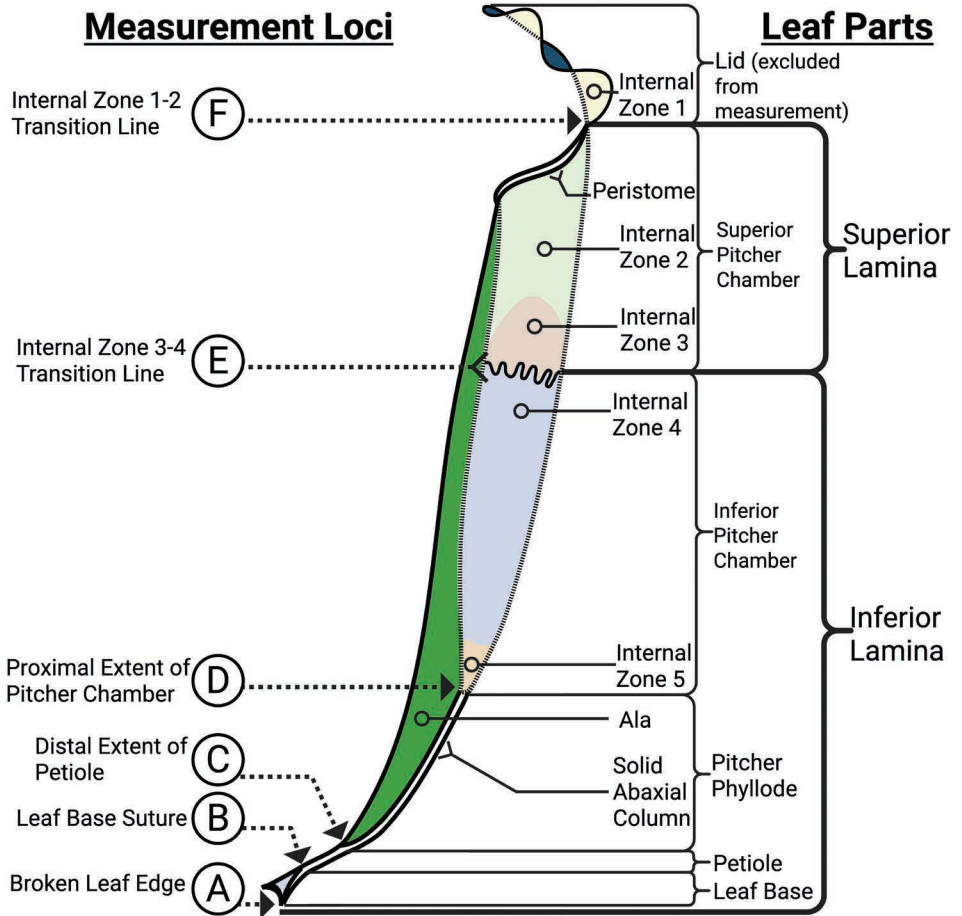


Figure 1. *Sarracenia* pitcher leaf model for longitudinal measurement.

## Hypotheses

This study hypothesizes that the *Sarracenia* leaf is comprised of parts that are delimited by structural and dynamic properties at transversal boundaries along the length of the leaf, and that substructures and their plastic properties are homologous across *Sarracenia*, but that certain substructures and concatenations thereof differ critically between taxa and leaf cohorts within taxa. Boundaries between substructures were observed where vascular, structural, and plastic leaf dimensions changed at consistent points of transition upon the exterior and/or internal surfaces of pitcher leaves. Five points of transition between substructures were selected to be measurement loci.

The pitcher phyllode, once considered part of the petiole, is hypothesized to be an alate substructure between the pitcher chamber and the petiole. The petiole is hypothesized to be a solid, rigid cylindrical structure of uniform diameter located distal to the leaf base's adaxial suture and proximal to either the pitcher chamber or unchambered phyllode. Locus #E (at the iZ3-4; Fig. 1) was noted to be the only place where internal and external leaf substructure boundaries (including internal Zones and external leaf halves) transition together at a single transversal location, indicated by the mutual termination of structural and dynamic properties on either side of it. Locus #E divides the pitcher leaf into the same superior and inferior parts and concatenations in all measured taxa (Fig. 1). The halves are called the inferior and superior laminae.

## Materials and methods

### Excursions

Fieldwork revolved around visits to natural sites of *Sarracenia wherryi* and *S. chrysea* in southwest Alabama. Excursions occurred in May-June and September 2022; April and September 2023; April and August-September 2024; and April-May and October 2025. Excursions coincided with the production of the first cohort of leaves in spring and climax leaf cohorts in late summer.

### Specimen data

Data derive from leaves produced by plants growing in full sun. Herbarized collections included leaves and plants of *Sarracenia chrysea*, *S. wherryi*, *S. alata*, *S. flava*, *S. leucophylla*, *S. alabamensis*, and *S. ×ahlesii* Bell & Case (= *S. alata* × *S. wherryi*). Supplementary field data were taken on all the above taxa for the inferior lamina to whole leaf index except *S. ×ahlesii*. All collections from private property were made with the knowledgeable consent of landowners. No collections were taken in Florida or publicly-stewarded habitat in Alabama. Vouchers of *S. alabamensis* of Central Alabama were only prepared from cultivated material and no wild material was taken of that taxon. All herbarized data of *S. flava*, and some of *S. alata* and *S. leucophylla*, come from cultivated plants, grown under methods following Farin (2018).

*Sarracenia ×ahlesii* was sampled to compare it and its parent taxa. *Sarracenia alata* and *S. ×ahlesii* samples were taken at the same location where *S. wherryi* was also abundant. To avoid mixing up *S. wherryi* with look-alike hybrids, it was sampled from a nearby site where it was the only *Sarracenia* taxon present. The hybrid was identified in the field by its intermediate size, spatial proximity to parent taxa in-site, incompletely erect-upright rosetted leaf carriage, orange or yellow-streaked petals, and other intermediate characteristics.

### Herbarized specimen protocol

Leaves were pulled from rhizomes to preserve the petiole and leaf base. Vouchers were transported back to base in closed containers with damaged edges submerged in water. All herbarized specimens were dorsiventrally pressed and opened. Some leaves were dorsiventrally dissected before pressing. Dissected leaves were cut longitudinally from the peristome or immediately proximal to it down the adaxial meridian of the tube to expose the internal Zones. Dissected living leaves were interred to the plant press with internal surfaces appressed to newsprint under rubber band restraints.

### Measurement protocol

All loci were simultaneously measured per sample. Specimens were fixed atop a foam board and loci indicated with colored ball-head pins. For locus #A, the zeroth millimeter mark on the tape measure was situated at the broken edge of the base where it attached to the rhizome and fixed with a black pin. For locus #B, the distal terminus of the basal adaxial suture was marked with a yellow pin. For locus #C, caliper tines were closely calibrated to the adaxial and abaxial faces of the petiole at the point immediately distal to the terminus of the basal suture. These were tracked along the succeeding distal length of the petiole, following the abaxial and adaxial faces across the inherent torsion of the primary veins until tines were immobilized by an increase in petiole diameter (where the adaxial four primary veins diverge from the abaxial six, forming the ala); this was determined to be the distal boundary of the petiole and marked with a red pin. Changes in petiole structure at #C were visually confirmed with a lens. Locus #D was found by incising the leaf and marking the proximal terminus of the pitcher chamber with a blue pin. Locus #E was found by incising the leaf and marking the iZ3-4 with a green pin. Locus #F was marked with a white pin at the point where the peristome unraveled to form the lid margin. A flexible tape measure was then led between pins following the natural abaxial contour of the pitcher leaf. Pinned constellations were then photographed from the side to capture points of measurement on the tape measure where it encountered pins, and from above to index the preparation in sequence with others. Field data were collected with a meterstick or ruler on live plants in habitat without removing leaves.

### Statistical calculation protocol

Data analyses were performed in Microsoft Excel version 16.103.4. Statistical comparisons between taxa or leaf cohorts involved samples of unlike size, and used Excel's built-in t-test calibrated for samples of unequal variance,  $\alpha = 0.05$  (Welch's t-test).

## Results and analysis

### Explanation of selected index distributions:

- Inferior lamina: length of segment AE/length of segment AF (Fig. 1).
- Petiole to whole leaf (excl. leaf base): BC/BF.
- Pitcher phyllode to whole leaf (excl. petiole and leaf base): CD/CF.
- Whole pitcher chamber to whole leaf: DF/AF.

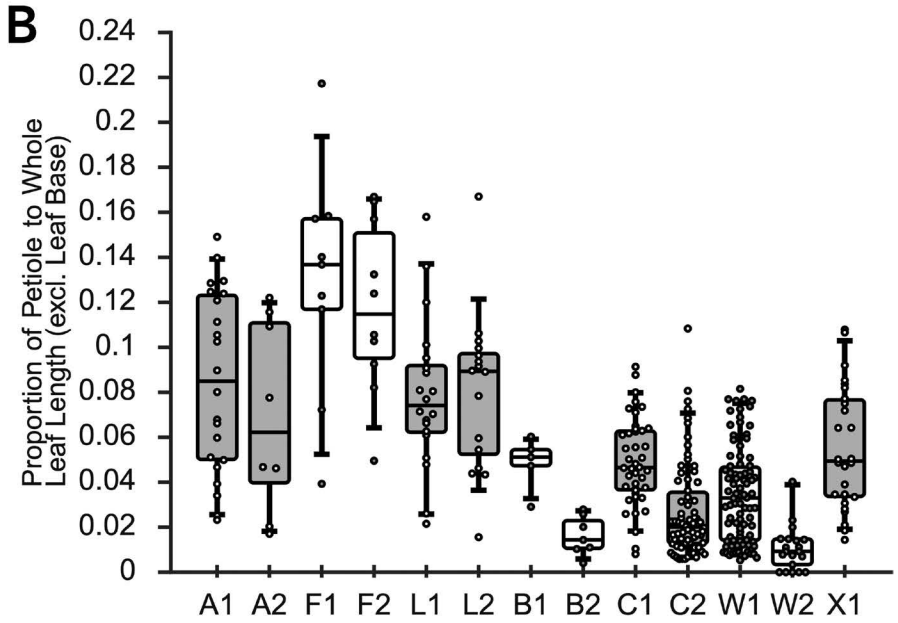
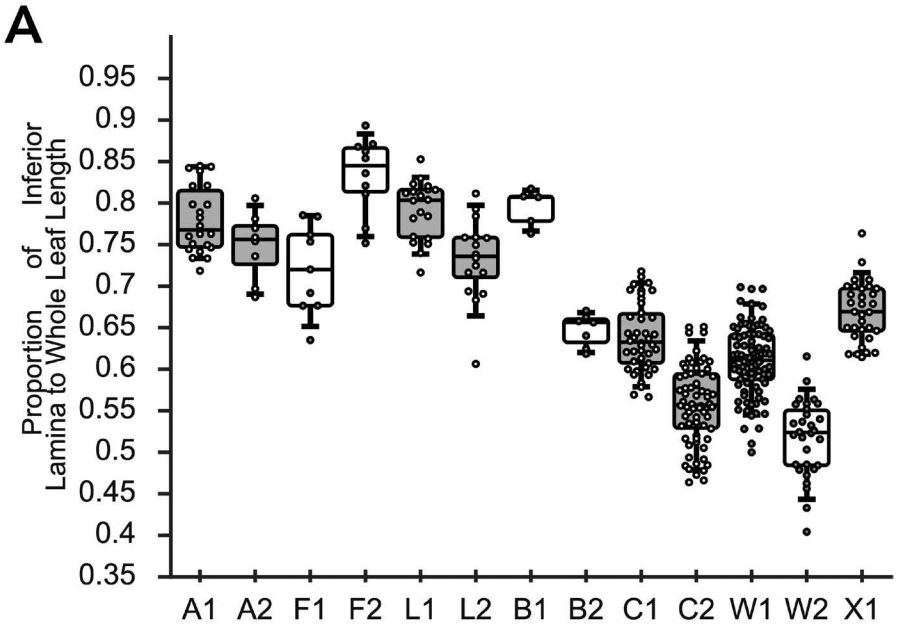
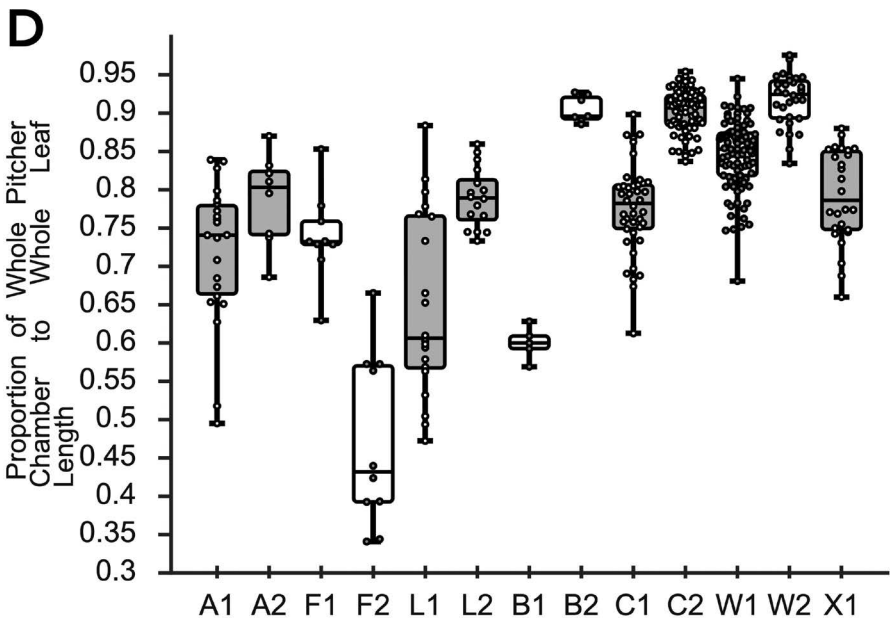
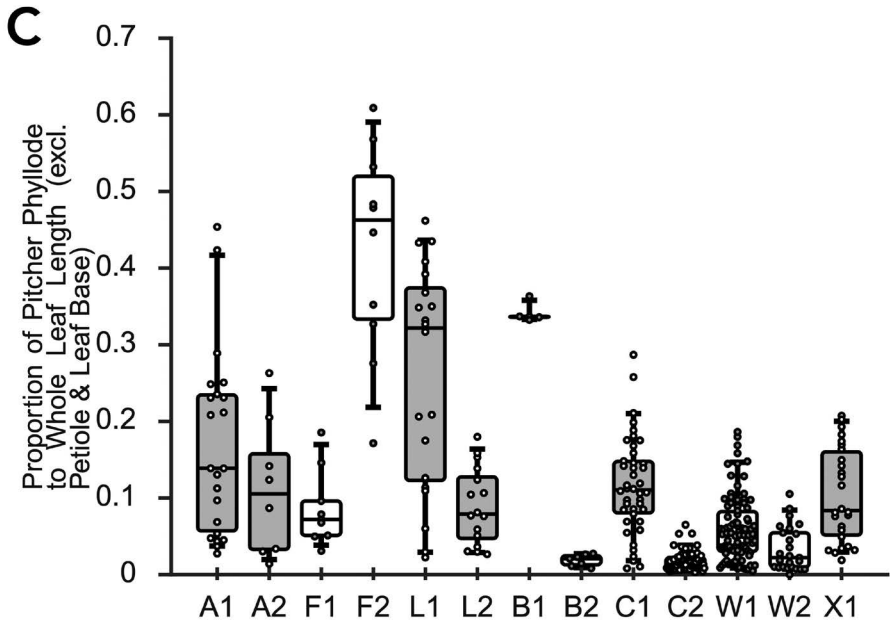


Figure 2. (A) Inferior lamina index. (B) Petiole index. (C) Pitcher phyllode index. (D) Whole pitcher chamber index. Boxes depict the interquartile range (Q1-Q3). Horizontal center lines depict the median. Whiskers extend to the 5<sup>th</sup> and 95<sup>th</sup> percentiles.



A1 = *Sarracenia alata* first cohort leaves ( $n = 22$ ). A2 = *S. alata* climax cohort leaves ( $n = 8$ ). F1 = *S. flava* first cohort ( $n = 9$ ). F2 = *S. flava* climax cohort ( $n = 10$ ). L1 = *S. leucophylla* first cohort ( $n = 20$ ). L2 = *S. leucophylla* climax cohort ( $n = 16$ ). B1 = *S. alabamensis* first cohort ( $n = 5$ ). B2 = *S. alabamensis* mid-season cohort ( $n = 7$ ). C1 = *S. chrysea* first cohort ( $n = 42$ ). C2 = *S. chrysea* climax cohort ( $n = 70$ ). W1 = *S. wherryi* first cohort ( $n = 90$ ). W2 = *S. wherryi* climax cohort ( $n = 30$ ). X1 = *S. xahlesii* first cohort ( $n = 33$ ).

Table 1. Statistical comparison of *Sarracenia chrysea* vs. *S. wherryi*.

Index	Cohort	Mean difference	t(df)	p
Inferior lamina	First	0.03	(82) = 3.57	< 0.001
	Climax	0.04	(55) = 3.97	< 0.001
Petiole	First	0.02	(87) = 3.87	< 0.001
	Climax	0.02	(63) = 4.30	< 0.001
Pitcher phyllode	First	0.06	(59) = 5.29	< 0.001
	Climax	-0.02	(27) = -2.71	= 0.011

Table 2. Statistical comparison of *Sarracenia alata* vs. *S. leucophylla*.

Index	Cohort	Mean difference	t(df)	p
Inferior lamina	First	-0.01	(40) = -1.00	= 0.32
	Climax	0.02	(17) = 0.86	= 0.40
Pitcher phyllode	First	-0.09	(37) = -2.21	= 0.03
	Climax	0.02	(9) = 0.67	= 0.15

Table 3. *Sarracenia ×ahlesii* vs. parent taxa.

Trait	<i>Sarracenia alata</i>	<i>S. ×ahlesii</i>	<i>S. wherryi</i>	Statistics
Leaf length (cm)	M = 46.71 ± 11.10	M = 26.95 ± 6.97	M = 17.76 ± 6.13	All pairwise $p < 0.001$
Inferior lamina index	M = 0.78 ± 0.04	M = 0.67 ± 0.04	M = 0.61 ± 0.04	<i>S. ×ahlesii</i> differs from both parents ( $p < 0.001$ )
Pitcher phyllode index	M = 0.17 ± 0.12	M = 0.10 ± 0.06	M = 0.06 ± 0.04	<i>S. ×ahlesii</i> ≠ <i>S. wherryi</i> ; moderate difference from <i>S. alata</i>

Notes: Sample sizes for Tables 1-3 are the same as for Fig. 2.

Table 4 and pairwise Welch's t-test results for Table 3 are available in an online supplement at the CPN website via <https://doi.org/10.55360/cpn552.ct552> redirect.

Figure 2A; Table 4A: The inferior lamina index decreases significantly from first to climax cohorts in all taxa except *Sarracenia flava*, whose climax cohort index increases. Herbarium data for *S. alata* show no significant difference between cohorts, but results from field data indicate a decrease in index values in climax cohorts like *S. flava*. Field data corroborates herbarium data in direction of mean difference except for *S. alata*, where statistical results indicate a significant difference between cohorts.

Figures 2B, 2C, 2D; Table 4B: Petioles comprise less than 10% leaf length on average for all taxa except *S. flava*. Climax cohorts tend to decrease in proportion or not at all. Pitcher phyllode indices

differ between first and climax cohorts for all taxa except *S. alata*. *Sarracenia flava* is the only taxon whose pitcher phyllode proportion increases in the climax cohort. Whole pitcher chamber index changes from first to climax cohorts resemble inversions of the pitcher phyllode indices.

Table 4C: Coefficients of variation disclose different degrees of within-cohort variability (plasticity) between measurement loci. The most plastic segment is the pitcher phyllode (Fig. 1, loci CD), which is typically longest of the plastic segments. The petiole is comparably plastic but occupies a much smaller part of the leaf (Fig. 1, loci BC). The pitcher chamber (Fig. 1, loci DF) CV values are higher in phyllodous cohorts than in aphyllodous cohorts (except for *S. alabamensis*). The inferior lamina (Fig. 1, loci AE) is invariably the least plastic segment within cohorts. A higher CV value in the inferior lamina index does not correlate with more phyllodous or aphyllodous cohorts for taxa. Cropping the petiole from truncations minimally alters relative variability.

The inferior lamina index differs between cohorts for all taxa except *Sarracenia alata* (Fig. 2A, Table 4A). The petiole index (Fig. 2B, Table 4B) shifts across cohorts significantly for *S. chrysea* and *S. wherryi*, while *S. alabamensis* undergoes a moderate shift. The pitcher phyllode index (Fig. 2C, Table 4B) changes markedly between cohorts in all taxa. The whole pitcher chamber index (Fig. 2D, Table 4B) is always greater in aphyllodous pitchers.

Comparisons of some *Sarracenia* taxa

Table 1: *Sarracenia chrysea* vs. *S. wherryi*

There are significant differences in inferior lamina, petiole, and pitcher phyllode indices between *S. wherryi* and *S. chrysea* in both cohorts. Climax cohorts of *S. wherryi* often lacked pitcher phyllodes and petioles since pitcher chambers of *S. wherryi* sometimes originate within the leaf base. Therefore, locus D sometimes linearly preceded locus B. Incommensurate results for 9 samples in the pitcher phyllode index and 5 samples under the petiole index in climax cohorts of *S. wherryi* were omitted from figures, tables, and analysis.

Table 2: *Sarracenia alata* vs. *S. leucophylla*

T-tests show a noticeable statistical difference in the pitcher phyllode index in first cohort leaves.

Table 3: First cohort leaves of *Sarracenia* × *ahlesii* (= *S. alata* × *wherryi*) vs. those of *S. alata* and *S. wherryi*

*Sarracenia* × *ahlesii* had an inferior lamina index intermediate to and statistically separate from either parent taxon. For the pitcher phyllode index, *S. ×ahlesii* was also significantly different from *S. wherryi*, but was less so from *S. alata* (see also Fig. 2C). *Sarracenia alata* had significantly longer leaves than the other two taxa. Leaves of *S. ×ahlesii* were significantly longer than those of *S. wherryi*.

## Discussion

Preliminary observations and hypotheses are corroborated by results and analyses. Data and analysis disclose more substructures in the *Sarracenia* pitcher leaf than previously known. The internal consistency of results indicate that methods used to delimit leaf parts were sufficiently reproducible, and that the substructures they indicated for are homologous. Substructures are separated from each other by morphologic/physiologic changes along the length of the leaf, and

internally characterized by dynamic plastic signatures. The substructures of the petiole and pitcher phyllode exhibit independent and distinct plastic properties.

Analysis under this new model centralizes the iZ3-4, which is the only locus that is both stable and biologically significant. The iZ3-4 provides modular solidarity to the model and methodology, damping the influence of the inferior lamina substructures in the inferior lamina index in respect to relative variability. The iZ3-4 is a biological boundary between the inferior and superior laminae for both internal and external parts of the pitcher. It is especially significant as the only place where internal and external structures transition together at the same transversal place, partitioning plastic proximal regions of the leaf from distal morphology. The parts it separates operate in each species in respect to their development, allometry, and behavior. Differences between species sort into variations of size, presence/absence of parts, and potential for plasticity relative to the iZ3-4. This organization of the leaf around the iZ3-4 is applicable to all studied taxa.

The leaf halves that the iZ3-4 delimits, the inferior and superior laminae, are developmentally and functionally distinct, and serve separate but interrelated functions for *Sarracenia*. The inferior lamina contains many newly-recognized constituent dimensions that differentiate taxa, including measurable plasticity. The inferior lamina to whole leaf index varies minimally, and, among indices, it is the most reliable allometric characterization of leaf cohorts for taxa. Most taxa in this study can be contrasted by comparing heterophyllous cohorts using average inferior lamina to whole leaf index values. Field data of the inferior lamina to whole leaf index corroborates herbarized findings.

Older concepts of the *Sarracenia* “petiole” are now better disambiguated. The petiole may be present without the pitcher phyllode, but the pitcher phyllode never exists without the petiole. By contrast, the pitcher chamber may exist without a phyllode or petiole, and engages directly to either of these two (or to the leaf base in climax leaves of *S. wherryi* and most leaves of *S. psittacina*). The petiole is delimited by four indicators: four of the ten primary longitudinal veins distribute at the petiole’s distal boundary into the ala, the remainder comprise the solid abaxial column and/or dilate to form the pitcher tube; it is consistent in diameter along its length; all primary veins are parallel within the petiole; and petioles often twist transversally for some taxa (e.g., *S. leucophylla*), and torsioning of the primary veins stops at the petiole’s distal end.

This work discloses pitcher cohort heterophylly, characterized by different substructure proportions, and their variable degrees of plasticity. Cohorts differ by substructure assemblage and proportion. Leaf cohorts may be termed phyllodous or aphyllodous. For *S. wherryi*, the climax leaf cohort may lack petioles and phyllodes entirely (also seen in *S. psittacina*). Heterophylly itself is not phenological plasticity (agreeing with Schnell 1980). Plasticity is a differentiated and inherent response capacity of modular, homologous substructures with phenological implications. Aphyllodous cohorts may be bypassed or withheld from production in stressed plants, but phyllodous leaves are not produced in the sequential position of aphyllodous leaves as a replacement.

Patterns in heterophylly appear to be deeply programmed to taxa. The pitcher phyllode in particular is a critical point of difference between taxa of similar size and otherwise similar proportions, strongly defining taxon heterophylly. *Sarracenia flava* shows a sequence of aphyllodous to phyllodous leaf cohort production over the growing season, opposite to other Gulf Coast taxa that are phyllodous in the first cohort and aphyllodous in the climax cohort. Squamulae occupy their own cohort, typically forming summer and winter hibernacula. Cohorts of almost all taxa were sequentially separated by the presence of a summer hibernaculum. Summer hibernacula are produced around June after the first pitcher cohort as plants enter a period of growth arrest until early

September in the lower Coastal Plain taxa. Exceptions are *S. wherryi* and *S. psittacina*, which do not produce summer hibernacula (Trexler 2026).

All studied taxa with upright leaves can produce phyllodous pitcher leaves amongst flushes of independent phyllodia. Independent phyllodia were not seen to be produced cohorts separate from phyllodous pitcher leaves. Independent phyllodia are produced adjacent to or within cohorts of phyllodous pitchers, without sequential separation by a hibernaculum. Though some studied taxa like *S. flava* tend to produce only phyllodia in some cohorts, all were seen to produce phyllodous pitcher leaves within phyllode-dominated cohorts.

Some substructures have taxon-specific characteristics. For example, the abaxial column of the pitcher phyllode is laterally asymmetrically canaliculate in *S. leucophylla*, rhomboid in transversal cross-section in *S. alabamensis*, to terete in *S. flava*. Cohort heterophylly, variable substructure plasticity, and unique taxon traits compile into a matrix of characteristics for taxa.

The new methodology ultimately provides a new standardized way to analyze *Sarracenia* leaves modularly. This research provides a falsifiable method and model for analyzing *Sarracenia* leaf substructures anchored and delimited at referenceable, homologous, and biologically significant points of transition. The methodology operates at multiple scales, at concatenated or cropped substructure index permutations, the leaf half, leaf cohorts, and taxa. Parsing the pitcher leaf also helps locate and delimit other properties, especially plasticity, but also markings, colors, surface morphology, lifespan, etc. Analyses of parent taxa are corroborated in hybrids, which are shown to have intermediate proportions relative to parents, also in-line with earlier work. Allometric indices portray and identify taxon distinctions for analysis and comparison. The study verifies the existence of heterophyllous leaf cohorts, discloses patterns of relative index variability within cohorts, and recognizes these as new characteristics of *Sarracenia*. Since pitcher leaf substructure dimensions and properties characterize taxa, these characteristics may have bearing on *Sarracenia* taxonomy and ecology.

### Implications

Findings corroborate much about *Sarracenia* morphology that has long been assumed but which had not been substantiated, especially the presence of heterophyllous pitcher cohorts. While plasticity as expressed in highly etiolated leaves remains to be explored, new implications are also clear for ecological relationships of *Sarracenia*. Patterns of functional convergence can now be inferred in inferior laminae that group taxa into separate “classes”. Classes correlate with aspects of *Sarracenia* biology, distribution, and ecology to offer a dynamic, interrelated view of strategies to maintain phytocarnivory bound by differentiated homologous phenomorphology.

Cohort heterophylly offers striking perspectives for analyzing between taxa otherwise thought to be similar. *Sarracenia flava* is different from *S. oreophila* in lacking the latter’s third cohort. The climax cohort of *S. oreophila* is aphyllodous, apetiolate, has an inferior lamina to whole leaf ratio of nearly 1:1, and its pitcher chamber is engaged directly to the leaf base, like *S. wherryi*. The trimorphism of *S. oreophila* is even invocative of *S. alabamensis*. *Sarracenia alabamensis* itself has first cohort leaves that are truly unique in the genus, both in proportion and in stature (Trexler 2026). In hybrids, cohort-related differences inherited from the parents tend to scramble while presenting in extremely obvious ways, and some may require substructure analysis when parents have similar seasonal heterophylly (e.g., *S. alata* × *leucophylla*).

The inferior lamina as a whole is responsive to conditional changes, its substructures independently responding to above-ground ecology in upright *Sarracenia* taxa. Petioles extend the developing leaf apex away from the growth point, out of leaf litter, and into sunlight. Pitcher phyllodes elevate the pitcher chamber and attractive superior lamina above surrounding (and succeeding) vegetation. The ability of the leaf to increase visual prominence of the distal carnivorous element by means of a proximal substructure has implications for phytocarnivory strategies (prey capture, photosynthesis, and phenomorphological trade-offs) in rapidly succeeding fire ecologies. This makes the inferior lamina important to ecological relationships for *Sarracenia*.

In situations ungenial to carnivory like deep vegetative succession, pitcher phyllodes on tall upright taxa (not petioles) may variably replace the carnivorous pitcher chamber, resulting in highly laminar leaves with reduced carnivorous function (these may have high pitcher phyllode and inferior lamina indices orthogonal relative to sun-grown samples – C.A. Trexler unpublished data). While the pitcher phyllode and pitcher chamber may be a single physiological system, pitcher phyllodes sometimes exhibit important taxon-specific characteristics or functions distinct from the carnivorous chamber. In October 2025 in Baldwin County, Alabama, a large field of *S. leucophylla* was seen where almost every pitcher had been struck by *Exyra* sp. Dead girdled pitcher chambers were left dangling from innumerable still-living meter-long pitcher phyllodes, all capable of photosynthesis.

Ecological functionality of the phyllode is a clear point of difference between some taxa. Inferior lamina morphology, now disambiguated, seems to indicate for ecological niche partitioning of *Sarracenia* species. Species differ in how they compete with surrounding vegetation, attract preferred prey, growth habit (tall-graminoid, or short-rosetted), and phytocarnivorous niche (Gibson 1983). Rates of seedling height accrue and adult neoteny can be considered as well (Trexler 2026). This is corroborated by observed preferences of different *Sarracenia* taxa to specific ecological amplitudes relative to the fire cycle (Trexler 2026). Independent phyllodia, practically the same structures as pitcher phyllodes, are especially important for the largest and most widespread taxa. These aspects of *Sarracenia* relate foremost to the relative length and functionality of the inferior lamina while characterizing taxa relative to each other.

Convergence between *Sarracenia* taxa can be ascribed to inferior lamina morphology. Convergence appears to relate to overall size and stature, while varying in seasonal phenology. *Sarracenia alata*, *S. leucophylla*, and *S. flava*, similarly-sized taxa, demonstrably converge in both ecological niche and long-term survival strategy in diverse types of *Sarracenia* ecology (Gibson 1983). This is supported by similar inferior laminae. They have elongated erect-upright inferior laminae, which may co-scale with surrounding vegetation (Trexler pers. obs.); bear tall upright phyllodia reaching above surrounding vegetation; have fat starchy rhizomes capable of sustaining plants through long periods of dormancy in deep succession; and form vast, dense stands. These species occupy convergent niches, already illustrated by convergent morphology, aerial prey capture strategies, and modes of distribution in-habitat (Gibson 1983). They show similar leaf dimensions, heterophylly largely offset by circannual order of appearance. Their juveniles rapidly accrue height with each leaf. These species are altogether well-adapted to vegetative succession.

*Sarracenia wherryi* and *S. chrysea* are short taxa, and exhibit different strategies from taller upright congeners. They distribute very locally, adhering to strictly herbaceous habitat within bogs (Trexler 2026). They lack prominent pitcher phyllodes, and independent phyllodia they do produce are rare and shorter than their inferior laminae. Their inferior laminae are also mostly allocated to carnivory, with few demonstrable responses to vegetative succession and very reduced alae (Trexler 2026). Their prey niche is confined to ants (Gibson 1983; Trexler pers. obs. 2022-2025). Their

juveniles show none of the rapid growth the tall phyllodous taxa do, accruing size on a yearly basis instead of leaf-by-leaf (Trexler 2026). These two taxa do not compete with each other, nor do they probably directly compete with tall upright *Sarracenia*, or with surrounding vegetation. If mutual reduction of inferior lamina substructures is how these taxa converge (instead of necessarily proportion/size similarity), then the inferior lamina can be said to modify in tandem with niche, dually relevant to relationships with other *Sarracenia* taxa and to their strict ecological tolerances.

Inferior lamina characteristics appear to correlate with how *Sarracenia* engage with their ecology, and the ways they do tend to strongly characterize taxa. This has implications for the success or failure of primary hybrids whose parents differ in substructure assemblage, phenology, or proportion. The significance of the inferior lamina to ecological strategy also has clear implications for taxonomy and phylogeny. Given its role in sustaining carnivory through substructure plasticity, and how invariable its signature qualities are within taxa, the inferior lamina is taxonomically significant morphology worthy of consideration in *Sarracenia* systematics (e.g., in the sense favored in Bell 1967). The inferior lamina engenders the ability to change leaves from carnivorous to non-carnivorous organs in response to conditional signals, while orienting carnivorous elements of the leaf relative to surrounding vegetation and to attract preferred prey in a phytocarnivorous niche (Gibson 1983). Each of these dimensions separates taxa and ecologically situates them. Taxa may be ranked by morphology representing convergence or difference in such strategies. They may either have special ecological requirements, avoiding dense competing vegetation and taller congeners (the *S. rubra* complex), or have general tolerances to pressures from surrounding vegetation and be competitive with similar congeners (tall, widespread, phyllodous taxa). The superior lamina by contrast is dependent on the inferior lamina. Treatments prioritizing the superior lamina essentialize taxon similarity, resulting in extreme degrees of conflation (as in Wherry 1929 or Schnell 1977). Reliable, critical methods of determination are important for research in *Sarracenia*, a hybrid-prone genus with a history of challenging systematics. Genus-specific and biologically significant morphologic criteria in *Sarracenia* can inform critical sampling and determinations.

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