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POLLEN MORPHOLOGY AND ITS RELATIONSHIP TO TAXONOMY OF THE GENUS *SARRACENIA* (SARRACENIACEAE)

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ABSTRACT. Despite nearly a century of research, the systematic relationships among North American pitcher plants in the genus *Sarracenia* (Sarraceniaceae) remain unresolved. In this study we analyzed pollen morphology of the 11 currently recognized species of *Sarracenia* and examined how variations in key pollen characteristics relate to our current understanding of the taxonomy of this genus. We used principal components analysis to explore variations in pollen grain size (equatorial diameter and length) and shape (number of colpi) among *Sarracenia* species, and used cluster analysis to compare systematic groupings of *Sarracenia* based on floral, vegetative, and pollen characters. We compared these results with a previously published phylogeny based on molecular data. Groupings based on pollen characteristics alone did not align completely with those based on molecular or all morphological data. In clusters based on pollen alone and those using all morphological characters, *S. purpurea* and *S. rosea* formed a single group, and *S. flava*, *S. alata*, and *S. leucophylla* grouped together consistently. The pollen morphology of *S. jonesii* and *S. alabamensis* differed substantially from that of *S. rubra*, supporting the current systematic treatment of the genus that recognizes these three taxa as distinct species.

Key Words: carnivorous plants, morphology, pollen, *Sarracenia*, systematics

The ability to identify plants from their pollen has enabled botanists and ecologists to reconstruct past assemblages of plants and identify periods of environmental change (e.g., Fægri and Iversen 1989; Moore et al. 1991). Morphological characteristics of pollen grains also can be useful characters in studies of plant taxonomy because many pollen traits are influenced by the strong selective forces involved in various reproductive processes, including pollination, dispersal, and germination (e.g., Erdtman 1952; Moore et al. 1991; Nowicke and Skvarla 1979; Stuessy 1990). At the same time, characters subject to strong selection can be misleading if they reflect convergent evolution (similar evolutionary responses by unrelated taxa to similar environmental conditions). Thus, the use of pollen morphology as a taxonomic character is challenging, and pollen characteristics must be considered in concert with other characteristics in evolutionary reconstructions.

In this study we document pollen characteristics of members of the genus *Sarracenia* (Sarraceniaceae) and examine how these characters relate to our current understanding of the systematics of these pitcher plants. Our study differs substantively from the only other survey of pollen morphology in *Sarracenia* L. (Thanikaimoni and Vasanthy 1972). Those authors were primarily interested in interfamilial and ordinal relationships, whereas we have focused on discriminating species within the genus *Sarracenia*. Our work also reflects new systematic treatments (Mellichamp and Case 2009) and phylogenies based on allozymes and gene sequences (Bayer et al. 1996; Godt and Hamrick 1996, 1998, 1999; Neyland and Merchant 2006) that have been published since Thanikaimoni and Vasanthy did their work in the 1970s.

The genus *Sarracenia*. The 11 recognized species (Mellichamp and Case 2009) of pitcher plants in the genus *Sarracenia* are rosette-forming perennials with epiascidiate leaves that have been modified into pitcher-shaped traps (Adams and Smith 1977; Arber 1941), to which insects are attracted by nectar, odor, and/or color, and into which they fall, drown, and are digested (Bennett and Ellison 2009; Bhattarai and Horner 2009; Cresswell 1993; Green and Horner 2007; Macbride 1818; Schaefer and Ruxton 2008). All but one of the *Sarracenia* species are endemic to the southeastern United States (Godfrey and Wooten 1981). A recent phylogeny, based on

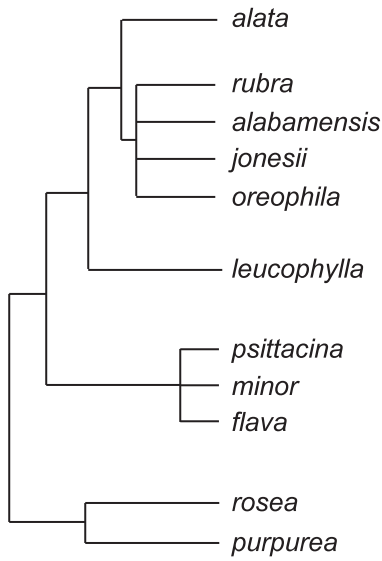

Figure 1. Current phylogeny (unrooted) of *Sarracenia*, redrawn from Neyland and Merchant (2006).

ITS-2 and 26S ribosomal RNA (Neyland and Merchant 2006), distinguished three clades, two of which contained all but one of the species that are restricted to the Southeast (Figure 1). One of these clades of southeastern species includes *S. psittacina* Michx., *S. minor* Walter, and *S. flava* L.; this clade was the only one identified by Neyland and Merchant (2006) that also received $> 50\%$ bootstrap support by Bayer et al. (1996). A second, larger clade included *S. alata* Wood, *S. leucophylla* Raf., *S. oreophila* (Kearney) Wherry, and *S. rubra* Walter *sensu lato*. Although neither Bayer et al. (1996) nor Neyland and Merchant (2006) supported the removal of *S. jonesii* Wherry and *S. alabamensis* Case & R.B. Case as separate species from the *S. rubra* complex, both *S. jonesii* and *S. alabamensis* are recognized as distinct species in Flora of North America (Mellichamp and Case 2009). However, these two taxa [as *S. rubra* subsp. *jonesii* (Wherry) Wherry and *S. rubra* subsp. *alabamensis* (Case & R.B. Case) D.E. Schnell, respectively] are listed, along with *S. oreophila*, as endangered under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 1979, 1988, 1989); thus, determining the distinctiveness of recognized taxa within the *S. rubra* complex has consequences for their legal conservation status.

The geographically widespread *Sarracenia purpurea* L., which occurs throughout the eastern United States and across Canada, is in a third clade (Figure 1; Neyland and Merchant 2006). Two subspecies of *S. purpurea* were recognized by Mellichamp and Case (2009): *S. purpurea* subsp. *purpurea* and *S. purpurea* subsp. *venosa* (Raf.) Wherry. *Sarracenia rosea* Naczi, Case & R.B. Case (formerly known as *S. purpurea* var. *burkii* D.E. Schnell) also was in the *S. purpurea* clade, but is geographically isolated along the coast of the northern Gulf of Mexico (Schnell 1993).

Whereas Nichols (1908) noted only a close similarity among the pollen of *Sarracenia flava*, *S. purpurea*, *S. rubra*, *S. psittacina*, and *S. variolaris* Michx. (= *S. minor*), Thanikaimoni and Vasanthy (1972) found substantial variance in pollen-grain length, equatorial diameter, and numbers of colpi among these same species, plus *S. alata* and *S. leucophylla*. In this paper, we revisit the pollen morphology of these species, and expand the analysis to include *S. rosea*, *S. oreophila*, *S. jonesii*, and *S. alabamensis*. Thus, we present comparative pollen morphology of all currently recognized species of *Sarracenia*. We then examine whether or not variation in pollen morphology maps onto the hypothesized different clades of *Sarracenia*, and also if this variance can help shed light on the apparent infraspecific differentiation in *S. purpurea* and *S. rubra*.

MATERIALS AND METHODS

Pollen from all species except *Sarracenia rosea* was obtained from 10-year-old greenhouse-grown plants. These plants have been propagated at Harvard Forest from wild-collected seeds (*S. alata*, *S. flava*, *S. leucophylla*, *S. minor*, *S. psittacina*) or local populations (*S. purpurea*), from outcrossed seeds from cultivated plants (*S. alabamensis*, *S. jonesii*, *S. rubra*), or from vegetative divisions of cultivated plants (*S. oreophila*). In all cases the seeds were derived from single populations near the center of the range of each species; complete provenance data and germination methods are given in Ellison (2001). Because our *S. rosea* plants did not flower during this study, we obtained one mature flower of *S. rosea* from each of five plants in a single population in the Appalachicola National Forest in Florida. The *S. rosea* flowers were collected at the end of April 2009, placed directly into 70% ethanol, and shipped to Harvard Forest for pollen analysis. We note that our samples do not reflect the entire geographic range of each species and that

intraspecific variability in pollen characters may have been underestimated. However, if, as is widely assumed, pollen characters are subject to strong selection, then this underestimate is likely to be small.

Anthers of 15–20 *Sarracenia* flowers from each species were pooled together, crushed with mortar and pestle, heated in 10% KOH, and processed with acetolysis; pollen residues were mounted in silicone oil (Fægri and Iversen 1989). Because we only had five flowers of *S. rosea*, we only used anthers from one of them and archived the others for future sampling, as needed. We measured 30 pollen grains from each species. For each grain, we measured length and equatorial diameter using image analysis software (Scion Image; Scion Corporation, Frederick, MD) and counted the number of colpi at 400× magnification. Post-hoc power analysis using the pwr library in R, version 2.9 (R Development Core Team 2010) indicated that our sample size provided a very high probability (power approached 1) of correctly inferring significant differences among species (with a critical level $\alpha = 0.05$), given the observed differences in length, equatorial diameter, and number of colpi.

Principal components analysis (function `prcomp` in R, version 2.9) was used to create composite "size" and "shape" scores for each pollen grain. We then plotted the mean principal axis scores for each species along with their 95% confidence intervals to visualize separation or overlap in pollen morphology among the 11 *Sarracenia* species. To determine whether or not pollen characteristics provided additional discrimination among *Sarracenia* species, we compared systematic groupings obtained from cluster analysis (average linkage method in function `hclust` of R, version 2.9) of the species based on morphological characteristics other than pollen characters, and on a complete character matrix including vegetative, floral, and pollen characters (Table 1). Values for vegetative characters were collated from Mellichamp and Case (2009), whereas those for floral characters were taken from Naczi et al. (1999) and Schnell (1978). Because these sources generally reported only averages and ranges, we used species' averages for pollen characters in the cluster analysis. Use of averages also avoided artificially inflating sample sizes and degrees of freedom.

Results of cluster analysis are reliable only when the number of variables (here, characters) does not exceed the number of observations (here, species). Because the number of measured

Table 1. Morphological characteristics of currently recognized *Sarracenia* species. Data for vegetative characters are from Mellichamp and Case (2009); those for flower characters are from Naczi et al. (1999) and Schnell (1978); and those for pollen characters are from this study. All measurements of continuous variables are in cm unless otherwise specified, and values for continuous variables are means as reported by the original authors. [1]Species key: alab = *alabamensis*; alat = *alata*; flav = *flava*; jone = *jonesii*; leuc = *leucophylla*; mino = *minor*; oreo = *oreophila*; psit = *psittacina*; purp = *purpurea*; rose = *rosea*; rubr = *rubra*.

Characters	*Sarracenia* Species[1]										
	alab	alat	flav	jone	leuc	mino	oreo	psit	purp	rose	rubr
Pitcher											
Presence (1) or absence (0) of white areolae on the pitcher	0	0	0	0	1	1	0	1	0	0	0
Pitchers erect (0) or decumbent (1)	0	0	0	0	0	0	0	1	1	1	0
Phyllodia seasonally produced (1) or not (0)	1	0	1	0	1	0	1	0	0	0	0
Length of pitcher (to base of hood)	40	45	52.5	47	62.5	28.5	46.5	19	15	17	31
Maximum width of pitcher wing	0.9	1.5	0.75	0.6	1	2	0.75	2.5	2	2.8	1.25
Maximum diameter of pitcher opening	3.7	3.5	4.5	2.5	4	2	3.25	0.75	2.5	3.5	2
Height of flower scape	36	37.5	37.5	51	55	33.5	57.5	25	50.5	25.5	44.5
Hood											
Length of hood	4.9	4.75	6.5	4.45	4.5	3.6	5	3	3.5	4	2.6
Width of hood	4.8	5	8.5	3.7	4	2.6	5.25	3	5	8	2.35
Width of neck of hood; 0 if absent	1	0.75	2	0.75	1	0	1.5	0	0	0	0.5
Length of apiculum	2	2	7.5	2.5	2.5	1	1.5	0	0	0	2
Rhizome											
Diameter of rhizome	1	1.15	1.75	1	1.75	1.5	1.25	0.65	0.9	1.3	1

Table 1. Continued.

Characters	*Sarracenia* Species[1]										
	alab	alat	flav	jone	leuc	mino	oreo	psit	purp	rose	rubr
Floral											
Total petal length	3.4	5.6	7.7	3.5	5.1	4.5	4.7	3.8	4.4	4.9	3.1
Maximum width of petal limb	1.8	2.9	2.9	1.8	1.9	1.8	1.5	1.6	1.9	2.8	1.6
Width of petal isthmus	1	2.2	1.8	1.1	2.1	1.1	1.9	0.9	1.3	1.8	0.9
Maximum width of petal base	0.5	1.4	1.4	0.5	1.2	0.8	1	0.8	1	1.4	0.4
Length of petal base	1.1	2	2.5	1.2	2.1	1.5	2	1.2	1.5	2.1	1
Length of petal limb	2.3	3.6	5.2	2.3	3	3	2.7	2.6	2.9	2.8	2.1
Bract length	0.7	1.25	1.5	1.5	0.75	0.85	0.9	0.7	0.65	0.65	0.7
Sepal length	2.5	4.5	4	3	4.25	2.5	4	2	3.2	3.85	2.1
Sepal diameter	1.5	3.25	2.75	1.75	2.4	2.5	2.5	1.5	2.5	2.75	2.3
Style diameter	3.25	6.5	7	3.25	6.5	3.5	6.75	2.5	4.5	6.1	2.75
Petal color (0 – yellow; 1 – pink; 2 – red)	2	0	0	2	2	0	0	2	2	1	2
Seed											
Diameter of capsule	0.9	1.5	1.7	0.9	1.75	1.3	1.65	1	1.5	1.75	1
Length of seed (mm)	1.35	2.1	2.15	1.35	1.8	1.2	1.9	1.75	1.85	2.05	1.35
Pollen											
Equatorial diameter (μm)	14.15	15.51	16.18	13.75	15.65	14.84	15.17	13.88	14.22	14.35	15.46
Length (μm)	12.33	14.02	14.28	12.18	14.33	13.46	13.89	12.02	13.05	13.06	13.24
Number of colpi	7.17	8.7	8.63	7.13	9.07	7.9	8	8.77	7.97	8.1	7.53

characters greatly exceeded the number of species, we first summarized the vegetative characters in a series of principal component scores—one each for flower, seed, and pollen characters, and two each for pitcher and hood characters. The number of principal component scores used was based on the proportion of variance explained. In the case of flower, seed, and pollen characters, the first principal axis explained the majority of the variance, whereas for pitcher and hood characters, two principal axes were needed to account for most of the variance in the data. Rhizome diameter was included as a separate variable; it was first centered and scaled [(observed mean − grand mean) ÷ standard deviation] so that its values were in the same range as the principal component scores (Table 2). Thus, the cluster analyses used either seven variables (cluster analysis without pollen data) or eight variables (cluster analysis with pollen data). We emphasize that the results of the cluster analyses do not provide information on phylogenetic relationships, as we have no information on character state polarity. Rather, the results of the cluster analysis simply illustrate groupings of species with similar morphological characters.

RESULTS

Sarracenia pollen grains are colpate, with the observed number of colpi ranging from 6 to 10. Equatorial diameter values ranged from 11.2 to 17.7 μm, and length ranged from 9.9 to 17 μm. Principal components analysis revealed five distinct groupings of species (Figure 2). Most taxa separated along the first principal axis, which reflected grain size (equatorial diameter and length) and accounted for 63% of the variance. Along this axis, the group including *S. leucophylla*, *S. alata*, and *S. flava* had very large grains (Table 1), whereas *S. alabamensis*, *S. jonesii*, and *S. psittacina* had the smallest grains (Table 1). Among the species with intermediate-sized grains, *S. purpurea* and *S. rosea* formed one group, and *S. rubra*, *S. minor*, and *S. oreophila* formed the other. The second principal axis accounted for an additional 25% of the variance and separated taxa primarily on the number of colpi. On this axis, *S. psittacina* was separated out from the rest of the "small-grain" group because it had an unusually large number of colpi given its small grain size. For the remaining taxa, the number of colpi increased with grain size.

Table 2. Principal axis scores of the multivariate data given in Table 1 and used in the cluster analyses. Because there was only one variable for rhizome (diameter), we did not subject it to PCA, but instead only scaled and centered it as described in text. [1]Species key: alab = *alabamensis*; alat = *alata*; flav = *flava*; jone = *jonesii*; leuc = *leucophylla*; mino = *minor*; oreo = *oreophila*; psit = *psittacina*; purp = *purpurea*; rose = *rosea*; rubr = *rubra.* Var. expl. = variance explained.

	Var. Expl. (%)	*Sarracenia* Species[1]										
		alab	alat	flav	jone	leuc	mino	oreo	psit	purp	rose	rubr
Principal Axis (Primary Characters Loading)												
Pitcher PC-1 (size)	54	−1.47	−0.53	−2.28	−1.02	−2.42	1.16	−2.00	3.26	2.53	2.48	0.28
Pitcher PC-2 (colpi)	18	0.12	0.25	0.18	−0.53	0.83	1.60	−0.94	1.69	−2.64	−0.09	−0.48
Hood PC-1 (all characters)	76	−0.61	−0.38	−4.29	−0.08	−0.37	1.52	−1.02	1.99	1.33	0.46	1.44
Hood PC-2 (length, width)	18	−0.11	0.09	0.00	−0.57	−0.58	−0.41	−0.10	−0.11	0.77	2.07	−1.06
Flower PC-1 (petals)	71	−3.06	3.75	4.69	−2.20	1.41	−0.76	1.22	−3.01	−0.64	1.93	−3.33
Seed PC-1 (both characters)	89	−1.68	1.08	1.59	−1.68	0.97	−1.18	0.97	−0.65	0.57	1.48	−1.47
Pollen PC-1 (size)	63	−1.90	1.54	2.19	−2.35	2.16	0.01	0.66	−1.13	−0.71	−0.50	0.03
Standardized variable												
Rhizome diameter	–	−0.59	−0.16	1.56	−0.59	1.56	0.85	0.13	−1.59	−0.87	0.27	−0.59

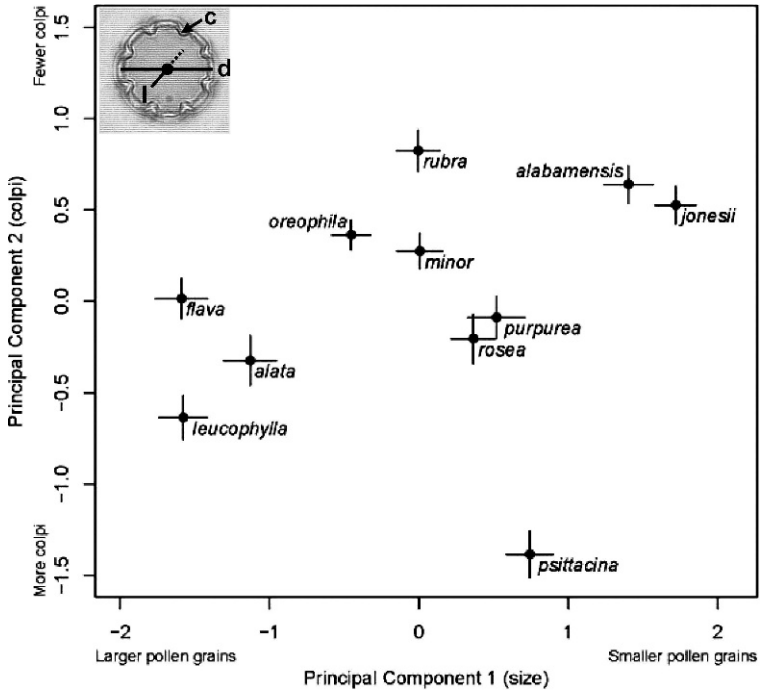

Figure 2. Separation in principal component space of the 11 species of *Sarracenia* based on pollen morphology. For each species, we plot the average score (N = 30) for each principal axis along with its 95% confidence interval. The inset shows a pollen grain of *S. oreophila* with colpi (c) and location of diameter measurement (d) indicated. Grain length (l) was measured from pole to pole after rotating the pollen grain.

Cluster analysis of the morphological data (Table 2), without including the pollen characteristics, identified four groups: the first included *Sarracenia flava*, *S. alata*, *S. leucophylla*, and *S. oreophila*; the second included *S. purpurea* and *S. rosea*; the third included *S. rubra*, *S. alabamensis*, and *S. jonesii*; and the fourth included *S. minor* and *S. psittacina* (Figure 3A). Because several of the other (composite) morphological variables were significantly correlated with pollen size (Table 3), the cluster analysis that included the pollen characteristics did not change the identity of groupings, although it did increase the branch distances by approximately 10% (Figure 3B). That is, the clusters were more clearly defined once pollen characteristics were included. Both dendrograms shown in Figure 3 had terminal clusters that differed from the groupings

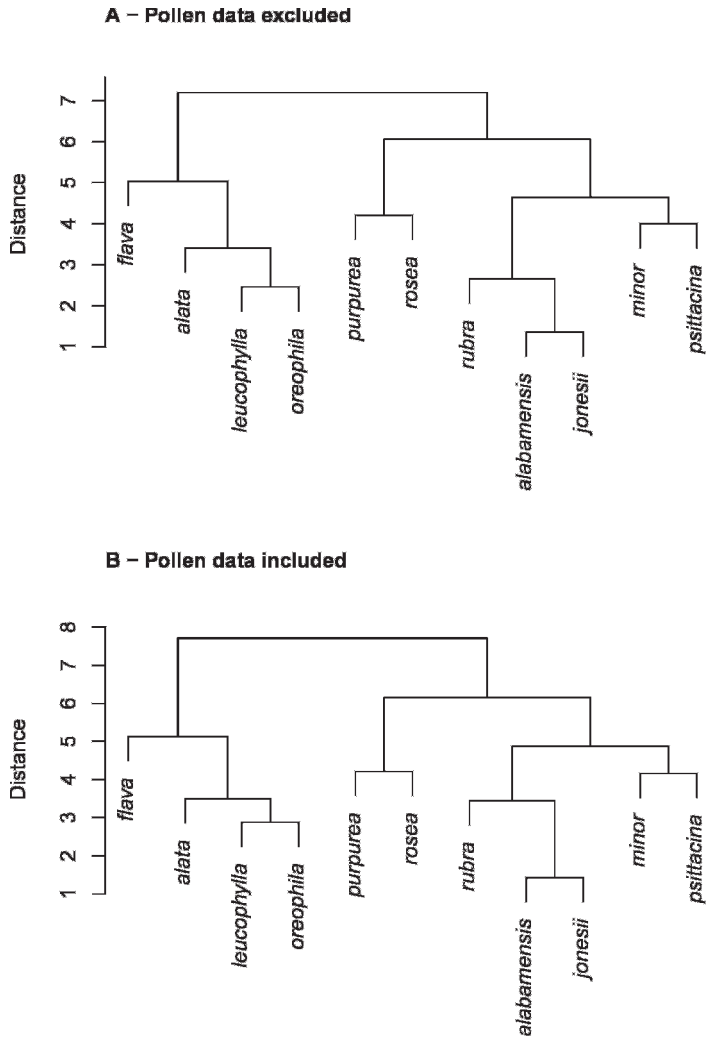

Figure 3. Dendrograms resulting from cluster analysis of the *Sarracenia* morphological data (Table 2) without (A) and with (B) the pollen characters included in the analysis.

identified on the basis of pollen alone (Figure 2). Salient differences in the PCA-based clusters based on pollen alone (Figure 2) included the separation of *S. jonesii* and *S. alabamensis* from *S. rubra*, the grouping of *S. oreophila* and *S. minor* with *S. rubra*, and the

Table 3. Correlation matrix of principal axis scores and standardized rhizome diameter. * indicates values that are significant at least at $p < 0.05$. Rhiz. = rhizome.

	Pitcher PC-1	Pitcher PC-2	Hood PC-1	Hood PC-2	Rhiz.	Flower PC-1	Seed PC-1
Pitcher PC-2	0.00						
Hood PC-1	0.75*	0.06					
Hood PC-2	0.48	−0.26	0.00				
Rhiz.	−0.57	0.24	−0.61*	−0.02			
Flower PC-1	−0.35	−0.02	−0.68*	0.37	0.69*		
Seed PC-1	−0.11	−0.17	−0.48	0.56*	0.50	0.89*	
Pollen PC-1	−0.44	0.16	−0.50	−0.09	0.74*	0.78*	0.71*

separation of *S. psittacina* from all other taxa. However, in both the clusters based on pollen alone (Figure 2) and those using all morphological characters (Figure 3), *S. purpurea* and *S. rosea* formed a single group, and *S. flava*, *S. alata*, and *S. leucophylla* consistently grouped together.

DISCUSSION

The genus *Sarracenia* has only a small number of species, but the pronounced intraspecific variability and common interspecific hybridization in this genus (Mellichamp and Case 2009) continue to puzzle taxonomists and phylogeneticists and suggest that *Sarracenia* has diversified very recently (Bayer et al. 1996; Godt and Hamrick 1998; Neyland and Merchant 2006; Romeo et al. 1977; Schnell and Krider 1976). Although morphological differences among named species can be quite spectacular (Schnell 2002), molecular analysis has found that fewer than 10 nucleotide substitutions separate species within distinguishable clades consisting of dramatically different taxa (e.g., <10 pair-wise differences in nucleotides among the tall green-pitchered *S. flava*, the hooded pitcher-plant, *S. minor*, and the recumbent parrot pitcher-plant, *S. psittacina*; Neyland and Merchant 2006). Our study of the morphology of pitcher-plant pollen illustrates both the strengths and limitations of pollen characteristics in helping to separate species within well-defined genera or clades, so it is perhaps not surprising that morphological characteristics of pitcher-plant pollen are not always congruent with either molecular or morphological traits used to distinguish among *Sarracenia* species.

Our groupings of *Sarracenia* species, based on pollen grain size and shape (Figure 2), did not map precisely onto clades based on sequence data (compare Figures 1 and 3). For example, *S. flava*, *S. leucophylla*, and *S. alata* pollen grains grouped together based on their relatively large size and many colpi (Figure 2), but molecular analyses placed *S. flava* in a group with *S. minor* and *S. psittacina*, and grouped *S. alata* and *S. leucophylla* together with *S. oreophila* and *S. rubra* (Figure 1; Neyland and Merchant 2006). Pollen morphology also failed to align perfectly with groupings of *Sarracenia* species based on other morphological characteristics (compare Figures 2 and 3).

Our data overlap to some extent with the measurements reported by Thanikaimoni and Vasanthy (1972). The number of colpi, for example, was similar for some species: *Sarracenia minor* had a mean of 7.9 in our study, versus 7.97 in Thanikaimoni and Vasanthy (1972), and for *S. rubra* the mean values were 7.53 and 7.64, respectively. On the other hand, the similarity was less for other species, including *S. leucophylla* (mean of 9.07 colpi in our study vs. 7.71 in Thanikaimoni and Vasanthy 1972), *S. flava* (8.63 vs. 7.02), *S. alata* (8.7 vs. 7.06), and *S. psittacina* (8.77 vs. 6.45). Discrepancies in size and shape could reflect intraspecific variation in pollen characters or differences in live versus dried material. We sampled from a single population of each species, whereas Thanikaimoni and Vasanthy (1972) sampled either single, cultivated plants or took pollen from herbarium sheets. In both cases, the samples in these two studies are of different provenance.

The identification of infraspecific taxa, both subspecies and varieties, adds further confusion to systematic treatments of *Sarracenia*. The differentiation and distinctiveness of the named subspecies and varieties of *S. rubra* and *S. purpurea* remain the most uncertain aspects of *Sarracenia* systematics (Case and Case 1974, 1976; Godt and Hamrick 1998; McDaniel 1966, 1971; Mellichamp and Case 2009; Neyland and Merchant 2006; Schnell 1977, 1979; Schnell and Krider 1976; Wherry 1929, 1933). Earlier treatments based on morphology suggested sufficient differences for establishing *S. jonesii* and *S. alabamensis* as unique species (Case and Case 1974; Wherry 1929); these distinctions have been upheld in the recent Flora of North America (Mellichamp and Case 2009). In contrast, the U.S. Fish and Wildlife Service used the designation as subspecies of *S. rubra* when they were listed as

federally endangered taxa (U.S. Fish and Wildlife Service 1988, 1989).

Although allozyme data (Godt and Hamrick 1998) and sequence data (Bayer et al. 1996; Neyland and Merchant 2006) provided scant evidence for separating these taxa, or any of the other named varieties, from *Sarracenia rubra sensu stricto*, pollen morphology supports the most recent systematic treatment of this genus (Mellichamp and Case 2009). These taxa differed significantly in pollen-grain size: the pollen of *S. rubra* was larger (mean length of 13.24 μm, diameter of 15.46 μm) than those of both *S. jonesii* and *S. alabamensis* (length of ~12 μm, diameter of ~14 μm). On the other hand, pollen morphologies of *S. purpurea* and *S. rosea* were much more similar (Table 1, Figure 3) than were other observed differences in morphology (Table 1; Naczi et al. 1999), germination (Ellison 2001), flavonoids (Romeo et al. 1977), allozymes (Godt and Hamrick 1998), and ribosomal RNA sequences (Neyland and Merchant 2006) that have been used to separate these species.

Overall, our results suggest that variations in key traits of pitcher plants that are associated with nutrient acquisition and reproduction—including the morphology of pitchers, flowers, pollen grains, and seed size, shape, and germination—are determined by complex interactions among various selective pressures. For example, germination requirements appear to be controlled by local environmental conditions (Ellison 2001), and pitcher morphology traits are influenced by the abundance of different prey groups (reviews in Ellison and Gotelli 2001, 2009). In contrast, variations in reproductive traits, such as floral and pollen morphology, more likely are determined by geographic isolation (e.g., Furness and Rudall 2004; Naczi et al. 1999). Further work on the systematics and phylogeny of the genus *Sarracenia* would be best served with a combined analysis of all available and reliable morphological and molecular data.

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