Contribution to knowledge of *Sarracenia* 'Adrian Slack' genetic background

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Sarracenia hybridization and genetics have been my interest since early 1990s. A cultivar looking like *Sarracenia* 'Adrian Slack' was my dream plant for a long time; I wanted to create such a plant and name it after my wonderful wife. When I opened the envelope with December issue of CPN in 2000, my jaw just fell to the ground: "Somebody else made it!". I read immediately that this splendid cultivar was named after Adrian Slack and it is a natural creation in fact. Although it has been nearly 20 years since *Sarracenia* 'Adrian Slack' (ADS later in text) was described, it is still one of the most elegant *Sarracenia* cultivars. It was obvious to be a superior clone of natural hybrid between *Sarracenia flava* and *S. leucophylla*. According to its original description ADS has inherited its fenestration after *S. leucophylla* and deep red veins after *S. flava* (Hanrahan & Meyers-Rice 2000). Heavily veined types of *S. flava* (as putative donors of intense venation) are referred to as *Sarracenia flava* var. *ornata* (Hort. Bull ex W. Robinson).

Exceptional beauty and transatlantic origin (from my point of view) together made absolutely clear it will be very difficult and pretty expensive to get a piece of this cultivar into my personal collection. Although it took me 11 years to get my personal "copy" of ADS, my creative fingers got fulfilled a bit earlier. I visited United Kingdom and the great collection of my good friend Mike King in the end of April 2006. I immediately spotted the new jewel in his collection, although the pitchers were just opening. And it was just in bloom! Most likely the first flowering of ADS in Europe! Mike was so kind and he allowed me to collect all of its pollen into prepared microtubes. In my collection I pollinated several carefully chosen flowers in order to obtain an offspring of similar qualities like original ADS. Results of these first eight crossings were seriously surprising to me as the offspring segregated in many more color types than expected. Moreover, these color types were present in certain frequency patterns. Most of these findings were observed repeatedly in countless crosses and backcrosses I performed using ADS since that time. Therefore, I decided to share this experience with all the CP community in this article.

Results and Discussion

Sarracenia flava var. *rugelii* was genetically involved and entire *S.* 'Adrian Slack' genotype is *S. flava* dominant:

The very first published photographs didn't indicate genetic influence of any other taxa than heavy veined *S. flava* (= var. *ornata*) and *S. leucophylla*. Characters such as extremely massive peristome, very slim column and perfectly cordate lid reminded me of a shape typical for *Sarracenia flava* var. *rugelii*. Such idea of mine was supported by photographs published later, which had clearly shown darker coloration of the cultivar's column. This was supported as well by results of my first breeding experiments listed above. Approximately half of the seedlings exhibited typical *S. f.* var *rugelii* throat patch even if it could not be inherited from the second parent used. Many of these red throat seedlings looked even like they we crossed not by × *moorei* but just with pure *S. f.* var. *rugelii*. The influence of *S. f.* var. *rugelii* is clearly visible e.g. in offspring of *S.* 'Leah Wilkerson' × ADS, famous combination that was repeatedly performed by several growers around the

globe. Aside of excellent cultivars like *S.* 'Legacy', such a cross always provided a high portion (about 10-15%) of plants that were indistinguishable from pure *S. f.* var. *rugelii* (Fig. 1). On the other hand, it is surprising, that combination *S.* 'Leah Wilkerson' × ADS probably never led to a plant looking like pure *S. leucophylla*. (*Sarracenia leucophylla*-like seedlings should be present if the *flava*:*leucophylla* portion in ADS genome were close to 50:50.)

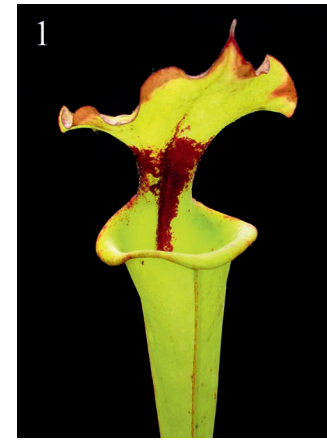


Figure 1: Selected seedling of *Sarracenia* 'Leah Wilkerson' × 'Adrian Slack' mimic of *S. flava* var. *rugelii*.

This was one of the signs which led me to a hypothesis that ADS is a greatly *S. flava* dominated genotype. Aside from the fact the offspring of ADS is biased to "*S. flava*" types in pitcher color and morphology, such a hypothesis can be supported by more phenotype markers. First of all, the offspring strongly tends to be yellow or orange flowered. Typical red tone and shape of *Sarracenia leucophylla* flowers are very rare even in crosses like *Sarracenia leucophylla* × ADS. Third evidence of *S. flava* dominance is morphology of the rhizomes of ADS offspring. The growth tip of most plants is bulbous like in *S. flava* and not same-sized compared to rhizome diameter like in *S. leucophylla*. The fourth and for me the strongest evidence is the year-round growth dynamics. The growth activity of ADS itself and all its offspring is strongly (but really strongly) spring-shifted, like in *Sarracenia flava* and its hybrids. The vigorous autumn growth typical for *Sarracenia leucophylla* is absent. The spring-shifted growth dynamics of ADS offspring is very uniform and so strong that ADS hybrids behave like they were crossed by pure *S. flava* and not by *S.* × *moorei*.

Sarracenia rubra subsp. *gulfensis* introgression:

Sarracenia × *moorei* (= *S. flava* × *leucophylla* hybrids *sensu lato*) are typically big monsters frequently reaching 1 meter tall. In some cases, ADS plants are not the tallest ones. The size of the pitchers is a tricky feature because size is greatly influenced by growth conditions. Moreover, it is controlled by quantitative genetics so the hybrid offspring diverges according to a Gaussian curve. It is hard to evaluate individual plants according to size therefore. I have several clones of *Sarracenia leucophylla* in my collection that typically provide very uniform offspring, including the height. I assume therefore, these "proven" clones have high level of homozygosity. When I crossed two of these clones with ADS, I obtained a very broad Gaussian curve of height in mature plants of both hybrid populations. For example, the plant shown in Figure 5c is nearly twice as tall as the plant in Figure 5b, although all of the plants in Figure 5 come from same cross and are grown side by side. Although pitcher height is problematic, it initiated my suspicion that one of the ADS ancestors was a small plant. *Sarracenia rubra* subsp. *gulfensis* came to my mind as a not very surprising "offender". *Sarracenia* ADS comes from the Milton area, Santa Rosa Co., Florida. Genetic introgression of *S. rubra* subsp. *gulfensis* in *S. leucophylla* populations is quite frequent in that area, even if the *S. rubra* subsp. *gulfensis* is not present itself in all the introgressed populations.

Although size variation is definitely not a significant proof in itself, about 10% of the seedlings in all of the ADS crosses that I made exhibited more rigorous features. These typical *S. rubra* phenotype characteristics present in the minor portion of ADS offspring are as follows:

1) Very fine veining, sometimes even with brown color tone typical for *S. r*. subsp. *gulfensis* (Fig. 2d,e).

Figure 2: *Sarracenia rubra* subsp. *gulfensis* color patterns observed in selected seedlings of *S.* 'Adrian Slack' offspring: a) *S. rubra* subsp. *gulfensis*; b) *S.* (*purpurea* × *leucophylla*) × ADS; c) *S. leucophylla* × ADS; d) *S.* (*leucophylla* × *minor* var. *okefenokeensis*) × ADS; e) *S.* 'Rudolf II' × ADS.

2) Creamy fenestration of ADS itself. This is bit disputable characteristics, but maybe some of the *Sarracenia* active enthusiasts would agree with me. In the *S. leucophylla* + *rubra* and *S. alata* + *leucophylla* mixed populations there are frequent hybrid plants exhibiting a large area of creamy-toned fenestration on their pitchers accompanied by very fine veining. This is one of the possible phenotypes rising from segregation of higher generations of *S.* × *areolata* or *S.* × *readii*. According to my color vision, the tone of the fenestration in ADS is the same.
3) Multiple flowers. It is a feature that is not usually seen in ADS itself, but I have observed it many times in most of the hybrids derived from ADS (see Fig. 3). Typically, there is just a single flower on the apex of the *Sarracenia* rhizome in the spring. But it might happen in some hybrids, that they produce 2–4 flowers in the growing tip. Such a feature could be sometimes observed in plants from the *Sarracenia rubra* complex. I have observed this anomaly more frequently in *S. flava* × *rubra* hybrids or in other complex hybrids where *S. flava* and *S. rubra* meet.
4) Pinkish coloration of the lower surface of the lid. Strong red/pinkish coloration of the lower side of the lid is frequent and exclusive for some *S. alata* and *S. rubra* types. Also, in *S. rubra* subsp. *gulfensis* (see Fig. 2a). This pattern of pinkish pigmentation can be seen on the lower surface of

the ADS lid as well. In some descendants of ADS, the pigmentation pattern of the lid is enormously evoking the *S. rubra* subsp. *gulfensis* lid (see Fig. 2a, b, c)

5) Probably the nicest evidence of *S. rubra* introgression in the ADS genome provides nectary distribution on the top parts of the pitchers. Nectaries of *Sarracenia flava* are located around the lid rim and throat area (Fig. 4a). Nectaries of *Sarracenia leucophylla* are present on the lower surface of the lid, dispersed in the hairy area of the lid. The peristome of these two species is waxy, sugar free. Same in the *S.* × *moorei* peristome (Fig. 4c). Nectaries in *S.* × *moorei* typically demonstrate overlapping distribution of *S. flava* and *S. leucophylla*. But the peristome of ADS holds a lot of active nectaria! (Fig. 4e). This is a typical feature of the peristome of *S. rubra* (Fig. 4d).

Figure 3: Multiple flowers are frequent in some seedlings raised from *Sarracenia* 'Adrian Slack' offspring. Here is mature plant of *S.* (*leucophylla* × *minor* var. *okefenokeensis*) × ADS.

Genetic linkage in color patterns:

Presence of a red throat in *Sarracenia* is encoded by a single locus (probably single gene?) according to my breeding experiments. (The extent of this article does not allow demonstration of the primary experimental data referring to this statement; a parallel article would be necessary.) I am not talking about size and shape of the red throat patch which is encoded independently in more complicated way. The character of the red throat itself demonstrates incomplete domination, which means in "negative" homozygotes the red throat is absent. In heterozygotes, it is present, but light red pigmented. A red throat is present and dark black in "positive" homozygotes.

Sarracenia 'Adrian Slack' appeared to be a heterozygote for this single locus character. Its offspring segregate exactly half to half when crossed with anything "red throat negative" like e.g. *S. leucophylla*. A classic single gene F2 pattern 1:2:1 was also proven in crosses of red throat heterozygotes, e.g. *S.* (*leucophylla* × *flava* var. *rugelii*) × ADS and other more complex crosses.

A surprising and very spectacular finding was a very frequent co-segregation of the overall color pattern of the pitchers together with presence/absence of a red throat patch in ADS offspring. That means most of the red throat positive seedlings of ADS are light colored (vein-less or pure veined) and the seedlings lacking a red throat are typically heavily veined (Fig. 5). Recombinant phenotypes like (red throat + heavy veins) or (absent red throat + light pitchers) are very rare, see Table 1. This indicate two conclusions:

1) "Red throat" locus is situated on the same chromosome of the ADS genome like the locus controlling pigmentation of veins of the pitchers. Both loci are situated quite close to each other as the power of genetic linkage can be estimated to about 4 centimorgans (cM). This value of chromosomal distance is calculated as ratio of recombined and non-recombined specimens; data presented in Table 1.

2) One parent of ADS needed to be red throat positive + light veined or more likely vein less. The second parent was heavily veined, lacking red throat. Alternative hypothesis of ADS heterozygote genotype originating from recombination of different looking parents would be 0.04 × 0.04 = 0.0016 (0.16%). Probability of primary hypothesis not taking recombination in count is therefore 99.84%.

Figure 4: Distribution of nectaria in *Sarracenia* 'Adrian Slack' related taxa: a) *S. flava* (example var. *atropurpurea*); b) *S. leucophylla*; c) *S.* × *moorei*; d) *S. rubra* subsp. *gulfensis*; e) *S.* 'Adrian Slack'.

Figure 5: Example of phenotype segregation in *Sarracenia* 'Adrian Slack' offspring – *S. leucophylla* × ADS; a) frequent phenotype = light colored pitchers with red throat patch; b) frequent phenotype = red veined without red throat patch; c) example of rare recombinant phenotype = light pitcher without red throat patch.

Table 1. Counts of phenotypes in selected hybrids used for genetic linkage estimation.				
Hybrid	Light pitchers + red throat	Heavy veined - red throat	Recombinants (all together)	cM estimation
S. leucophylla (white pitchers) × ADS	220	204	18	4.25
S. leucophylla (red veined) × ADS	131	148	12	4.30
S. (*leucophylla* × *flava* var. *ornata*) × ADS	67	78	6	4.13
S. (*leucophylla* × *minor* var. *okefenokeensis*) × ADS	106	98	7	3.43
Sum; cM estimation mean	524	528	43	4.03

What did the parents of *Sarracenia* 'Adrian Slack' look like?

This is a complete speculation, but we still have some more hints available. Due to the presented gene linkage we can assume one parent was light colored with throat patch, a second one was heavy veined, lacking throat patch. A second round of indications comes from the lid. The lid margin in ADS is straight; same in *S. flava*. According to results of my older experiments it seems, that the finest undulation of the lid rim of *Sarracenia leucophylla* is encoded also by a single gene and therefore inherited by the classic Mendelian model. Heterozygotes have lid undulation half prominent compared to fully undulated homozygotes e.g. *S. leucophylla*. As the lid of ADS has a straight rim (= homozygote for "flava – rim"), both parents must have carried at least one "flava - rim" allele for the straight lid. As I deduced in the beginning of the "Results and discussion" section, ADS is "flava" dominant. We can hypothesize one parent of the ADS might be *S. flava* var. *rugelii* itself. Although this could be possible according all the genetic evidence discussed above, I consider this case as not very likely. If one parent of ADS were pure *S. f.* var. *rugelii*, the result (ADS) would not have the rich fenestration that it has in the end. Therefore, I assume that the "light + red throat" parent was *S.* × *moorei* close to *S. f.* var. *rugelii* in its appearance. The second parent was likely a donor of the rich red vein pigmentation, had no red throat patch, and was most likely a dominant donor of the fenestration. We might hypothesize it could be "*S. leucophylla*" introgressed by *S. rubra* subsp. *gulfensis*. But the "red veined" parent must have been a more complex hybrid as we already know, both parents carried at least one allele of the straight "flava – rim" and the result (ADS) is a strongly "flava" dominant genotype. It is much more likely the "red veined" parent was a heavily veined "*S.* × *moorei*" with rich fenestration and some introgression of *S. rubra* subsp. *gulfensis*. Maybe something like the plants in Figures 2c or 5b.

Sarracenia flava var. *ornata* influence in *S.* 'Adrian Slack' genotype:

Honestly, after performing dozens of hybrids using ADS and evaluating countless number of seedlings, I cannot bring any clear proof that intense veining of ADS comes from *Sarracenia flava* as it was assumed in its original description (Hanrahan & Meyers-Rice 2000). It is very likely, as *Sarracenia flava* var. *ornata* types are frequent in the ADS native region. But on the other hand, prominent red veining could come from *Sarracenia leucophylla* or *S. rubra* subsp. *gulfensis* as discussed above. Obviously, there is a broad discussion on the origin of the heavy veined patterns in

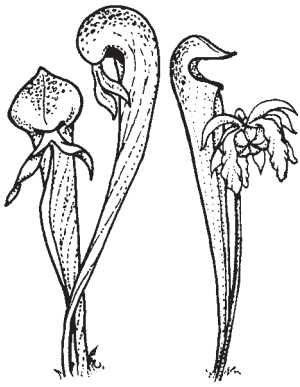
Sarracenia flava as such. So… Although at first glance ADS is a hybrid coming from *S. flava* var. *ornata*, the presence of this variety in ADS genome remains an open question for me.

Conclusion

Sarracenia 'Adrian Slack' seems to be a striking example of natural breeding process involving *S. flava* var. *rugelii*, *S. flava* var. *ornata*, *S. leucophylla* and very likely *S. rubra* subsp. *gulfensis*. It has been proven many times to be an excellent parent for horticultural breeding providing unbelievable color combinations in its offspring. Aside from the extreme color variability the typical features of ADS offspring are elegant shape of the pitchers, broad peristome and very vigorous, spring dominated growth.

References

Hanrahan, B., and Meyers-Rice, B. 2000. New cultivars. Carnivorous Plant Newsletter 29(4): 116-117.



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Front Cover: Maggie Chen admiring a nice *Darlingtonia californica* pitcher during the ICPS Conference field trip. Photo by Maggie Chen. Article on page 142.

Back Cover: A specimen of *Sarracenia* 'Adrian Slack' given directly from Bob Hanrahan to Barry Rice, where it is being grown at UC Davis. This individual has never been in tissue culture. Photo by Barry Rice. Article on page 160.

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