SHORT NOTES

THE KALEIDOSCOPE OF SARRACENIA

by D. E. Schnell

We have been asked to record our impressions, hypotheses and observations to date regarding the marked variations we have studied and considered in the genus Sarracenia. These few notes are necessarily brief and telegraphic to fit into the format and intent of CPN, but we would be happy to discuss details with individuals and we are presently engaged in further work with the probability of more formal and complete publication later on. These notes are based on repeated field studies in recorded areas as well as what has been learned by growing the plants under study rather than restriction to herbaria and a "flying field trip" or two.

At the outset, we would emphasize that complete, large scale and accurate field studies of this genus have become severely limited due to wholesale habitat destruction with a resultant precipitous fall in pitcher plant population in locations that were once vast stands of these plants. The loss of natural plant stands in our home state of Carolina is particularly distressing. Further south, into Georgia and the Mobile Bay area of Alabama, pretty good stands remain, but they are severely modified into artificially isolated islands by roads, drainage ditches and pasturing. One then sees an individual or relatively small copse of plants here and there in what once were good grass-sedge bogs, little "gardens" separated off unnaturally. For this reason, serious workers will wish to undertake careful review of the published field notes of older observers who worked in times of less disturbance.

I. Sarracenia flava

This species is rightly described as polymorphic, only S. rubra having at least as many important variations. The variation in S. flava would appear to be mainly in color and venation, although further study may likely turn up consistent anatomic or chemical variations as well. Interestingly, in 1881 Masters (Gardeners Chron., 16:11-12) presented a summary of names and descriptions for many of these forms, but since then formal designations have been discouraged by nearly all modern students. The forms listed in Masters' paper are partially erroneous since they are incomplete and mixed with what are now recognized species or hybrids, but we accept his basic intent as sound.

We believe one cannot simply dismiss these variations in S. flava as of minor interest or "just mutants." In light of current concepts, polymorphism in a species is certainly not casual. Polymorphism implies disruptive selection, an active evolutionary and ecologic process. The fact that these forms appear recurrently in considerable numbers in colonies of S. flava over nearly its entire range (although they are more often found in the range center), clearly indicates that they are not being "swamped" or absorbed into the gene pool as one would expect a simple, local genetic accident to be. Since they persist, we must seriously consider that they possess some selective advantage. This advantage need not necessarily lie in the vein and color variation itself (although this would have to be ruled out), but the morphologic variations may just be riders on chromosomal segments that offer physiologic advantage in some microvariation of habitat. To define such a possible habitat variation will require some study since to all appearances they grow mixed in with the typical form of S. flava, side by side in what would on the surface appear to be the same uniform habitat. If the habitat is indeed not significantly variable in relation to the precise positioning of these forms in a polymorphic colony, then perhaps directional selection is actually beginning to occur. We have noted grass-sedge bogs that have become artificially partitioned by roads, ditches and agriculture in which the "lesser" forms were actually dominant over the species typical forms in these instances of enforced isolation. Also, although difficult to judge in the field in colonies where the non-typical forms may be relatively few, flowering seems to be less; but growing plants of the variants in the greenhouse indicates that they do flower and produce viable seeds.

For these reasons, and for the purpose of communication, we would like to see these variants designated formally as forms, but certainly not as subspecies yet since they are all mutually sympatric. Tentatively, we recognize the following four basic forms:

1. The most common and "typical" one, having yellow or green lid (depending on sun exposure) with a prominent, irregular maroon pigmentation on the inside of the lid stalk, and slight to moderate venation radiating superiorly and inferiorly from the color spot. The only form present in relic piedmont bogs which may be of some phylogenetic significance and which we will consider in a later note.
2. The second most common form, having two types of rather diffuse maroon or deep red color to the pitcher:
    a. Red or maroon (or a coppery color if grown in less than full sun) of the external surface of the lid rather than green or yellow, lid stalk color spot present with moderate venation.
    b. Red or maroon of the top of the lid and externally extending nearly all the way or entirely to the rhizome.

    (Intermediates of a. and b. noted -- Crosses?)

3. A rather striking diffusely deep yellow or gold pitcher with very heavy, prominent red veins over the entire pitcher and lid resulting in a reticulate appearance with intervening patches of leaf puckering out between the vein net. Maroon pigment spot of inner lid stalk reduced.

4. A moderately uncommon anthocyanin-free form with pale green or yellow pitcher (cf. heterophylla form of S. purpurea).

As one observes many colonies over the range, one can easily note what empirically would seem to be crosses between these forms as well as with the typical forms, but laboratory pollination experiments will have to be completed to elucidate this as well as to illustrate if the above listed forms are actually irreducible. We have examples of these forms as well as putative field crosses under laboratory cultivation (and continuous observation in the field) and are beginning crossing experiments as well as self-pollinations to ascertain segregation of offspring and to see if the four basic forms are indeed absolute.

There is not doubt upon carefully considering all these specimens that they are of the taxon S. flava, and that they are not complexly introgressive hybrids with other species of the genus. The observation that the vein and color differences often fade to some degree when the plants are moved to tubs or greenhouse does not detract from the original thesis of genetic difference: How a plant may vary in different environments as compared to other members of the species which may vary differently or not at all in transplanting, is still likely biologically significant. One must remember that transplanting these forms may be introducing them to less than an ideal environment for expression of their full genetic complement. Actually, these cultural variances would seem to point more toward as yet undetected variations in microhabitat being important in the disruptive selection process.

II. Sarracenia purpurea

We concur with Wherry's original conclusion that the northern (S. purpurea purpurea) and southern (S. purpurea venosa) variants of this species do indeed deserve subspecific status. Except for the overlap area in New Jersey (the true nature of the overlap factor often passed over by critics of this proposal), the differences of pitcher form and tomentose condition, biological response to different climates and habitats on transplant, as well as the important ecologic difference of playing host to larvae of two different species of Wyeomyia with the insects "following" their hosts through the overlap area, are sufficiently consistent in our opinion and experience to warrant the formal subdesignation. (Plants of the species in the southern Appalachian mountains often assume an intermediate morphology between the two subspecies. These plants are venosa with ecophenic changes that disappear on reciprocal transplant.) Homogeneous environmental transplant experiments often result in plants assuming a tendency toward each other in appearance depending on the nature of the transplant environment, but there is never a total transformation according to our observations. Actually, the two subspecies may be considered extremes of a huge north-south (nearly transcontinental) cline, with some expected genetic intermingling at the central interface, not surprising considering the promiscuity of all Sarracenias. Since the two ends of the cline are obviously allopatric, subspecies is warranted over form. We have crossing experiments underway to determine the relative dominance of the subspecific characters.

But S. purpurea varies still more with three good forms to be considered under the appropriate subspecies:

1. Forma heterophylla--already formally described and well discussed in several papers.

2. A rare venosa variant mentioned by Wherry (Mobile Bay) and Bell (N. Florida) with pale pink petals, white style expansion, and green leaves. This variant has not been refound in the past twenty years to our knowledge and it certainly needs to be searched for and studied. Since current locations are not known, we rely on imperfect herbaria preparations, past descriptions, and make the perhaps unwarranted assumption that the plant is not some interspecific hybrid.

3. A diffusely deep red or maroon venosa occurring in colonies throughout the southern range, mainly the coastal plains, and more particularly on the Atlantic side. Our argument for this plant as a form would follow the same argument as the case for S. flava (v.s.). With Bell, we have noted that the plants tend to occur as a monoformic colony rather than evenly or inferiorly mixed with typical venosa, although occasional veined forms are found in maroon colonies, and apparent crosses between the two noted. But the maroon is only very rarely found as an occasional in a typically veined colony. Contrary to previous reports, even when shaded in deep summer grass, we have noted that newly sprouting pitchers in the late summer are still deeply and uniformly pigmented and remain so to maturity. We have not noted fading of these shaded later pitchers in natural areas, provided one is observing a pure maroon form with no evidence of venation in older pitchers. In culture, though (in very wet sphagnum), the plants do need full sun to retain the deep color, but control plants of veined forms do not become so deeply red under like conditions, indicating genetic differences. One wonders what drier conditions and/or the particular constituents of the sandy coastal plain soil may play in expression of the maroon trait.

III. Sarracenia leucophylla

We have not perceived any other forms than those well known:

1. Those plants with a pure white top (green veined), large lid and flaring pitcher opening. "Typical" form.
2. Plants with varying degrees of pink to red venation with very pale pink pigment spilling into the intervenous portions, smaller, more flexed lid, and somewhat narrower mouth. Caution is called for here since the species hybridizes readily with the westernly sympatric S. alata, but we believe we can sort these hybrids and back-hybrids. Still, introgressive hybridization as a mechanism in formation of this form cannot be ruled out and is likely.

IV. Sarracenia alata

This species is sympatric with S. leucophylla over most of both ranges but extends farther west. As above, varying degrees of hybridization are a problem, but we believe there are two main forms:

1. A largely green form with moderate venation (in sunlight) of the upper portions of the pitcher, pitcher form and flower otherwise characteristic of formal S. alata species descriptions. This form is most common in the eastern portion of the range.
2. A form with decreased venation but deep red or maroon pigmentation primarily of the lid and upper pitcher interior, extending externally in large plants in full sun. These forms are more common from Biloxi west, although there is wide intergrade, and the colonies in sloping wet meadows are very striking.

V. and VI. Sarracenia minor and S. psittacina

We are considering these two together since in our opinion there are no recognizable morphologic forms confirmed in either species. There remains the interesting and oft cited problem of the very large plants of these two species on the "prairies" of the Okefenokee. It has been said, although I cannot find detailed documentation, that samples of these plants removed to outside locations and greenhouses quickly assume ordinary size. What is lacking, of course, is the reciprocal part of such an experiment without which the unilateral results are meaningless: the placement of smaller coastal plain plants of each species from various areas into marked Okefenokee sites for observation. The simple waning of Okefenokee plants in greenhouse and other culture means nothing until the capabilities of both source plants are reciprocally studied. If the difference in size then proves to be ecotypic rather than ecophenic after all, then of course even this capability of the Okefenokee plants to be larger in home habitat would have clear biologic significance in spite of what happened to the plants in an outside environment which for the plants might be suboptimal for expression of the size trait. The Okefenokee plants seem to flower quite abundantly, by the way, so we doubt if there is a "ploid" involved.

As an aside, we have noted that largest plants of S. minor removed from Carolina coastal plain sandy soils (summer drying) and grown in wet living sphagnum in the greenhouse under bright light become more robust (after two years or so to catch up over transplant setback) than in the original location or control plants in coastal plain soil grown beside the sphagnum tubs.

VII. Sarracenia oreophila

We will pass on this species for the time being, yielding to our friend Randy Troup whom we expect will be telling us of his continuing, lifelong observations soon, and who certainly knows more of the variations and temperament of this species than anyone we know of.

We would like to make one comment though. Contrary to previous published observations, we have noted a definite "feline" or "musty" S. flava-like scent in flowers of this species from at least two locations. Steve Clemesha, growing the plants in Australia, concurs. The plants were otherwise typical S. oreophila in all respects. The strength of the flower scent is about 25% that of S. flava. Although out of place but somewhat appropriate here, we might mention that we have also noted a strong, similar scent in S. alata flowers from many locations and in both color forms. Here the strength of the odor is stronger, about 70% of S. flava. Since these species are all widely allopatric, there is no chance that any were S. flava or flava hybrids. This flower scent was noted in freshly opened (which may be the reason it was missed before in field plants) flowers in the field as well as in the greenhouse. The scent character of the flowers as well as flower color and some aspects of pitcher form suggest a close phylogenetic relationship between these three species. However, placement of these three plants as subspecies under one species would be a severe phylogenetic and taxonomic error.

VIII. Sarracenia rubra

This is one of the most fascinating "species" upon which one can speculate regarding biology, form, geography and phylogeny. Again, space precludes a rational development of thesis here, but we are beginning to consider that the lowland plants of S. rubra may more nearly approximate the primordial plants of the species than the upland jonesii plants. If indeed prior to

the tertiary uplift some 60 million years ago the present southeastern mountains and piedmont were a vast peneplain similar to the present coastal plain, dotted with bogs and laced with slowly moving waterways, then one might suggest that the plants "descended" from the now higher lands to the coastal plain after the uplift could be the ones following a more compatible environment while the mountain form was able to remain because of physiologic adaptations and selection to the now colder habitat; and likely through isolation over such a long period it underwent further evolution. Thus, in this early pre-uplift bog-plain, there may have been the condition of disruptive selection that we presently see with S. flava and that probably exists with other Sarracenias as well, the selection then becoming locally linear as habitat demanded. Of course, it was clearly serendipitous that a variant capable of survival was present when needed, and one wonders how many other early Sarracenias have come and gone during ancient environmental upheavals. There is some present biological indication of this hypothesis: Typical lowland S. rubras of the Carolina coastal plain will not grow or develop as well outdoors in mountain or piedmont bogs, the plants becoming stunted and juvenile. On the other hand, the mountain plants will not do as well in the warmer environments, although they will survive.

Therefore, in light of true morphologic differences (in fully developed plants in all cases), geographic isolation and important biologic variances, we certainly agree with Dr. Wherry's current suggestion of subspecies status for the mountain plants (jonesii). But, viewed in the overall perspective of the genus Sarracenia and S. rubra as an acceptable taxon, species designation would not be appropriate. The fact is the mountain plants are still more like S. rubra than unlike it. Contrary to previously published reports, there is a very strong violet-like scent to the flowers of jonesii, as in the Atlantic coastal plain plants of S. rubra. Also, we would disagree with previously published concepts of intermediate and lowlands pitcher forms occurring as taxa in the mountains. Observation of growing plants indicates that such pitchers are a natural occurrence in maturation of the jonesii plants, the pitchers being juvenile. The fact that juvenile pitchers of jonesii resemble so much the mature pitchers of lowlands S. rubra would further indicate that the mountain plants are more evolved.

There remain variations in the lowland plants. We are still studying the two color-vein variants in the Atlantic coastal plain and sand hills, the plants tending to occur in mixed colonies: One reticulately veined over a tan to green-tan background of lid and upper pitcher, the other with veins less prominent and with a rather diffuse red color of the outer lid and upper portions of the pitcher but with a lighter tan, still veined lid inner surface. These forms are clearly genetic as evidenced by their occurrence in mixed colonies and retention of characters in various transplants. We have found that relative scape length is extremely variable, certainly more so than pitcher characters, as any form, species and subspecies is moved about. Herbarium specimens, of course, could not indicate this but living with the plants certainly does.

Finally, there is the fascinating plant of the Gulf coast which reaches its zenith in western Alabama but can easily be found in western Florida and was once suggested to be a displaced portion of jonesii range. This it is not. The plant is moderately tall, the rubra odor of the flower is absent, the adaxial ala is not as strong as lowland rubras but still more prominent than a well-developed jonesii pitcher, the lid is more reflected away from the pitcher opening (which has a different shape) with the stalk of the larger lid somewhat reflexed, and there is not quite the bulge-like dilatation of the upper pitcher as in jonesii, the contours of the pitcher being smoother. There is more diffuse red pigmentation admixed with fine venation and the lid is frequently somewhat undulate on the margins. These characters follow in transplants. This variant is still under study and at present we have no conclusion regarding its taxonomic status which ultimately could fall anywhere from a rubra form (lack of flower odor and lid differences are disconcerting) to a separate species.

In the lowland plants of S. rubra one can see much ecophenic variation clearly related to water supply and planting medium. The drier sandy savannahs tend to produce small, almost juvenile pitchers even at flowering age, while the sphagnum filled roadside ditches and wetter bogs and bays produce larger, more robust plants. Reciprocal transplants confirm this impression. These variants obviously do not deserve taxonomic status.

HOW TO GROW ALDROVANDA VESICULOSA

by Mr. Ohtaki and Mr. Katagiri

Aldrovanda is a delicate aquatic plant which grows under very narrow environmental conditions. To be successful, certain conditions must be carried out in order that the plant continues its rapid rate of growth. Such conditions are:

1. Observation: You must observe your plants closely especially with respect to the shape of the growing point. If the growing point is rounded and onion-shaped, it is in quite good condition. If not, you should change the whole water soon, and trace the origin of the failure. The acidity of the water is very important and should be checked daily with either indicator dyes or pH paper which can be purchased in tropical fish stores. This species is much more sensitive to pH changes than the genus Utricularia. Under quite favorable conditions, Aldrovanda increases rapidly by branching, about eight times a month, and grows at the rate of seven to nine nodes per ten days. The optimum range