Drosera × *hybrida* rest in peace

John Brittnacher • Ashland, Oregon • USA • john@carnivorousplants.org

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In the final years of the 19th century, the Scottish botanist John Muirhead Macfarlane was uniquely situated to discover, describe, and understand a plant he named *Drosera hybrida* (Macfarlane 1899). He was classically trained in all the minutia related to structural botany and probably spent a large part of his early life sitting at a microscope. His scientific method was to observe and describe nature, then philosophize about what he discovered.

Macfarlane's major passions were evolution and heredity. He was an adherent of Charles Darwin's theory of evolution from an early age and much of his life's work was exploring the mechanisms of evolution (see Macfarlane 1909). He understood that one of the key, but inadequately explained aspects of evolutionary theory in the late 19th century was the mechanism for generating variation that was the grist for the struggle of the fittest. The gradualism of Darwin was slow and did not explain how so many different species could evolve so fast. Through his study of *Nepenthes* in general and *Nepenthes* hybrids in particular, Macfarlane saw that the generation of new species by hybridization could be a significant factor in evolution (Macfarlane 1889, 1893). These new species were a blend of the existing species and, as he observed, could combine the best of both parents.

In his pre-rediscovery of Mendel world, Macfarlane was squarely in the blending inheritance camp. Under blending inheritance, the "generative substance" in the cells of hybrids was thought to blend like paint colors producing a new species intermediate in appearance between the parent species. The generative substance was thought not to segregate or unblend in the offspring of hybrids. The hybrids were considered a new stable type and thus a new species. In 1892 while at the University of Edinburg, Macfarlane published a major paper on plant hybrids: *A comparison of the minute structure of plant hybrids with that of their parents, and its bearing on biological problems* (Macfarlane 1892a). In the paper he illustrated in exquisite detail how hybrids are a mix of characters present in the parents. He focused mainly on microstructural elements, measuring a range of variation in the parents and comparing them to the hybrid. To Macfarlane, the mixing of the parental traits was proof of blending inheritance and a way to produce instant species.

Macfarlane also lived in a pre-modern philosophy of science world. Before the philosopher Karl Popper in the 1930s pointed out that it was impossible to prove a theory is correct (see Popper 1959), scientists spent their time trying to amass as much data supporting their theories under the assumption that the theory with the most support was correct. After Popper, science became a more iterative process of hypothesis, prediction, and testing where scientists are involved in proving a prediction of a hypothesis is wrong rather than correct. In his attempts to prove blending inheritance was true, Macfarlane did note that occasionally he found characters that more closely match one parent or the other and wondered in his writing how that worked. But he dismissed those cases as not the norm rather than use them to question blending inheritance. What baffled him most was that unlike in his study of *Nepenthes* where all the hybrids were fertile, *Drosera* × *hybrida* and a few other hybrids he examined were sterile and had pollen, ovules, and mature seeds not intermediate between the parents (Macfarlane 1892a). These observations did not square with his understanding of inheritance and he presumed the generative substance for sexual characteristics is unable to blend properly. Today instead of saying, “OK, so a few observations don’t fit my theory but in bulk it is true” we would focus on the observations that do not fit and say the theory is wrong. But Macfarlane was not there yet. He was on the lookout for plant hybrids, especially ones between very different parents, to accumulate yet more data to support his theories.

Macfarlane was very much interested in carnivorous plants from the start of his career. In the mid 1880s, he performed a major study of the pitcher plants *Nepenthes*, *Sarracenia*, *Heliamphora*, *Darlingtonia*, and *Cephalotus* (Macfarlane 1889, 1893). This *tour de force* included descriptions of the morphology and histology of pitchers and flowers as well as arrangements for pollination and, of course, a study of *Nepenthes* and *Sarracenia* hybrids. In 1891 Macfarlane visited the USA to give a talk on *Dionaea muscipula* at an American Association for the Advancement of Science conference. After the conference he spent three months on the east coast studying carnivorous plants including additional detailed observations on trap closure in *Dionaea muscipula* (Macfarlane 1892b, 1892c). The abstract for his talk could have been used for a talk that was given at the ICPS 2000 conference 109 years later: timing of triggering of the trigger hairs, triggering the trap by poking the leaf anywhere on the lamina, and chemical triggering, along with a discussion of parallels between what happens in *Dionaea* leaves and animal nerves. While on that trip he was offered a job at the University of Pennsylvania and moved there in 1893 becoming a professor of botany (Steckbeck 1943).

It comes as no surprise that when Macfarlane arrived at Penn he visited local carnivorous plant sites and it is even less of a surprise what he did when he found a hybrid between two very different sundew species. This would provide more data for his theory of inheritance! In his 1899 paper he described the trip where he discovered *Drosera* × *hybrida*:

> ACCOMPANIED by a few of my students, an excursion was made, during the third week of June, to the rich botanizing grounds near Atco, N. J. Amongst the pine-barren swamps of that locality was an area several acres in extent, that was partially flooded, but clothed with a profuse surface vegetation of swamp or bog plants. These consisted almost entirely of the four species, *Eriocaulon septangulare* [*Eriocaulon aquaticum*, Seven-angle pipewort], *Drosera intermedia*, *D. filiformis*, and a yellow-flowered *Utricularia*.
>
> The later blooms of *D. filiformis* were still abundant, but the involute flower stalks of *D. intermedia* were just unrolling, and as was proved later, these did not bloom fully till the second week of July. Casting one’s eye across the swampy mass of vegetation, the clusters of pale pink elongated leaves of *D. filiformis* contrasted strongly with the short, dense clusters of crimson-pink leaves belonging to *D. intermedia*.
>
> After a considerable stretch of the marsh had been examined, my attention was arrested by a rather distant group of plants, somewhat intermediate in height and color between the two common species around. A nearer examination of the eleven plants composing the group, suggested the possibility of their being natural hybrids between the above-named species. They were carefully removed, without injury, to one of the greenhouses in the University Botanic Garden, where they have since been grown and watched. A continued and careful exploration of the swamp failed to reveal the presence of additional plants or plant clusters like those already found.
>
> Detailed comparison of the leaves, flower stalks, inflorescence, flowers and period of blooming, still further confirmed the suspicion entertained on finding them. Histological investigation of the three, as well as of *D. rotundifolia*, which was only sparingly present in the marsh, shows that the last-named species does not contribute to the formation of the plants in

question. It equally demonstrates a minute blending, in all parts of the hybrids, of the histological peculiarities of *D. filiformis* and *D. intermedia*.

When the eleven specimens were collected, care was taken to remove sods of both parent species, and all three were grown in neighboring flats in the greenhouse.

In other words, John Muirhead Macfarlane, an expert on plant hybrids with a keen interest in carnivorous plants, went to one of his favorite botanizing locations and found eleven hybrid sundew plants. He then shovel collected ALL of them plus "sods" of the parental species so he could add to his proof of blending inheritance. So it goes for *Drosera* × *hybrida* at the type location.

Macfarlane's study of *Drosera* × *hybrida* is a classic example of late 19th century botany. He measured what today we would consider all the important taxonomic details of the plants but then went into great detail about cell size, stomata size and location, chloroplast sizes and distribution among cell types, the trachea and cell structure in tentacular hairs, and then apologized for not going into the minute details of the flower ovaries and seeds. On top of this it was almost unheard of for scientific papers of this era to have tables of data. So Macfarlane was not forced to put his data in a form that required some consistency and is easy to visualize. And forget about statistics, it did not exist yet. Table 1 summarizes his key data as described in the text of his paper. Figure 1 shows flowers of the parents and three different hybrid clones; Figure 2 is a reproduction of the plate accompanying the text.

Table 1. Taxonomically relevant measurements from Macfarlane (1899). Measurements in English units were converted to metric.

Character	*D. filiformis*	*D.* × *hybrida*	*D. intermedia*
Leaf length	20 cm average, to 25-28 cm summer	4.4-5.1 cm spring, 9 cm average summer	3.8 cm average
Leaf petiole length	1.0-1.6 cm	1.3-1.6 cm spring, 2.2-2.5 cm summer	not mentioned in text, 2.6 cm from Plate XII
Tentacular hair color	head crimson	head + top 1/3 to 1/2 stalk crimson	head + top 2/3 stalk crimson
Tentacle head size	220 µ × 165 µ	210 µ × 125 µ	230 µ × 105 µ
Scape length	25 cm average	17 cm average	14 cm average
Number flowers	14 average	10 average	8 average
Bloom size	22 mm	9.5 mm	6.4 mm
Bloom period	7 - 28 June	until 3 August	3 July - 15 August
Bloom color	purple-pink	white/faint pink flush	white
Sepal glandular hairs	180 - 380 µ long	1/4 to 1/3 *D. filiformis*	not present
Sepal sessile glands	2 and 4 celled	2 and 4 celled, both in reduced number	2 celled
Pollen	richly granular, up to 56 µ across	empty, 48 – 50 µ across	granular and plump, 44 µ across
Ovules	normal	small, empty or nearly empty	normal

Figure 1: Flowers of *Drosera filiformis* and *D. intermedia* left to right on the top row. Three clones of *D. × hybrida* on the bottom row. The images are approximately proportional to the actual sizes. Note how the stigmas of the species are close to the stamens while in the hybrid the styles are relatively longer putting the stigmas beyond stamens. This could affect the efficiency of self-pollination.

Macfarlane summarized his data saying:

> A glance at the comparative results, however, equally demonstrates that in this, as in some other hybrids studied, certain parts or organs tend more toward one parent than another. The balance of development throughout in the present case is evidently toward *D. intermedia*. Thus, in the relative size of the tentacular hair heads, in the amount of thickening of the indurated cortex cells, in the greatly reduced size of the glandular hairs of the sepals as inherited from *D. filiformis*, and in the color and size of the flowers, there is a decided preponderance in morphological detail of *D. intermedia* over the other parent, or the former exercises a certain swamping-effect on the growth vigor handed down from the latter parent. This is all the more remarkable when one considers that the apparently prepotent parent is the smaller and more delicate species.

Macfarlane then went on to frame the result of *D.* × *hybrida* being more like *D. intermedia* than *D. filiformis* shoehorned into blending inheritance terms. And notice how his normally beautiful classic English prose degenerates as he starts making things up to support his theory.

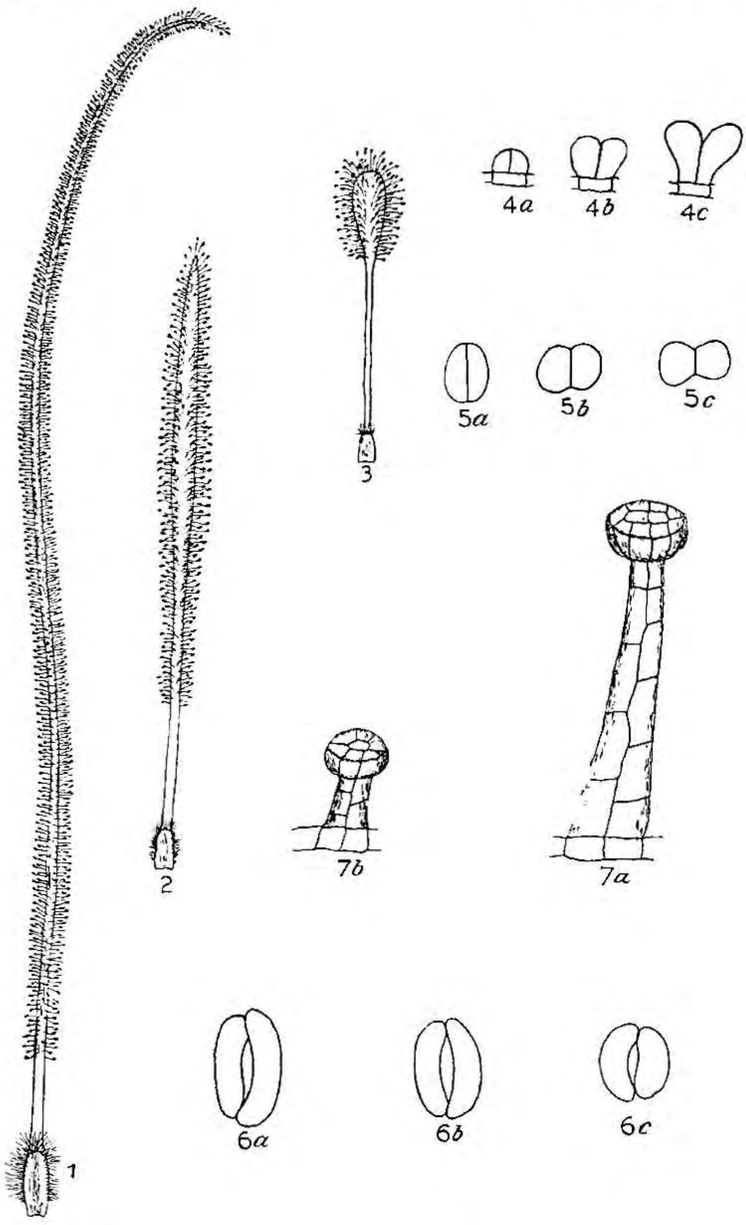
> The phenomenon which the writer termed bisexual hybridity [in Macfarlane 1892a] receives several striking exemplifications. Where two more or less diverse growths occurred, one on either parent, these have been shown to be reproduced not in blended fashion, but as distinct structures reduced either in size or number or both. The elongated glandular hairs on the sepals of *D. filiformis*, and the sessile two-celled glands of *D. intermedia* alike appear in the hybrid. Such a morphological pattern is frequent in hybrids whose parents are somewhat removed in systematic affinity, and suggests interesting cytological speculation. For, if every cell in the hybrid be, as its structure proclaims it to be, a combined effect of two parental conditions each reduced by half, some appropriate explanation must be given to the special case before us. […] It will be more consonant with the principles of heredity, if we suppose that at a certain cell centre in the epidermis, a special growth-potentiality is inherited from one parent, that stimulates to the formation of a hair characteristic of it, and that while the hereditary influence of the other parent, that is devoid of such hairs, is sufficient to reduce or check back growth of the hair to at least half the size of the parental one, it fails to prevent the development of a structure peculiar to one parent alone. Neither is there any need to suppose that there is a separation or sorting out of chromatic elements in the process.

The last sentence is a stab at the nascent field of genetics. Macfarlane used his data to narrate his version of heredity and developmental biology, waving his arms where he got an unexpected result, producing a modified version of blending inheritance for traits that do not blend equally. He was not prepared to believe that blending inheritance is not true or that new hybrids are not instant species. For this result Macfarlane sacrificed his new *Drosera hybrida* on the altar of science! Had Macfarlane instead focused on the traits that did not fit blending inheritance he might have made key discoveries that would have contributed to the modern synthesis of genetics and evolution. To do this he would have had to do actual experiments testing hypotheses. Macfarlane did not do experiments.

What did Macfarlane get right? Macfarlane could not have been more correct about the importance of hybridization in plant evolution and speciation. The importance of hybridization has been known at some level from the time of Carl Linnaeus but the full understanding has required genetic studies, many of which are summarized by Grant (1981). Hybridization is not only a major factor in the production of new plant species but also facilitates gene transfer between related species (Cronn & Wendel 2004). However hybridization does not produce instant species. It may be a first step in speciation but a species is more than just one or a handful of unique individuals. Macfarlane was also right that interspecific hybrids in general are a blend of the parents. But virtually sterile interspecific hybrids are not the appropriate plants to study if you want to know how heredity works. To understand heredity requires using hybrids that are fully fertile and not only making first generation hybrids but also selfing the hybrids and backcrossing the hybrids to the parents. This way you can see the segregation of the genes responsible for discrete character differences. Had Macfarlane wanted to and been able to do crosses with *D.* × *hybrida* he probably could have seen the segregation of flower color in the next generation and convinced himself that blending inheritance was wrong.

What would someone in Macfarlane's position 110 years later do if they stumbled across a previously unknown plant hybrid in nature? Remember Macfarlane was a professor at a preeminent university. His job promotions and stature in the scientific community would depend on publishing

Vol. II Plate XII. *Bot. Contrib. Univ. Penn.*



MACFARLANE ON HYBRID DROSERAS.

Figure 2: Plate from Macfarlane (1899). 1. Leaf of *Drosera filiformis.* 2. Leaf of *Drosera × hybrida*. 3. Leaf of *Drosera intermedia.* 4a. Gland cells of *Drosera filiformis;* 4b of *D. × hybrida;* 4c of *D. intermedia,* all in vertical view. 5a, 5b, 5c. Surface views of last. 6a. Stoma of *D. filiformis;* 6b of *D. × hybrida;* 6c of *D. intermedia.* 7a. Capitate glandular hair from sepal of *D. filiformis;* 7b of *D. × hybrida.*

significant contributions to the field of botany. According to Steckbeck (1943) Macfarlane enjoyed teaching and interacting with students and in fact was out in the field with his students when he found his hybrid so I expect a modern Macfarlane would think “this would be a great project for my undergraduate field botany class”. It would not be something on which he would spend much of his own personal research time. Hybrids are expected whenever two closely related species grow near each other, bloom at the same time, and share pollinators. But he would hedge his bets because the parental species in this case do not normally grow with each other or bloom at the same time so he might find something worth a research publication. He might even bother to publish a name for the hybrid. Unfortunately the modern Macfarlane cannot go back to the Atco botanizing site and do a follow up to see if any more hybridization occurred. Rich Sivertsen (pers. comm.) spent years looking for *D.* × *hybrida* in the Atco area and concluded after talking to residents that the Atco bog was where a drag strip and motocross racetrack are located today.

This would be the end of the story of *Drosera* × *hybrida* if Rich Sivertsen and Dave Kutt (Sivertsen 2008) had not accidentally discovered it in 1974 at Lake Absegami, New Jersey, 38 km southeast of Atco. Lake Absegami is an artificial lake in the Bass River State Forest, Burlington County, New Jersey. The lake has a sandy beach with a boat launch area. The higher than historical water level brought together *D. intermedia*, a species usually found in or near shallow water, and *D. filiformis*, which is usually found in sandy areas with the water level below the soil surface. Peter D’Amato (2011) related this story about *D. intermedia* from a visit to the lake as a teenager:

> Once as a kid I saw a woman move away from the people on the main part of the beach and she laid her towel on the sand closest to where the cove was, I think she wanted to be alone. To my teenage horror, she threw her towel right over some sundews. I went over to her and said something like “Excuse me, you’re crushing rare plants lying there!” She sat up on her elbows and a sundew was uprooted sticking to her arm! I told her “that’s a carnivorous plant eating your arm!” She rapidly moved to the main beach area not because she cared about sundews but because I think she thought I was insane.

As Macfarlane noted, *D. intermedia* and *D. filiformis* do not usually bloom at the same time. For some reason the two species did bloom together at Lake Absegami, probably from *D. filiformis* having delayed flowering after being stepped on, and produced a new population of *D.* × *hybrida*. Initially Sivertsen noticed stunted “*D. filiformis*” near the boat launch in an area of heavy traffic and thought those plants would be killed anyway so why not collect some of them during the spring while dormant for himself and Kutt who was visiting from Ohio. By summer Sivertsen and Kutt realized something was wrong with their new “*D. filiformis*”. The leaves were short and wide with petioles too long plus the flowers opened white and closed with a light purple flush. Sivertsen sent plants to Don Schnell and Joe Mazrimas for identification. Schnell responded that the plant was the long lost *D.* × *hybrida*. Sivertsen distributed the plants widely including Europe and Japan.

Schnell visited the Lake Absegami plants with Sivertsen later in 1974 (Schnell *et al.* 1974). It was noted that the *D.* × *hybrida* plants occurred singly and in clumps among the parent species and that there seemed to be variation among the hybrids. Some plants were more *D. filiformis*-like but most were definite intermediates between the parents. I wonder what Macfarlane would have thought of the *D. filiformis*-like plants! The last known record of *D.* × *hybrida* at this location was May 2008 (see Front Cover). Sivertsen (pers. comm.) visited Lake Absegami in August 2011 and failed to find any *D.* × *hybrida*. No *D. filiformis* were present either and had not been for a few years

Figure 3: *Drosera filiformis* seedlings growing from seedpods on an intact flower stalk. The Martha Furnace *Drosera* × *hybrida* were found under a similar situation although the plants were almost blooming size. Photo by Jason Ksepka.

so a regeneration of the hybrid could not happen there again. So it goes for the second coming of *D.* × *hybrida* in a natural population.

In 1978, Jim Bockowski, while giving Philip Sheridan and Mike Hunt a tour of the pine barrens (Sheridan 1978) discovered *D.* × *hybrida* near the ruins of Martha Furnace, Burlington County, New Jersey. Martha Furnace was an early 19th century bog iron smelter along a branch of the Oswego River in the pine barrens 10 km northwest of Lake Absegami. The ore deposits were scraped off the banks of the rivers, melted into pigs at the furnace, and boated down the rivers to the coast. The location where the plants were found was where a bank had eroded into an inlet to the river branch forming a sandy area with *D. intermedia* growing in a solid mat along and in the water and thousands of *D. filiformis* growing a meter or two from the water. Several clumps of *D.* × *hybrida* plants were growing out of the seedpods of one flower stalk in the mud near the *D. intermedia* (Bockowski pers. comm., see Fig. 3). Bockowski collected one of the clumps and over the next few years distributed plants and leaf cuttings widely. Bockowski and others have returned to the location several times since 1978 but have not been able to find any *D.* × *hybrida*. So it goes for the third coming of *D.* × *hybrida*.

Was the Lake Absegami *D.* × *hybrida* actually a "natural" population and for that matter was Macfarlane's roadside bog "natural" or Bockowki's sand slump? Lake Absegami is a very disturbed area ecologically. The plants are in the middle of a recreational area where families go to play. Sivertsen regularly took his family there on vacation. D'Amato was there with his family. It is highly possible the Atco bog was also not fully natural. In the mid to late 19th century, Atco, New Jersey, was in a major glass producing area with a 3000-acre production area nearby (The Atco Town Crier 2008). The Martha Furnace location was in an area with major disturbance a century prior to the plants being there. Bockowski did not think it looked "disturbed" at the time although it was not exactly a stable or typical site. What is apparent is that it takes special circumstances to produce an environment where the hybridization can occur and those locations may be transient.

Whether it takes human disturbance or not to produce *Drosera* × *hybrida*, it has not been found anywhere else. In well over 40 years exploring the New Jersey pine barrens, Sivertsen and others have observed many sites where both *D. intermedia* and *D. filiformis* occur in very close proximity without finding any hybrids between them. Schnell (2002) reports that he also failed to find *D.* × *hybrida* where *D. intermedia* and *D. filiformis* grow together in North Carolina and Florida. Again, the most likely reason for this is *D. filiformis* blooms in the early summer while *D. intermedia* blooms in the late summer. To get the hybrid, something has to happen to make *D. intermedia* bloom early or *D. filiformis* bloom late.

As far as is known, all *D.* × *hybrida* in cultivation are either from an area the size of a dining room table at Lake Absegami, one clump of plants from one seedpod at Martha Furnace, or are artificial hybrids. It is not known how many clones of *D.* × *hybrida* exist. It is possible there are clones produced from seeds. As Macfarlane found, the plants produce pollen and seeds but all the ones he examined were hollow. This means that at an extremely low rate *D.* × *hybrida* should produce viable seed because the plants have the functional machinery to produce pollen and seeds. During meiosis the unpaired chromosomes segregate more or less at random or do not segregate at all. This is what causes the apparent sterility. For *D.* × *hybrida* the pollen and ovules could contain no genetic material, or all 20 chromosomes, or any number of chromosomes in between. To get a viable seed would require an ovule to be pollinated with pollen containing a complementary set of chromosomes. Any of the rare viable seeds with a full complement of chromosomes, and thus the new plants, could be an exact duplicate of the original clone (the exact same 20 chromosomes), aneuploids (uneven assortment of chromosomes), triploids (double set from one parent and single set from the other with 30 chromosomes), or tetraploids (double duplicate of the original with 40 chromosomes). Anyone who has enough of the plants should be able to produce progeny of each of these types via seed. However I think most if not all the clones represented in captivity result from different hybridization events. It is quite possible each of the plants collected by Sivertsen represented different clones. I have identified clones with different leaf lengths and flower colors. Of these the only one I can confidently trace back to Lake Absegami has the longest leaves and pale pink flowers. The most common clone on the west coast probably descends from the plants Sivertsen sent to Joe Mazrimas and it has relatively short leaves and almost white flowers. I cannot confirm this because Mazrimas (pers. comm.) was unable to maintain the plants long term at his house in the mild climate of the San Francisco bay area. We could maintain what appeared to be a different clone in Davis 90 km to the northeast but the plants were dormant 8 months of the year and thus quite boring. They were discarded. Because we were dealing with virtually sterile clones there was no easy way to select for a clone that grew well in captivity.

Even though no natural *D.* × *hybrida* are now known in the wild, that is no reason to plant out the plants on private property you do not own or on public property or even at the locations where they were discovered. There is nothing special from a modern scientific or conservation point of view about *D.* × *hybrida* and especially the original wild clones. Macfarlane did an excellent job characterizing the nature of the hybrid. What he did not understand is how common plant hybrids are and the vast majority of them suffer the same fate as *D.* × *hybrida*. From a conservation standpoint, *D.* × *hybrida* is not a plant typical of the New Jersey pine barrens. The plants at Lake Absegami cannot predate the artificial lake, it is unlikely the eleven plants at Atco predate the sand mining and logging of the 19th century, and the few plants at Martha Furnace could not have been more than one or two years old.

For horticulturalists *D.* × *hybrida* is a fascinating plant. There are nice diploid clones of *D.* × *hybrida* available from artificial crosses and some day there will be a fertile tetraploid available. The

Lake Absegami clones are not the easiest to grow. They are temperate plants with a very short growing season. Forget about growing them long term in a terrarium or outside in a mild climate. What would be most interesting is to make new clones of *D.* × *hybrida* with parents from different locations, say the Florida *D. filiformis* and the Cuban *D. intermedia*. These plants would make better hobby plants. It may also be possible to make hybrids between *D. tracyi* and *D. intermedia*. That could be a fun plant! All you need is plants of both species blooming at the same time to make your own hybrid.

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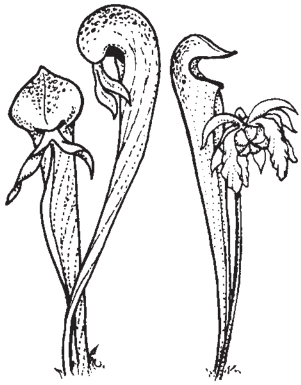

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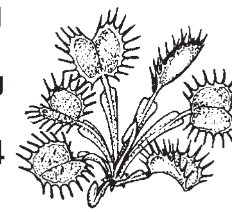

Front Cover: Possibly the last photo of *Drosera* x *hybrida* at Lake Absegami, New Jersey. Photo taken 11 May 2008 by Jason Ksepka. Article on page 112.

Back Cover: *Sarracenia* 'Deep Throat'. Photo by Damon Collingsworth. Article on page 139.

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ICPS, Inc.
2530 Patra Drive
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icps@carnivorousplants.org

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