

DROSERA HYBRIDA, THE NEXT GENERATION

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Plants are generally known for being promiscuous and *Drosera* is no exception. Many *Drosera* hybrids occur in nature and many more can be made artificially (see Ziemer 2017 and Brittnacher 2010 for examples). Natural hybrids between species that are very closely related and have fertile offspring can be a pain for hobbyists, botanists, and taxonomists because the plants pass characters back and forth and it is hard to know exactly what you are studying or growing. Natural hybrids between species with sterile offspring are more easily studied and are interesting because if the sterility is due to chromosomal pairing issues, the sterility can be resolved via polyploidy. The resulting fertile allopolyploid plants are essentially instant species in the evolutionary sense. Allopolyploid speciation is the most common form of hybrid speciation (Mallet 2007; Soltis *et al.* 2003) and changes in ploidy may represent about 2% to 4% of speciation events in flowering plants (Otto & Whitton 2000). In carnivorous plants, the best examples of hybrid speciation via allopolyploidy are *D. anglica* (Wood 1955) and *D. tokaiensis* (Shirakawa *et al.* 2012). In the case of *D. tokaiensis* in Japan, *D. spatulata* and *D. rotundifolia* crossed and produced sterile offspring. When chromosome doubling events occurred, either sexually or somatically, fertile *D. tokaiensis* resulted. Polyploidization set the population of *D. tokaiensis* on an evolutionary trajectory where at some point the plants in the wild will no longer be the same as the original hybrid. Over time, polyploids tend to become essentially diploids and excess genomic material is trimmed out or repurposed. In order to determine how much *D. tokaiensis* has evolved so far, Tungkajiwangkoon *et al.* (2016) compared the genome sizes of wild plants with the genome sizes of artificially produced *D. tokaiensis* and the parents. The genome size of the wild *D. tokaiensis* was found to be 15% less than expected. This indicates that *D. tokaiensis* is measurably into the polyploidization/diploidization/genome trimming cycle that has been a major factor in plant evolution (Marchant *et al.* 2016).

Drosera hybrida is an example of a potential instant species in that it immediately becomes a new independent evolutionary unit when a fertile population arises in the wild from its sterile, hybrid progenitors. The parents of the hybrid are the unlikely pair *D. filiformis* and *D. intermedia*. Sterile natural hybrids have been found and are known in New Jersey but no fertile plants have been found there yet (Ksepka 2017). Fertile hybrids were found in California where the plants were planted out in a protected botanical area (D'Amato 2013), so it is quite possible that someday fertile plants will also be found in its native range. When this happens, it is up to taxonomists to decide how to refer to the different plants. In this paper, I use "*Drosera hybrida*" primarily to refer to the fertile plant (the next generation) but cannot avoid using that name for the sterile hybrid as well. Article H3 of the ICN (McNeill *et al.* 2012) allows for not using the "×" in front of the epithet of a hybrid species.

Drosera filiformis and *D. intermedia* are unlikely parents of a hybrid because the plants are so reproductively different. The fact that one is a tall thread-leaved plant and the other a small, ground hugging, spoon-leaved plant is not important. It is the flowers that matter. *D. filiformis* has pink flowers about 20 mm across borne at least 200 mm above the ground. *D. intermedia* has white flowers about 9 mm across about 70 mm above the ground. *D. filiformis* blooms during the late spring and early summer before *D. intermedia* or overlapping a week or two depending on the location and

weather. Even when they bloom at the same time, individual *D. filiformis* flowers start opening at sunrise and close at noon. *D. intermedia* flowers open two or three hours after sunrise and close one or two hours after noon. With all these differences, it would be unlikely for them to share pollinators. Figure 1A shows a sweat bee (family Halictidae) pollinating a *D. filiformis* flower. The bee walked in a circle around the whorl of stamens, harvesting pollen from the anthers. The outer side of the bee and its leg pollen basket touched the stigmas as it moved past them leaving pollen. The styles appear to lie near or against the petals to not be in the way of the bee and the distance of the stigmas to the anthers was just right for the bee to pollinate the flower with pollen from a different flower. *D. intermedia* is probably also pollinated by sweat bees although they need to be smaller and be active later in the season than the bees that pollinate *D. filiformis*. These bees crawl over the stigmas to get to the anthers to collect pollen. Tiny sweat bees could easily visit late season *D. filiformis* flowers to harvest pollen and then if they did not get enough pollen, visit a *D. intermedia* flower harvesting the *D. intermedia* pollen but leaving some *D. filiformis* pollen on the stigmas. I am sure other insects visit the flowers and other scenarios are possible.

The observation by Jim Bockowski at Martha Furnace, New Jersey, of multiple clumps of hybrid *D. hybrida* plants growing out of old seed capsules on a fallen *D. filiformis* scape (Brittnacher 2011) has bothered me for a long time. We are talking about a rare event happening in multiple flowers on the same scape or a very rare case of a sterile *D. hybrida* having false vivipary at multiple nodes along a scape. After the paper was published, I noticed one of my *D. filiformis* plants failed to produce seeds one year. Normally *D. filiformis* flowers self-pollinate as the petals close. My first thought was a male sterile. That would be perfect. I had tried pollinating flowers to make hybrids without removing the anthers. I got no hybrids. That indicated to me that own-species pollen will outcompete other-species pollen if both kinds of pollen are present on the stigmas. A male sterile plant would always have to outcross. But it turned out my plant without seeds produces longer than typical styles and shorter stamens under certain conditions—I think cold weather but have not done a proper study. The styles can be so long relative to the stamens that the flowers do not self-pollinate when they close (Fig. 1B,C). Typically, *D. tracyi* flowers have a low rate of self-pollination for the same reason. An unusual *D. filiformis* plant with extra-long styles blooming late near a clump of *D. intermedia* could account for Jim's observation.

The next major stumbling block in generating a fertile *D. hybrida* is doubling of chromosomes. This can happen via meiotic chromosome non-disjunction during pollen and ovule production assuming there are no other pollen and ovule development, post fertilization, or genomic interaction issues in the otherwise sterile hybrid (Martienssen 2010). A second way to double the chromosomes is mitotic chromosome non-disjunction in a stem cell producing a chimeric plant that is part diploid and part tetraploid. There are no reports of this happening in New Jersey but it did occur in California.

Between 1985 and 1990, two carnivore fanatics planted out many *D. hybrida* plants they reproduced from leaf cuttings in the Butterfly Valley Botanical Area near Quincy, California (Brittnacher 2012a). Their purpose was to set up a sanctuary for the hybrid because they had difficulty keeping the plant alive in the central valley of California. After a few failures, the plants became established and did exceedingly well (Anon. pers. comm. 2011). In 2006, Harry Tryon (pers. comm. 2012) found the plants while visiting the site. He grew *D. hybrida* at home but did not recognize these plants as being the same. I had visited the site with Barry Rice two years earlier, in 2004, at the request of the USDA Forest Service botanist in charge of the Botanical Area. The botanist was regularly having to remove exotic plants from the Botanical Area but was not sure what a particular sundew was. We were not sure what it was either. The scapes looked like *D. filiformis*; the leaves

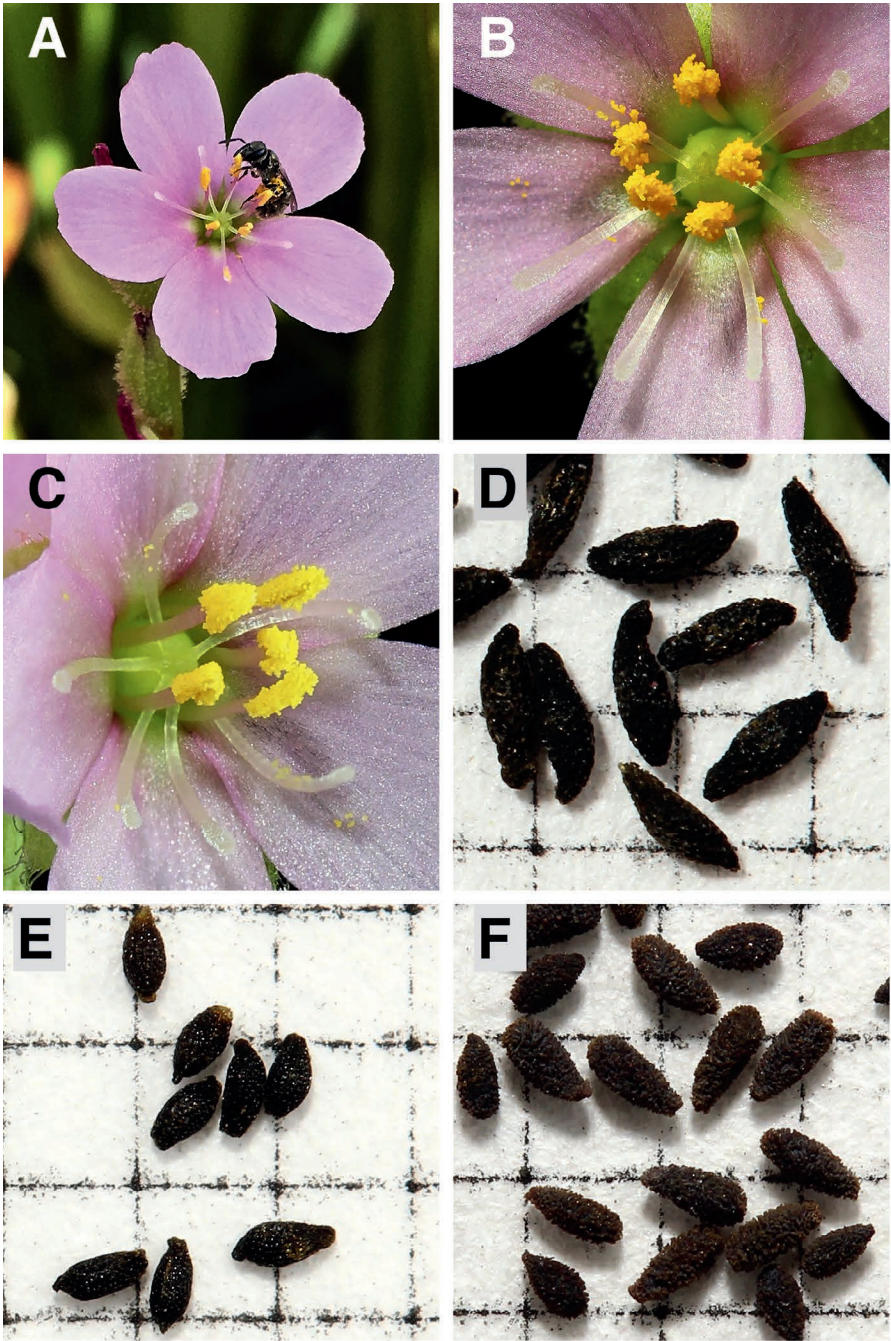


Figure 1: (A) Sweat bee (family Halictidae) harvesting pollen on a *Drosera filiformis* flower. (B) Detail of a *D. filiformis* flower with long styles and short stamens. (C) A more typical *D. filiformis* flower as it starts to close. (D) *D. hybrida* seeds on a 1 mm grid. (E) *D. filiformis*, New Jersey, seeds. (F) *D. intermedia*, New Jersey, seeds.



Figure 2: *Drosera hybrida* plants at the Butterfly Valley Botanical Area, near Quincy, California, in 2004. The plants have since been removed.

definitely were not (Fig. 2). We grew *D. hybrida* at the UC Davis Botanical Conservatory but they were nasty little things in comparison. We did not find seeds in the capsules so knew it must be a hybrid, but what? We brought back a few plants to Davis and were able to confirm they were *D. hybrida*. Starting in 2007, Barry assisted the Forest Service in removing all the *D. hybrida* from the Botanical Area. Barry sent me some of the plants that were removed. Although we did not find seeds in 2004, Harry did find seeds in 2006, the year before the plants were removed. He planted the seeds at his home. Harry gave me divisions from his plants in 2011. He also distributed fertile plants at the July 2011 California Carnivores open house. After getting the fertile plants from Harry, I decided

to characterize how the fertile plants were different under common growing conditions from all the various clones I had acquired.

In general, the fertile *D. hybrida* are nothing to get excited about for a general hobbyist (Fig. 3c). There are nicer clones that are more vigorous and bloom more often. They just don't produce seeds. Whatever happened to "hybrid vigor"? Polyploidy introduces a physiological load on a plant. Many genes are closely regulated to produce only so much product. There are now twice as many of those genes and they are producing twice what the plant needs. In a normal plant that is not as big a deal as it is for a nutrient-limited carnivore. That is why some of the smallest genomes are in carnivorous plants. With *D. hybrida* we are talking about plants that have not had the time for diploidization or "normalization" of gene expression to occur. What is bigger in the fertile plants? The seeds are larger than either of the parents' seeds (Fig. 1D-F) and the leaves tend to be a little wider although they may be shorter. The flowers of the fertile tetraploid plants are identical to sterile plants. Both kinds of plants can have stamens too short or styles too long to self-pollinate when the flower closes (Fig. 3a,b). This has led some people to question the fertility of the tetraploid (D'Amato 2015). The tetraploid cannot produce seeds if pollination fails for mechanical reasons.

One significant difference between the fertile plants and sterile plants is that the fertile plants do not bloom as often. In 2017, only 16% of my fertile plants bloomed compared to 61% of my New Jersey-sourced plants (Table 1). This is not totally surprising. I have over 30 tetraploid *D. eloisiana* plants and 6 *D. 'Nightmare'* plants. None of them bloomed in the past two seasons! But what was surprising to me was that I have had four fertile plants "appear" in pots with the Butterfly Valley Botanical Area plants sent to me in 2007. Yes, there could have been a re-potting error. Yes, I could have made a mistake while taking leaf cuttings. But given that the tetraploids bloom about once every 6 years, there could have been a tetraploid plant among the ones I received direct from the Botanical Area and it just didn't become obvious until years later when it and its leaf cutting offspring first bloomed for me.

In the Butterfly Valley Botanical Area plant-out drama, none of the leading and supporting actors recall the exact source of the Botanical Area *D. hybrida* plants. There were at last two New Jersey sources of different clones at that time (Brittnacher 2011; Ksepka 2017). It is apparent from the vigor of the plants and number of flowers per scape grown under my conditions, there is a difference between the plants I sourced from California and those I sourced from New Jersey. It is not as if the California plants cannot look like the New Jersey plants under the right conditions. The plants at the Botanical Area in Figure 2 have the same number of flowers per scape as the Burlington Co., New Jersey, plants in the wild (Ksepka 2017). In any case, the California-sourced plants were a clone that was not as vigorous as others available now.

Is there anything special about the Butterfly Valley Botanical Area that could have contributed to the polyploidization event? I very much doubt the Botanical Area contains a cosmic vortex but there are botanists who might disagree. The Botanical Area has a tremendous variety of rare plants (Cheatham 1976). This is most likely the result of the site being wetter at a lower elevation than is likely in the Sierra Nevada. Peter D'Amato (2015) suggested that a late frost while flowering could have caused plants to produce polyploid seeds. There is some basis to make this suggestion because polyploids are more common at higher latitudes and elevations. However, most research on polyploids more or less assumes polyploids will happen. Polyploidy itself is more likely to be advantageous and thus to persist in cold environments (Soltis *et al.* 2003; Brochmann *et al.* 2004). Also, the Botanical Area is only at 1150 m elevation. Barry Rice (pers. comm.) has been to a large population of the hybrid between *D. anglica* and *D. rotundifolia* in the Oregon Cascades at a similar elevation and not found any fertile *D. obovata* plants. The large population at that location can be

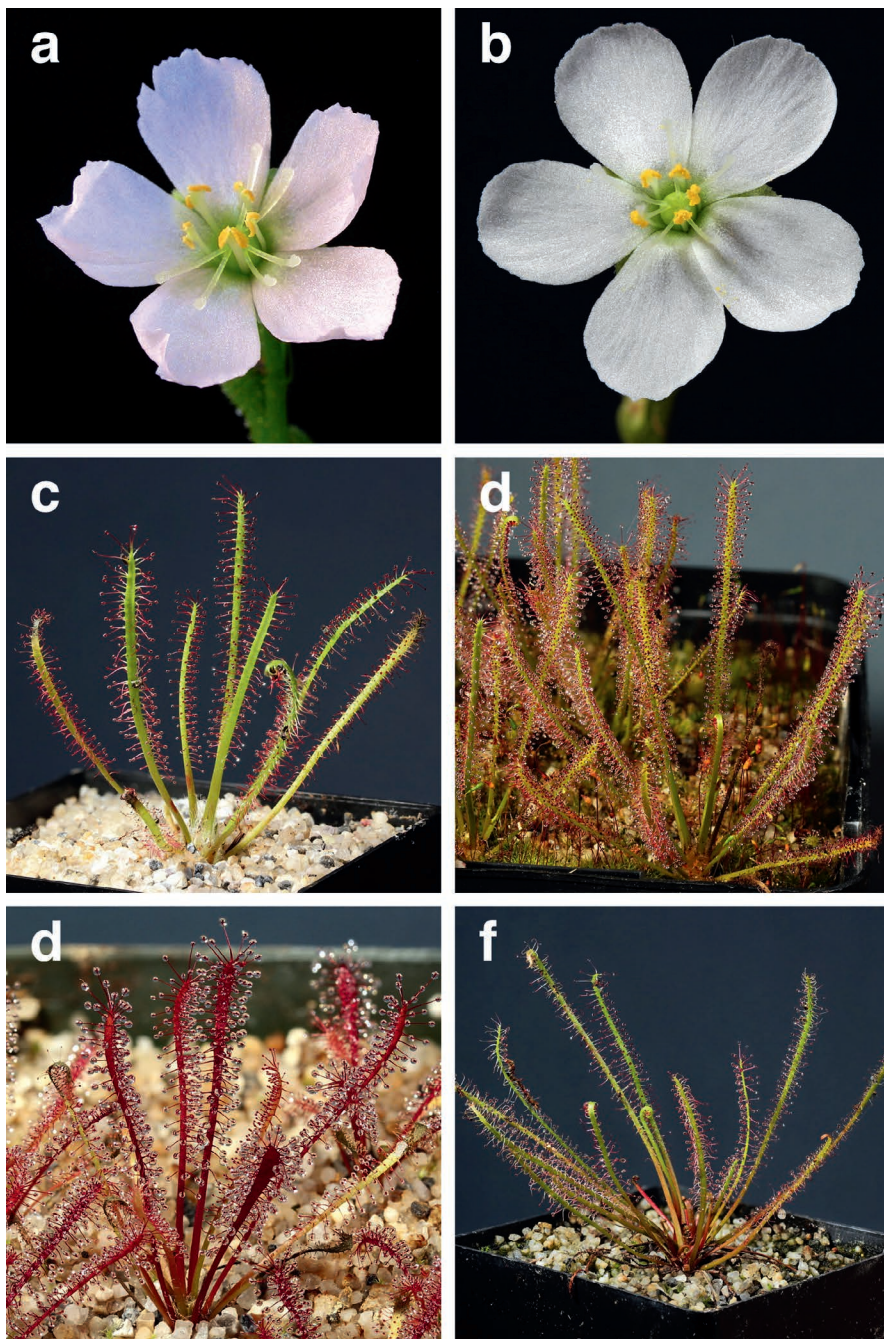


Figure 3: (a) *Drosera hybrida*, HT06 tetraploid flower. (b) *D. intermedia* × 'California Sunset' flower. (c) *D. hybrida*, HT06 tetraploid plant. (d) *D. filiformis* × *intermedia*, new hybrid. (e) *D. filiformis* var. *floridana* × *intermedia* plant. (f.) *D. intermedia* × 'California Sunset' plant.

Table 1. Scape per plant and flower number per scape for <i>D. hybrida</i> grown under identical conditions during 2017 in Ashland, Oregon.			
Clone ¹	Number of Plants	Scapes per Plant	Flowers per Scape
Tetraploid ²			
HT06	47	0.17	3.25
BV07PS	22	0.09	3.00
California ^{2,3}			
BV07	23	0.35	3.88
BV04	17	0.59	4.80 ⁴
HTCC	16	0.69	3.36
New Jersey ^{2,3}			
LakeA	27	0.63	6.24
Burlington	29	0.59	6.00 ⁴

¹Personal clone names: HT06 are initially from Harry Tryon from seed collected at Butterfly Valley Botanical Area, California, in 2006, propagated by division, leaf cuttings, and seeds; BV07PS are BV07 plants that produced seeds or were accidentally mixed up from HT06, propagated by leaf cuttings and seeds; BV07 are plants directly from the 2007 Butterfly Valley Botanical Area eradication, propagated by leaf cuttings; BV04 are plants propagated from the 2004 Butterfly Valley Botanical Area sampling maintained at UC Davis; HTCC are from Harry Tryon that he got from California Carnivores; LakeA are from plants collected at Lake Absegami, New Jersey, by Rich Sivertsen (see Brittnacher 2011); Burlington are propagated by leaf cuttings from plants collected with permission in Burlington Co., New Jersey (Ksepka 2017).

²The tetraploid plants had significantly fewer scapes per plant than the non-tetraploid plants (Chi-squared test, $p < 0.01$).

³The California-sourced plants had significantly fewer flowers per scape than the New Jersey-sourced plants (Chi-squared test, $p < 0.01$).

⁴Photos of plants at the Butterfly Valley Botanical Area, California, (Fig. 2) show most scapes on the plants having about 10 to 12 flowers per scape, similar to plants in Burlington Co., New Jersey (Ksepka 2017 (Fig. 1 p. 149 this issue)).

explained by animal disturbance and false vivipary so it is not as if the presence of so many plants indicates there should be fertile individuals. In another example, the tetraploid *D. anglica* is a cool to cold climate-associated plant. If it didn't exist before the last ice age, it could have arisen near the USA/Canada border mid-continent where one of its parents, *D. linearis*, is found today. If the species is older, which I think it is because of its extensive range, all bets are off about its history.

Why is *D. hybrida* only found in New Jersey while the parents coexist in other locations as well? It could be an issue in which the flowering times of *D. filiformis* and *D. intermedia* do not overlap, or do not overlap very often. Or it could be the available pollinators are not interested or do not exhibit the right behaviors. But that does not mean we cannot make our own if we can "encourage" our plants to bloom at the same time. Figure 3d shows one of a number of new hybrids I have made between *D. filiformis* and *D. intermedia*. They are easy to make IF you can get the parents to bloom at the same time and you can make the crosses between 10 and 11 a.m. and the flowers have not been visited by a pollinator when you get around to it and you are careful to remove the anthers without accidentally getting pollen on the stigmas and in the case of *D. intermedia* you remove the anthers

without also removing the styles. For me, some years there is more bloom overlap than others. Figure 3e shows *D. filiformis* var. *floridana* × *intermedia* using a typical, minimal dormancy clone of *D. filiformis* var. *floridana*. The plants produced so far are rather small and not very vigorous. The *D. intermedia* × ‘California Sunset’ (Fig. 3b,f) are more encouraging.

The polyploid nature of *D. hybrida*, *D. anglica*, and *D. tokaiensis* is not a mere curiosity. The scientific study of relatively recent polyploids gives us insights into the evolution of *Drosera* species in general. The progenitors of all carnivorous plant species have been through the genome polyploidization/diploidization/genome trimming cycle many times (Marchant *et al.* 2016). These cycles have helped provide the genetic tools for the plants to build unique structures and to adapt to extreme environments. Within the genus *Drosera* there are numerous examples of ancient polyploidy. Most *Drosera* species in Africa and many in South America are diploidized tetraploids as are *D. neocaledonica*, *D. ultramafica*, *D. ob lanceolata*, and many *D. spatulata* populations in Australia, Oceania and Asia (see Brittnacher 2012b for more examples). The progenitors of these species at some point in the distant past probably were in the same tenuous situation as *D. hybrida* is today.

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