Contents

Drosera anglica Huds. vs. *Drosera* × *anglica*: What Is the Difference?

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Summary

Drosera anglica Huds. is of hybrid, amphiploid origin (*Drosera linearis* Goldie and *D. rotundifolia* L. being the parents) and generally is not difficult to identify in its largely circumboreal distribution. However, in the northern Great Lakes region of North America where *D. anglica* occurs sporadically with *D. linearis* and *D. rotundifolia*, problems occur when hybrids (*D.* × *anglica*) and the true species may be sympatric. Furthermore, there is evidence that amphiploidy and therefore speciation is ongoing in the area. A discussion of the origin of *D. anglica,* some ecologic factors, problems with identification, and finally suggestions for distinguishing between the species and hybrid is presented.

Introduction And Background

Drosera anglica Huds. is a north temperate to circumboreal species that can be found in appropriate habitat in much of the northern tier and some sub-tier of the United States and in southern Canada, extending into Eurasia as far south as southern Europe (Schlauer, *in litt.*), and into Japan and the Hawaiian island of Kauai (Diels, 1906; Wynne, 1944). There has been some nomenclatural confusion in the past with *D. longifolia* being used at times either synonymously or in precedence. The latter has been recently resurrected in one flora and Cheek (1998) has applied for rejection of *D. longifolia* altogether (see the cited paper for a detailed history and reasons for suggested rejection). I will use what I also regard as the preferred combination, *D. anglica.*

The presence of the species on the Alakai Swamp on Kauai in the Hawaiian archipelago is of interest (Mazrimas, 1987; Gon, 1994; G. Newman, *in litt.)* since the species is considered northern and Hawai'i is generally tropical. In fact the bogs in which the plants occur are at 1200 to 1800 m (4000 to 6000 feet) elevation.

Therefore, the local climate is not truly tropical in these specific locations. There is no actual frost as there is in wintertime abundance in the more common *D. anglica* habitat, but nocturnal winter temperatures often descend to just above freezing, and summer nights are cooler as well. Approaching winter dormancy in northern continental habitats, the plant forms a tight winter bud (hibernaculum) at ground level. This does not occur on Kauai, but during partial dormancy new leaves are far shorter and atypical in appearance. The plants are also generally smaller in this location and the smaller size and winter behavior are a constant in plants grown from seed in temperate North America.

This article will concentrate on *D. anglica* as it is found in the northern Great Lakes region of North America, particularly in northern Michigan (including the upper peninsula). This area is of interest because there is strong evidence that the species is of hybrid origin and this is the only area where the putative parents, *D. linearis* Goldie and *D. rotundifolia* L., can be found easily with *D. anglica* (not uncommonly in the same fen) (Wood, 1955; personal observation). Interestingly, other hybrids may be found including *D.* × *obovata* (*D. anglica* × *D. rotundifolia*) rarely, and even the hybrid between *D. anglica* and *D. linearis* recently has been identified in nature (Schnell, 1995a). Finally, the hybrid *D.* × *anglica* is also found and this can create immense confusion. So seemingly difficult are *D. anglica* and *D.* × *anglica* to tell apart that Voss, in his recently completed Michigan Flora (Part II 1985), has decided that all the *Drosera anglica*-like plants in Michigan should be referred to as *D.* × *anglica* for simplicity's sake. Of course, this conclusion should not be applied in areas where *D. anglica* and *D. linearis* are not sympatric since *D.* × *anglica* would be impossible in that situation. I hope to show that the two can be discerned, even in the field, where *D. anglica* and *D.* × *anglica* are sympatric.

The species and hybrid in the area we will be discussing occur in a habitat best described as a marl fen (Figure 1; see also description and photos in detail in Schnell, 1980, 1982). Scattered across most marl fens in this region one finds variably sized hummocks of sandy peat and *Sphagnum* mosses (Figure 2). These little islands in the very wet sandy, marly peat of the fen may vary from centimeters to several meters across, the latter supporting shrubs and small trees. The fens are generally surrounded by a 'shoreline' of similar constitution as the hummocks, and then dense forest. These hummocks and borders are usually acid in reaction while the marl flats are basic to circumneutral. Of the *Drosera* we are considering, *D. linearis* grows preferably in shallow water (1-2 cm) over the marl flat, although occasional plants can be found growing on the hummocks and even on wet, decaying logs. *Drosera rotundifolia* grows most often on the tops of hummocks and above waterline on the sphagnous fen margins. *Drosera anglica* and *D.* × *anglica* usually can be found at the bases of hummocks or fen margins, at or near the waterline—an intermediate position. After careful searching, I have found that most of the upper Michigan fens have at least a few to relatively many *D.* × *anglica* and fewer contain *D. anglica,* but those that do often have them in abundance. The latter are found more easily in the many fens of the eastern half of the upper peninsula.

We must consider some of the breeding activity of these *Drosera*. In habitat, the plants begin flowering more or less synchronously in late June to early July. There is a raceme of flowers on the flower stalk (peduncle) and these open and close daily in succession. Each flower opening that day does so by mid-morning (if a bright, sunny day) and then closes by mid-afternoon, and that is it for that particular flower. If a still unknown pollinating agent has not acted in that brief time, the flower undergoes self-pollination as the petals close and press the pollen-bearing anthers against the stigma. Thus, seed is assured, even if not cross-pollinated. The seedpods rapidly expand to 3-4 mm and yield mature seed by late August into early September.

Figure 1: Aerial view of northern Michigan fen. Note interstate highway above. Aerial survey is a good way to identify sites for later surface study.

Figure 2: Typical marl flat in a northern fen with a small hummock. *Drosera linearis* is scattered thinly over the flat. The hummock has *Sarracenia purpurea* subsp. *purpurea* and a few bright green *Pinguicula vulgaris*.

Also to be considered is the fact that hybrids or all North American *Drosera* are sterile (Wynne, 1944; Wood, 1955; Cheek, 1993; Schnell, 1995b). The hybrids cannot breed with each other or the parents, in contrast to the well known opposite situation with *Sarracenia,* for example. In fact this sterility rule can be used as evidence in certain taxonomic problems, such as determining whether *D. filiformis* var. *filiformis* and *D. filiformis* var. *tracyi* should be considered as varieties of one species or two separate species. Since the hybrid between the two is quite fertile, this points to an infraspecific placement, as it is usually classified (Schnell, 1995b).

In 1955, Wood detailed a compelling argument for the hybrid origin of *D. anglica.* Noting that the species had a chromosome count of 2n=40 whereas all other northern *Drosera* were 2n=20, he hypothesized that chromosome doubling had occurred in a hybrid in order to overcome the sterility barrier in northern *Drosera* hybrids. (Those unfamiliar with the n, 2n and x chromosome number designations as well as meiosis vs. mitosis may wish to consult the appropriate chapters of a basic biology or botany text.) Working out of the Douglass Lake University of Michigan Biological Station, he studied the *Drosera* of several bogs and fens in Michigan over several years. He noted the presence of *D. anglica* as well as *D.* × *anglica* in several locations and deduced that the parent plants were likely *D. linearis* and *D. rotundifolia* based on sympatry and morphology.

How does a sterile hybrid of *D. linearis* and *D. rotundifolia* become a fertile species? Studies indicate that the sterile hybrid chromosome count is 2n=20 as expected, and the same as all other northern *Drosera* species. If one examines the early flower buds of such sterile hybrids by dissecting out anthers and ovaries and doing squash preparations or microscopic sections early in development, one notes that the special kind of cell division at certain stages of the development of pollen and ovules known as meiosis is highly disturbed. Both meiosis and mitosis are a precise sort of genetic dance in which chromosomes pair, divide and then disjoin in a highly even manner to produce new nuclei. But in sterile hybrids, some of the chromosomes lag, divide tardily, and form bridges and fragments resulting in highly abnormal nuclei, all of which can be observed by staining and microscopically examining tissue. It is no wonder that such hybrids are sterile.

However, if some little-understood accident results in retardation of meiosis altogether, fertile pollen and ovules with an unreduced chromosome number occur which can then result in viable embryos and seed. The chromosome number of the seed embryo and resulting seedling and plant has now doubled. This process is known as allopolyploidy, or more often by the synonym amphiploidy (*e.g.* Grant, 1981; Briggs & Walters, 1997). Since the amphiploid plant's chromosomes may now pair up properly with the equivalent from the same contributing parent plant during meiosis, the now amphiploid plant is capable of producing viable seed normally generation after generation. Generally, such amphiploids are then recognized as species rather than hybrids.

This then creates a problem for us in the field where parents, hybrids and amphiploid species occur together: How do we easily tell the amphiploid species from the hybrid in a consistent way? Wood (1955) accomplished this by using chromosome counts of root tip (chosen because of active growth and many mitoses being present) squashed and stained preparations and squashes of developing anthers and ovules. He also determined that the flat surface epithelium cells and stoma guard cells of leaf epithelium differed in size, the species generally being larger in this respect, presumably due to a greater chromosome complement than the hybrid. Because the species had larger cells and nuclei, Wood was able to measure these and separate the plants for his research. Having found and discerned the *D.* × *anglica* hybrid in several northern Michigan fens, he described it, naming it by formula (*D. linearis* × *D. rotundifolia*). But he was not always certain of separating the hybrid and species from each other by inspection of whole plants in the field.

Next, Wood discovered something of great evolutionary interest—the origin of *D. anglica* is apparently polytopic; that is, it has occurred by amphiploidy of the hybrid in more than one place, and this process is probably ongoing. This phenomenon has been noted in several other non-carnivorous genera and species (*e.g.* Wood, 1955; Grant, 1981; Briggs and Walters, 1997). Likely, the unknown stimulus for amphiploidy has worked and is working in several different fen locations. Wood was able to deduce this by noting a very few clusters or single plants of the fertile species in large fens with many thousands of other *Drosera* species and a even a few of their hybrids, and also noting that small populations or individual plants of *D. anglica* (species) were often in fens located many miles apart.

One wonders how *D. anglica* has developed such a wide present day distribution nearly around the world while one of its evolutionary parents, *D. linearis*, has remained so localized to the Great Lakes region (but with a few disjunct populations in the Canadian maritimes and at least one small population in northern Maine (Diels, 1906; Wynne, 1944)). Did *D. linearis* at one time have a greater distribution than at present and is receding into its present redoubt and perhaps further in the future? Marly fens to which *D. linearis* seems confined are very fragile habitats. I have seen several Lake Huron shoreline beach pool fens destroyed in one season by severe winter storms and dune blowouts. Or have plants of *D. anglica* simply been distributed widely away from the present Great Lakes area to pioneer in suitable habitats nearly around the world? *Drosera anglica* is ultimately a much more flexible species in its habitat requirements than *D. linearis* in my observations in the field and in cultivating the material. If distribution is the factor, what were or are the carrying agents? Seed on bird feet, as the postulation of plovers bringing propagules of *D. anglica* from Alaska to Kauai. Or was it the prevailing winds bringing seed from Japan to the Alakai Swamp (Mazrimas, 1987; Gon, 1994)? We do not know.

Differentiating *Drosera anglica* From *Drosera* × *anglica*

I conclude this paper by listing and briefly discussing ways to tell *D. anglica* from *D.* × *anglica*. I will discuss the most technical and complex methods that have been used first, then work down to some more easily accomplished field methods. The most technical procedures are of course most definitive at this time. However, they often require sophisticated equipment and the processes themselves are usually beyond the expertise of even the most dedicated amateur and often many professional botanists. Some molecular biological procedures, such as DNA, isoenzyme and FISH (fluorescent in situ hybridization), have not yet been recorded for this problem, but have good potential, especially FISH.

Highly Technical Procedures

1. Microscopic sections prepared by standard histotechnological methods of developing flower buds with staining to discern cells and features, and looking particularly for developing anthers and ovaries to evaluate meiosis. One searches for abnormal chromosome segregation and homologous pairing with lagging and unmatched chromosomes and fragments (*e.g.* Grant, 1981). Technical help is required for making the slides, and considerable experience in evaluating them under the compound microscope.

2. Microscopic examination of stripped or peeled epithelium of the leaf undersurfaces (to avoid glands) (Wood, 1955). Because of amphiploidy, epithelial pavement and guard cells of stomata in *D. anglica* are larger than those of the hybrid. These cells can be measured by planimetry.

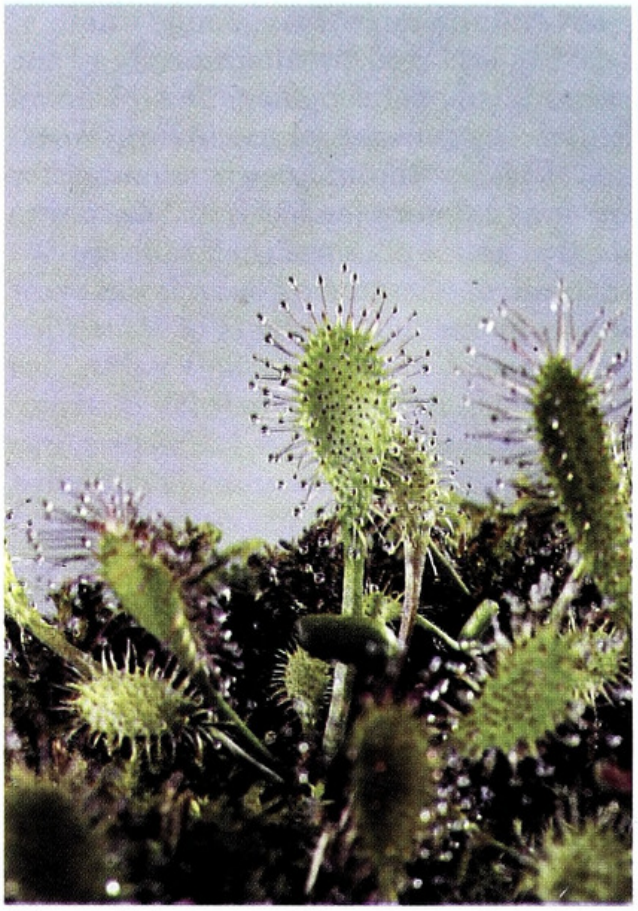

Figure 3: Leaves of *Drosera* × *obovata*.

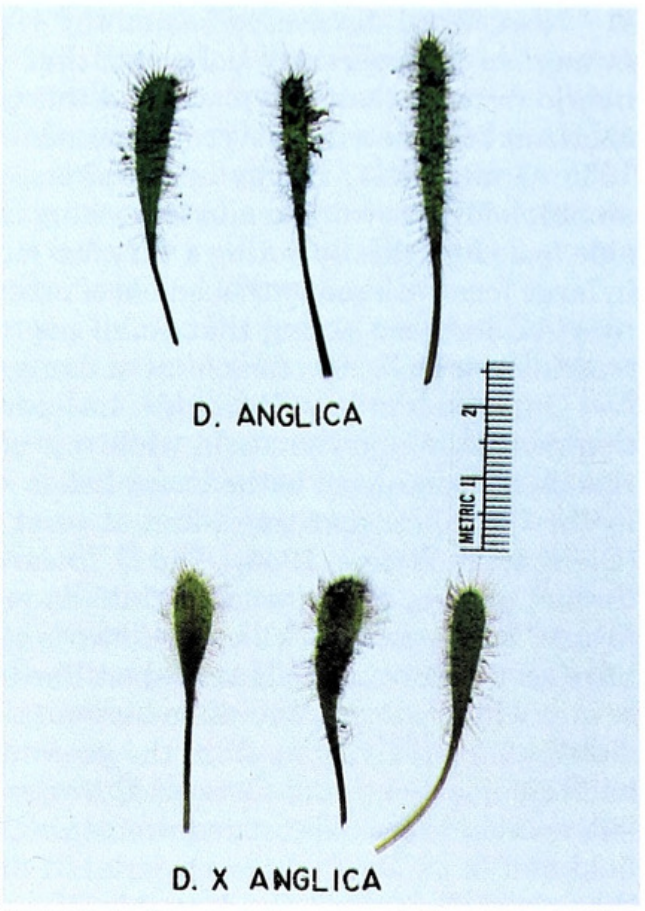

Figure 4: Average leaves of *Drosera anglica* and *Drosera* × *anglica*. Compare with *Drosera* × *obovata* in Figure 3.

Figure 5: *Drosera anglica* in northern Michigan. Note the thicker peduncles compared to *D.* × *anglica* in Figure 6.

Figure 6: *Drosera* × *anglica* in northern Michigan. Note the more slender peduncles compared to *D. anglica* in Figure 5.

3. Somewhat more accessible than above but requiring manual skill, experience, stains, a compound microscope and often some luck, one can prepare squashes of root tips (where there is a lot of mitosis going on) and even developing anthers and ovaries of dissected flower buds to count and evaluate chromosomes. In this case, we are interested in the 2n=20 vs. 2n=40 status of the root tip cells, and evaluating meiosis in good preparations of the flower parts cells. There is a huge body of scattered literature on how to do this so I will not list it here. We are overdue a current single volume describing the most prominent methods in detail with critiques.

Less Technical Procedures

4. The 'less technical' here is relative since at least one stain and a compound microscope (Do we not all carry one in our vans while in the field?) are required. However, the procedure is not difficult to do and evaluate. Pollen staining is based on the premise that viable or living pollen grains capable of fertilizing an ovum will take up certain stains while many sterile hybrids of plants produce only empty or incompletely staining grains. A good reference for pollen viability procedures is Kearns and Inouye (1993) who evaluate several of the pollen staining procedures and find some lacking and/or little controlled on exactly how useful they are. It is probably relative and some are likely more useful in certain plant groups than others. I have had considerable experience with the stain lactol phenol cotton blue on *Sarracenia* and *Drosera*, using known and unknown hybrids compared to species, and find that it is useful and consistent. One simply dusts a small amount of pollen (do not overdo it or you will exhaust your stain and get false negative grains) on the center of a clean, dry glass microslide, add a drop of the stain, mix the stain and pollen thoroughly with a one-time use toothpick and put a coverslip over the preparation.

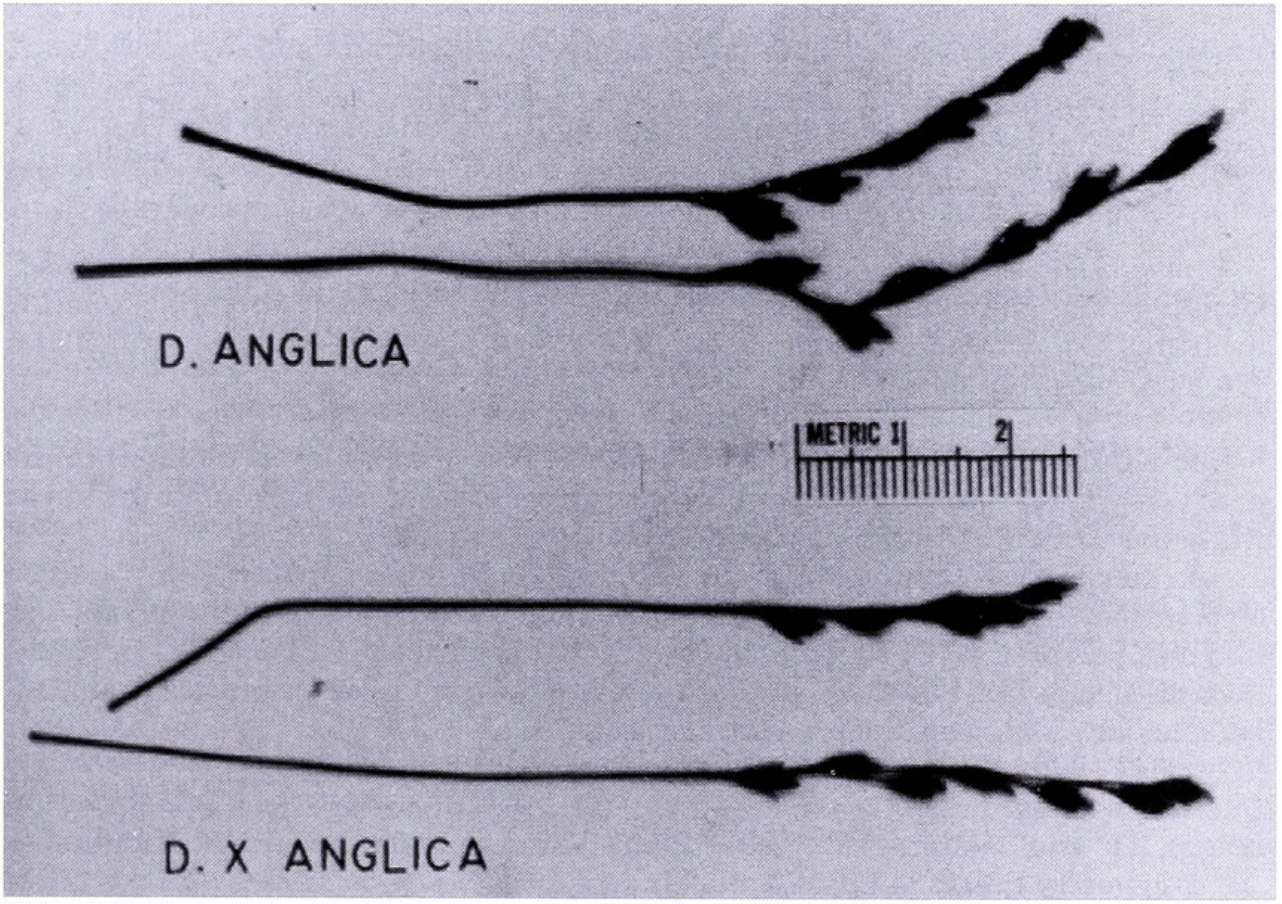

Figure 7: Comparison of late season peduncles with spent flowers of *Drosera anglica* (above) and *Drosera* × *anglica* (below). Besides having peduncles with greater thickness (see text for measurement ranges), *Drosera anglica* also has maturing seedpods.

Viable grains of species and fertile hybrids (e.g. as in *Sarracenia*) stain a deep blue across the entire grain. Grains of sterile hybrids are empty and take no or far less stain. A few hints not mentioned in the usual procedure instructions: After covering your preparation with the coverslip, let it set for about four to six hours for the stain to absorb. Secondly, to get used to what you are looking for, try a few known fertile related species for comparison and also control. Finally, remember nothing is 100% in testing. There will be some (usually less than 5%) empty grains in perfectly fertile species, and a very few grains staining positive in sterile hybrid preparations.

Procedures More Adaptable For Field Use

5. The next consideration is leaf shape. In his 1955 paper, Wood states that *D. anglica* and *D.* × *anglica* cannot be distinguished in the field by leaf shape, but a page later goes on to say that the leaves of *D.* × *anglica* have more the shape of another hybrid, *D.* × *obovata* (*D. anglica* × *D. rotundifolia*)—that is, obovate-spatulate—while the species *D. anglica* is linear-spatulate (Figures 3 and 4). Actually, both statements are true! On average when examining many leaves of many plants, the hybrid *D.* × *anglica* is indeed distinguishable from *D. anglica* (as is the case when pulling three representative leaves of each taxon for Figure 4 out of hundreds collected and pressed). But as is often the case in statistical situations, there is overlap in single cases and individuals may present a problem. To further confound the situation, *D.* × *obovata* is occasionally found with our two problem taxa in the same fen. Usually, when you find only a few widely scattered or small clumps of anglica-like plants in a fen, you are more likely dealing with *D.* × *anglica* since when *D. anglica* is present, it is usually in relatively large clumps and/or numbers. Leaf shape can be helpful but its limitations must be appreciated.

6. One can take advantage of the fertility of the species and the sterility of the hybrid to observe whether *Drosera anglica*-like plants have maturing seedpods, and even collect seed to compare with the fine Wynne (1944) drawings. If you are bogging in the spring or early summer before seedset, you can flag your plants and examine them later in the season.

7. I have noted that the species has a consistently larger corolla than the hybrid, similar to the epithelial cell sizes mentioned in item 2 above. *Drosera* × *anglica* measures 6-7 mm across, while *D. anglica* is 8-10 mm. This is very useful if you catch the plants in flower.

8. Comparable to item 7 above, the peduncles or flower stalks are of different thickness (see Figure 5,6,7): The hybrid consistently measures 1.0-1.2 mm in thickness while the species is 2.0-2.2 mm. This is also very helpful.

In summary, what do I do? Technically, I do indeed use pollen viability studies on occasion. Leaf shape is also very helpful when correlated with other factors and taken in perspective. Of course, seed production is quite definitive in the field and horticulturally. But I have found that there are flowers and/or peduncles nearly all summer, and sizes of these are the most helpful.

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Special Reviews: Videos by Hartmeyer Productions

In recent issues of Carnivorous Plant Newsletter (26:2, 27:4) and on the internet, there have been occasional references to two videos produced by Siegfried and Irmgard Hartmeyer. I contacted the Hartmeyers, and they were good enough to provide copies for the ICPS to review.

Both videos (Beautiful & Hungry—Carnivorous Plants, parts I and II) are travelogues that follow the Hartmeyers as they journeyed through Singapore, Australia, Germany, and Switzerland. While both videos have all the charm of home movies, the second is probably more interesting to the dedicated carnivorous plant grower. Less time is spent on holiday activities like scuba diving and parasailing, and more on carnivorous plants. Particularly interesting is this video's devotion to arthropods that live on sticky plants and dine on the unfortunate prey trapped by the adhesive leaves. These arthropods and their associated plants are shifting and blurring the distinctions between carnivorous and non-carnivorous plants.

In the making of both videos, the Hartmeyers encountered bizarre and unfortunate circumstances that prevented them from finding all the plants they hoped to see. To compensate for this, they show plants from their own collections.

It may be difficult for many ICPS members to view the Hartmeyer videos because of videotape incompatibilities (for example, the US videoplayers are unable to play these European videos). However, interested parties should contact the Hartmeyers at Wittlinger Str. 5, D-79576 Weil am Rhein, Germany, email: S.Hartmeyer@t-online.de. The Hartmeyers plan to produce future products on more universal, digital formats. (BAMR)