Dionaea traps selectively allow small animals to escape

Siegfried R. H. Hartmeyer and Irmgard Hartmeyer • Wittlinger Str. 5 • D-79576 Weil am Rhein • Germany • s.hartmeyer@t-online.de
Stephen E. Williams • Emeritus Professor • Lebanon Valley College • Annville • Pennsylvania 17003 • USA • williams@lvc.edu

Abstract: *Dionaea muscipula* selectively allows small animals to escape using a system of interlocking features that complement each other very efficiently. Ants of the species *Lasius neglectus* (length 3.5 mm) ran through open traps, pausing on the alluring glands along the rim of the trap moving their mouthparts over them. Analysis of videos revealed the ants primarily passed along the trap rim, over the alluring glands, but sometimes ran down to the leaf base through the trigger hairs occasionally brushing by a hair without triggering the trap, because they did not deliver the two stimuli needed to trigger trap closure.

Traps observed for four weeks were estimated from sampled observations to have had a total of about 15,000 trap visits by ants during this time period. Six ants were captured during four weeks indicating a risk of capture of about 0.04%. During this same period ten prey other than ants were captured. Visits for prey other than ants was mostly nocturnal and so low that no visits were observed during the observation period. Compared with the large number of ant visits all other prey visits were orders of magnitude fewer. The selective system that allows small animals to escape includes:

1) Attraction of the ants away from the trigger hairs by alluring glands.
2) Clear visibility of the trigger hairs to a 3.5 mm ant.
3) The requirement of two stimuli for triggering trap closure.
4) The escape allowed for small animals by openings between the marginal bristles during the slower phase of trap closure that follows the rapid snap of the trap.

Since ants are known to compose about one third of the captures by *Dionaea* in its native habitat, selection against the capture of small ants not worth the energy expenditure by the plant is an adaptive mechanism.

Introduction

There has been considerable interest in Charles Darwin's (1875) idea that *Dionaea* has a mechanism that would mainly capture moderately large insects and allow most of the small ones to escape. While doing research to test Darwin's hypothesis, entomologist Frank Morton Jones (1923) conceived of a second mechanism that would prevent the capture of small animals. The aim of this study is to reinvestigate their hypothesis and to examine in a statistically reliable manner if small animals (ants in this study) have a significantly reduced risk of being captured.

Darwin's hypothesis: The mechanism Darwin (1875) proposed for this involves the escape of prey through the openings between the projections from the edge of the leaf that remain partly open after the early rapid snap of the capture movement and during the slow closure that finally seals the trap and the fate of the prey. Darwin noted the saving in time that would result in digesting only prey that would provide sufficient nutrition and stated, "this advantage is secured by the slowly intercrossing marginal spikes, which act like the meshes of a fishing net, allowing the small and useless fry to escape" (Fig. 1).

Jones' hypothesis: Frank Morton Jones (1923) noticed that small ants were attracted to glands along the upper margins of the trap lobes. These ants moved in and out of traps without disturbing them while working their mouthparts on the marginal areas where alluring glands occur (Fig. 1). Jones proposed that small ants and other animals attracted to the glands along the leaf margin, that were too small to reach from that position to the trigger hairs, would fail to spring the trap. The result is selection of prey larger than small ants without the trap even having to bear the cost of reopening after being triggered.

Figure 1: Top: Traps directly after closure. Darwin hypothesized small prey escapes through the overlapping spikes. Bottom: Open traps with visitors. Jones, in addition to accepting Darwin's idea, also hypothesized the alluring glands guide small animals away from the triggers.

Darwin's and Jones' hypotheses are not mutually exclusive, either or both can select for prey that is sufficiently large to offset the expenditure of energy by the capture mechanism. Jones (1923) suggested that both mechanisms are involved in the selection of prey by *Dionaea*. Of course, Jones' mechanism would only act on animals attracted to the marginal glands while Darwin's mechanism would act on all prey captured.

Alluring glands: Jones (1923) observed ants attracted to areas near the rim of *Dionaea* traps and Lloyd (1942) accurately described Jones' ideas in his classic work "Carnivorous Plants", adopting the term "alluring glands" for structures in the area that attracted the ants thus making it the standard term for these structures.

The function of the trap area with alluring glands described by Frank Jones (1923) was to attract small animals, especially ants, away from the trigger hairs so that only those long enough to touch them when their mouthparts were engaged would be captured. Since about one third of the prey captured by *Dionaea* in its natural habitat are ants (Williams & Hartmeyer 2017) this function is likely to be very important.

In most papers since the 1980s the alluring glands are proposed as a lure that draws prey into the trap where it trips the trigger hairs and is captured. This is likely due to this role for the glands being described in Juniper, Robins and Joel's classic book "The Carnivorous Plants" (1989). While there clearly is an attractant produced that draws ants (Jones 1923) and flies (Williams & Hartmeyer 2017) it does not seem to draw prey into the trap from a distance.

Analysis of prey: Prey capture success by three different sized traps has been determined to have no correlation with prey size (Hutchens & Luken 2009; Luken 2019). More recent laboratory research by Davis *et al*. (2019) found larger trap size correlated with a substantial increased probability of capture. Prey mass resulted in a slightly smaller probability of successful captures. In these experiments cultivated flytraps of 5-30 mm were exposed to lab grown crickets of 7-23 mm. Since the traps were exposed to prey of moderate to large size relative to the trap and not to small animals neither Darwin's nor Jones' hypothesis was tested in the experiment.

It is unclear if the correlations observed by Hutchens and Luken (2009) and by Davis *et al*. (2019) demonstrate that smaller prey is escaping through the leaf spines and moderate sized prey is

retained. The calculations are based on prey captured. We know very little about prey that got away. Since prey capture is a relatively rare event, testing of Darwin's hypothesis is likely to be difficult but Frank Jones' (1923) descriptions of ants being frequently noticed on the leaves indicate that it may be possible to test his hypothesis.

The objective of this paper is to repeat Frank Jones' observations and measure the frequency of small ants that escaped from active traps without closing them and to measure and identify the captured prey.

Methods

Dionaea muscipula in this experiment are a population of plants established more than 20 years ago in a 40 cm pot inside a garden pond in Weil am Rhein (Southwestern Germany, Fig. 2). These plants, similar to those found in the wild, are the same ones used in a previous 80-day study of prey captured by *Dionaea* in various habitats by Williams and Hartmeyer (2017).

Ants (*Lasius neglectus*, length 3.5 mm) observed in the study had established themselves in the 40 cm pot near the *Dionaea* since the 2017 Williams and Hartmeyer study. All ants and prey animals are those occurring in the garden with no manipulation by the experimenters.

Observations and video (Hartmeyer & Hartmeyer 2019) of ant visits to the traps were made. In spring 2019, the ant population settled for the first time inside a large pot with *Dionaea*, *Drosera rotundifolia*, and *Sarracenia minor* var. *okefenokeensis*, directly beside the established *Dionaea* that started to sprout again after winter dormancy. The behavior of the ants and their interaction with the active traps was observed.

Scheduled observations: Ant visits to the population of *Dionaea* traps were observed continuously during 24 ten-minute intervals spread over six days. These observation periods were made at different times of day. The time, weather, and number of open and closed traps were recorded. The prey found in reopened traps was measured and identified along with the length of the reopened traps. During the experiment the number of active traps increased from 24 to 38. The distance from the alluring glands to the nearest trigger hair was measured for traps of a range of sizes. The median length and the lengths of the largest and smallest traps were determined. Blackening or inactive looking traps were removed to keep the setup clear. However, except for

Figure 2: Garden pond population of *Dionaea*.

that, the plants were left to themselves. In addition to the removal of blackened-inactive traps new traps developed; therefore, the total of open and closed traps in the log changes. Only healthy active traps have been counted. In summer 2016, the same population of traps was documented for prey capture during 80 days (Williams & Hartmeyer 2017), which provides comparable data of the usual prey capture without ant nest beside the plants.

Photography and videography were done with an Olympus SH-2 (photos & HD-video) and a Huawei P20 Pro (4K-videos). The photographs were improved for image quality with MAGIX Photo and Graphic Designer. The original 4K-videos were edited with EDIUS Pro 9 for display details, image quality, and stabilization and then rendered to HD-format. The image stabilization was necessary because the setup is placed inside a garden pond and it was impossible to install a tripod for suitable macro shots. Therefore, the manually shot macro videos were strongly blurred. The resolution was greatly improved with the previously mentioned stabilization filter. However, no video content has been manipulated with editing software.

Results and Discussion

Observations and video of ant visits to the traps showed ants nesting in the 40 cm pot frequently moved over the plants and through the traps without being captured. The numerous ants that entered the stand of *Dionaea* in the garden pond were continuously active throughout daylight. They crawled over the plants and ran through open traps, pausing on the visibly-dry alluring glands and moving their mouthparts over them (Front Cover). Their interest in these structures was striking and is clearly visible on the shots. Analysis of the videos revealed the ants primarily passed along the trap rim, over the alluring glands. Due to the ants' small size they did not reach the trigger hairs when they passed along the rim of the trap. Even when they suddenly ran down to the leaf base through the trigger hairs, we never observed them trigger the trap. Occasionally they passed close to a trigger hair and may have brushed against it but since two stimulations of a hair or hairs within 20 sec are required to trigger closure of a trap it is very rare that this happens. When the mouthparts were on the alluring glands the 3.5 mm ants stretched only about 0.7 of the median distance to the trigger hairs closest to the rim. While they were longer than the alluring gland to trigger hair distance in the smallest trap (ratio 1.17), the ants were usually nearly horizontal to the rim of the trap and well away from trigger hairs. They did not trigger a response this way. Our observations

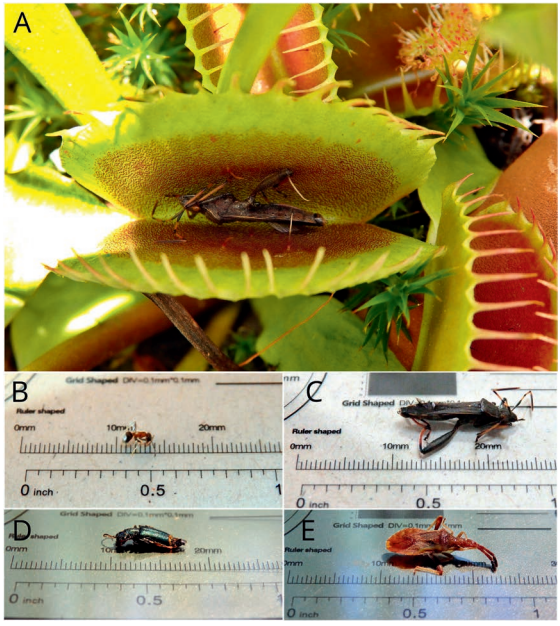


Figure 3: A&C = prey predatory bug (13 mm). B = *Lasius neglectus* (3.5 mm). D = prey beetle (7 mm). E = prey true bug (9 mm).

agree exactly with those of Jones (1923) and support his hypothesis that the alluring glands drew the small ants away from the trigger hairs and prevented their capture.

When the observations started on May 27th only three of 24 different sized active traps were closed with prey despite the heavy ant traffic. For example, in the early afternoon, 15 ant visits occurred within ten minutes, yet no captures were made that day. The first closed leaf opened in June revealing a large predatory bug (Reduviidae, Hemiptera; Fig. 3). Jones predicts that smaller animals attracted to the alluring glands will not trigger trap closure, larger animals would reach the trigger hairs and would have a high probability of being captured. Since three independent studies (Jones 1923; Lichtner & Williams 1977; Hutchens & Luken 2009) show that about one third of the prey captured by *Dionaea* in its native habitat are ants, it is clear that selection of size is important for this class of prey. Without prey size selection, almost all traps would be closed on ubiquitous small ants.

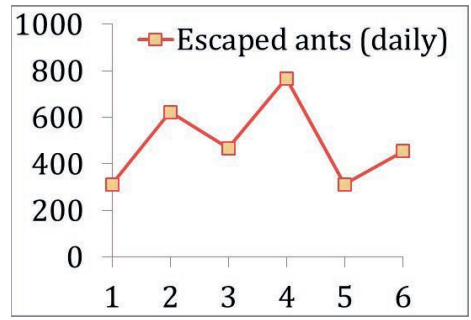


Figure 4: Ant escapes during 24 ten-minute intervals over six days, extrapolated to daily events. Average = 520 escapes daily or 14,560 in four weeks.

Scheduled observations of ant visits: During the 10-minute intervals all ants leaving any trap without triggering closing were counted. Adding all ants counted in 24 ten-minute intervals is equivalent to 240 minutes or four hours of precise counting, we achieved a sum of 158 escaped individuals. During this period an average of 40 ants per hour entered and left the traps without triggering them. Extrapolated to a daily period of 13 hours (counting between 9 am-10 pm) 520 problem-free trap visits daily (Fig. 4) or about 15,000 (extrapolated 14,560) during the four-week observation time. Only six ants were captured during the 4 weeks (Table 1). The risk of *Lasius neglectus* being captured is thus very low, about 0.04%. For comparison: The risk of mortality by medical malprac-

Table 1. Prey capture by the garden pond population of *Dionaea* over four weeks.

Captured Prey During Four Weeks	Number Captured	Prey Length (mm)	Trap Length (mm)	Remarks
Hymenoptera (*Lasius neglectus*)	6	3.5	13-23	3 single captures. 2 ants caught at once, each carrying 4-5 mm long item. 1 ant caught together with a crab spider.
Arachnida	1	4	22	likely *Misumena vatia*
Coleoptera	5	6.5-7	18-26	Beetles, all *Malachius bipustulatus*.
Diptera	2	4 & 6.5	14 & 20	Mosquitos
Hemiptera	2	9 & 13	31 & 25	Different true bugs
Unidentified	2	3-6	2 × 20	Jelly & droppings, excluded from calculation.
Total: 16 prey animals in four weeks = 4 captures per week by 24-38 traps.				

tice for a human in a German hospital is 0.1% (BMG 2007) and thus 2.5 times higher than the risk that small ants will be captured by a *Dionaea* trap.

Prey other than ants captured during four weeks of observation (10, Table 1) consisted of five beetles (6.5 - 7 mm), two true bugs (9 & 13 mm), two mosquitos (4 & 6.5 mm) and one small crab spider (4 mm) that was captured together with an ant in one trap. All these prey animals were larger than the 3.5 mm ants, often reaching a multiple of the ant length (Fig. 5). Two ants, each carrying 4-5 mm long items of nesting material through a trap were captured in a single trap closure possibly due to their extended size. Only three ants were captured alone; however, to keep our calculation conservative we included all six captured ants, disregarding the circumstances of capture. Data on the risk of capture for prey animals other than ants is unavailable because their visits, which are mainly nocturnal, are far less frequent. Measuring their captures and escapes would require 24-hour observations for several weeks; therefore, this type of measurement has not been done. The beetles, true bugs, and mosquitos were all captured over night, when the ant traffic around the *Dionaea* paused. Compared with the large number of ant visits (maximum counted escapes in ten minutes = 21, minimum 1), all other animal visits were orders of magnitude fewer. That means even a conservative estimate of their risk of being captured is orders of magnitude higher than 0.04%. Therefore, our experiments show clearly that *Dionaea* sorts out prey of insufficient size, particularly small ants, thus increasing the chance to capture medium to large prey.

Figure 5: 1) The alluring glands draw ants away from the triggers. 2) The trigger hairs are large enough to be visible to ants crossing the trap. 3) One accidental touching of a trigger hair does not close the trap. 4) Even if the trap closes, gaps between the bristles allow small prey to escape.

Dionaea's complex prey selection mechanism results in selection of prey of sufficient size to offset the costs of the snap trap capture mechanism. Capture of prey involves loss of resources to the plant:

1) The closed trap has reduced photosynthesis due to the change in orientation of the leaf to the sun, decreased flow of CO_2 and changes in metabolism (Pavlovic 2010).
2) Energy is used in closing and reopening the trap.
3) Energy is expended in digesting prey.
4) Traps can make only 3 to 4 closures; each closure is slower than the previous one. The snap of a trap is therefore a limited resource (Brown 1916; Davis *et al*. 2019).

The advantages of prey selection relate to the relative costs in capturing prey of different size. Small prey probably have an energy expense out of proportion to any advantage gained. While the

advantages of carnivory in *Dionaea* are related to procuring nutrients rather than energy the energy expenditure must still be worth the gain in the overall budget of the plant.

The *Dionaea* prey selection mechanism is a system of at least four different interlocking features which complement each other very efficiently.

1) The dry alluring glands attract some animals, such as ants and flies, away from the trigger hairs. Of the animals attracted only those long enough to reach from the alluring glands to the trigger hairs have a high probability of being captured (Jones' mechanism). These visitors often pause and move their mouthparts over these glands which occur near the marginal spikes and they leave and enter the traps often through the spaces between the spikes or at the space at the petiole without crossing the dangerous trigger zone (see Hartmeyer & Hartmeyer 2019 video and Fig. 5).
2) Frequently, ants suddenly walk down to the leaf base and pass the dangerous trigger hair region. However, ants are unlikely to run headlong into visible obstacles. With a length of approximately two millimeters, the trigger hairs should be clearly visible for a 3.5 mm sized ant (see Hartmeyer & Hartmeyer 2019 video and Fig. 5).
3) Even if a leg or antenna touches a trigger hair accidentally nothing happens, the traps remain open. *Dionaea* responds within about 20 seconds for a second contact. Without it, the trap remains open and the memory of the first stimulus fades and another two stimuli are required for closure.
4) After stimulation by prey a *Dionaea* trap will rapidly snap closed but the closure is not complete. A gap remains between the lobes for several minutes. During this period the escape of large prey is barred by the marginal spikes, which cross over each other along the open edge of the trap. Animals that are small enough have a chance to escape between the marginal spikes (Darwin's mechanism). This mechanism will allow the escape of small animals regardless of whether or not they are attracted to the alluring glands.

The interaction of all these features enables small ants to visit *Dionaea* traps with a risk of only 0.04% of being captured. This amazingly small risk suggests that *Dionaea* clearly has complex mechanisms that prevent the capture of small ants. Other small prey, not attracted to alluring glands, can still escape by mechanisms 2, 3, and 4 if they are agile enough. However, observations that would prove this in detail have yet to be made.

Previous experiments on prey selection have been inspired by Darwin's suggestion that small potential prey escapes during the later phase of closure when gaps between the marginal spines provide an escape route. This is an ingenious idea and also attracts attention because it was the famous Charles Darwin who suggested it. Three of the studies based their conclusions on measurements of the prey captured in the field. Darwin (1875) believed that his limited observations supported his hypothesis and Jones (1923) felt his observations supported both Darwin's and his hypothesis although the results were not definitive. Hutchens and Luken (2009) found no significant correlation between prey size and trap size and concluded that, attractive as Darwin's hypothesis was, the evidence does not support it. All of these studies looked only at prey captured and had no measurements of small animals that escaped. If either hypothesis is correct it must be demonstrated that small potential prey has a much larger chance of escaping than large prey so none of the studies is conclusive. Davis *et al*. (2019) did measure the probability that crickets of a range of sizes would be captured under laboratory conditions and therefore had a chance of testing Darwin's hypothesis when crickets are the prey. However, their data shows smaller crickets have a higher probability of being captured than larger ones, exactly the reverse of what would be expected if Darwin's hypothesis was correct. However, since the crickets range between 7-23 mm while the traps range from

5-30 mm (except for one small trap) the crickets should be considered medium to large prey. They did not investigate potential prey small enough to test Darwin's hypothesis rigorously.

Jones' mechanism of attraction of ants away from the trigger hairs toward alluring glands on the rim of the trap allowing them to escape is effective. Darwin's mechanism of allowing small prey to escape through openings between the marginal spines along the lobes of the trap during the slow final phase of closure probably also works, but more observations and experiments are needed to confirm this in detail. An experiment like that of Davis *et al*. (2019), where the probability of capture of medium sized and large prey but with small potential prey like the ants in our experiments included is probably the best way to test Darwin's hypothesis. Considering the amazing fact that during our experiment, which was done over four weeks, only six of 15,000 ant visits triggered a closing makes it very likely that such an effective sorting out of small animals is based, not on just one mechanism, but on a sophisticated system of several interlocking features that include the mechanisms of Jones (1923) and Darwin (1875).

References

Brown, W.H. 1916. The mechanism of movement and the duration of the effect of stimulation in the leaves of *Dionaea*. American Journal of Botany 3(2): 68-90.

Bundesministerium für Gesundheit (BMG 2007). Sachverständigenrat zur Begutachtung der Entwicklung im Gesundheitswesen. Kooperation und Verantwortung. Voraussetzungen einer zielorientierten Gesundheitsversorgung. Gutachten 2007, Langfassung, 2007 1-462. http://dipbt.bundestag.de/dip21/btd/16/063/1606339.pdf

Darwin, C. 1875. Insectivorous Plants. John Murray, London.

Davis, A.L., Babb, M.H., Lowe, M.C., Yeh, A.T., Lee, B.T., and Martin, C.H. 2019. Testing Darwin's hypothesis about the wonderful Venus flytrap: Marginal spikes form a "horrid prison" for moderate-sized insect prey. The American Naturalist 193: 309-317.

Hartmeyer, S.R.H., and Hartmeyer, I. 2019. Video: *Dionaea* traps selectively allow small animals to escape. https://youtu.be/JJYAa0n_h0w

Hutchens, J.J., and Luken, J.O. 2009. Prey capture in the Venus flytrap: collection or selection? Botany 87:1007-1010.

Jones, F.M. 1923. The most wonderful plant in the world. Natural History 23(6): 589-596.

Juniper, B.E., Robins, R.J., and Joel, D.M. 1989. The Carnivorous Plants. Academic Press, London.

Jürgens, A., El-Sayed, A.M., and Suckling, D.M. 2009. Do carnivorous plants use volatiles for attracting prey insects? Functional Ecology 23: 875-887.

Kreuzwieser, J., Scheerer, U., Kruse, J., Burzlaff, T., Honsel, A., Alfarraj, S., Georgiev, P., Schnitzler, J.-P., Ghirardo, A., Kreuzer, I., Hedrich, R., and Rennenberg, H. 2014. The Venus flytrap attracts insects by the release of volatile organic compounds. Journal of Experimental Botany 65(2): 755-766.

Lichtner, F.T., and Williams, S.E. 1977. Prey capture and factors controlling trap narrowing in *Dionaea* (Droseraceae). American Journal of Botany 64(7): 881-886.

Luken, J.O. 2019. The Venus flytrap: Subsistence or trophy hunter? Natural History 127(5): 14-15.

Lloyd, F.E. 1942. Carnivorous Plants. Chronica Botanica Company, Waltham.

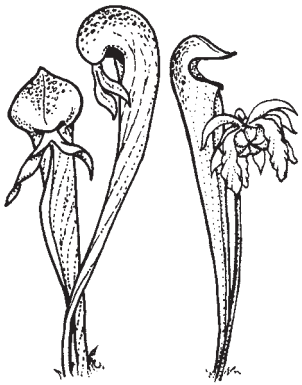
Pavlovic, A., Demko, V., and Hudák, J. 2010. Trap closure and prey retention in Venus flytrap (*Dionaea muscipula*) temporarily reduces photosynthesis and stimulates respiration. Ann Bot. 105(1): 37-44.

Williams, S.E., and Hartmeyer, S.R.H. 2017. Prey capture by *Dionaea muscipula* A review of scientific literature with supplementary original research. Carniv. Pl. Newslett. 46(2): 44-61.

CARNIVOROUS PLANT NEWSLETTER

Journal of the International Carnivorous Plant Society

Volume 48, No. 4 December 2019



CARNIVOROUS PLANT NEWSLETTER

Journal of the International Carnivorous Plant Society
www.carnivorousplants.org

Volume 48, Number 4
December 2019

Front Cover: A small ant (*Lasius neglectus*) attracted by the alluring glands inside a *Dionaea* trap. Photo by Siegfried R. H. Hartmeyer. Article on page 153.

Back Cover: Venus flytraps can be grown for years indoors without dormancy. Photo by John Brittnacher. Article on page 178.

Carnivorous Plant Newsletter is dedicated to spreading knowledge and news related to carnivorous plants. Reader contributions are essential for this mission to be successful. Do not hesitate to contact the editors with information about your plants, conservation projects, field trips, or noteworthy events. Advertisers should contact the editors. Views expressed in this publication are those of the authors, not the editorial staff.

All correspondence regarding dues, address changes and missing issues should be sent to the Membership Coordinator at the ICPS. Do not send such correspondence to the editors. Checks for subscriptions should be made to the International Carnivorous Plant Society in US funds. Dues, including a subscription, are $30 per year.

International Carnivorous Plant Society, Inc.
2121 N. California Blvd., Suite 290
Walnut Creek, CA 94596-7351, USA
icps@carnivorousplants.org

Date of effective publication of the September 2019 issue of Carnivorous Plant Newsletter: July 31, 2019.

The ICPS is the International Cultivar Registration Authority (ICRA) for the names of cultivated carnivorous plants according to the International Code of Nomenclature for Cultivated Plants. Send relevant correspondence to the ICPS, Inc.

Carnivorous Plant Newsletter is published quarterly in March, June, September, and December by the ICPS, Inc., 2121 N. California Blvd., Suite 290, Walnut Creek, CA 94596, USA. Periodicals postage paid at Walnut Creek, CA and additional mailing offices. Postmaster: Send address changes to ICPS, Inc., 2121 N. California Blvd., Suite 290, Walnut Creek, CA 94596, USA. Printed by Allen Press, Inc., 810 E. 10th Street, Lawrence, KS 66044. Logo and masthead art: Paul Milauskas.
 ISSN #0190-9215