

# CARNIVOROUS PLANT NEWSLETTER

Journal of the International Carnivorous Plant Society

Volume 36, No. 1

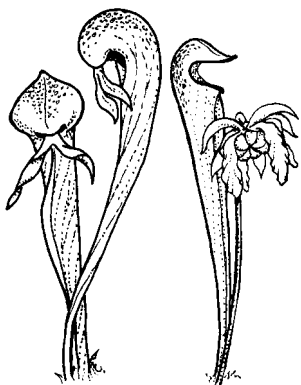
March 2007



# CARNIVOROUS PLANT NEWSLETTER

Journal of the International  
Carnivorous Plant Society  
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Volume 36, Number 1  
March 2007



Front Cover: Group of *Pinguicula chilensis* with immature seed pods growing in the shade along a small creek at Las Turberas. Article on page 6. Photograph by Oliver Gluch.

Back Cover: The entrance corridor into *Sarracenia psittacina* pitcher. Article on page 23. Photograph by Barry Rice.

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. Contributors should review the "Instructions to Authors" printed in the March issue of each year. Advertisers should contact the editors. Views expressed in this publication are those of the authors, not the editorial staff.

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<i>Byblis liniflora</i> <i>Darlingtonia californica</i> <i>Dionaea muscipula</i> <i>Drosera aliciae</i> <i>D. anglica</i> <i>D. binata</i> <i>D. binata</i> —Coromandel, NZ <i>D. burmannii</i> <i>D. capensis</i> ‘Albino’—white flower <i>D. capensis</i> —narrow leaf <i>D. dielsiana</i> <i>D. filiformis</i> var. <i>filiformis</i> <i>D. filiformis</i> var. <i>filiformis</i> —Florida, USA, all red <i>D. filiformis</i> var. <i>tracyi</i> <i>D. glanduligera</i> <i>D. indica</i> <i>D. intermedia</i> —Cuba <i>D. intermedia</i> —New Jersey, USA <i>D. intermedia</i> —North Carolina, USA <i>D. intermedia</i> —Rhode Island, USA <i>D. peltata</i> subsp. <i>auriculata</i>	<i>D. peltata</i> subsp. <i>peltata</i> <i>D. rotundifolia</i> —Alaska, USA <i>D. rotundifolia</i> ‘Charles Darwin’ <i>D. rotundifolia</i> —Washington, USA <i>D. spatulata</i> <i>D. tokaiensis</i> <i>Ibicella lutea</i> <i>Pinguicula alpina</i> <i>Sarracenia flava</i> <i>S. leucophylla</i> <i>S. leucophylla</i> —Alabama, USA <i>S. oreophila</i> <i>S. purpurea</i> subsp. <i>purpurea</i> <i>S. purpurea</i> subsp. <i>venosa</i> <i>S. rubra</i> <i>S. rubra</i> subsp. <i>alabamensis</i> —ESA/CITES, USA sales only <i>S. rubra</i> subsp. <i>jonesii</i> —ESA/CITES, USA sales only <i>S.</i> —various hybrids
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PLEASE NOTE the new address for the ICPS Seedbank!

This is a partial list of the seeds available. A complete list is online at the ICPS web site, <http://www.carnivorousplants.org/> or by sending a self-addressed, stamped (if USA), envelope to the seed bank address.

Seed packets are US\$1 each. Please include US\$3 postage and handling for each order. You may pay by cash, check, or money order in US\$. Many members pay with cash. Please make checks and money orders payable to “ICPS Seed Bank”.

The seed bank is a members-only benefit. The quantity of seed available to each member is 1 packet of each variety per month and 40 packets total in any 12 month period. Please list alternative seed selections, as other orders will arrive before yours. If you have an e-mail address, please include it so we can correspond should any issues arise. Seeds purchased through the seed bank are intended for your personal use only and may not be sold.

You are encouraged to stock the seed bank with seed produced by cultivated plants. The ICPS policy on wild seed collection is on line at the ICPS web site. Cultivation-produced seeds of species protected by the US Endangered Species Act are distributed within the US only, and in accordance with the ICPS’s US Fish & Wildlife Service permit TE061005-1.

Donate seed and get credit for free seed from the seed bank. Seeds of selected varieties are available free to teachers for use in the classroom and to scientists and conservation organizations. It is ICPS policy not to sell internationally seed of plants protected by CITES Appendix I or the US Endangered Species Act.

John Brittnacher, Manager • [john@carnivorousplants.org](mailto:john@carnivorousplants.org)

# LETTER FROM THE EDITOR

Barry Rice

We are deep in the new year, a year that has brought new leadership to the International Carnivorous Plant Society. We have said goodbye to outgoing ICPS president Carl Mazur and Steve LaWarre, and are greeting long-time ICPS members Doug Darnowski and Bob Ziemer to the ICPS board. Doug has already started duties with Carnivorous Plant Newsletter (he is the new ICPS president and is also in charge of literature reviews). Meanwhile, in June Bob will have exciting news about back issues of Carnivorous Plant Newsletter.

For me and the ICPS, this is a year of particular significance. Jan Schlauer and I have officially completed decade of editorial duties for Carnivorous Plant Newsletter. I look back at the previous ten years and see many changes have occurred in the ICPS and Carnivorous Plant Newsletter, and in general they have been for the better. Some noteworthy events include the following:

1)After much sturm und drang, the ICPS graduated from a club of murky legal status, to the ranks of a real and true nonprofit organization. This was a crucial development.

2)With its nonprofit status in hand, the ICPS was able to start processing credit card memberships inexpensively. If I told you of the ICPS resources that had been wasted trying to recover money from bounced membership checks, you'd be shocked!

3)The ICPS finally developed a Conservation Program, and began awarding grants to nonprofits that are working on targeted conservation projects that enhance carnivorous plant sites. The ICPS Conservation Program is the largest conservation grant program in the world that is focused exclusively on enhancing carnivorous plant stewardship.

4)The ICPS website was born. If you haven't seen it, what are you waiting for?

5)The ICPS seed bank was restructured into a living entity that seed bank manager John Brittnacher updates on a constant basis. The seed bank works with the ICPS Conservation Program to maintain permits from the US Fish & Wildlife Service, so it can distribute seeds of US Federally Threatened and Endangered species, at least within the USA. Now, if we can only find the resources to address CITES concerns, we could go international!

6)Jan Schlauer has established the ICPS as the International Cultivar Registration Authority (ICRA) for carnivorous plants. While there are those who feel that the international cultivar registration system does not adequately address carnivorous plants, with the ICPS fulfilling its requirements as ICRA for carnivorous plants there is at least a system in place for those who want to use it!

7)Three quiet heroes continue to perform key roles for the ICPS. For about the last decade Cindy Slezak has processed the membership of every member of the ICPS. She has done this with extraordinary grace and perseverance. Steve Baker continues to perform the layout and design of each CPN issue, as he has since dinosaurs roamed the Earth. And former ICPS-President Rick Walker continues to maintain the ICPS membership database.

8)Finally, the look and feel of Carnivorous Plant Newsletter has evolved. Compared to ten years ago, it looks perhaps somewhat more professional and official. Some of this is due to the enormous attention to detail and accountability the editors demand of themselves and the contributing writers. However, I believe that most of the change in CPN has come from technological changes in human society itself. During the first few decades of the ICPS's existence, its main function was to provide a way for its members to communicate with each other. While it did a good job at this when it had no competition, the internet—with its instant email and countless personal home pages—raced in during the 1990s and made the original mandate for the ICPS obsolete. Indeed are there really any functions left for small specialist societies of any kind, when email and web-based communication forums are common and essentially free? Why write a "News & Views" piece or a full-fledged article, when it can be posted on the internet tonight? Why renew one's membership in the ICPS at all?

I believe that the world still does need membership-based carnivorous plant societies like the ICPS and the ACPS, AIPC, BACPS, CCPS, CPS, ECPS, GFP, IPS, JCPS, LACPS, NECPS, NZCPS, OCPS, and VCPS; as well as those groups that are not so prone to acronyms such as Carnivora, Darwiniana, Association Dionée, and Drosera v.z.w., and finally any other society I may have accidentally overlooked! But it will be the heady charge of leadership for these societies to reinvent themselves so they are not marginalized by the internet. After all, if these societies disappear, what will happen to the seed banks and conservation programs? Where will you go for information that has also been reviewed by other people for accuracy and rigor?

Change is the only constancy. The ICPS continues to change. We have a new and energized board of directors, and I am confident it will continue to guide the ICPS well as we move into the undiscovered future!

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PINGUICULA CHILENSIS—HABITAT OBSERVATIONS FROM THE  
NAHUELBUTA NATIONAL PARK IN CHILE

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Keywords: observations: *Pinguicula chilensis*, Chile.

The butterwort species *Pinguicula chilensis* Clos is one of two species known to grow in Chile (the other being *P. antarctica*). According to Casper (1966), *P. chilensis* occurs along the Central Andean Mountain Range, ranging from 35° southern latitude (Laguna del Maule) to 38° southern latitude (Parque Nacional Nahuel Huapi). It is also found in the Valdivian Coastal Cordillera. The Andean habitat of *P. chilensis* is wet meadows (locally called mallín) at the edge of melting snow fields on volcanoes and other high mountains. The plants grow in altitudes of 1700 to 3000 m. Little is known about the habitat in the Valdivian Coastal Mountains.

In addition to this range, Rodriguez *et al.* (2000) mention that *P. chilensis* also grows in the Parque Nacional Nahuelbuta, located about 300 km north of the habitats in the Valdivian Coastal Cordillera. I had the opportunity to visit the National Park four times between 2004 and 2006.

The National Park is located in the Cordillera de Nahuelbuta (east of the city of Angol in the Province of Malleco at 37° southern latitude) and comprises an area of 6832 hectares. This National Park is the last refugium of an *Araucaria araucana* (monkey puzzle tree) coastal forest. The two highest peaks are Alto Nahuelbuta (1530 m a.s.l.) and Cerro Nahuel (1472 m a.s.l.). The annual precipitation is 1200-1500 mm. While in the dry summer the highest daily temperatures can be around 20°C (68°F), in winter (July to September) frosts occur and snow accumulation can be up to 1 meter (3 feet) deep in the highest regions of the mountains. Typical trees of the forest are *Araucaria araucana* (the oldest tree found in the park has an age of about 1500 years!), *Nothofagus antarctica* (Spanish: ñirre), *Nothofagus pumilio* (Spanish: lenga) and *Nothofagus dombeyi* (Spanish: coigüe). Very attractive when in flower is also the parasitic plant *Desmaria mutabilis*, which lives on *Nothofagus* species and is pollinated by a hummingbird. As there are often clouds coming up into the mountains from the sea, the high humidity favours the growth of epiphytic *Usnea barbata* mosses. In winter the *Nothofagus* species have no leaves, which gives the landscape a quite mystic image.

*Pinguicula chilensis* at Nahuelbuta National Park occurs in two different habitats. Small populations can be found in the forest at springs along the El Aguilucho trail at an altitude of about 1260 m. These plants mainly grow with mosses in shade under trees and shrubs. The soil is wet year-round, is consists exclusively of organic material. However, the main habitat in the National Park is the Las Turberas area. This is a plateau at an altitude of 1250 m where several small creeks form a kind of a bog, with small islands with grasses and shrubs. There is no *Sphagnum*, but the soil is high in organic matter. *Pinguicula chilensis* grows mainly in shaded places under grasses. During the summer months (December-February) the rosettes can reach a size of up to 5-8 cm (2-3 inches). Some plants grow in direct sun. The leaves of these plants are red-yellowish and the rosettes are smaller. In January the soil where most of the plants occurred was damp, only at few places were plants growing in very wet conditions. At this location, *Drosera uniflora* also occurs.

Like all other temperate *Pinguicula* species of South America, the plants do not form hibernacula but instead overwinter with a rosette. In September leaf rosettes are only up to 3.5 cm (1.4 inches) in diameter and the rosette is more compact with upturned leaf margins. During the winter, plants growing in vertical habitats near the flowing water are probably not protected by a blanket of snow, therefore they should be able to survive temperatures below freezing. However, it is not known what are the lowest temperatures are the plants could survive.





Figure 1: *Pinguicula chilensis* habitat at Las Turberas.



Figure 2: Front and side view of flower at Las Turberas.

Flowering begins at the end of December and ends in February. Ernst (1961) mentioned that one of the distinctive characters of this species is the almost glabrous flower stalks (i.e. they do not have glands or hairs). In the Las Turberas area most of the flower stalks did not bear glands, but at the El Aguilucho trail site I saw plants with quite a number of glands on the pedicels. Therefore an almost glabrous flower stalk is not a unique character of the species. The maximum number of flowers per plant found was three, while most of the plants formed one or two flowers. The flower stalks of *P. chilensis* at both locations did not exceed 2 cm (0.8 inches), and were often shorter. The sizes of all the corolla lobes are very similar (beside the slightly longer middle lobe of the lower lip). The lobes are obovate and most are shallowly notched up to 1 mm. The palate on the middle lobe of the lower lip consists of two separate parts and bears long yellow hairs. The position of the palate is a main distinguishing feature to *P. antarctica*. While the palate in *P. chilensis* can be found in the tube close to the apex of the middle lobe of the lower lip, in *P. antarctica* the palate is located at the base of the middle lobe of the lower lip, closer to the spur (Ernst 1961) The 2-3 mm long, tubular spur is pale green. The conical tube is much longer than the tubes of other South American *Pinguicula* (Casper 1966). The corolla is white or pale-violet, showing a violet venation on the proximal part of the lobes (i.e. near the corolla tube). The tube is veined dark violet. The flower venation was very pale at the smaller El Aguilucho trail population; at Las Turberas most of flowers have very dark venation, very similar to *P. antarctica*. The weaker venation could be due to shade.

Very few tiny insects could be found on the leaves during December and January, while in October almost no insects were present on the leaves. How the flowers are pollinated is not known, but I believe they probably mostly self-pollinate because the flowers are small and hidden under grasses. Plants in cultivation produce seed without pollination.

The habitat of *P. chilensis* in the Nahuelbuta National Park is currently not in danger. The park is well managed and the main habitats are not shown on maps. Furthermore climatic changes are not likely to have an immediate impact on the habitat even if the annual rainfall were to decrease slightly.

Acknowledgements: I would like to thank the CONAF personnel of the Parque Nacional Nahuelbuta for their habitat information.

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- Casper, S.J. 1966. Monographie der Gattung *Pinguicula* L. Bibliotheca Botanica, 127/128, 1-209.
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## LOOKING BACK: CPN 25 YEARS AGO

Editor Don Schnell wrote: "Carnivorous Plant Newsletter is now entering its eleventh year, and those who have been with us all the way or at least of for a greater part of those ten previous years have watched this publication grow from a small offset looseleaf format to our present fine journal with wide-ranging articles and features serving many interests worldwide. CPN is widely respected, is now being carried by more libraries, and even crops up now and then in formal journal or book bibliographies." Don continued to give compliments to the ICPS seed bank, then run by Patrick Dwyer (who else remembers Patrick?). Reading Don's comments inspired me (BR) to write this issue's editorial on Jan's and my last ten years with CPN. Who will be writing "Looking Back" 25 years from now?



AN INTERESTING OBSERVATION ON THE MYCORRHIZAL  
SYMBIOSIS IN THE INSECTIVOROUS PLANT, *DROSERA PELTATA*  
SM., IN MEGHALAYA, NORTH-EAST INDIA

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Keywords: Ecology: *Drosera peltata*, *Suillus luteus* — physiology: *Drosera peltata*.

Abstract

The work deals with new observations of a mycorrhizal symbiotic association in the corms and subterranean lateral foliar organs of *Drosera peltata* Sm. North-East, India. The fungal species is *Suillus luteus*, an indigenous common mycobiont in this region. This mycobiont enhances the efficiency of mineral uptake, particularly phosphorous. Calcofluor fluorochrome does not fluoresce at the subepidermal region of the corm, due to a mycorrhizal Hartig net. This is an additional report of mycorrhizal symbiosis in the carnivorous plant *Drosera peltata* after Fuchs & Haselwandter (2004) in *Drosera intermedia*.

Introduction

In angiosperms about 645 species have evolved a carnivorous habit to capture prey (Rice 2006, pers. comm.), secreting digestive enzymes, reabsorbing the digested products and benefiting from the supplementary nutrition to the usual nutrition of plants (Fahn 1979; Heslop-Harrison 1976b). The carnivorous habit is most important in supplementing nitrogen supply (Heslop-Harrison 1976a). However, the experiments conducted by Pringsheim & Pringsheim (1962, 1967) and Harder (1963) on *Utricularia*, and Harder & Zemlin (1967, 1968) on *Pinguicula* showed that carnivory may contribute to the supply of other mineral elements.

The association of fungi with roots or underground plant organs is the chief organ of nutrient uptake by many land plants (Smith & Read 1994). Harley & Smith (1983) reported that 118 angiosperm genera in 35 families and 10 gymnosperm genera have mycorrhizal associations. Recent research work of Fuchs & Haselwandter (2004) showed the occurrence of vesicular arbuscular mycorrhiza in *Drosera intermedia*, Hayne an endangered carnivorous plant in Salzburg, Austria. There is some evidence of mycorrhizal association in the roots of *Nepenthes* (Moran, in Clarke, 2001). During the course of study on the developmental aspects of secretory glands in the carnivorous plants of Meghalaya, the authors came across an interesting observation of the mycorrhizal symbiosis in *Drosera peltata*. The underground organs of *Drosera peltata* consist of a corm, vertical shoot, and numerous lateral foliar organs produced exogenously, that while appear rootlike, lack a root cap and true root hairs. Goebel (1923) described them as “dubious roots.”

*Drosera peltata* is a seasonal perennial plant that commences above-ground growth in the month of July and completes its life cycle at the end of October. Globally, *Drosera peltata* occurs throughout much of southeast Asia, Australia, and New Zealand. *Drosera peltata* grows in certain areas of Meghalaya such as Jarain, Sohrarim and Mawsynram where the soil has a low nutrient content. During the dry, hot winter these plants survive as underground corms. The corms and poorly developed lateral foliar organs are sheathed by a mycorrhizal mantle. *Drosera peltata* perennates by these corms, which are filled with abundant starch grains.

Materials and Methods

The corms and lateral foliar organs of *Drosera peltata* were fixed in FAA and sections were taken 8-10 mm thickness after dehydration and paraffinization. The sections were stained with

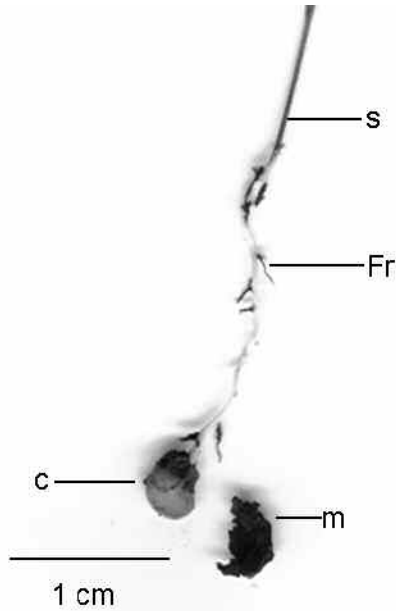


Figure 1: An enlarged portion of the *Drosera peltata* root system showing the corm (c) with detached mycorrhizal mantle (m), dark lateral foliar "roots" (Fr) covered with mycorrhiza and the main stem (s). Scale bar = 1 cm.

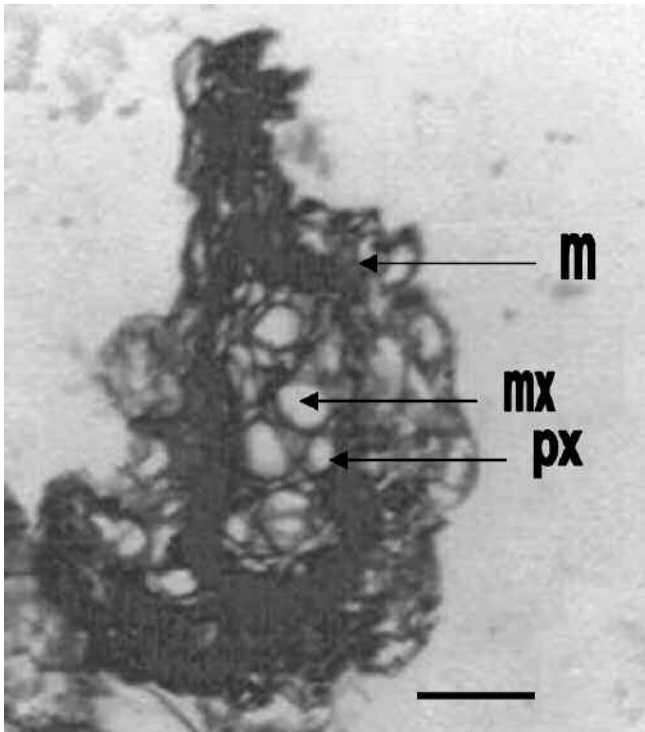


Figure 2: Transverse section of a lateral foliar "root" showing mantle (m), the disorganised vasculature of the protoxylem (px) and metaxylem (mx). Scale bar = 60 $\mu$ m.

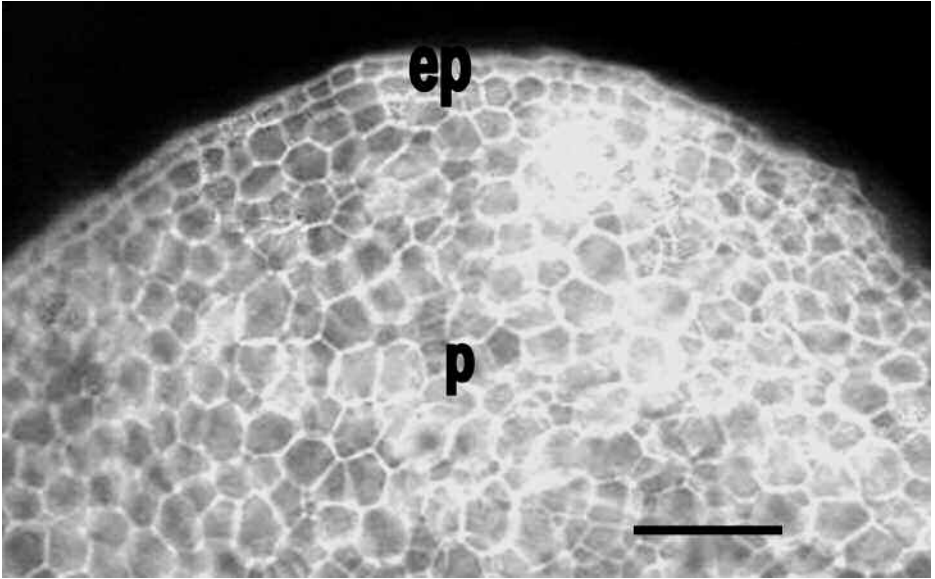


Figure 3: Fluorescence micrograph of transverse section of *Drosera peltata* corm illustrating the difference between the non-mycorrhizal and mycorrhizal zones. The hartig net is absent below the epidermis. Note the fluorescing epidermal (ep) and peridermal (p) layers. Scale bar = 240  $\mu\text{m}$ .

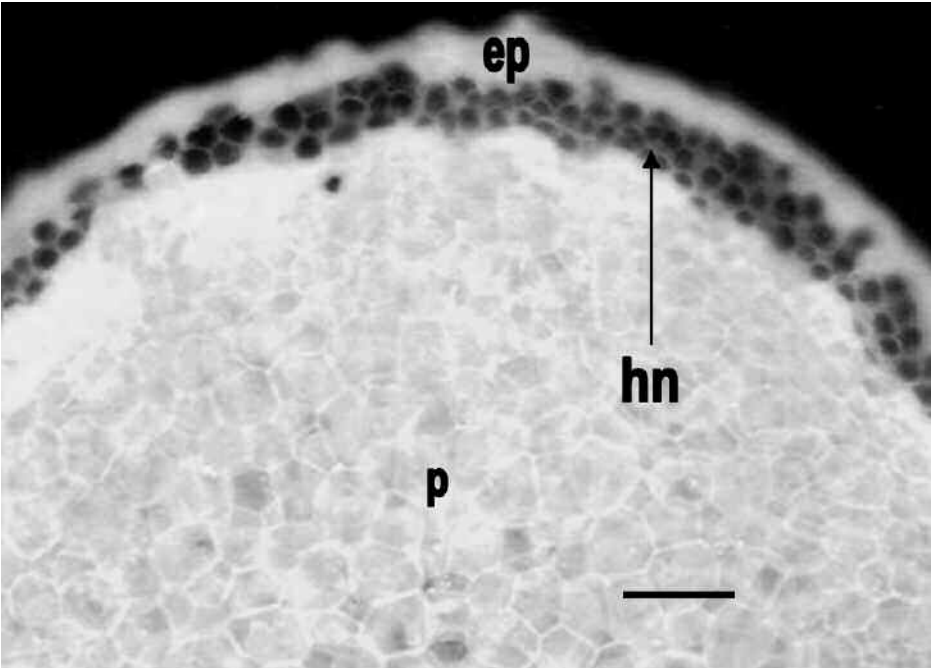


Figure 4: Fluorescence micrograph of transverse section of *Drosera peltata* corm showing the mycorrhizal zone. Note the subepidermal location of the mycobiont *Suillus luteus* and the absence of fluorescence in the mycorrhizal zone due to the presence of hartig net (hn), and the fluorescing epidermal (ep) and peridermal (p) layers. Scale bar = 240  $\mu\text{m}$ .

Aniline blue and Cotton blue (Johansen 1940; O'Brien & McCully 1981). Mycorrhizal spores were extracted from the 50 g of soil surrounding the corm. This extraction was performed using the sieving method (Daniels & Skipper 1982; Brundrett *et al.* 1996) and centrifugation using a 60% sucrose gradient. Spores were extracted from the supernatant by pipette and mounted in polyvinyl alcohol-lacto-glycerol (PVLG) without staining. The spores were observed under Nikon E 600 microscope. The spores are smooth, hyaline, broadly ellipsoid to sub-globose, ochraceous or buff coloured, and measured 3-4x4-7  $\mu\text{m}$ . Identification of the fungus as *Suillus luteus* was based on spore wall structure and followed published descriptions (Schenck & Perez 1990). Moreover, *Drosera peltata* grows in the understory of *Pinus kesiya* Royle ex Gordén, which is also associated with *Suillus luteus*. Fluorescence microphotographs were taken by using Leitz Biomed Fluorescence microscope. Phosphatase activity was measured using the method described in Dodd *et al.* (1987). The mantle portion of mycorrhiza was removed and washed with double distilled water. The total phosphorus content in the root and corm was estimated after an acid wet oxidation in  $\text{HNO}_3 + \text{H}_2\text{SO}_4 + \text{HClO}_4$ ; analyses were performed for phosphorus as suggested by Allen (1974). Translocation percent of phosphorus to the shoot was calculated as described by Theodorou & Bowen (1993): %P (translocated)=100%  $\times$  shoot P (mg)/total P (mg).

### Result and discussion

In *Drosera peltata* the "root" system (i.e. the lateral foliar organs described in the Introduction) is frail, weak and thin. The lateral "roots" are 5-10mm in length and 1-2 mm in diameter completely covered by dark colored mycorrhizal sheath. In transverse section the "roots" have an outer most epidermis in which the cells are radially stretched. The epidermal layer does not produce any root hairs. The cortex consists of 1-2 layers of isodiametric cells with starch grains. The xylem of the "roots" is either di- or tri-arch. The corm is devoid of any lateral true roots. In addition to the modified "lateral roots", at the junction of the corm and the main stem arise small horizontal shoots that during the growing season can form the new shoot, or during the end of the season or winter can produce the resting corm (Adlassnig *et al.* 2005; Slack 2000). In transverse section, the Hartig net is 3-5 cells thick in the peripheral portion of the corms. This region does not fluoresce with Calcofluor.

The primary mycobiont was identified as being *Suillus luteus*. Phosphatase activity ( $375.0 \pm 29.50 \mu\text{g P-nitrophenol g}^{-1} \text{ dry wt.}^{-1}\text{h}$ ) in the underground organs was greater in plants associated with the mycobiont than in plants without the mycorrhizal association ( $190.0 \pm 12.40 \mu\text{g P-nitrophenol g}^{-1} \text{ dry wt.}^{-1}\text{h}$ ). Similarly, phosphorus content of the shoot and corm was greater in mycobiont-associated plants ( $86.0 \pm 6.75 \mu\text{m/gm}$ ) than in plants without mycorrhizal associations ( $45.0 \pm 1.90 \mu\text{m/gm}$ ). Translocation efficiency of phosphorus (52%) from soil to the shoot by plants was higher in *Suillus luteus* infected plants. Plants without *Suillus luteus* had lower translocation efficiency (39%). The results depict that mycorrhizal infection and production was better in plants associated with *Suillus luteus* as compared to plants without the symbiont.

*Drosera peltata* frequently grows with grasses and other vegetation, and as such the soil is likely have enhanced amounts of organic material. Mycorrhizal fungi can degrade these composts and make them available to the associated plants (Schisler & Linderman 1989).

The improved phosphorus uptake in mycorrhizal associated plants, as we observed in *Drosera peltata* is supported by other authors (Stribley *et al.* 1980; Lodge *et al.* 1994; Robinson 1994). Higher nutrient uptake by mycorrhizal plants is due to improved hyphal growth and improved exploitation of the soil volume by *S. luteus*. Higher phosphate uptake by plants is correlated to higher rate of phosphatase activity in mycorrhizal than non- mycorrhizal ones (Tarafdar & Marschner 1994).

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## DROSERACEAE GLAND AND GERMINATION PATTERNS REVISITED: SUPPORT FOR RECENT MOLECULAR PHYLOGENETIC STUDIES

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### Abstract

Droseraceae germination and leaf gland and microgland character state patterns were re-examined in the light of new molecular phylogenetic relationships. Phanerocotylar germination is basal in the family, with cryptocotylar germination having evolved at least twice; once in *Aldrovanda*, and again in *Drosera* within the *Bryastrum/Ergaleium* clade. Gland patterns also support major clades; with the *Bryastrum* clade taxa having marginal and *Rorella*-type glands whereas the terminal branch of the *Drosera* clade had marginal glands and most of the clade possessed biseriate type 3 glands. The gland and germination patterns are supported by growth habit features, suggesting that the family and the main clades within *Drosera* in particular have undergone major adaptive radiations for these characters.

### Introduction

Relationships between the genera and species of Droseraceae have been the subject of numerous studies, with a range of morphology-based systems produced, mainly using traditional characters such as habit, leaf-associated features and specialised propagation techniques (e.g. Planchon 1848; Diels 1906). Character evolution of traps has also been considered important in carnivorous plants (Juniper *et al.* 1989; Jobson & Albert 2002) and glandular patterns (Seine & Barthlott 1992, 1993; Länger *et al.* 1995) were considered important at the sectional level, as well as providing possible evidence of relationships and/or patterns with related families such as Plumbaginaceae (Wilson 1890; Schlauer 1997).

In addition, studies of characters such as cytology (e.g. Kondo 1976; Kondo & Lavarack 1984), germination (Conran *et al.* 1997), pollen structure (Takahashi & Sohma 1982) and phytochemistry (Culham & Gornall 1994) have added to the overall understanding of relationships in the family, contributing to several proposed classification realignments (Marchant *et al.* 1982; Seine & Barthlott 1994; Schlauer 1996).

Molecular sequence data were useful for showing the evolution of trap complexity in Lentibulariaceae (Jobson & Albert 2002) and relationships within Nepenthaceae where convergent morphology had made phylogenetic interpretation difficult (Meimberg *et al.* 2001). Molecular phylogenetic information also allowed the exploration of snap trap evolution in Droseraceae through character mapping of trapping morphology and mechanisms onto clades (Cameron *et al.* 2002), as well as for exploring the development predisposition for, and possible loss of carnivory in the Caryophyllidae (Meimberg *et al.* 2000). The development of new molecular phylogenies within Droseraceae has helped to resolve some of the ongoing controversies, such as the position of *Drosophyllum* (and support for its removal from the family) and the position of morphologically unusual or “isolated” *Drosera* species (Albert *et al.* 1992; Williams *et al.* 1994; Rivadavia *et al.* 2003). However, one of the biggest advantages of these molecular phylogenies is to assist in the study of character evolution, as well as the evaluation of different character set patterns for their usefulness in supporting classification within the family and exploring evolution and biogeography. For example, the Droseraceae molecular data are supported in part by chromosome number and biogeographic patterns, suggesting support for a possible southern hemisphere African-Australian origin of the family (Rivadavia *et al.* 2003).

Accordingly, this study re-examines germination data for the family and combines them with sig-

nificantly expanded leaf gland and microgland data to test the hypothesis that these characters show phylogenetically useful patterns under the revised molecular phylogeny for Droseraceae of Rivadavia *et al.* (2003).

### Materials and Methods

Gland diversity was investigated using both light and scanning electron microscopy. Specimens for whole-mount examination were immersed in 26% vol/vol lactic acid until cleared, then mounted in lactic acid and examined under a transmission light microscope. Material for scanning electron microscopy was fixed in 5% glutaraldehyde for 30 minutes, dehydrated through a graded ethanol series, critical point dried and coated using and Eiko IB. 5 ion sputter coater. Specimens were observed with a Hitachi S-570 scanning electron microscope at 5-15 kV, and the location and structure of any glands was classified relative to those reported by Seine & Barthlott (1992; 1993) and Langer *et al.* (1995).

Germination data from Conran *et al.* (1997), gland and microgland data from Seine & Barthlott (1993), Langer *et al.* (1995), and our own unpublished gland/microgland data for 180 species, subspecies, varieties, cultivars and morphotypes of *Drosera*, *Dionaea* and *Aldrovanda* were assembled for each of the different character states at the sectional level. However, as the previous two studies did not code gland types in the same manner, direct comparison between them was difficult. In an attempt to reconcile their respective leaf microgland classifications, the data for their studies and ours are summarised at sectional level with the respective gland classifications indicated in Table 1. These character state distributions were then mapped onto a condensed sectional-level cladogram derived from the clades obtained by Rivadavia *et al.* (2003), using the sectional classification of Schlauer (1996) and the clade-exploration program MacClade 3.06 (Maddison & Maddison 1996). Phylogenetically useful patterns of character states were then discussed in terms of evolution within the family.

Taxon	No. of taxa examined	St	Ma	T1 B, F, bi	T1 E, G, H, bi	T2 bi	T3 C, bi	T4-5 D, mu	T6 mu	T7-9 I, mu	T10-12 mu	Ge	GC	NC
<i>Aldrovanda</i>	1	0	0	F1	G1	a	0	0	0	0	0	CR	0	1
<i>Dionaea</i>	1	0	0	0	H1	a	0	0	0	0	0	HE	0	0
<i>Drosera</i>														
Subgenus <i>Arcturia</i>	1	1	0	0	0	0	0	0	0	1	0	PH	0	0
Subgenus <i>Bryastrum</i>														
Section <i>Bryastrum</i>	1	1	1	0	0	1	0	0	0	0	0	CR	0	0
Section <i>Lamprolepis</i>	43	43	34	B4	E2	0	0	43	0	1	4	CR	0	0
Subgenus <i>Coelophylla</i>	1	1	1	0	E1	0	0	1	0	0	0	CR	0	0
Subgenus <i>Drosera</i>														
Section <i>Arachnopus</i>	1	1	0	0	0	0	0	0	1	0	0	PH	0	0
Section <i>Drosera</i>	26	26	21	B8	E3	1	15	0	0	1	3	PH	16	0
Section <i>Oösperma</i>	16	16	13	B5	E4	0	10	0	0	2	0	PH	9	0
Section <i>Prolifera</i>	3	3	0	B2	E1	0	0	0	1	0	0	HE	0	0
Section <i>Psychophila</i>	2	2	0	B2	0	0	0	0	0	0	0	PH	0	0
Section <i>Ptycnostigma</i>	7	7	7	0	E4	0	1	0	0	2	1	PH	1	0
Subgenus <i>Ergaleium</i>														
Section <i>Ergaleium</i>	35	35	0	B3	E28	0	0	0	0	10	2	CR	0	0
Section <i>Stolonifera</i>	8	8	0	0	E6	0	0	0	0	4	0	CR	0	0
Section <i>Erythrorhiza</i>	17	17	0	0	E9	0	0	0	0	9	1	CR	0	0
Subgenus <i>Lasiocephala</i>	9	9	4	B8	E1	0	0	0	0	0	0	CR	0	0
Subgenus <i>Meristocaulis</i>	1	1	1	0	0	1	0	0	0	0	1	?	?	?
Subgenus <i>Phycopsis</i>	1	1	1	0	E1	0	0	0	0	1	0	PH	0	0
Subgenus <i>Regiae</i>	1	1	0	0	0	0	0	0	0	1	0	PH	0	0
Subgenus <i>Stelogyne</i>	1	1	1	0	0	0	1	0	0	0	0	PH	0	0
Subgenus <i>Thelocalyx</i>	2	2	2	0	E2	0	0	2	1	1	0	PH	2	0

Table 1: Numbers of taxa exhibiting gland and germination features for Droseraceae, summarised by genus, subgenus and section following Schlauer (1996) unless a section or species group was separated in Rivadavia *et al.* (2003): St = stalked central glands; Ma = stalked marginal unifacial glands; T1-T11 = sessile leaf microgland types as classified by Langer *et al.* (1995); B-1 = sessile microgland types as classified by Seine & Barthlott (1993); a = a related gland type not differentiated by Seine & Barthlott (1993); bi = biseriolate microglands; mu = multiseriolate microglands; Ge = germination type (P = phanerocotylar, C = cryptocotylar, H = hemicycotylar); GC = glandular cotyledons; NC = first leaves non-carnivorous. Gland data for subgenus *Meristocaulis* from Seine & Barthlott (1993) and Langer *et al.* (1995).

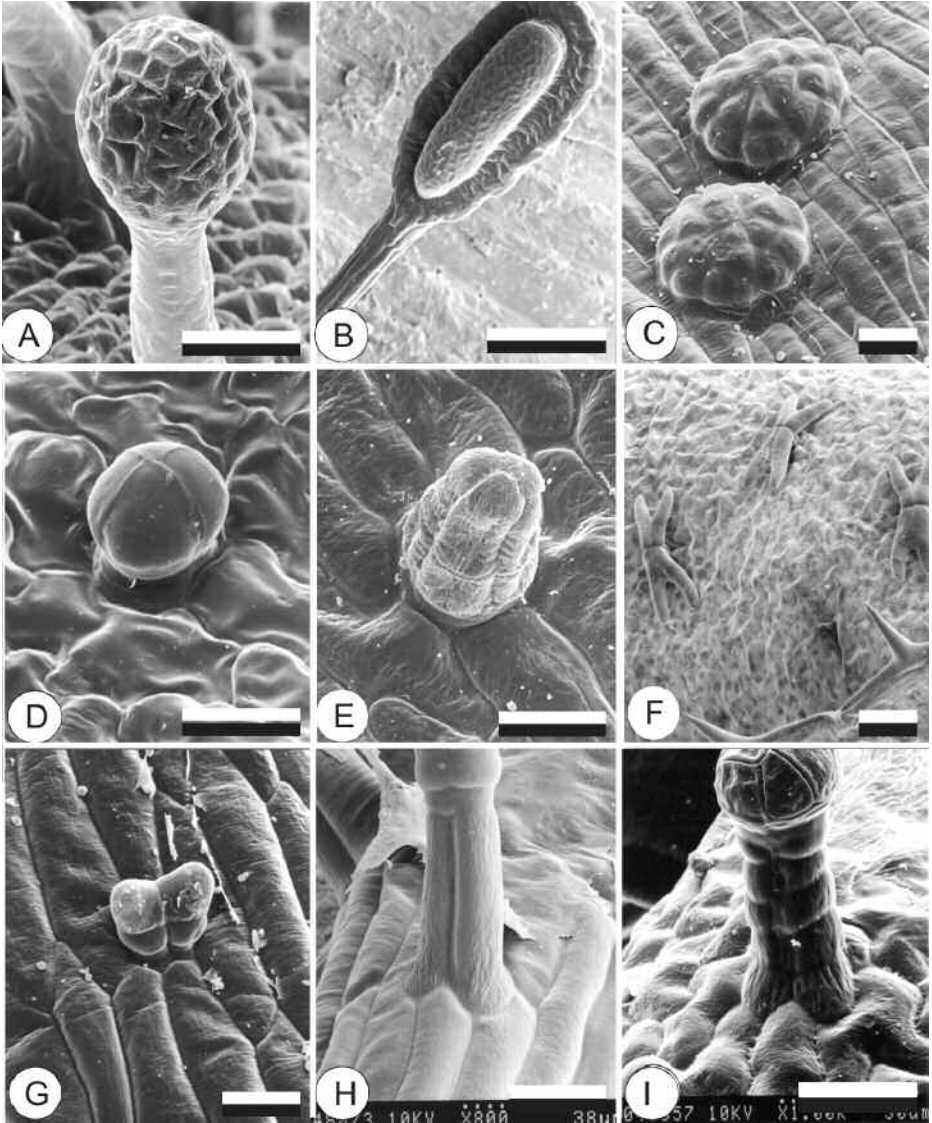


Figure 1: Droseraceae taxonomically informative gland types. A: *Drosera trinervia* Spreng. stalked gland; B: *D. capillaris* Poir. marginal unifacial gland; C: *Dionaea muscipula* Soland ex Ellis sessile multicellular glands; D: *Drosera menziesii* R.Br. ex DC. type 1B multiseriate gland; E: *Drosera erythrorhiza* Lindl. type 1E sessile multiseriate gland; F: *Aldrovanda vesiculosa* L. elongated sessile multiseriate glands; G: *Drosera capillaris* type 3 biseriate gland; H: *Drosera sewelliae* Diels type 4-5 sessile biseriate (*Rorella*-type) gland; I: *Drosera andersoniana* W.Fitzg. ex Ewart. & White type 11 inflorescence gland. Scale bars A, B = 50  $\mu$ m, C-I = 25  $\mu$ m.

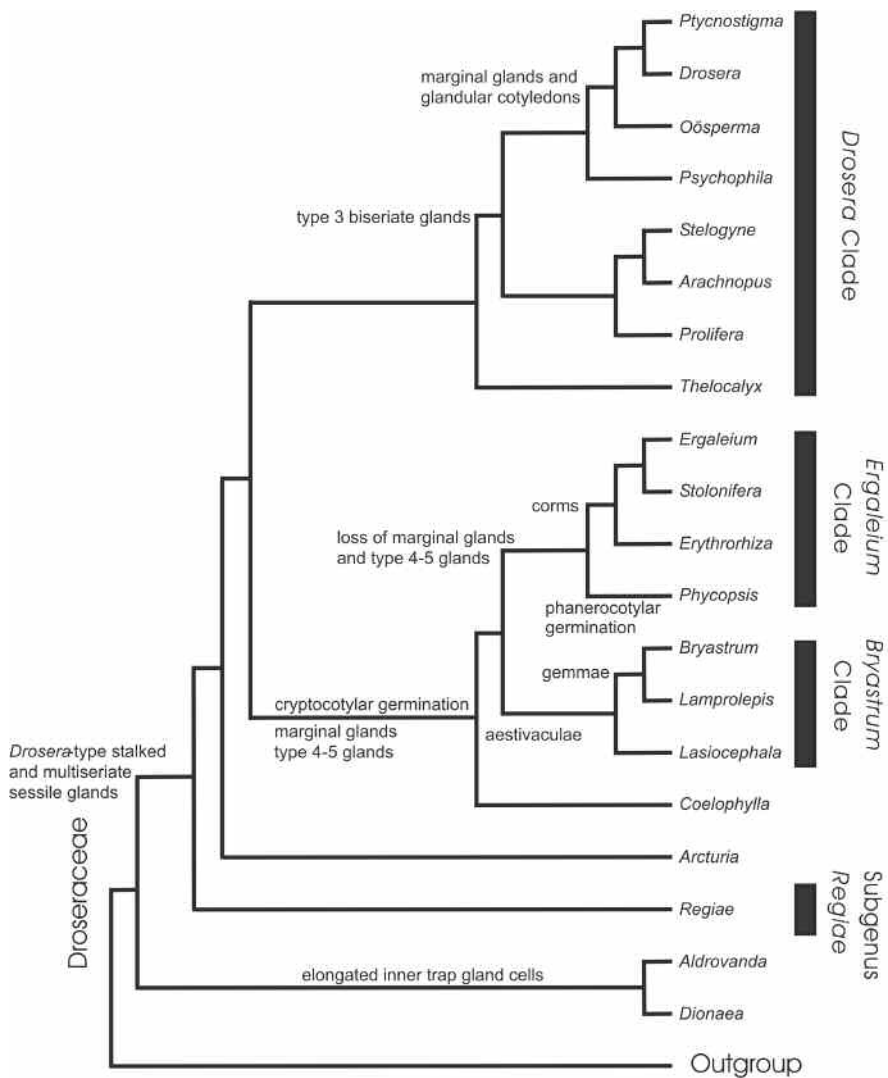


Figure 2. Condensed cladogram showing major groups derived from the molecular analysis of Rivadavia *et al.* (2003) and showing the relationship of the clades to various gland, germination and asexual reproductive features.

## Results

Gland patterns showed that *Drosera* was distinguished from its relatives by the presence of multiseriate sessile glands in addition to the distinctive *Drosera*-type stalked glands. All taxa possessing Type 3 biseriate glands (*sensu* Länger *et al.* (1995)) were located within the *Drosera* clade, and those with marginal glands were in a terminal clade containing sections *Drosera*, *Oösperma* and *Ptycnostigma*, as well as in the taxa now comprising the *Bryastrum* clade. The biseriate glands with elongated basal cells classed as Types 4 and 5 by Länger *et al.* (1995) were listed as *Rorella*-type glands by Seine & Barthlott (1993) because they were seen in subgenus *Bryastrum* (= *Rorella* auct. non Hall. ex All.: N. Marchant). The expanded data confirm this, with all taxa possessing these glands being members of the *Bryastrum* clade *sensu* Schlauer (1996) possessing these glands, as well as subgenus *Coelophylla* (*D. glanduligera* Lehm.) which was basal to the *Bryastrum*/*Ergaleium* clade pair.

When mapped onto the revised cladogram of Rivadavia *et al.* (2003), cryptocotylar germination becomes a synapomorphy for the clade representing the subgenera *Bryastrum*, *Coelophylla*, and *Ergaleium* (see Figure 2). With the exception of section *Phycopsis* (*D. binata* Labill.) all species in the clade so far germinated are cryptocotylar. The basal *Drosera* taxa are phanerocotylar with eglandular cotyledons, whereas those species that have glands on the cotyledons are restricted to the terminal clade containing sections *Drosera*, *Oösperma* and *Ptycnostigma*. These patterns are also supported by other features such as growth form (e.g. the tuberous habit of the *Ergaleium* clade taxa), distinctive petiolate leaves and the formation of summer-dormant aestivaculæ (Gaff 1981) shared between sections *Lamprolepis*, *Bryastrum* and *Lasiocephala*. There is also a propensity of cryptocotylar germination in dry-land habitat species (Pate & Dixon 1982) and those with asexual reproduction such as gemmae and tubers (Karlsson & Pate 1992) as seen in members of the cryptocotylar *Ergaleium* and *Bryastrum* clades.

## Discussion

Although some of the taxa studied here for gland data were also reported by Seine & Barthlott (1993) and Länger *et al.* (1995), our study provides data for a further 107 species, varieties, cultivars and morphotypes. In particular, we included many more taxa from sections *Lamprolepis* and *Lasiocephala*, so that between these three studies, most taxa within the family have now been surveyed. Our gland survey results for the additional taxa largely agree with those of the earlier studies. The *Ergaleium* clade was uniform in lacking marginal unifacial or spoon glands, as well as only possessing multiseriate microglands. There was considerable variability in inter-taxon gland types in the *Drosera* and *Bryastrum* clades. As with the earlier studies, there were both taxa with and without, marginal unifacial glands, but the dichotomy into taxa with multiseriate versus biseriate microglands was also observed.

Schlauer (1997) noted that gland studies in angiosperms related to Droseraceae were not new. *Dionaea*, *Aldrovanda*, *Drosophyllum*, *Polygonum* (Lersten & Curtis 1992), Nepenthaceae (Fahn 1979), Frankeniaceae, Plumbaginaceae and Tamaricaceae (Wilson 1890) all possess flat modified multicellular glands of sub-epidermal origin, which in Plumbaginaceae at least are thought to be derived from calcium carbonate-secreting Mettenian glands and developed into mucilage glands via intermediate forms. There are also symmetrical multicellular stalked glands, both vascularised and non-vascularised in Plumbaginaceae, Ancistrocladaceae and Dioncophyllaceae that are similar to those in *Drosera* and *Drosophyllum*. This indicates that the precursors for the trapping and glandular structures seen in Droseraceae are widespread in nearby outgroup Carophyllid families, possibly helping to explain the multiple development of carnivory within the group, or as suggested by Meimberg *et al.* (2000), the loss of carnivory in Ancistrocladaceae and most Dioncophyllaceae. This development is further seen within Droseraceae, where the basal taxa (section *Arcturia* and subgenus *Regiae*) are those with multicellular glands and unspecialised stalked glands, whereas the more derived *Drosera* and *Bryastrum* clades are where biseriate glands developed. Unifacial marginal glands seem to have developed several times, but also appear to have been lost secondarily in subgenus *Ergaleium*. Similarly, glandular cotyledons although found in the terminal *Drosera* clade, are also widespread in the outgroup families suggesting that this feature is ancestral and that its absence in various Droseraceae taxa possibly represents multiple loss.

Subgenus *Meristocaulis* was not included in the molecular phylogeny and its germination pattern is not known. The gland patterns (Table 1) are ambiguous, with marginal glands and Type T2 biseriate



and T11-12 multiseriate sessile glands. This pattern is seen in members of both the *Drosera* and *Bryastrum* clades, so that in the absence of germination data, the position of *Meristocaulis* is still uncertain.

Germination patterns show that cryptocotyly has apparently evolved several times in the family (Fig. 2). In comparison with outgroup families; although Drosophyllaceae are cryptocotylar, the other related families (Tamaricaceae, Nepenthaceae, Polygonaceae, Plumbaginaceae and Limoniaceae) are all phanerocotylar, which is also the most common germination condition in the Caryophyllales (Clifford 1981; Clifford 1991). Conran *et al.* (1997) also described the germination pattern of hemicyptocotyly, where the cotyledons emerge partially from the testa and are photosynthetic, but the apices remain enclosed in the seed. This pattern, seen in both *Dionaea* and *D. adelae* F.Muell. seedlings, seems to be an intermediate stage between crypto- and phanerocotyly. Cryptocotyly is a condition generally associated with large-seeded taxa, often from rainforests, and its occurrence in Droseraceae is considered unusual (Clifford 1984). The fact that it occurs in *Drosophyllum*, *Aldrovanda* and the *Ergaleium/Bryastrum* clade in *Drosera* suggests that there is an ecological association, as these are the taxa where there is often a need for long-term seed dormancy. This may be due to fire- (e.g. Ortega Olivencia *et al.* 1995 for *Drosophyllum*) or inundation-triggered germination (e.g. Kozschinski 1886 in the case of *Aldrovanda*). This applies especially in SW Western Australia where both summer fire or smoke exposure and then cool moist winter conditions are needed to stimulate germination in many angiosperm taxa including both Byblidaceae and some Droseraceae (e.g. Bell *et al.* 1993; Roche *et al.* 1998; Wills & Read 2002). Accordingly, the evolution of a larger seed reserve with a smaller embryo may be an advantage for long-term survival of these small seeds until environmental conditions are right for germination.

Seine & Barthlott (1994) and Conran *et al.* (1997) noted that there were gland and germination patterns supporting classification changes in Droseraceae, and the molecular data support the placement of *Ptycnostigma* and *Stelogyne* with *Drosera* and *Oöesperma* (along with sections *Arachnopus*, *Prolifera*, *Psychophila*, and subgenus *Thelocalyx*) in the phanerocotylar *Drosera* clade (Rivadavia *et al.* (2003)). Similarly, the taxa representing the *Bryastrum* clade are also united by *Rorella*-type glands and cryptocotylar germination, agreeing with many of the changes suggested by Conran *et al.* (1997), as well as some of the realignments of Schlauer (1996). Nevertheless, a number of the latter's subgenera could be returned to sectional level within expanded subgenera representing the *Drosera*, *Bryastrum* and *Ergaleium* clades. These data show that the molecular clades have an underlying basis in both anatomy and trap evolution, but also in ancestral ecological choices – the linkage in *Drosera* of dry-land-growing, asexually reproductive taxa with cryptocotylar germination, for example, shows that ecological adaptation seems to have been a major driving force for evolution within Droseraceae.

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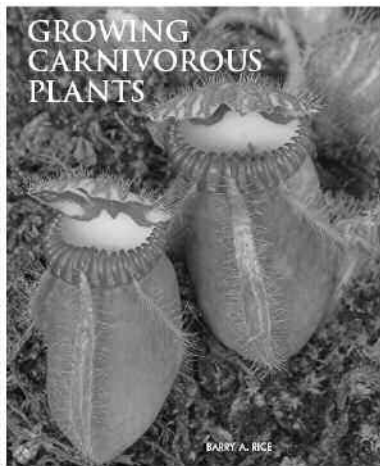
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## BOOK REVIEW



Rice, Barry. 2006. *Growing Carnivorous Plants*. Timber Press, Portland. ISBN-13: 978-0-88192-807-5, 224 p., approximately 329 color photographs, figures and maps. Hardcover, 28.5 × 22.5 cm (11.25 × 9 in), US\$39.95, shipping extra.

Reviewed by Jan Schlauser

While there are already a few books on the cultivation of carnivorous plants (the ones by Adrian Slack and Peter D'Amato being noteworthy examples), this is the first publication in the genre combining comprehensive state-of-the-art guidelines with accurate cultivar nomenclature. This book can be recommended to absolute beginners as well as to experienced growers who have not lost the ability to learn. But do not expect a bone dry compilation of data. Remember the author is noted for his particular style of humour and his skills in emulsion photography (abusing the standard material for simple carnivorous plant enzyme tests that once used to be popular for picture generation, providing continuous colour gradients and non-rasterized resolution), quite a bit of these arts being reproduced in the present work. As could be expected from a conservation professional, the book does contain notes on threats to carnivorous plant habitats but it also provides guidelines for responsible behaviour and a perspective to sustainable appreciation of these wonders of nature both in the wild and in cultivation. I particularly enjoyed the author's encouragement to field explorers, "Hundreds of human bodies have been recovered from peat bogs....You could be one too!" This is (to my knowledge) the second book by Timber Press on carnivorous plants (after Don Schnell's second edition of "Carnivorous Plants of the United States and Canada"), and while it is very different in scope and style it meets the same high standards that are so characteristic for this publisher.

Interested buyers can buy books from Timber Press, Amazon.com, etc. Autographed copies can be purchased from the author via <http://www.sarracenia.com/cp.html>.

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### NAMES OF CULTIVARS REGISTERED IN 2006

- Sarracenia* 'Belly of Blood', B.Rice, *Growing Carniv. Pl.* 147 (2006), 6 Dec.  
*Sarracenia* 'Chagall', J.Lechtman, *Carniv.Pl.Newslett.* 35:68 (2006), 16 Oct.  
*Sarracenia* 'Frogman', B.Rice, *Growing Carniv. Pl.* 147 (2006), 6 Dec.  
*Sarracenia* 'Langford Williams', L.Williams, *Carniv.Pl.Soc.J.(UK)* 28:30 (2006), 3 June  
*Sarracenia* 'Vintage Slack', P.D'Amato, *Carniv.Pl.Newslett.* 29:117 (2000), 27 Aug.  
*Dionaea* 'B52', B.Rice, *Growing Carniv. Pl.* 79 (2006), 6 Dec.  
*Dionaea* 'Justina Davis', B.Rice, *Growing Carniv. Pl.* 80 (2006), 6 Dec.  
*Dionaea* 'Wacky Traps', B.Rice, *Growing Carniv. Pl.* 81 (2006), 6 Dec.  
*Drosera* 'Charles Darwin', I.Snyder, *Carniv.Pl.Newslett.* 35:68 (2006), 16 Oct.  
*Drosera* 'Emerald's Envy', W.J.Clemens, *Carniv.Pl.Newslett.* 35:12 (2006), 3 June

## NEWS AND VIEWS

Katsuhiko Kondo (kkondo@hiroshima-u.ac.jp), known to us all for his years of work in carnivorous plants, wrote to the ICPS with great news about his out of print book. I (BR) have taken the liberty of summarizing his correspondence: Ten thousand copies of “Carnivorous Plants of the World in Color” was originally published in 1983 by Ienohikari Association Publisher (Tokyo). Ienohikari Association considered ways to republish an updated version of this book, and decided to supplement the original photographs with new images. The new book, released in July 2006, is entitled “The Carnivorous Plants,” is 192 pages and contains 400 pictures (on 192 pages) of approximately 200 species and 400 photographs of carnivorous plants. Many of the high-quality photographs have great value because they show carnivorous plants listed by the IUCN and CITES; having images of such plants in their natural habitats is important. The 56 pages of text (in Japanese) describes taxonomy, cultivation (including tissue culture and micropropagation), recent research, conservation, human use, etc. The book measures approximately 12.5 × 17.6cm (5×7 inches).



Copies can be purchased directly from Katsuhiko Kondo; copies cost 3500 Japanese Yen including postage (approximately \$30). Professor Kondo can accept VISA/MasterCard, international bank checks, and postal money orders—contact him for details via email or at: Katsuhiko Kondo, Laboratory of Plant Chromosome and Gene Stock, Graduate School of Science, Hiroshima University, 1-4-3 Kagamiyama, Higashi-Hiroshima City, 739-8526, Japan.

Carl Mazur (ccp@vaxxine.com) writes: In a recent paper that I wrote with Jay Lechtman (Carnivorous Plant Newsletter, 2005, 34:3, p79-84.), we used the term “veinless” to describe specimens of *Sarracenia purpurea* that lacked brightly colored venation, but that were not *Sarracenia purpurea* f. *heterophylla*. In our paper we noted that we had coined this term. In communication with Phil Sheridan, he indicated that he and his colleagues had previously used this term to describe similar plants. Although Mr. Sheridan and his colleagues had not formally published this descriptor, they have been using it for a number of years and in their catalogs to describe *Sarracenia* that do not exhibit colored venation. In no way did we mean any disrespect in not mentioning this fact in our paper.

Les Mehrhoff (les.mehrhoff@uconn.edu) reported an interesting sighting of *Darlingtonia californica* in Pennsylvania—well out of its range, yes, but doing quite well on the gravestone for William Darlington (1782-1863). The genus *Darlingtonia* was named after William Darlington by his friend John Torrey. Darlington’s grave is in Oaklands Cemetery in West Chester, Pennsylvania. See the photograph, below, provided by Les.



## CARNIVOROUS PLANTS WITH HYBRID TRAPPING STRATEGIES

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Keywords: carnivory: *Darlingtonia californica*, *Drosophyllum lusitanicum*, *Nepenthes ampullaria*, *N. inermis*, *Sarracenia psittacina*.

Recently I wrote a general book on carnivorous plants, and while creating that work I spent a great deal of time pondering some of the bigger issues within the phenomenon of carnivory in plants. One of the basic decisions I had to make was select what plants to include in my book.

Even at the genus level, it is not at all trivial to produce a definitive list of all the carnivorous plants. Seventeen plant genera are commonly accused of being carnivorous, but not everyone agrees on their dietary classifications—arguments about the status of *Roridula* can result in fistfights!<sup>1</sup> Recent discoveries within the indisputably carnivorous genera are adding to this quandary. *Nepenthes lowii* might function to capture excrement from birds (Clarke 1997), and *Nepenthes ampullaria* might be at least partly vegetarian in using its clusters of ground pitchers to capture the dead vegetable material that rains onto the forest floor (Moran *et al.* 2003). There is also research that suggests that the primary function of *Utricularia purpurea* bladders may be unrelated to carnivory (Richards 2001). Could it be that not all *Drosera*, *Nepenthes*, *Sarracenia*, or *Utricularia* are carnivorous? Meanwhile, should we take a closer look at *Stylidium*, *Dipsacus*, and others? What, really, are the carnivorous plants?

Part of this problem comes from the very foundation of how we think of carnivorous plants. When drafting introductory papers or book chapters, we usually frequently oversimplify the strategies that carnivorous plants use to capture prey. For example, the following classification scheme of carnivorous plant strategies probably looks familiar:

Snap traps (or bear traps): *Aldrovanda*, *Dionaea*.

Flypaper plants: *Byblis*, *Drosera*, *Drosophyllum*, *Pinguicula*, *Roridula*, *Triphyophyllum*.

Pitfall traps: *Brocchinia*, *Catopsis*, *Cephalotus*, *Darlingtonia*, *Heliamphora*, *Sarracenia*, *Nepenthes*.

Suction traps: *Utricularia*.

Lobster pot traps (or eel traps): *Genlisea*.

However, as happens in all simple classification systems for living organisms, there are examples that span categories. These are cases where carnivorous species have hybrid strategies in capturing prey. In this paper I will describe a few of them.

### Flypaper-pitfall hybrids

The genus *Nepenthes* has more species than any other genus of pitfall carnivores, so it is not a surprise that some of its members have evolved into forms that use extraordinary strategies to obtain valuable nutrients.

*Nepenthes inermis* is an interesting highland species from Sumatra that has funnel-shaped pitchers that lack a peristome. The tiny pitcher lid of this species is little more than a thin strap held high above the pitcher. It was long assumed that this *Nepenthes* was simply another pitfall carnivore. But is it? Why is the inner surface of the pitcher coated with a thin layer of mucilaginous slime? Clarke (2001) reviews various observations and ideas that have been presented for this species, and concludes that *Nepenthes inermis* pitchers probably function as hybrid flypaper-pitfall traps. Insects are attracted to the pitchers, perhaps because of their bright green color or aromatic fragrance. But instead of foraging on a peristome, the insects become mired on the sticky surface on the inner surface of the pitcher. Gravity then causes the captured prey to slowly slide down the pitcher surface until they enter the bath of fluid in the lower portion of the pitcher. A depressing end for the insects, indeed!

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<sup>1</sup>In this paper, I will accept as “carnivorous” those plants that do not produce their own enzymes, but which may use associates or commensals to complete the digestion process.





Figure 1: Inside a *Darlingtonia* pitcher, looking out. Notice how difficult it would be to reach the entrance corridor once prey find themselves inside the pitcher. The treacherous pitfall is at the far right. Note how dark the escape aperture is, when compared to the illuminated pitfall. Photograph made in natural light.



Figure 2: The entrance corridor into a *Nepenthes ampullaria* pitcher.

Pitfall traps and lobster pot traps have many commonalities. Both types of traps rely upon the prey entering a chamber from which they cannot escape. The key difference between these trap strategies is in how the prey are conveyed to their doom. In pitfall traps, the prey errs by losing its grip on a slippery or otherwise challenging surface, and in this temporary lapse of navigational control it plummets—in accordance with Newton's law of gravitation—into a chamber from which it cannot escape. In contrast, a lobster pot works by producing obstacles that effectively act as one-way valves, much like the turnstiles that guide the traffic flow of human commuters at public transportation facilities. Prey enter the trap under their own powers of movement (instead of being ushered in by gravity, as in a pitfall trap).

Erect *Sarracenia* are exemplars of respectable pitfall traps. Once an insect topples into a *Sarracenia* pitcher its options for escape are limited by the exceedingly slippery pitcher walls. Even victims with wings are in great danger, since nearly all flying insects fly in a mostly-lateral direction—in order to fly out of a pitcher, an insect must be skilled at flying vertically in very cramped quarters. Gravity takes its toll, and the plant receives its meal.

However, one species—*Sarracenia psittacina*—is clearly not a pitfall plant. The pitcher of this species is tilted at 45° to the horizontal, or very often is perfectly horizontal. If held at such angles, conventional *Sarracenia* traps would be essentially harmless. But the pitcher opening in *Sarracenia psittacina* is uniquely modified. Instead of gaping like a hungry mouth, the trap opening is shaped as a lateral entry tunnel that provides access to a large, globose, internal cavity inside the pitcher trap (see Back Cover). Once an insect passes through the tunnel and drops into the internal cavity, escape is extremely difficult. This escape route is very small, and is also very hard to get to because its opening is held high above the floor of the pitcher cavity. These two attributes of the escape route—small size and difficulty of access—are classic lobster pot features.

Meanwhile, another passage is presented to the prey; one much easier to enter, and so very inviting. This tube is lined with long hairs that point ever deeper into the trap, and which allow entry but prohibit exit. But woe to the insect that enters this passage: *Ergo insectum moriturum!*

Clearly, Slack (1979) was correct when he listed *Sarracenia psittacina* as a lobster pot, along with *Genlisea*. But is this the only case of a lobster pot carnivore masquerading as a pitfall plant? Consider *Darlingtonia californica*. In strategic structure, it is almost identical to *Sarracenia psittacina*—the only significant difference is that the trap is rotated ninety degrees so the pitcher tube is once again vertical, as is usual in a pitfall plant. Prey, mostly daytime foragers, land on the fanglike appendages dangling under the pitcher orifice. These insects crawl up and through a cylindrical entry corridor with confidence because the inside of the pitcher is brilliantly illuminated by the glassy windows on the pitchers.<sup>2</sup> Climbing into the pitcher, the insects clamber to the end of the entry corridor and vault over the edge, dropping a short distance onto the flat floor of the expanded pitcher head. Now, the only real escape lies in backtracking, but this would be difficult because it would require scaling the steep outer edge of the entry corridor, which has an overhanging ledge<sup>3</sup> (see Figure 1). Flying insects are unlikely to escape aerially because the pitcher roof, confusingly sealed with transparent windows, is nearly as bright as the daytime sky, while the real avenue of escape—directly downwards through a comparatively small opening—is relatively dark because it points down towards the ground.

Meanwhile, another avenue is easily accessed. Brightly illuminated with glassy windows, it is the descending pitcher tube that leads to death by drowning, and a hoard of hungry *Metriocnemus* larvae...

*Darlingtonia*, then, has the two key attributes of a lobster pot: a small portal that is difficult to find again once entered and which is difficult to access even if found. Are there any other examples of lobster pot-pitfall traps? Possibly, depending upon how much you wish to blur the boundaries. The peristomes of both *Nepenthes ampullaria* and *N. aristolochioides* are modified so that the entry

<sup>2</sup>While the fenestrations in *Sarracenia* pitchers are translucent at best, in *Darlingtonia* they are truly, and remarkably, as perfectly transparent as a paper-thin sheet of mica.

<sup>3</sup>There is, however, a small gap in the *Darlingtonia* entry corridor, and lucky is the insect that can find it!

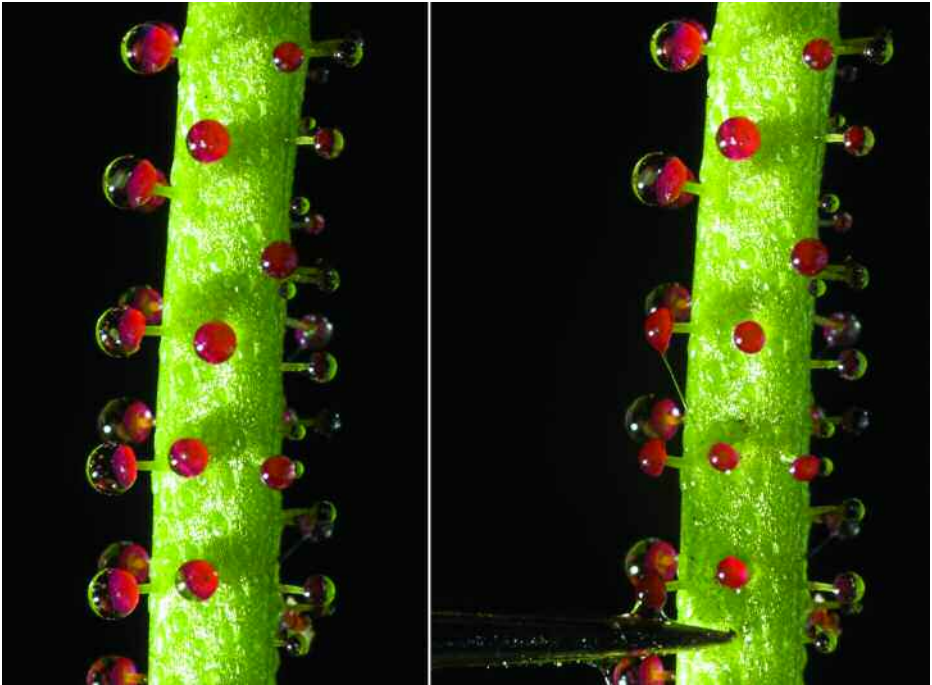


Figure 3: Left: A fresh *Drosophyllum* leaf with the mucous glands and sessile digestive glands easily visible. Right: The same leaf, swept with the tip of a metal pin. Notice how mucus is transferred onto the pin.



Figure 4: Extremely high power imagery showing the mushroom-like shape of *Drosophyllum* mucous glands.

into the pitcher is transformed into an entry corridor (see Figure 2), much as in *Darlingtonia* or *Sarracenia psittacina*. The peristomes of other *Nepenthes* species, such as *N. jacquelineae* or *N. mirabilis* var. *echinostoma* give their pitchers a bit of lobster pot flavor, too. Even *Cephalotus* pitchers have, interior to their peristomes, a second ledge which impedes the escape of prey. But at this point, the suggestion of a lobster pot is probably stretching the definition. Even if one were to concede that the peristome structures of *Nepenthes* pitchers have a retentive function that is effective because it has an element of the lobster pot strategy, these are still gravity-driven pitfall traps...mostly.

#### Another flypaper-pitfall hybrid

Flypaper plants capture prey by generating sticky droplets on the leaves. Bugs contacting these droplets cannot escape. The adhesive glue from each gland acts like a rope, tying the prey to the gland tip, and thus to the leaf. As a necessary result, so obvious it may first escape your notice, is the simple fact that while prey may struggle and thrash, they eventually succumb very close to the point of original leaf contact.

*Drosophyllum lusitanicum*, the large glandular plant from Portugal, Spain, and Morocco, uses a different strategy. Stalked glands cover the leaf surface, and the plant appears to be yet another passive flypaper. And indeed, tiny prey that are trapped by leaves adhere to these glands as in a conventional flypaper. But when *Drosophyllum* captures much grander prey, a new strategy emerges.

When a large insect lurches against a *Drosophyllum* mucous gland, an extraordinary event occurs. Instead of forming a long strand binding the prey to the gland, the entire load of mucus is neatly transferred onto the prey (see Figure 3). *Drosophyllum* gland heads have an interesting mushroom-shape unlike any *Drosera* glands, and this shape may be key in effectively transferring the mucus (see Figure 4). The insect responds by blundering into another gland, which again transfers its burden of mucus onto the prey. The bewildered insect moves about the leaf as it tries to rid itself of the unwanted mucus. *Drosophyllum* leaves spend the majority of their lives oriented vertically, or are at least steeply ascending. This ensures that the struggling, ever-more-beslimed insect is guided gravitationally down the length of the leaf. After several glands have been contacted, the prey is sufficiently coated with slime so it can no longer breathe: it suffocates (or drowns), ironically perched in an aerial location on a threadlike leaf. The sessile glands then contribute to the digestion process by releasing additional fluids.

*Drosophyllum* therefore differs from conventional flypaper plants in that it uses gravity to drop the prey downwards, until it is surrounded by fluid in which it drowns. This exact sentence could be used to describe a pitfall carnivore such as *Nepenthes*. Indeed, the trap of *Drosophyllum* is in essence a pitfall-flypaper, even though there is no pit!

The previous examples of carnivorous plants with hybrid foraging strategies show how our simple classification schemes are inadequate. Nature often creates situations that confound our attempts at simple analyses. Be very cautious, I say, when labeling one carnivore a “pitfall trap” and another a “flypaper plant.” And in the same way, we must remember that some plants may blend the boundaries between carnivory and noncarnivory. We must keep our eyes open for these intermediate cases, and prepare ourselves for long arguments about carnivory! As for me, I’ve recently obtained a few *Stylidium* plants, and will be watching them very carefully!

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## LITERATURE REVIEWS

Clarke, C., Lee, C. & McPherson, S. 2006. *Nepenthes chaniana* (Nepenthaceae), a New Species from North-Western Borneo. Sabah Parks Nature Journal 7: 53-66

At long last the authors finally acknowledge that the material from Northern (Malaysian) Borneo prematurely assigned to *Nepenthes pilosa* by Smythies (1964) and almost all subsequent authors (ignoring the fact that the type specimen collected in Kalimantan has quite different, broadly infundibuliform pitchers that were compared to *N. burbidgeae* by the original author Danser!) is in fact distinct at species level. The “new” species *N. chaniana* (with comparatively narrow tubular pitchers) is actually the most widespread and best known from a group of three (*N. pilosa*, *N. chaniana*, and the recently described *N. glandulifera* v.i.), to which the even more widespread *N. fallax* (syn. *N. stenophylla* auct. non Mast: Danser) can be added as a “sister.” (JS)

Estes, D. 2006. Tennessee’s Lost Emerald: The Green Pitcher Plant. Tennessee Conservationist

Botanists and native plant enthusiasts from Tennessee have doubtless heard some of the tale of Tennessee’s only pitcher plant, *Sarracenia oreophila*. In 1935, a single living plant was found in the wild and placed in a University greenhouse in an attempt to produce flowers for positive identification. Due to a mishap, the plant was lost in cultivation and no herbarium specimen was made. The entire record of *Sarracenia* in Tennessee is based on this anecdote. The author presents the people and events surrounding the fate of possibly the last wild pitcher plant in Tennessee. Optimistically, Estes suggests *S. oreophila* could still exist in the state, as evidenced by additional reports and potential sightings around the Cumberland Plateau. The article is well illustrated with photos of early plant collectors, *Sarracenia oreophila* in habitat (in Alabama) and other native plants which could be confused with the pitcher plant (Reviewer: M. Chamberland).

Gomez-Laurito, J. 2005. *Utricularia uxoris* (Lentibulariaceae), una nueva especie costarricense de la sect. *Orchidioides*. Lankesteriana 5: 137-139.

The new bladderwort species described in this paper looks like a *Utricularia jamesoniana* with smaller, green (not white suffused with pink) and less hairy flowers. The lower lip of the corolla is less deeply lobed. Given the variability of *U. jamesoniana* across its large range in central and South America, it is difficult to judge whether specific segregation is really justified. (JS)

Krol E., Dzubinska H., Stolarz M., and Trebacz K. 2006. Effects of ion channel inhibitors on cold- and electrically-induced action potentials in *Dionaea muscipula*. Biol. Plant. 50: 411-416.

The trap-closing of *Dionaea*, and its sister genus *Aldrovanda*, has long been known to involve electrical signals. These signals involve pulses of electrical potential, also found in animal cells, called action potentials. Here, the authors studied the nature of the generation of these signals using inhibitors of the transport of various ions, and they used either sudden decreases in temperature or shocks with direct current to induce the action potentials involved in closing. It is interesting to note the nature of action potentials involved in closing, since for both stimuli, anions, potassium ions, and calcium ions were involved, but not to the same degree. Thus the plants can in some way differentiate among triggers and produce their action potentials in different ways for different stimuli. (DWD)

Lee, C.C. 2004. New Records and a New Species of *Nepenthes* (Nepenthaceae) from Sarawak. Sandakaniana 15: 93-103

The newly described species *N. glandulifera* is the most recent addition to the Bornean



group of *Regiae* with long brown hairs. It differs from its relatives by a missing appendage on the lower lid surface and by dark glands at stems, leaf bases, and lower parts of pitchers (only on petioles and nodes in *N. pilosa*, and missing in *N. chaniana*). (JS)

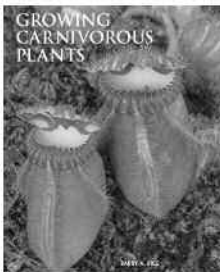
Matusikova I., Salaj J., Moravcikova J., Mlynarova L., Nap. J.-P., and Libantova J. 2005. Tentacles of in vitro-grown round-leaf sundew (*Drosera rotundifolia* L.) show induction of chitinase activity upon mimicking the presence of prey. *Planta* 222: 1020-1027.

Carnivorous plants secrete a range of enzymes for the digestion of their prey, and one obvious but often-overlooked or under-explored enzyme from this group is chitinase. This enzyme decomposes chitin, the principal component of fungal cell walls and, more importantly, the exoskeletons of insects and crustaceans. *Drosera rotundifolia*, raised in tissue culture to prevent any surface microorganisms from contaminating the plants, adjusted enzyme expression to match the material offered, making more proteases in response to the protein in gelatin and more chitinases in response to chitin isolated from crustaceans. This very sensible and efficient sort of response is perhaps not surprising but nonetheless very interesting for physiologists. The authors are quite thorough, examining the expression of chitinase not only at the protein level but also at the level of mRNA—this strengthens the identification of chitinase as being produced by the plants themselves. Chitinase was only expressed in the secretory parts of the glandular hairs in response to chitin being applied to the plants. (DWD)

Neyland, R., and Merchant, M. 2006. Systematic Relationships of Sarraceniaceae inferred from Nuclear Ribosomal DNA Sequences. *Madrono* 53: 223-232.

Using molecular methods that are so popular, the authors explore the relationships among *Darlingtonia*, *Sarracenia*, and *Heliamphora*. Their displayed consensus tree is intriguing, and suggests that *Sarracenia purpurea* is a sister clade to all the other species in its genus. The remaining species are grouped in two groups (one including *S. flava*, *S. minor*, *S. psittacina*; the other containing *S. alata*, *S. leucophylla*, *S. oreophila*, and *S. rubra*). No phylogenetic structure could be detected among plants in the *S. rubra* complex, here discussed as five subspecies. Within *Sarracenia purpurea*, the var. *burkii* taxon is apparently a sister group to the rest of *S. purpurea*, supporting recent moves to elevate the taxon to species status (i.e. *S. rosea*). On the generic level, *Darlingtonia* is seen to be a sister clade to *Heliamphora/Sarracenia*, which does not provide much clarity into the question of the geographic origin of the Sarraceniaceae.

This paper is marred by the apparent ignorance of the authors as to the correct nomenclature regarding infraspecific taxa in *Sarracenia purpurea*. In this paper, the northern subspecies is treated as “*Sarracenia purpurea* subsp. *gibbosa*” and the southern subspecies is treated as “*Sarracenia purpurea* subsp. *purpurea*.” The origin for this confusion is summarized in Cheek, M. CPN 2001, p29-30. (BR)



## Growing Carnivorous Plants (the book)

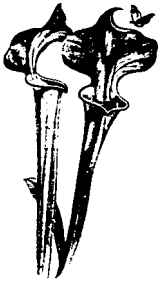
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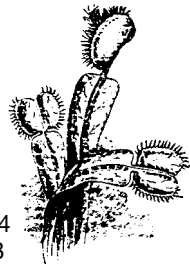
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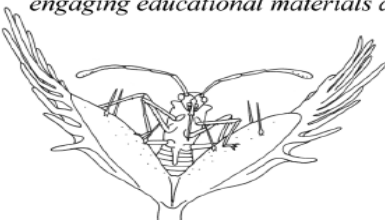
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