

OBSERVATIONS ON *CEPHALOTUS FOLLICULARIS* REPRODUCTIVE BIOLOGY

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Keywords: *Cephalotus follicularis*, flowers, seeds, seed germination, stolons.

Received: 12 August 2022

<https://doi.org/10.55360/cpn514.jb756>

Abstract: Aspects of *Cephalotus follicularis* reproductive biology are documented to gain a better understanding of this enigmatic plant. Detailed observations of seed germination, seedling development, and vegetative reproduction provide a description of the uncommon events in the process.

Cephalotus follicularis (Cephalotaceae, Oxalidales) is found in bog and swamp margins, fens, and seeps in southwestern Australia. The area has a winter rainy season and summer dry season. Localized flooding can occur during the winter. Bushfires are an integral part of the ecology of southwestern Australia during the dry season. *Cephalotus* has particular adaptations to survive overgrowth by shrubs and to take advantage of the fires that remove the overgrowth (DeBuhr 1976; Lowrie 1978; Gibson 1999; Mann 2005; Nunn 2014; Cross *et al.* 2019). The plants ecological adaptations are reflected in its reproductive biology.

Materials and methods

The *Cephalotus* plants used in this study were initially grown from seeds donated to the ICPS Seed Bank in 2000 and 2006 by Phill Mann or were the cultivars *Cephalotus* ‘OG Black’ and *Cephalotus* ‘Hummer’s Giant’. The plants had been rejuvenated multiple times from stolon cuttings. They were grown under natural light by a garage window supplemented with artificial lighting on a local sunrise/sunset cycle to induce flowering. Flowers were pollinated by hand and by flies. Observations of the flowering process were made to make seed production more productive. Seven flowers were followed closely. Achenes were collected and seeds removed to determine seed set.

The seedling study was done either planting seeds in pots with finely chopped long fibered New Zealand *Sphagnum* or in plastic petri dishes with filtration disks. For the petri dishes, attempts were made to adequately sterilize the seeds and filtration disks using sulfur powder and a hydrogen peroxide solution. What worked best was dusting sulfur powder onto filtration disks, putting another disk over and two under it to give a stack of four disks to hold moisture. The stacks were placed in the petri dishes with the same inside dimensions as the diameter of the disks. Seeds were placed in a 1% hydrogen peroxide solution in a microtiter tube for 5 minutes then the seeds and solution poured onto the disks in the petri dishes. Additional water was added as necessary. The dishes were put in plastic Ziploc bags to minimize evaporation. Seeds were stratified either in a refrigerator “butter keeper” at 4°C or a wine refrigerator at about 14°C. The seeds in the butter keeper were moved to the wine refrigerator after two months because they were not germinating. When germination was observed, the pots or petri dishes were placed under artificial lighting at room temperature.

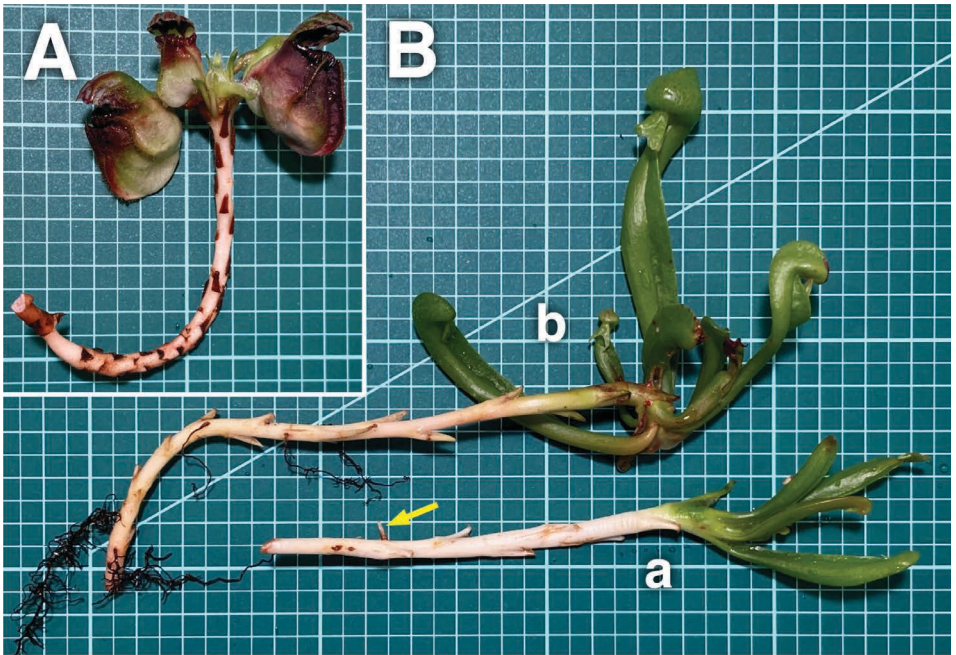


Figure 1: A: Excavated *Cephalotus* stolon with plant that will form a vertical stem at the tip. B: *Darlingtonia* stolons with plants at the tip that will become rhizomatous. Yellow arrow indicates emerging root on stolon. Photographed on a 5 mm grid.

Terminology

The common term for the underground stem-like parts of *Cephalotus* is “rhizome” (c.f. Cross *et al.* 2019). This usage is understandable for instances where herbarium sheets are used to describe a plant and the presence of roots is used to distinguish rhizomes from stolons. However, this usage is misleading in that it mischaracterizes how the plant actually grows and vegetatively reproduces. The root distinction will not be used here.

Cephalotus does not creep along the ground like *Sarracenia*, which unquestionably has rhizomes. Instead, single growth point plants from seed have a short vertical, above ground stem and a tap root. Multi growth point plants are more complicated. Mature plants spread and reproduce vegetatively via subterranean stolons that are typical of other plants that send out stolons on or just below the soil surface. That is, the plants send out elongated stem-like shoots with radial symmetry for the purpose of asexual reproduction. *Darlingtonia* is an example of a plant that sends out stolons and has rhizomes at the stolon tips. In Figure 1Ba, the stolon is in its second year of growth with new leaves at the tip and a few emerging roots. The first year there was no indication of a plant at the tip. Figure 1Bb shows a stolon in its third year with a more mature plant and obvious roots along the stolon. My observation based on digging up stolons and dividing plants is the stolons typically send out roots after the tip starts to become rhizomatous. However, it is quite possible to find stolons doing the unexpected such as a few small pitchers among the scale-like leaves in the middle of a very long stolon. *Cephalotus* stolons produce new plants with vertical stems when they reach the soil surface (Fig. 1A). As the stolons age, they change form and become stolon tubers which

produce roots and additional stolons as shown below. *Cephalotus* stolons can produce roots directly as in the case of propagation by stolon cuttings and can naturally branch as reported by Lowrie (2014) and Cross *et al.* (2019).

Flower and seed observations

The basic description of flowers with the phases of flowering in *Cephalotus* are outlined in detail in Cross *et al.* (2019). The observations reported here provide a more detailed timeline.

Cephalotus has rather simple flowers. Typical flowers have 6 tepals, 12 stamens, 6 stigmas and produce up to 6 seeds (Fig. 2). Flowers open in late spring and summer. On the day flowers open (day 1), by midafternoon, there is shed pollen evident on many of the anthers, but the stigmas have not matured. Additional anthers shed pollen on days 2 and 3. The stigmas start to separate and mature on day 4. The anthers turn brown on about day 9 (range 6–12, $n=7$), and the flowers start to close and nod down.

Cephalotus pollen is very powdery. It does not stick to small inexpensive natural hair watercolor brushes that work well to pollinate most *Sarracenia* flowers. If the flowers are not disturbed until about day 5, a brush can be used to dislodge a small cloud of pollen from the anthers to self-pollinate a flower. Plucking pollen-laden stamens with a needle nosed forceps and dusting the stigmas of an older flower may work if it can be done gently enough. House flies (Muscidae) and flower flies (Syrphidae) were observed visiting flowers during this study and interfered with observations.

The achenes with seeds dry and splay out about day 30 (range 28–33, $n=3$) (back cover). An achene with the seed is very light and the long hairs allow the structure to blow in the slightest breeze (Fig. 3A). When closely handling the achenes, it is advised to wear a face mask to keep from breathing on the achenes and scattering them. Just *et al.* (2019) consider that the seeds with achenes are primarily wind dispersed. They will also float on water, which would be advantageous to both dispersal and placement at higher locations in a bog during seasonal flooding, as was reported by DeBuhr (1976) and like what was observed for *Drosera* species (Ksepka 2019; Bourke 2021). I have observed that the achenes are strikingly similar to *Darlingtonia* seeds and could be dispersed long distance by clinging to the fur of an animal visiting nearby exposed water as described in Collingsworth (2015) for *Darlingtonia*. *Cephalotus* does not have all the seed dispersal mechanisms of *Darlingtonia*. The most significant is *Darlingtonia* can fling seeds onto a host (personal observation). *Darlingtonia*, like *Cephalotus*, has very tall flower stalks that can swing when disturbed. In the field, just brushing past a mature *Darlingtonia* seed capsule will result in seeds being thrown



Figure 2: *Cephalotus* 'OG Black' flowers. Note some flowers have unusual numbers of tepals and stigmas.

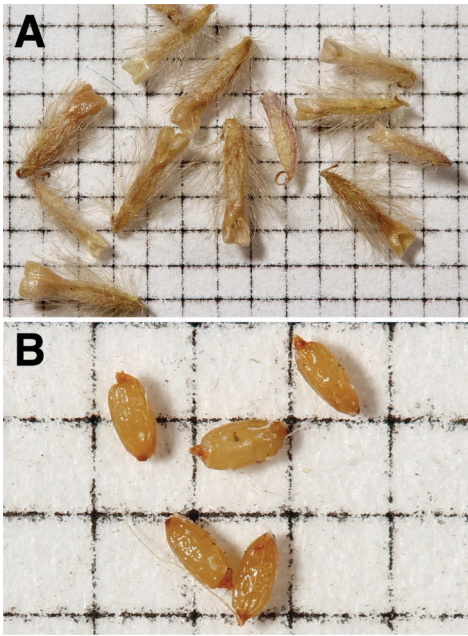


Figure 3: *Cephalotus* achenes (A) and seeds (B) photographed on a 1 mm grid.

out of the capsule. This is very advantageous for *Darlingtonia* because the plants send out large numbers of stolons that can completely colonize all the immediate habitat capable of supporting the plants in a few years to decades depending on the site. There is a distinct advantage for the seeds to go to other wetlands in the area as there would be few opportunities in the immediate vicinity. *Cephalotus* flower stalks do not hold the individual seeds very long but do mature seeds daily for about two months. In addition, the stolons that *Cephalotus* plants produce tend not to make massive long term stands in their usual habitat (Nunn 2014). Hitching rides on animals should be possible for less common but important longer distance dispersal between bogs.

Cephalotus sometimes produces achenes without seeds. Note in Figure 3A that at least four of the achenes appear not to be large enough to contain a seed (Fig. 3B). In a sample of achenes from this study in 2021, 44 seeds were collected from 94 achenes (47% contained seeds).

Because some of those achenes were collected with forceps which can eject seeds from the achenes and forceps can damage seeds as well, the trial was repeated in 2022 collecting seeds carefully into a large bowl. No free seeds were found in the bowl after collection. In this sample, only 59 seeds were collected from 197 achenes (30% contained seeds). The conditions the plants were growing under were not natural, but this general observation could account for the results of Just *et al.* (2019) that they had a substantially lower rate of seedling success when the seeds were not removed from the achenes. Under natural conditions there is an advantage for the seeds to remain in the achene. The achene is more likely to remain on the surface of the soil. As seen in the next section, seedling development is most amenable to being on the surface of the soil.

Seedling development

Just *et al.* (2019) studied *Cephalotus* seed germination in the context of its ecology and conservation biology. They did extensive studies of seed storage and germination requirements. As part of their study, they determined the best conditions to induce seed germination. The most important factors were to hydrate the seeds and to stratify them at 15°C. This is not “cold stratification” in the usual sense. As they found and I reproduced, stratifying seeds colder was not helpful and they would not germinate properly until moved to about 15°C. They needed to be at 15°C about 6 to 10 weeks. Just *et al.* (2019) found the seeds that did not germinate properly were not necessarily dead. They could generally be coaxed to germinate with longer stratification at 15°C or with the hormone GA3. Figure 4 displays the terminology used in describing seedlings.

Cephalotus seeds appear not to contain small embryonic plantlets as are typical in common flowering plants. Instead, it appears there is simply a mass of undifferentiated embryonic cells from

which the plantlet structures differentiate and grow after germination, defining germination as when the seed expands and the embryonic tissue starts to extrude (Fig. 5A-B). Cross *et al.* (2019) have a photo of a longitudinal section of a seed. They interpret the photo to show a small white linear embryo at the distal tip of the seed surrounded by endosperm. It is presumed during stratification the endosperm breaks down nourishing the embryo so that at the time of germination, the remains of the endosperm become the membrane-like structure enclosing the embryo which at that time fills the seed. This process needs more study because at the beginning of germination, there is no outward evidence of any differentiation of the embryo. Instead, it appears that as the undifferentiated embryonic cells expand at germination and the seed coat splits, an opening occurs at the distal end of the enclosing membrane, and the embryonic cells are extruded (Fig. 5B-C). It is not clear how much of this extrusion process is powered from the embryonic cells expanding and how much is from hidden differentiation and development of the hypocotyl and later, the cotyledons within the seed coat and membrane (Figs. 5C-E, 6A-B). It is unclear how the cotyledons get out of the enclosing membrane because it appears intact after cotyledons are out. Conran & Denton (1996) refer to the embryonic cells as a hypocotyl extension, but developmentally it appears the hypocotyl sprouts from the cells.

The result of this delayed differentiation is the immediate development of a seedling substantially larger than the seed (Fig. 5E, 6B). Most seedlings maintain the mass of embryonic cells between the hypocotyl and radicle (Fig. 6C). A few seedlings were observed that did not have an obvious mass of undifferentiated cells (left side of Fig. 5E). These seedlings were much smaller. After the seedlings exit the seeds, it appears the embryonic cells do not provide much substance to the seedlings and may only play a developmental role that is complete when the seedling is complete. Figure 6D shows a seedling six months after being planted out. The blue arrow points to the embryonic cells that have become a knob at the hypocotyl-radicle junction. The embryonic cells and hypocotyl appear to have become a typical stem and the radicle a fleshy stem-like tap root. Note the typical adventitious roots pointed to by the yellow arrows.

Jan Schlauer (pers. comm.) suggested that what here are called undifferentiated embryonic cells could be a tuber-like storage structure formed from the primary root, and the observed root is a secondary, adventitious root. This is an interesting hypothesis that offers a more traditional interpretation of what is seen in the seedlings. Figure 7 shows more of the variation among the seedlings. There are seedlings with the hypocotyl on the proximal end of the cell mass and the “radicle” on the distal end. However, most seedlings have both the hypocotyl and radicle attached laterally to the mass after it is out of the seed coat. If the shape of the cell mass does not reflect the prior shape inside the seed and the hypocotyl and cotyledons existed before germination, the tuber hypothesis

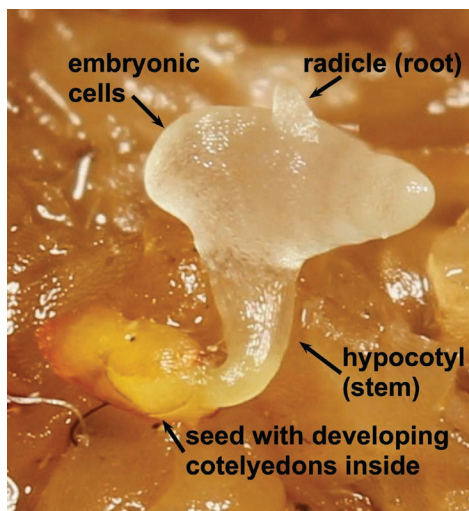


Figure 4: *Cephalotus* seedling emerging from seed. It appears the seed initially just contains embryonic cells. The hypocotyl and radicle sprout from the cell mass as the seedling develops at germination.

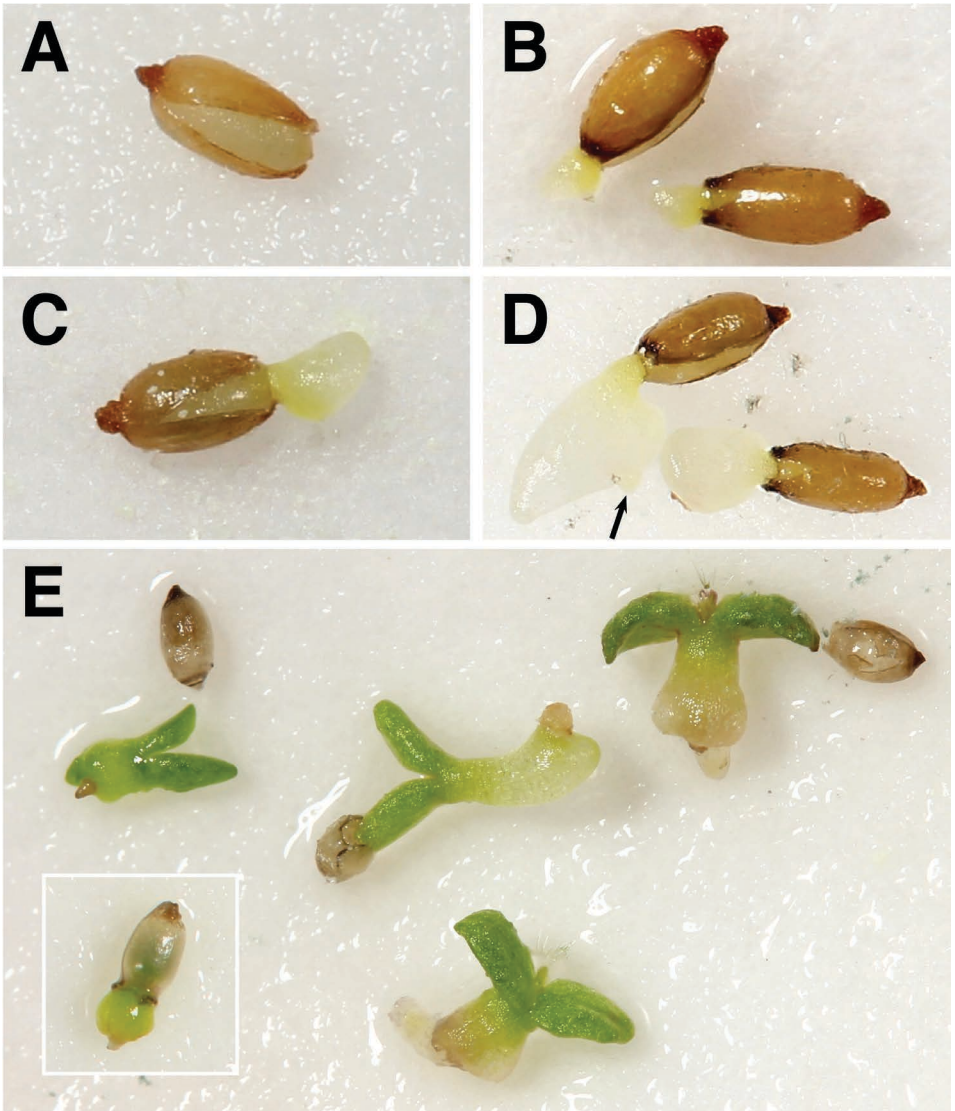


Figure 5: *Cephalotus* stages in seedling development. A: Embryo swells and seed coat splits. B-C: Embryonic cells continue to swell and extrude out of the enclosing membrane. D: Embryonic cells are out of the seed membrane. The hypocotyl is beginning to emerge. Arrow indicates differentiating root. E: Fully developed and emerged seedlings. Inset was taken 15 days earlier showing cotyledons still within seed membrane. A-D were in darkness. E was arranged with seed coats for scale—the upper left seed coat may not go with that seedling. Inset may not be the same seedling as above it.

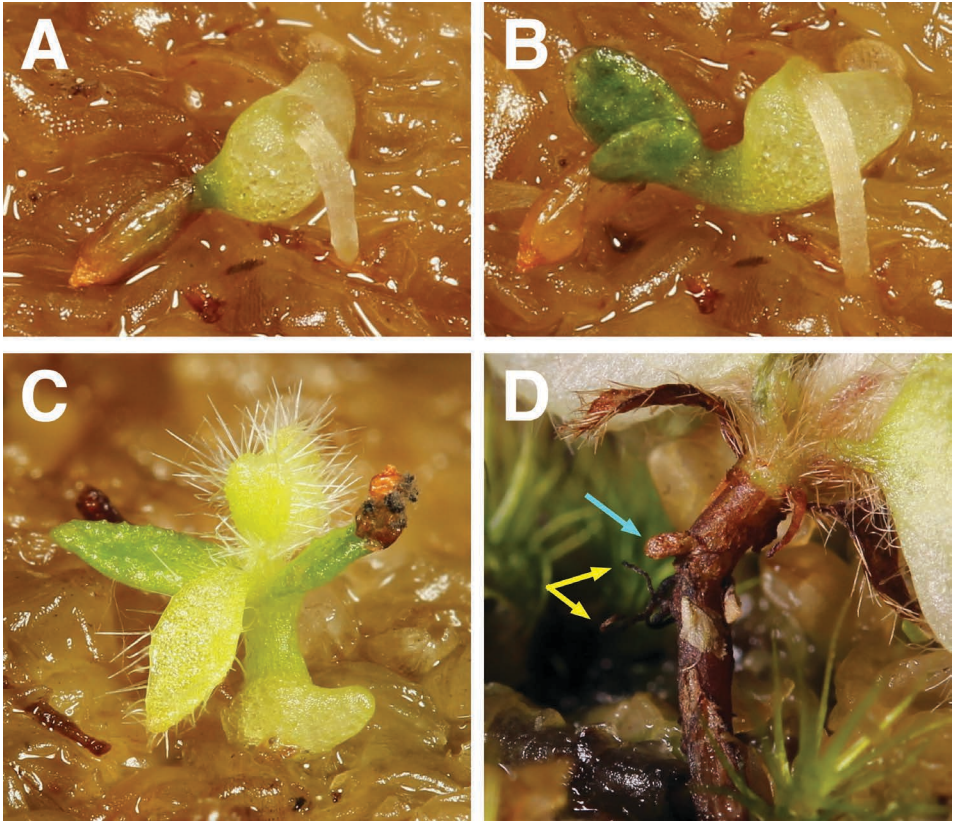


Figure 6: *Cephalotus* advanced stages in seedling development. A-B: Embryo with radicle entering the soil before and after release of cotyledons from the seed coat. C: Planted seedling showing the first leaf which is a foliage leaf and the second leaf which is a pitcher. This is typical. D: Partly excavated seedling six months after planting. The blue arrow points to the remains of the embryonic cells at the hypocotyl-radicle junction. The yellow arrows point to typical *Cephalotus* adventitious roots emanating from the radicle (tap root).

would be possible. To determine how typical or unique *Cephalotus* germination is, it would require a classical 19th century microscope study of seed development and germination.

In the wild, *Cephalotus* seeds should germinate during the cool, rainy winter. Six months later they will be presented with a warm to hot, dry summer. To survive the summer, the seedlings need moisture. Having relatively large seedlings and a fleshy tap root for water and nutrient storage could be critical for the seedling survival on the drier edges of bogs and seasonally variable seeps where they are found.

Reproduction via stolons

According to my observations from propagating and growing *Cephalotus*, it appears that the plants immediately from seed have short taproots that ultimately become thickened and tuberous. The tubers bud off adventitious roots (Fig. 6D). Older plants from seed spread via stolons. These stolons form short leafy vertical stems at the soil surface.



Figure 7: *Cephalotus* seedlings showing the variation found. The same seedlings may appear more than once but at different growth stages.

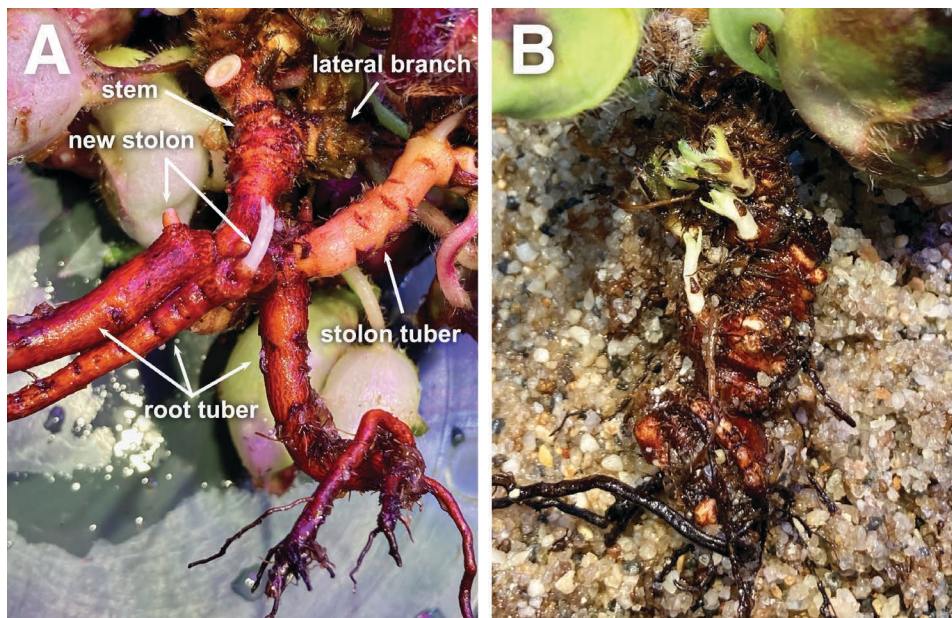


Figure 8: A: *Cephalotus* 'OG Black' plant two years after propagation via division. New stolons are originating on root tubers. An older stolon is tuberous. Lateral branches off the main stem tend to be short lived. B: *Cephalotus* (from Denbarker, WA seed) plant two years after propagation via stem cutting. Stolons are sprouting from the stem after the main growth point died post blooming. The underground part of the stem has become knobby and tuber-like. This clone tends not to be as prolific at producing root tubers compared to the clone in A.

The above ground stems of *Cephalotus* are usually no longer than a few cm. Growth tips die when the plant blooms or, if the plant does not get the appropriate light cues to bloom, just dies with age. This event usually initiates the production of stolons and lateral stem branches (Fig. 8).

The subterranean parts of mature *Cephalotus* plants are typically a tangled mass of stolons, roots, and buried stems. Most of the stolons and some of the roots are in the form of tubers. It can be difficult to tell the stolon tubers from the root tubers (Fig. 8A). Buried stems become knobby and somewhat tuberous (Fig. 8B). New stolons sprout from the stolon tubers, root tubers, and buried stems. Cross *et al.* (2019) have a photo of a cross section of a tuber showing a mass of parenchyma cells around the original root or rhizome. Having relatively large storage and freely reproducing subterranean structures allows *Cephalotus* plants to quickly recover after bush fires (Nunn 2014). They also make the plant easy to propagate in cultivation.

Acknowledgments: I thank Jan Schlauer, Richard Nunn, John Conran, and Bob Ziemer for helpful comments on the manuscript.

References

Bourke, G. 2021. Splash-cups, springboards, and sink or swim – Preliminary study of the strategies for vegetative propagule dispersal in Pygmy *Drosera*. *Carniv. Pl. Newslett.* 50(2): 52-59. <https://doi.org/10.55360/cpn502.gb841>

- Collingsworth, D. 2015. Do bears disperse *Darlingtonia*? Carniv. Pl. Newslett. 44(2): 44-47.
<https://doi.org/10.55360/cpn442.dc725>
- Conran, J.G., and Denton, M.D. 1996. Germination in the Western Australian Pitcher Plant *Cephalotus follicularis* and its unusual early seedling development. W. A. Nat. 21(1): 37-42.
- Cross, A., Kalfas, N., Nunn, R., and Conran, J. 2019. *Cephalotus* – the Albany Pitcher Plant. Redfern Natural History Productions, Poole, Dorset, England.
- DeBuhr, L. 1976. Field Notes on *Cephalotus follicularis* in Western Australia. Carniv. Pl. Newslett. 5(1): 8-9. <https://doi.org/10.55360/cpn051.ld803>
- Gibson, R. 1999. Observations on *Cephalotus* in the wild. Carniv. Pl. Newslett. 28(1): 30-31.
<https://doi.org/10.55360/cpn281.rg416>
- Ksepka, J. 2019. A note on *Drosera* seed dispersal. Carniv. Pl. Newslett. 48(3): 137.
<https://doi.org/10.55360/cpn483.jk704>
- Lowrie, A. 1978. *Cephalotus* hunting in the deep S.W. of Australia. Carniv. Pl. Newslett. 7(4): 119-121. <https://doi.org/10.55360/cpn074.al244>
- Lowrie, A. 2014. Carnivorous Plants of Australia. Magnum Opus, Vol. 1. Redfern Natural History, Poole, Dorset, England.
- Mann, P. 2005. Observations on *Cephalotus follicularis* and *Drosera binata* in Western Australia. Carniv. Pl. Newslett. 34(3): 68-70. <https://doi.org/10.55360/cpn343.pm291>
- Just, M.P., Merritt, D.J., Turner, S.R., Conran, J.G., Cross, A.T. 2019. Seed germination biology of the Albany pitcher plant, *Cephalotus follicularis*. Australian Journal of Botany, 67: 480-489.
<https://doi.org/10.1071/BT19053>
- Nunn, R. 2014 New insights into the growth cycle of *Cephalotus follicularis*. Carniv. Pl. Newslett. 43(3): 93-96. <https://doi.org/10.55360/cpn433.rm450>



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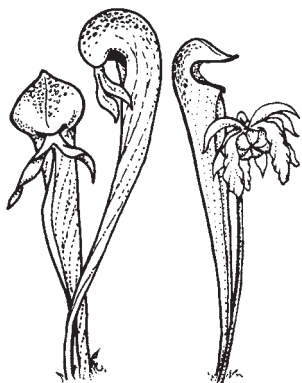
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CARNIVOROUS PLANT NEWSLETTER

Journal of the International
Carnivorous Plant Society
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Volume 51, Number 4
December 2022



Front Cover: *Utricularia minor*, Eldorado County, California, USA. Photo by Barry Rice.
Article on page 194.

Back Cover: *Cephalotus* flowers at different stages from blooming to releasing seeds.
Image by John Brittnacher. Article on page 168.

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Date of effective publication of the September 2022 issue of Carnivorous Plant Newsletter: August 10, 2022.

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.
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