

4 Carnivorous Plants

Carnivorous plants produce elaborate and highly specialized traps to capture invertebrate prey. These traps arise from modified leaf structures. However, to be truly carnivorous, a species must also demonstrate an ability to produce digestive enzymes (that can break down invertebrate tissues) and absorb the resulting nutrient-enriched solution. Some genera demonstrate protocarnivory (they have some, but not all features of carnivory). For example glands on the peduncle and flowers of some *Stylidium* species produce digestive enzymes (Darnowski *et al.*, 2006), but experiments are still required to determine if nutrient uptake occurs. Resin glands on the scapes, bracts and leaves of *Grevillea leucopteris* capture many insects but there is no mechanism for their digestion.

Western Australia's carnivorous plants are confined to five genera (*Drosera*, *Byblis*, *Cephalotus*, *Utricularia*, and *Aldrovandra*) that each displays a different capturing technique, with the greatest number of species in Australia occurring in the SouthWest. Carnivorous plants typically grow in habitats that are nutrient-impooverished ranging from highly leached soils to bogs and swamps where organic compounds acidify the water, reducing the rate of decomposition and hence nutrient availability. *Aldrovandra* is a monotypic genus and has only recently been recorded in southwestern Australia near Esperance, but is not in great abundance. There is an additional record of the genus occurring in the Kimberley.

4.1 *Drosera*

Drosera (Droseraceae) has its worldwide centre of diversity in the SouthWest and exhibits a range of growth forms (Rivadavia *et al.*, 2003; Yesson & Culham, 2006; Lowrie, 2014). SouthWest species are mostly perennial and are classified into three subgenera: the tuberous *Eryaleium* includes species that have rosettes of leaves (section *Erythrorhizae*), leaf clusters on short stems (section *Stolonifera*) or climb (section *Ergaleium*), and the subgenus *Bryastrum* (pygmy droseras) (Fig. 4.1). The annual, sometimes ephemeral, *D. glanduligera*, is the sole species of subgenus *Coelophylla* and possesses a combination of sticky and snap trap tentacles, unlike other species. Snap traps occur in the venus fly trap [*Dionaea muscipula* (Droseraceae) native to North and South Carolina, USA] but the mechanism here is quite different. Originating 40 Ma (Yesson & Culham, 2006), *D. glanduligera* inhabits moist low-lying, well drained soils, and is a relict of these ancient mesic Eocene landscapes.

The leaves bear sticky, multicellular hairs (tentacles) that capture arthropods, attracted by colours, the glistening mucilage produced by the tentacles, or scent (Gibson & Waller, 2009). These tentacles respond to the smallest touch, causing the tentacles to slowly bend towards the prey and downwards. This response is transmitted to the other tentacles. The greater the prey struggles, the more widespread is tentacle

movement towards it. The captured prey becomes covered in mucilaginous fluid secreted by the glands that have captured it. *Drosera* is derived from the Greek *drosos* (dewy) and refers to the glandular hairs that give the appearance of being covered in dew, hence the common name, sundews.

Stickiness of the tentacles (Fig. 4.2) is due to the production of mucilage that contains proteolytic and other hydrolysing enzymes that break down proteins and other compounds in the prey. Chitinous exozymes (chitinases) are also produced by bacteria that break down the prey's tough exoskeleton (Fig. 4.3). Absorption of digested products occurs by the same gland that secretes the digestive enzymes, accounting for 50-80% of drosera nitrogen uptake (Dixon, Pate & Bailey, 1980) and utilization (Schulze *et al.*, 1991). After a few days the tentacles resume their original position, the undigested remnants drop away and the modified leaf is ready to capture more prey.



Fig. 4.1: *Drosera* species display great diversity in their habit. (upper left) *D. rupicola* in flower showing peltate leaves with glands in the leaf concavity (5 mm wide). (upper middle) the SouthWest is a biodiversity centre for pygmy droseras. Pictured is *D. nitidula* (1 cm diameter) displaying relatively long glandular tentacles arising from the modified leaves. (upper right). Close up of the 'dewy' stalked glands (tentacles) of *D. auriculata* with remains of a digested insect in the lamina (lamina 5 mm wide). (lower) erect (*D. porrecta*), climbing (*D. erythroyne*) and rosette (*D. rosulata*) droseras. Many species produce new shoots from an underground tuber in response to the winter rains. Images of *D. auriculata*, *D. erythroyne*, *D. nitidula* and *D. porrecta* provided by Allen Lowrie.

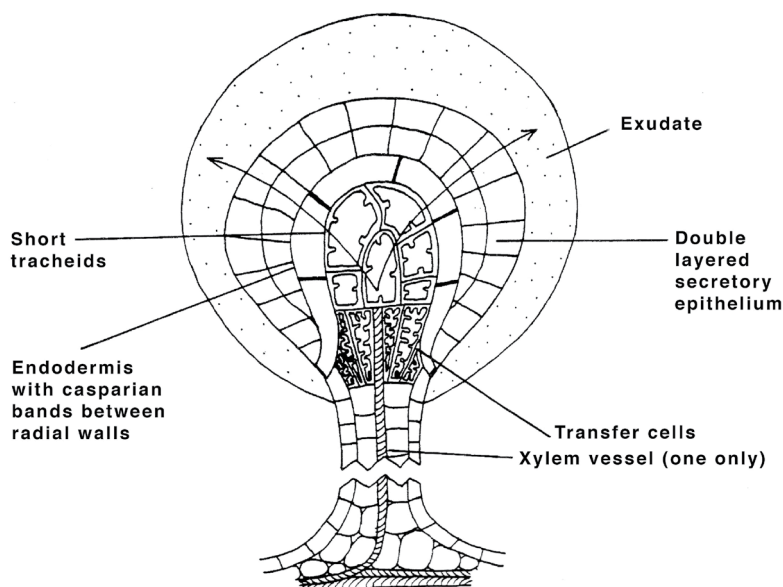


Fig. 4.2: Longitudinal section through a *Drosera* tentacle. The glandular head of a tentacle is usually reddish and covered with droplets of mucilage. The glandular head consists of external and internal layers of secretory cells and tracheids in the centre. The tracheids are separated from glandular cells by a row of barrier cells consisting of cutinized cell walls that appear to control transport. In the basal part of the tentacle there are some outer (epidermal) and inner (parenchyma) stalk cells and a single vessel connecting the glandular head with the stalk and hence the leaf. Head 0.5 mm wide.

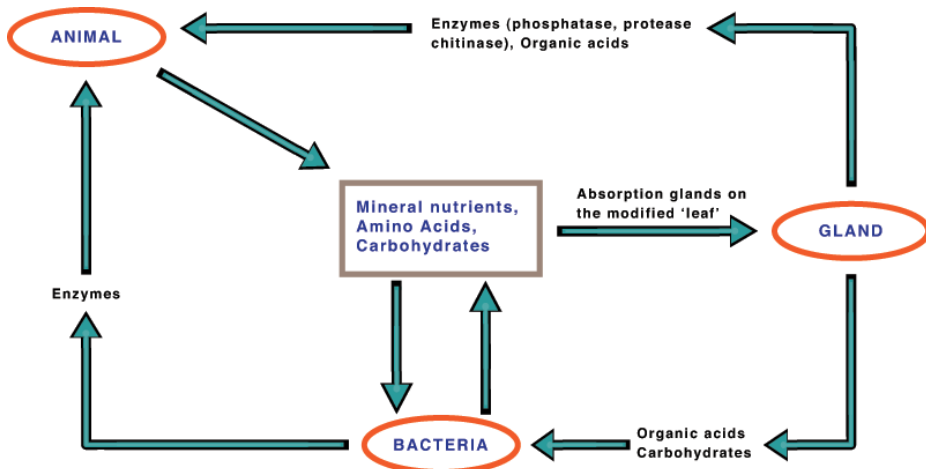


Fig. 4.3: Schematic representation of the digestive and absorption processes involving exudates produced by a *Drosera* tentacle. *Drosera erythrorhiza* can capture on average 80 arthropods $\text{cm}^{-2} \text{day}^{-1}$ in mid-spring (Dixon *et al.*, 1980), and are a more effective source of N than soil-supplied N.

4.2 *Byblis*

Two species of *Byblis* (Byblidaceae) inhabit southwestern Australia (*B. gigantea*, *B. lamellata*) (Lowrie *et al.*, 2002). Both are perennial subshrubs, regenerating each year from the stump of the previous year's stem. The remaining four species occur in northern Western Australia and are all annual herbs, relying on seed production for species survival. *Byblis* is named after a princess of classical Greek mythology who fell in love with her brother; she eventually hanged herself and turned into a fountain. This refers to the stem and leaves of the plant that are covered with glandular hairs glistening in the sun 'like dripping tears'.

The leaves and stems of all *Byblis* species are densely covered with glandular hairs that secrete a mucilaginous fluid (Fig. 4.4). These serve to attract small insects that are ensnared when touching the sticky secretions. Unless they are strong enough to escape, the insect prey either dies from exhaustion or asphyxiates as the mucilage envelops it. Unlike the sundews, however, *Byblis* are unable to bend their tentacles or leaf lamina to trap or digest prey. As a result, they are classified as a "passive trap".

Byblis has two types of glands - stalked and sessile glands (Fig. 4.4). Stalked glands capture and twist down after prey capture. Sessile glands secrete the digestive juices and absorb the products of digestion, and are five to ten times as numerous as the stalked glands.



Fig. 4.4: (left) *Byblis lamellata* growing in seasonally damp sands at Eneabba. Glands cover the needle-shaped leaves, stems and sepals. Above plant is 25 cm wide. (right) Electron micrograph of a *Byblis* leaf showing the stalked and sessile glands covering the surface. Stomates (leaf pores) on the leaf surface are also visible. Leaf is 2 mm wide.

4.3 *Cephalotus*

Cephalotus has only one species and that is the only species in the family Cephalotaceae (thus it is a monotypic family). Locally known as Albany pitcher plant, the species grows in peaty swamps along the south coast of southwestern Australia. The name *Cephalotus* is derived from the Greek *kephale* (having a head). This refers to the head of pollen at the end of the stamen.

The trap, a modified leaf, lures prey by a combination of coloured markings on the rim and lid, its odour (decaying prey) (Fig. 4.5), presence of a reward (nectar along the rim) and transmitted light through the translucent lid and wall tissues that suggest a passage (Parkes & Hallam, 1984). It is an effective arthropod-trapping device because:

1. The reddish-purple mouth has a slippery surface ribbed with downwardly-pointing teeth arching over the pitcher, so that an insect tends to slip into the pitcher rather than escape from it.

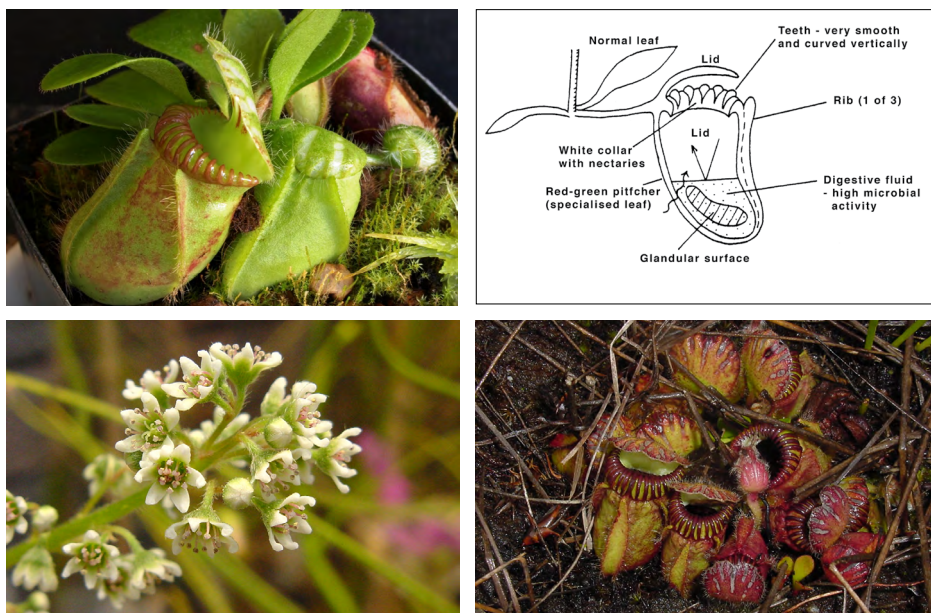


Fig. 4.5: *Cephalotus follicularis*. (upper left) Note the mature (left), immature (middle) and embryonic (right) pitchers. These pitchers are modified leaves. Mature pitcher is 4 cm long. (upper right) Drawing of a longitudinal section through a *Cephalotus* pitcher. Pitcher is 4 cm long. (lower left) insect-pollinated flowers. The species epithet refers to its hooded stamens. (lower right) *Cephalotus* plants occur near or in swamps and bogs in the south coastal SouthWest. Plant pictured is 15 cm wide. Images provided by Melissa Darling (upper left), Allen Lowrie (lower left) and Aaron Gove (lower right).

2. The inside rim (collar) curves downward to form a ledge and is glandular and slippery making it difficult for an insect inside the pitcher to climb out.
3. Smooth pitcher walls.
4. The translucent lid and walls make it difficult to distinguish the exit for any insect flying into the pitcher.
5. The liquid pool at the bottom of the pitcher also reflects light, as well as capturing and drowning its prey.

Arthropods that fall into the pitcher drown in the digestive fluid. Glands in two mounds on the pitcher wall exude digestive enzymes and absorb the resulting nutrient-enriched solution. Large *Cephalotus* plants obtain, on average, 26% of their nitrogen requirement from captured prey (Schulze *et al.*, 1997).

4.4 *Utricularia*

Of the 40 species known in Western Australia, thirteen occur in the SouthWest. Although *Utricularia* species mostly occur in moist peat, some occur on sand and in depressions on rock outcrops, while others are completely aquatic (with only the flowers appearing above water). They can survive almost anywhere where there is fresh water for at least part of the year. Many Australian species will grow only during the wet season, reducing themselves to tubers only 10 mm long and remaining dormant during the dry season.

Utricularia possesses the most complex traps of all carnivorous plants (Fig. 4.6). Called ‘bladders’ (utricles) they are matchhead in size, and are modified leaf segments (aquatic species) or whole leaves arising directly beneath a rosette of normal leaves (non-aquatic species). The name *Utricularia* is derived from the Latin *utriculus* (small skin or leather bottle) in reference to the bladder. Each trap is partially water-filled, and has a door surrounded by sensitive hairs that direct prey to the opening. The trapdoor opens inwards upon irritation by a passing animal such as a mosquito larva. After the prey brushes against the trigger hairs, it is sucked in because of the release of negative pressure maintained inside the utricle, engorging several times its resting volume. Traps are connected to the plant *via* stolons, stalks or leaves. Plants may even be rootless.

After firing, the trap restores the negative pressure by removing water from the lumen until the original compressed shape is returned. After this process is completed, which lasts about 30 minutes, the trap is ready to fire again.

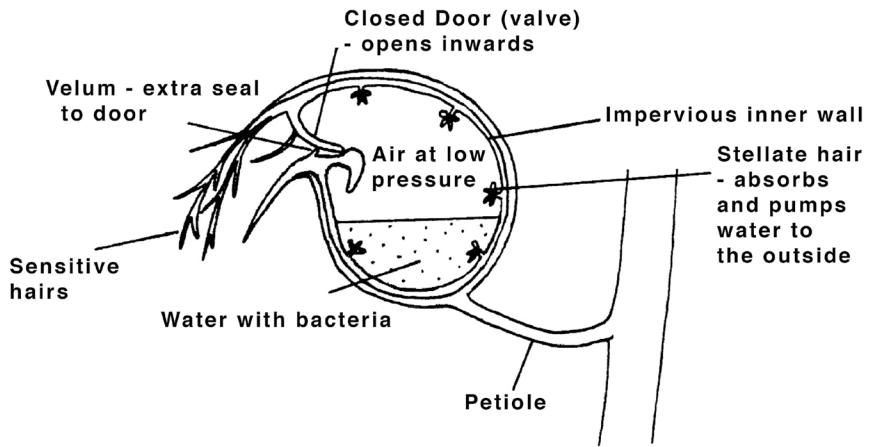


Fig. 4.6: (upper) *Utricularia menziesii*, 3 cm tall. (lower) Diagram of a longitudinal section through a *Utricularia* bladder. The trap is a hollow utricle, mostly two cells thick, partly filled with water, and under negative pressure. Traps are usually 1–4 mm long.