

AN ACCOUNT OF THE ANTENNAE-FLOWERED *UTRICULARIA*
OF NORTHERN AUSTRALIA¹

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Abstract: In northern Australia there grows a most remarkable group of 6 species of *Utricularia* with flesh-coloured flowers and an upper or lower corolla lip that has transformed into a pair of tall, erect antennae-like flower lobes. These characters are quite unusual for the genus, and there are numerous hypotheses as to the reasons for these adaptations, the most likely being sexual floral mimicry to attract a pollinator. The aim of this paper is to provide an overview of this highly unusual complex, which includes a botanical history and summarised treatments of each species to provide the reader with the key characters necessary to identify these taxa in the field.

Introduction

The genus *Utricularia* L. (Lentibulariaceae) contains approximately 250 monographed species worldwide (Taylor 1989; Fleischmann 2012, 2015; Lowrie 2014), with 88 of these found in Australia (Nunn 2022). In northern Australia there is a most remarkable group of 6 species, *Utricularia albertiana* R.W.Jobson & Baleeiro, *U. dunlopilii* P.Taylor, *U. capilliflora* F.Muell, *U. dunstaniae* F.E.Lloyd, *U. antennifera* P.Taylor and *U. lowriei* R.W.Jobson, that each, with flesh-coloured flowers, have an upper or lower corolla lip that has transformed into a pair of tall, erect antennae-like flower lobes. In *U. lowriei*, *U. antennifera*, *U. albertiana*, and *U. dunstaniae*, these appendages are formed by the lower lip of the corolla, whereas in *U. capilliflora* and *U. dunlopilii*, they arise from the upper lip of the corolla (Taylor 1989; Jobson 2013; Lowrie 2013).

These characters are quite unusual for the genus, and there are numerous hypotheses as to the reasons for these adaptations. Taylor (1979) suggests one can only conjecture that the two erect filamentous corolla lobes are connected in some way with pollination by some particular insect. Lowrie (1995, 2001), postulates that flowers of these species much resemble insects (sexual floral mimicry), suggesting that pollination may occur by pseudocopulation. Plachno *et al.* (2016) point out that flowers of sexually deceptive taxa generally possess a set of morphological and physiological characters that mimic their insect pollinators. Reut and Jobson (2010) through molecular studies show that those species having upper corolla appendages have arisen twice independently. The overall floral form in species sharing the filiform appendages, both upper- and lower-lobed, is strikingly similar, with all sharing apricot/flesh-coloured flowers, and the presence of filiform appendages of either type, corresponding strongly with the floral colour. This result provides evidence for Taylor's (1989) hypothesis that mimicry-driven sexual selection may have been a factor during the parallel evolution of filiform corolla lobes.

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Lowrie (1995 and 2001) makes some further interesting field observations, and these are supported by the author who has seen populations of these species in the Northern Territory in 2011, 2012, 2013, 2016, 2018, 2021, Cape York in 2014, and the Kimberley in 2016. Due to the colour and diminutive size of the flowers, they are extremely difficult to see during normal daylight hours and it takes the seasoned observer some time to adjust one's vision to find them. At sunrise and sunset, the angle of the sun is at approximately 15 degrees and the flesh-coloured antenna reflect the sunlight and glow a yellow-bronze colour whilst other low herbaceous plants are dark in colour and don't stand out. Insect activity is at its highest at these times of the day (Lowrie 1995) and further adaptations that position the flowers for maximum illumination, and their scapes somewhat in the background, give the appearance of being airborne, this is enhanced by the slightest gentle breeze making the flowers shimmer back and forward.

Botanical history

The botanical history of the antennae-flowered *Utricularia* dates back to the late 19th century and spans the 20th and early 21st centuries and includes some of the great botanical names of the past, Mueller, Lloyd, and Taylor.

Baron Ferdinand von Mueller published the first of the antennae-flowered *Utricularia*, *U. capilliflora* in 1891 (Mueller 1891). Mueller was appointed Government Botanist for Victoria by Governor Charles La Trobe in 1853 and in the same year, Mueller established the National Herbarium of Victoria (MEL). From 1857 to 1873, he was director of the Royal Botanic Gardens, Melbourne. He described many new plant species sent by botanists from other parts of Australia, notably from Maurice William Holtze in the Northern Territory. Holtze was the director of the Botanic Garden at Port Darwin and with the assistance of his son, Nicholas, collected many new and undescribed species from the Darwin and Arnhem Land area. One such collection by Nicholas Holtze from the Adelaide River, was described by Mueller as a new species, *U. capilliflora*. In his description, Mueller noted that this was one of the most delicate of all vascular plants and the two long hairlet like segments of the upper corolla were quite exceptional in the genus.

In order to extend his knowledge of Australian *Utricularia* species, Francis Ernest Lloyd examined all accessible specimens and in doing so he was able to describe four new species (Lloyd 1936), one of which being *Utricularia dunstaniae*. Baron Ferdinand von Mueller's collection at the National Herbarium, Melbourne, which contained the type specimen of *U. capilliflora*, also contained another specimen that von Mueller had labelled *U. capilliflora*, which turned out to be quite distinct. Collected by N. Holtze (*Holtze 1340*) along the Adelaide River, Northern Territory in 1891, this specimen had similar morphological characters to *U. capilliflora*. However, on close examination by Lloyd was found to have the two antenna-shaped lateral lobes arising from the lower corolla lip and the lower corolla lip was triangular shaped, in *U. capilliflora* these lobes arise from the upper lip. With these distinct differences Lloyd was able to describe this specimen as a new species, *U. dunstaniae*.

Peter Taylor, Kew Botanist, world authority on *Utricularia* and author of the most comprehensive monograph on the genus, made two trips to Australia (Taylor 1989), for 6 weeks in 1979 where he visited all the mainland states, and he returned in May 1980 to spend two weeks in the Northern Territory. These visits to Australia yielded two new species of antennae-flowered *Utricularia*. Whilst in the Northern Territory, Taylor was assisted by Clyde Dunlop, Curator of the Northern Territory Herbarium, to see most of the *Utricularia* native to that region. Taylor was also able to view Dunlop's collections and from *Dunlop 4737*, a collection from Little Nourlangie Rock, described

and later published (Taylor 1986) a new species of antennae-flowered *Utricularia*. This species he named *Utricularia dunlopii*, in honour of Clyde Dunlop. Clyde Dunlop also made extensive collections of plants in the Kimberley region of northern Western Australia, and another of his collections, *Dunlop 5320* from the Mitchell Plains was described and published by Taylor (1986) as *Utricularia antennifera*.

Allen Lowrie (1995) first mentioned a putative new species of antennae-flowered *Utricularia* as *Utricularia* species “Cape York” which he described from a single inflorescence collected by Ann G. Gunness, at Namaleta Creek, c. 90 km N of Weipa, (*AG 2306*, 11 Apr 1994; specimen held in Herbarium Lowrieianum, Perth). Although specimen *AG-2306* was poorly preserved, an interpretation of the inflorescence by Allen Lowrie suggested that this was a new species and would extend the range of antenna flowered *Utricularia* by approximately 1000 km from their Northern Territory locations. Lowrie’s suspicions of a new taxa and range extensions were confirmed by Richard Jobson who formally described this new species and named it in honour of Lowrie in 2013. He discovered it north of Cooktown whilst working on the rediscovery of *U. albiflora*. A further range extension was discovered in 2014, when on an ICPS field trip to the northern most point of Australia, Greg Bourke and Charles Clarke, found this taxon growing at Jacky Jacky and Sanamere.

The most recently described member of this complex is *Utricularia albertiana* (Jobson & Baleeiro 2018). In his monograph, Peter Taylor (1989) recognised the Kimberley form of *U. dunstaniae* (*Beauglehole 58874*) as conspecific with the type specimen from near Darwin, NT. In his description of the species, the corolla spur is described as narrowly scrotiform with apex bilobed, the lobes obtuse [= *U. albertiana*] or subacute [= *U. dunstaniae*]. Hence *U. albertiana* was previously thought to be a Kimberley form of the Northern Territory species *U. dunstaniae*. However, a recent molecular phylogenetic study (Jobson 2013; Jobson *et al.* 2018) that included specimens from two of the three known populations of *U. albertiana* and three of *U. dunstaniae* from the Darwin region, placed *U. albertiana* as strongly supported sister species to *U. antennifera*, while *U. dunstaniae* was placed sister to the Cape York endemic *U. lowriei*.

Taxonomy

The following are summarised treatments of each species to provide the reader with the key characters necessary to identify these taxa in the field. The author has drawn on the detailed descriptions of Lowrie (2014), Jobson (2013), and Jobson and Baleeiro (2018) as well as his own field observations.

Utricularia albertiana R.W.Jobson & Baleeiro 2018 (Fig. 1)



Figure 1: *Utricularia albertiana*, Theda Station, Kimberley, Western Australia. Photo R. Nunn.

Description: Small annual, affixed subaquatic herb. *Rhizoids* numerous. *Stolons* few. *Leaves* few, petiolate; lamina obovate or narrowly obovate, apex rounded. *Traps* few at base of peduncle, one or two at nodes of stolon, and singly on internodes, ovoid. *Inflorescence* erect, solitary 60–120 mm long; *Bracts* and *bracteoles* similar, basifixed, sparsely glandular, ovate with apex subacute, slightly gibbous at base. *Flowers* 1, 4–5 mm long (excluding erect appendages); *Corolla* reddish-brown to apricot; upper lip erect, obovate, strongly convex; lower lip 5-lobed with lateral pair filiform, erect, 40–50 mm long, of the three central lobes, two outer lobes absent, central lobe descending, subulate, 2–5 mm long, usually two or three times the length of the spur; palate glabrous, with raised rim; spur inflated, broadly scrotiform, mostly glabrous.

Etymology: The specific epithet honours Prof. Victor A. Albert, botanist and evolutionary biologist in the Department of Biological Sciences at the University at Buffalo, State University of New York.

Phenology: Flowering between February and April. Lowrie records this species also flowering in July to August in the dry season.

Distribution and ecology: Known from three locations in the Northern Kimberley region, Western Australia. The type location is at King Edward River, while a second collection site is c. 50 km to the west (*Dunlop 5320*), also Theda Station.

Grows in shallow pools on sandstone pavement and outcrops.

Notes: *Utricularia albertiana* was previously confused with *U. dunstaniae* from the Northern Territory and differs in having spur apex rounded/obtuse, central corolla lower lip lobe longer than the spur, calyx lower lip almost as long as the spur, and trap dorsal appendage usually present.

Utricularia antennifera P.Taylor 1986 (Fig. 2)

Description: Small annual herb, occasionally perennial, terrestrial or affixed aquatic. *Rhizoids* numerous, *Stolons* few. *Leaves* usually 1 to 4 arising from peduncle bases and from each stolon node; lamina narrowly obovate, apex rounded, petiolate. *Traps* white-translucent, ovoid. *Inflorescence* erect, arising at random along stolons, 6–12 cm long. *Bracts* and *bracteoles* similar, basifixed, ovate, apex rounded. *Flowers* solitary 3–3.5 mm long (excluding 2 very long semi-erect appendages). *Corolla* main body fleshy looking; lower lip adaxial surface pale yellow, abaxial surface similar, 5-lobed, 2 upper appendages antennae-like, bearing a prominent tooth-like appendage at their base, that together surround, but remain well gapped and not touching each other at upper part of open throat (leading to stigma and anthers), very long semi-erect appendages 2.5–5.5 cm long, upper lip pale yellow.



Figure 2: *Utricularia antennifera*, Theda Station, Kimberley, Western Australia. Photo R. Nunn.

low, oblong, apex rounded or emarginate. *Palate* similar colour to corolla, lower part of throat bearing a crenate raised rim, papillose. *Spur* positioned at 80 degrees to lower corolla lip lobes, similar colour to corolla, from base conical, constricted near middle, then soon dilated into an inflated transversely ellipsoidal figure with apex rounded, slightly curved forwards.

Etymology: The epithet *antennifera* is Latin for “antennae-bearing” in reference to its long lateral, semi-erect, antennae-like appendages towering above the main body of the flower.

Phenology: Collected in flower in February and March.

Distribution and ecology: Kimberley region: Mitchell Plateau; near Theda Station Homestead; Beverley Springs Station.

Grows in shallow depressions in wet, black, silty sand skeletal soils over sheet sandstone on the margins of creeks and wet sand on the edges of large, wet season depressions. In gravel or sand over basalt and sandstone in shallow water at low altitude.

Utricularia capilliflora F.Muell. 1891 (Fig. 3)

Description: Small annual to perennial herb, an affixed aquatic. *Rhizoids* numerous, *Stolons* few. *Leaves* usually 1 to 2 arising from peduncle bases and from each stolon node, narrowly ovate, apex rounded, petiolate. *Traps* white-translucent, ovoid. *Inflorescence* erect, arising at random along stolons, 5–8 cm long. *Bracts* and *bracteoles* similar, basifixed, ovate, apex rounded, bases gibbous. *Flowers* solitary, rarely up to 3 on a scape 4.5–4.6 mm long, (excluding 2 very long semi-erect appendages); *Corolla* main body fleshy looking, pale yellow; lower lip adaxial surface pale yellow, abaxial surface similar, 5 lobed, equally extended over an angle of 140 degrees, subulate, upper lateral pair set 20 degrees below horizontal, each bearing a prominent tooth-like appendage at their base that together are nearly surrounding, but are well gapped and not touching each other at upper part of open throat (leading to stigma and anthers), next lateral pair set 45 degrees at either side of central line, lower lobe shorter and set on central line; upper lip pale yellow, triangular at base, forming basal portions of 2 upper antennae-like appendages, crossed over each other near their base, 1.5–2.5 cm long. *Palate* similar colour to corolla, lower part of throat bearing a raised rim. *Spur* positioned at 60 degrees to lower corolla lip lobes, similar in colour to corolla, from base conical, constricted near middle, then soon dilated into an inflated scrotiform figure.

Etymology: The epithet, *capilliflora*, is from the Latin *capillus* (hair-like) and *floris* (flower), in reference to its long, lateral, semi-erect, antennae-like appendages, which arise from the upper lip of the corolla and tower above the main body of the flower, as well as its 5, hair-like, lower lip appendages.

Phenology: Flowers March to May.

Distribution and ecology: Northern Territory. Common in the Darwin region: Howard Springs; Girraween; Noonamah; Freds



Figure 3: *Utricularia capilliflora* Howard Springs, Northern Territory. Photo R. Nunn.

Pass; Humpty Doo; and scattered locations eastwards along the Arnhem Highway to Jabiru, at the foot of the Arnhem Land escarpment.

Grows in damp sand at the edge of creeks and on sand plains in open vegetation at low altitude.

Utricularia dunlopii P.Taylor 1986 (Figs. 4, 7, and front cover)

Description: Small annual to perennial herb, terrestrial, an affixed aquatic when not flowering. *Rhizoids* numerous, *Stolons* few. *Leaves* usually 1 to 6 arising from peduncle bases and from each stolon node; lamina narrowly obovate-apex rounded, petiolate. Traps white-translucent, ovoid. *In-florescence* erect, arising at random along stolons, 8–10 cm long. *Bracts* and *bracteoles*, similar, basisolute, upper parts ovate, apex acute. *Flowers* solitary 2.5–3 mm long, (excluding 2 very long semi-erect appendages), and commonly branched to support 2–3 flowers; *Corolla* main body fleshy looking, pale pinkish bronze, lower lip adaxial surface pale pinkish bronze, abaxial surface similar, 3-lobed, equally extended over an angle of 100 degrees, subulate, upper lateral pair set below horizontal at 30 degrees, each flared at their base and together forming part of palate on lower part of open throat (leading to stigma and anthers), lower lobe much shorter and set to one side of central line; upper lip pale pinkish bronze, forming basal portions of 2 upper antennae-like appendages, 1.5–2 cm long. *Palate* similar colour to corolla, lower part of throat bearing a raised rim. *Spur* positioned parallel to lower corolla lip lateral lobes, similar in colour to corolla, from base conical, constricted near middle, then soon dilated into an inflated compressed ovoid figure, slightly curved forwards.



Figure 4: *Utricularia dunlopii*, Howard Springs, Northern Territory. Photo R. Nunn.

Etymology: *Utricularia dunlopii*, named in honour of Clyde Dunlop who, by his numerous and careful collections of northern Australian *Utricularia*, has contributed enormously to our knowledge of these plants and who also, by his generous assistance and carefully planned programme, enabled Peter Taylor to see most of the Northern Territory species in the brief space of two weeks in May 1980.

Phenology: Flowers February to May.

Distribution and ecology: Western Australia and Northern Territory. In Western Australia known from a few collections from the Mitchell and King Edward River region and in Northern Territory near Darwin and several locations from the Arnhem Land Plateau.

In the eastern and western limits of its range, grows in damp depressions in sandstone pavement but near Darwin in damp sandy ground in swamps in open vegetation.

Notes: *Utricularia dunlopii* is easily distinguished from its five relatives by its scapes, which are the only in the complex that are commonly multi-flowered

Utricularia dunstaniae F.E.Lloyd 1936 (Fig. 5)

Description: Small annual to perennial herb, terrestrial or affixed aquatic. *Rhizoids* numerous, *Stolons* few. *Leaves* usually 1 to 2 arising from peduncle bases and from each stolon node; lamina narrowly obovate-apex rounded. Traps white-translucent, broadly ovoid. *Inflorescence* erect, arising at random along stolons, 6–12 cm long. *Bracts* and *bracteoles* similar, basifixed, ovate, apex rounded. *Flowers* solitary 4.6–5 mm long, (excluding 2 very long semi-erect appendages); *Corolla* main body fleshy; lower lip adaxial surface pale yellow, abaxial surface similar, 3–5-lobed, 2 upper appendages flesh pink, antennae-like, bearing a prominent tooth-like appendage at their base well-spaced and not touching each other and positioned either side of upper part of open throat (leading to stigma and anthers), very long semi-erect appendages, 1.5–4 cm, gradually tapering towards apex, of remaining 3 lobes, 2 lateral lobes are often absent or very short and variable, central lower lobe is always present, narrowly triangular; upper lip pale yellow, circular, apex mostly rounded sometimes emarginate, positioned above upper calyx lobe. *Palate* similar colour to corolla lower lip, lower part of throat bearing a prominent raised rim, papillose. *Spur* positioned at 40 degrees to lower corolla throat rim, beige and flesh pink in colour, from base conical, constricted near middle, then soon dilated into an inflated scrotiform figure.

Etymology: The epithet, *dunstaniae*, honours Marjorie Lillian Stewart Dunstan (née Carnell) wife of William Dunstan (1895–1957), army officer and Victoria Cross recipient, manager of the Herald in Melbourne, Victoria. Lloyd said of Mrs. Dunstan “...whose sympathetic attitude has done much to foster the love and appreciation of natural history.”

Phenology: Collected in flower in March to May

Distribution and ecology: Northern Territory: near Darwin - Howard Springs and McMinns area; Stuart Highway ca. 38.4 km S of Darwin; also, a solitary record from near Jabiru at the foot of the Arnhem Land Escarpment.

Grows in wet sand, often in shallow water, in open vegetation and in sandy, skeletal soils over sheet sandstone on the margins of rivulets, creeks and rivers.

Notes: Of all the antennae-flowered *Utricularia*, this species is the most difficult to locate in the field and has proven elusive on 6 attempts by the author to locate and photograph.

Utricularia lowriei R.W.Jobson 2013 (Fig. 6)

Description: Small probably annual, terrestrial or affixed subaquatic herb. *Rhizoids* numerous, *Stolons* few. *Leaves* few, two or three from base of peduncle and 1 from stolon internodes, peti-



Figure 5: *Utricularia dunstaniae*, Howard Springs, Northern Territory. Photo G. Bourke.



Figure 6: *Utricularia lowriei*, Sanamere Lagoon, Queensland. Photo R. Nunn.

olate; lamina narrowly obovate. *Traps* several at base of peduncle and one at nodes of stolon, ovoid. *Inflorescence* erect, solitary 40–70 mm long; *Bracts* and *bracteoles* similar, basifixed, ovate with rounded apex. *Flowers* 1, 2–5 mm long (excluding erect appendages). *Corolla* reddish-brown to apricot; lower lip 5-lobed with lateral pair filiform, erect 9–15 mm long, three central lobes descending, subulate/filiform, mostly equal length, usually twice the length of the spur; *Spur* scrotiform, glabrous, from a cylindrical base, longer than the calyx lobe, apex bilobed with each lobe more or less rounded.

Etymology: The specific epithet honours the late botanist and naturalist Allen Lowrie (1948-2021), who has greatly advanced the study of *Drosera*, *Stylidium*, and *Utricularia*.

Phenology: Flowers recorded in July.

Distribution and Ecology: Type location north of Cooktown and the northern most point of Cape York, Sanamere and Jacky Jacky.

Found growing in shallow water at edge of depression on deep sand.



Figure 7: *Utricularia dunlopiana* growing in its typical sandstone seepage habitat on the Arnhem Plateau, Northern Territory. Photo Thilo Krueger

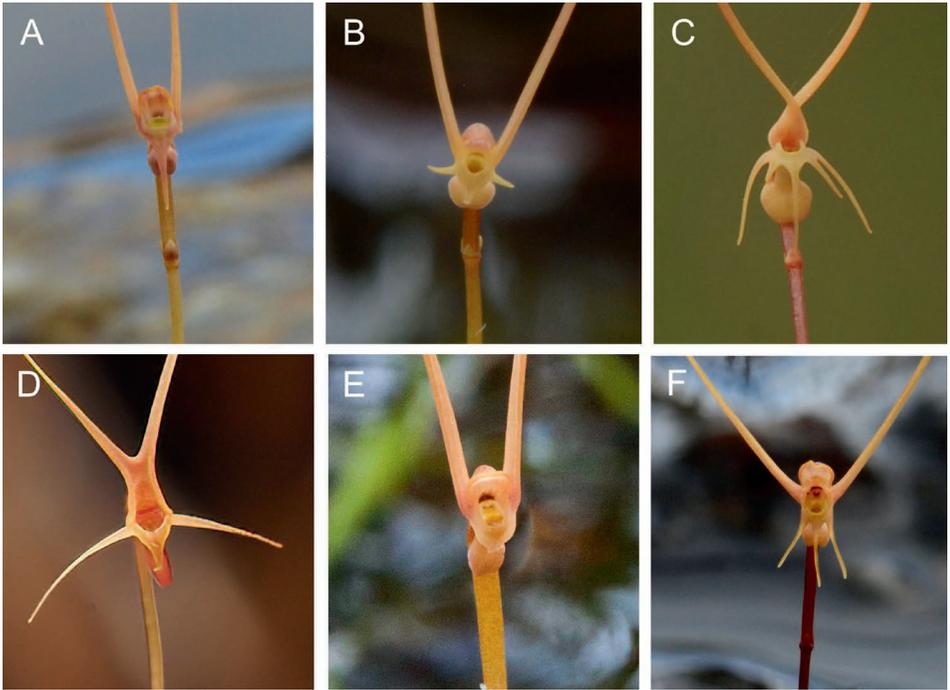


Figure 8: Detail of flowers (A) *Utricularia albertiana*, (B) *U. antennifera*, (C) *U. capilliflora*, (D) *U. dunlopilii*, (E) *U. dunstaniae*, (F) *U. lowriei*. Photos (A)-(D), (F) R. Nunn, (E) G. Bourke.

Key to the Australian antennae-flowered *Utricularia* species (modified from Taylor 1989 and Jobson 2013).

- 1a. Corolla with 2 capillary lobes arising from the corolla upper.....2
- 1b. Corolla with 2 capillary lobes arising from the corolla lower lip.....3
- 2a. Corolla lower lip 5-lobed (Fig. 8C).....*U. capilliflora*
- 2b. Corolla lower lip 3-lobed (Fig. 8D).....*U. dunlopilii*
- 3a. Three central lower lip lobes, central lobe longer than the spur.....4
- 3b. Three central lower lip lobes reduced or deltoid, shorter than the spur5
- 4a. Two outer central lower lip lobes filiform, longer than the spur (Fig. 8F)..... *U. lowriei*
- 4b. Two outer central lower lip lobes absent (Fig. 8A)*U. albertiana*
- 5a. Dorsal bladder-trap appendage always absent (Fig. 8E)*U. dunstaniae*
- 5b. Dorsal bladder-trap appendage long and filiform (Fig. 8B)..... *U. antennifera*

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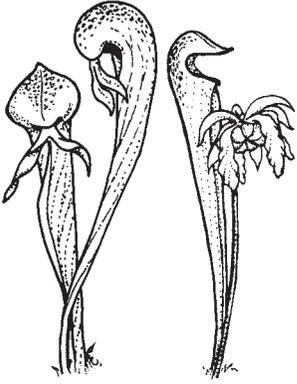
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Front Cover: Flower of *Utricularia dunlopiae*, Howard Springs, Northern Territory, Australia. Photo by Richard Nunn. Article on page 133.

Back Cover: Flower of *Pinguicula zecheri* 'Faulisi'. Photo by Howard Bramble. Article on page 156.

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