

WHEN THREE BECOME TWO: *DROSERA COALARA* LINKS
DROSERA CITRINA WITH *DROSERA NIVEA*

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The pygmy sundews (*Drosera* section *Bryastrum*) are the second-largest group of Australian *Drosera* in terms of species number following the tuberous sundews. According to the latest revisions (Fleischmann *et al.* 2018; Robinson *et al.* 2018) they currently comprise 51 species in southwest Western Australia and six named natural hybrids (Lowrie 2014; Lowrie *et al.* 2017). Within the pygmy *Drosera*, a wide range of flower colors can be found, ranging from pure white, various shades of pink, metallic orange, and red to yellow colors, quite often with bi- or rarely even tricolored petals (Lowrie 1989; Robinson *et al.* 2018). The color combination of lime yellow petals with white base has thus far been considered to be unique to *D. citrina* (Lowrie & Carlquist 1992; Lowrie 2014; Lowrie *et al.* 2017).

When first discovered in flower, *Drosera citrina* was described by Lowrie (1989; initially mistaken for *D. rechingeri*, until correctly classified by Lowrie & Carlquist 1992) to be one of the most unique pygmy *Drosera* due to its striking flower color. The white-flowered *D. nivea* was denoted as its closest relative by Lowrie & Carlquist (1992), but considered to represent a variety of *D. citrina* by Schlauer (1996) – the latter classification was not adopted by most *Drosera* taxonomists (e.g., Lowrie 1998, 2014; Lowrie *et al.* 2017; Fleischmann *et al.* 2018). With the description of *D. coalara* by Lowrie (2014), another closely related taxon was added

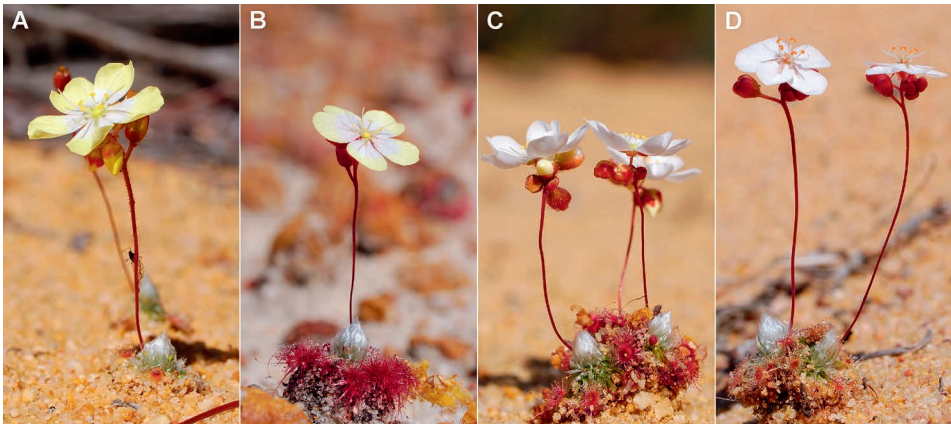


Figure 1: Comparison of *Drosera citrina* (Moora, A), *D. coalara* (from two different localities NE of Badgingarra, B, C), and *D. nivea* (Coorow, D). Photos: Thilo Krueger.



Figure 2: Sympatric occurrence of white- and yellow-flowered color morphs of *Drosera coalara*, northeast of Badgingarra, Western Australia. Photo: Thilo Krueger.

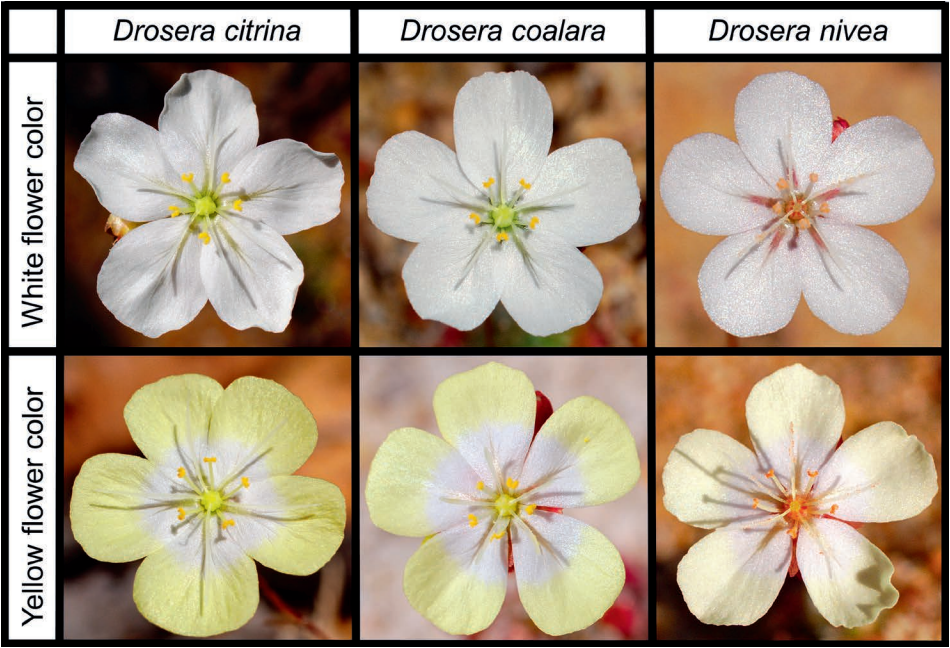


Figure 3: Comparison of white- and yellow-flowered color morphs of *Drosera citrina*, *D. coalara*, and *D. nivea*. *Drosera citrina*: both from Moora; *D. coalara*: both northeast of Badgingarra; *D. nivea*: top from Coorow, bottom southwest of Coorow. Photos: Thilo Krueger.

to this affinity of species from the northern sand plains of southwest Western Australia (Fig. 1). At the time of its description, *D. coalara* was considered to be entirely white-flowered, just like *D. nivea*. Expeditions and field work by the first author in Western Australia revealed not only additional localities of the white-flowered variant of *D. citrina* (one of them already known to Lowrie (1989: 154): “An all-white-flower form of this species occurs at one location near Moora.”), but also found white- and yellow-flowered *D. coalara* in mixed populations (Fig. 2), and surprisingly also yellow-flowered populations of *D. nivea*, hence all three species are now known to consist of both white- and yellow-flowered individuals (Fig. 3). Therefore, the diagnostic characters delimiting these three species were re-investigated in the light of the new populations and data discovered, and some characters such as stipule shape and flower number as described by Lowrie (2014) were examined on a wider range of specimens and populations (including the type localities for all three taxa, as well as the type specimens).

Distribution and Habitats

All three taxa are confined to the sand plains and heathlands between Coorow and Gingin in southwest Western Australia (Fig. 4). *Drosera citrina* only occurs in deep yellow sands in open *Banksia* forests (or rarely in heathland) on the Dandaragan Plateau between Moora and Gingin. It is currently known from ca. 10 populations (Fig. 4). White-flowered plants of *D. citrina* from near Moora were first reported by Lowrie (1989; erroneously as “*D. rechingeri*” at the time). *Drosera nivea* inhabits deep white to beige sands on sand-plains among low heath vegetation (Lowrie 1998, 2014), and it has been recorded from seven sites between the towns of Coorow and Watheroo (Fig. 3). In Lowrie (2014), the range of *D. nivea* was erroneously illustrated ca. 100 km to the east of its actual range. *Drosera coalara* was only known from two localities according to the original description, namely the type locality northeast of Badgingarra, and a small roadside population west of Mogumber, which is ca. 96 km distant to the south (Lowrie 2014). According to the authors of the present work, the Mogumber population reported by Lowrie likely represents white-flowered *D. citrina* due to their relatively long peduncles (curiously, the Mogumber site also has not been included in the species’ range map by Lowrie 2014). This would leave only the *locus classicus* for *D. coalara*. In September 2019, the first author of this work discovered at least seven additional populations of *D. coalara*, most of which lie within the ca. 100 km diameter circle that was drawn around the type locality of *D. coalara* to illustrate the species’ distribution in Lowrie (2014). Two of these populations were, however, found near Wannamal, more than 100 km south of the type locality. *Drosera coalara* grows in a wide range of different heathland habitats, including deep yellow, beige, and gray sands and even almost pure laterite (pers. obs; Lowrie 2014).

Drosera citrina and *D. nivea* show allopatric distribution (their ranges do not overlap, both species are separated geographically by ca. 50 km between the closest localities, Fig. 4), *D. coalara* is parapatric with *D. nivea* (the ranges touch in a narrow border zone but do not overlap much) and sympatric distribution with *D. citrina*. The ranges of all three species seem to represent a continuum (Fig. 4) – and it might be better to consider only two taxa, *D. citrina* in the south, *D. nivea* in the north, both mediated by transitional forms in-between, which have been described as *D. coalara*. In the range border zones, transitional forms occur (especially between *D. nivea* and *D. coalara*), but we did not observe sympatric occurrence of two or more of the above-mentioned three taxa.

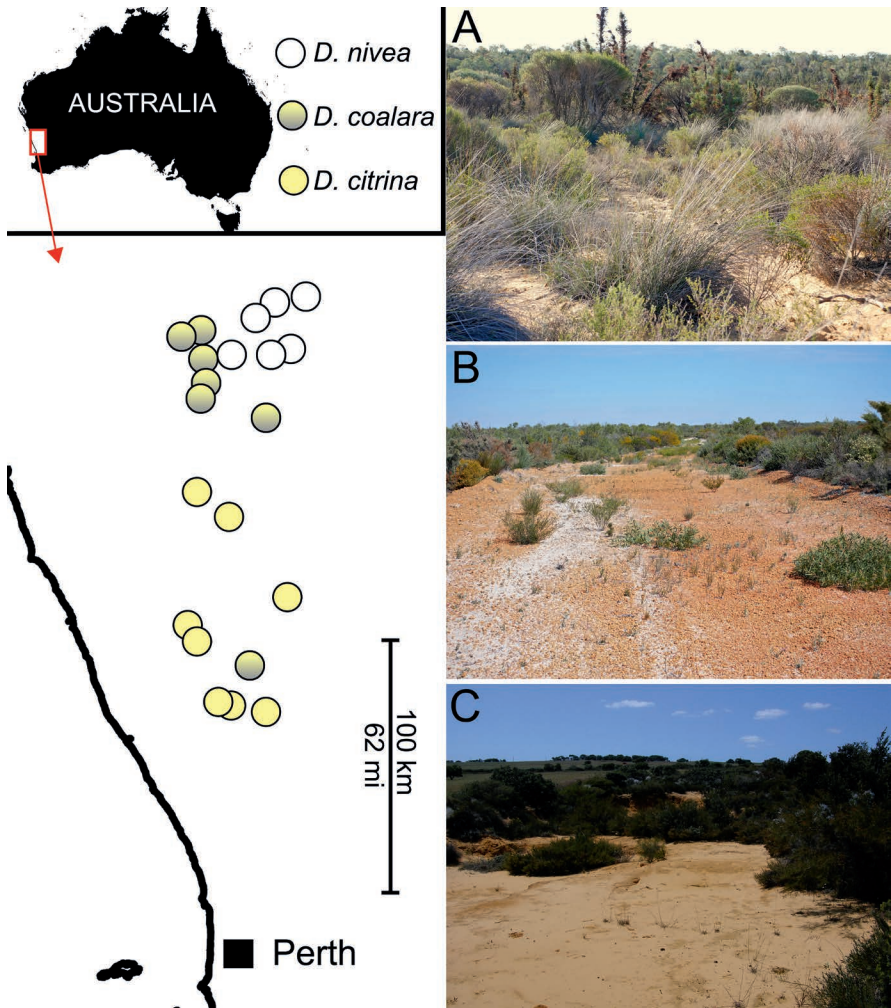


Figure 4: Distribution map based on Atlas of Living Australia (2019), Lowrie *et al.* (2017) and personal observations. All localities have been visited and confirmed by the authors of this work. Instead of three distinct species, the range can also be interpreted as a grade from *D. citrina* (predominantly yellow flowers) in the south to *D. nivea* (predominately white flowers) in the north, geographically and morphologically linked by *D. coalara* in the middle. Right: typical habitats of *D. nivea* (A, near Coorow), *D. coalara* (B, near Badgingarra) and *D. citrina* (C, near Regans Ford). Photos: A, B by Thilo Krueger, C and Map by A. Fleischmann.

Discussion

Pollinators apparently do not distinguish between yellow- and white-flower color morphs – so why should botanists do so and call them different species?

Both yellow- and white-flowered individuals of *D. coalara* were found intermixed within the same population at all eight sites (including at the type locality) with varying percent-



Figure 5: This white-flowered morph of *D. coalara* (right) was visited – and very likely also pollinated – by the same individual of the bee-fly *Choristus* (Diptera: Bombyliidae; genus identified by X. Li) just four seconds after floral visit at a yellow morph (left). Note the *Drosera* pollen sticking to its left foreleg (arrow) from the first flower visit, enabling potential cross-pollination. Photos: Thilo Krueger.

age distributions of flower colors. Since all plants were flowering at the same time, and without any morphological difference of the plants apart from flower color (T. Krueger, pers. obs. 2019; Figs. 2, 5), these can be considered color morphs of one and the same species (not even worth being recognized taxonomically on forma rank). A pollinating bee-fly of the genus *Choristus* (family Bombyliidae; genus identified by X. Li) was observed by the first author to freely choose between the yellow and white flowers, without avoiding any of them, enabling cross-pollination (Fig. 5). Therefore, the mixed petal colors of *D. coalara* certainly belong to the same population's gene pool. Populations containing different color morphs are not unusual among flowering plants in general, and in *Drosera* in particular (e.g., most of the woolly sundews of *D. sect. Lasioccephala* occur in white- and pink-petalled individuals within the same population; pers. obs.). Intraspecific flower color variation (as observed by the human eye) was often found to be effectively invisible to specific pollinators in other plants, hence will persist in the population by genetic drift/neutral evolution (Paine *et al.* 2019).

Different small beetles have been observed by the authors as floral visitors of *D. citrina* and *D. nivea*, the latter species additionally shows signs of myophily (pers. obs.). Populations of *D. citrina* are predominately yellow-flowered, with occasional occurrence of white-flowered individuals among the populations. We did not find entirely white-flowered populations of *D. citrina*. In fact,

Table 1. Taxonomic comparison between *Drosera citrina*, *D. coalara*, and *D. nivea*. Data based on Lowrie & Carlquist (1992), Lowrie (1989, 1998, 2014), and own observations from the field and from cultivation. Note the wide morphological overlap of *D. coalara* with the two other species, especially with *D. citrina*.

character	<i>Drosera citrina</i>	<i>Drosera coalara</i>	<i>Drosera nivea</i>
peduncle length	1.7-4.5 cm	1.5-3.0 cm	2.5-3.5 cm
number of flowers per scape	(4)6-12(-16)	(2)3-6(-10)	(2)4-6(-10)
petal color	predominantly white with yellow margin, rarely pure white	white or white with yellow margin	white, occasionally white with pale yellow (cream) margin
ovary color	yellowish-green	yellowish-green	pale red, rarely green
pollen color	yellow	yellow	orange
habitat	yellow sand on heathland	yellow, beige or gray sand, rarely laterite	deep beige sands on sand plains and heathland

***Drosera citrina* Lowrie & Carlquist**, Phytologia 73(2): 99 (1992)

=*Drosera rechingeri* auct. non A.Strid, Carniv. Pl. Austral. 2: 154-157, xviii, xxxiv (1989).

=*Drosera chrysochila* Schlauer, Palmengarten 1992(3): 190 (1992).

=*Drosera coalara* Lowrie & Conran, Carniv. Pl. Austral. Magnum Opus 3: 1269 (2014), **syn. nov.**

***Drosera nivea* Lowrie & Carlquist**, Phytologia 73(2): 104 (1992)

=*Drosera citrina* var. *nivea* (Lowrie & Carlquist) Schlauer, Carniv. Pl. Newslett. 25(3): 72 (1996).

the white-flowered forms were extremely rare within the populations. The first author observed less than 10 white-flowered *D. citrina* amongst tens of thousands of yellow-flowered plants at a population near Moora. While most populations of *D. nivea* are predominantly white-flowered, intermixed and even purely yellow-flowered populations have been found by the first author.

Three species, two, or a single variable one?

Given the new data on variation and range overlap of the three taxa, the question arises how to best classify them – especially in the case of *D. citrina* and *D. nivea*. Intraspecific classification might be more appropriate in this case than two separate species. Schlauer (1996) suggested to distinguish the two taxa on variety rank – however, in his concept that would suggest sympatry (which has never been observed so far), and so the rank of subspecies (i.e., allopatric distribution) might be more appropriate. However, in the present work, we distinguish both taxa on species rank, with *D. coalara* treated as conspecific with *D. citrina*. We do so because typical plants of *D. citrina* and *D. nivea* can still be reliably separated based on habitat, distribution range, and few morphological characters (see also Table 1).

Lowrie and Conran (1992) and Lowrie (1998, 2014) consider the pedicel length to be a key character to delineate *D. citrina* from *D. nivea* (pedicel length 2.5-3.0 mm in *D. citrina* vs. 1.5-2.0 mm in *D. nivea*). Although *D. nivea* at its type population near Coorow has relatively longer pedicels than *D. citrina* from the southern part of its range, in a greater picture, the pedicel length of all known populations (including *D. coalara*: pedicel length 1.0-1.5 mm sensu Lowrie 2014) shows



Figure 6: The peduncle and also pedicel length of *D. coalara* is extremely variable, even within the same population. The left and the right individuals were found less than 10 m apart, the one with shorter scapes at an area much more exposed to full sun. Photos: Thilo Krueger.

much variation and size overlap (Figs. 1, 6). Therefore, we do not consider this character to be of taxonomic value to tell apart these species.

Drosera nivea often has notably longer peduncles than *D. coalara* and *D. citrina* (pers. obs.), however especially the latter has more flowers (up to 16, compared to 4-6 (rarely up to 10) flowers in *D. nivea*; Lowrie 2014; however, the total number of flowers per scape in *D. citrina* has some geographic bias, with populations in the south bearing more flowers per scape, often 10-14, compared to mostly 6-8 flowers in northern populations), so that the total height/length of the flower scapes is similar in both species. However, both species frequently develop a second inflorescence, which is shorter in height and fewer-flowered – hence distinguishing features given here in Table 1 are based on the season's primary inflorescence. *Drosera coalara* generally produces the shortest peduncles of the three species (Fig. 1), although peduncle length is quite variable in that taxon (even within the same population). Some individuals were observed to produce relatively long scapes, and hence closely resemble *D. nivea* except for ovary and pollen color (compare Fig. 1D with Fig. 6 left), while less than 10 m away plants with much shorter peduncles occurred (Fig. 6). Notably, individuals growing in more exposed parts of the habitat generally produced shorter and more reddish peduncles.

Lowrie (2014) describes upward-curved styles as a diagnostic feature of *D. coalara* (in contrast to the horizontally spread styles of *D. citrina* and *D. nivea*). However, horizontally spread styles

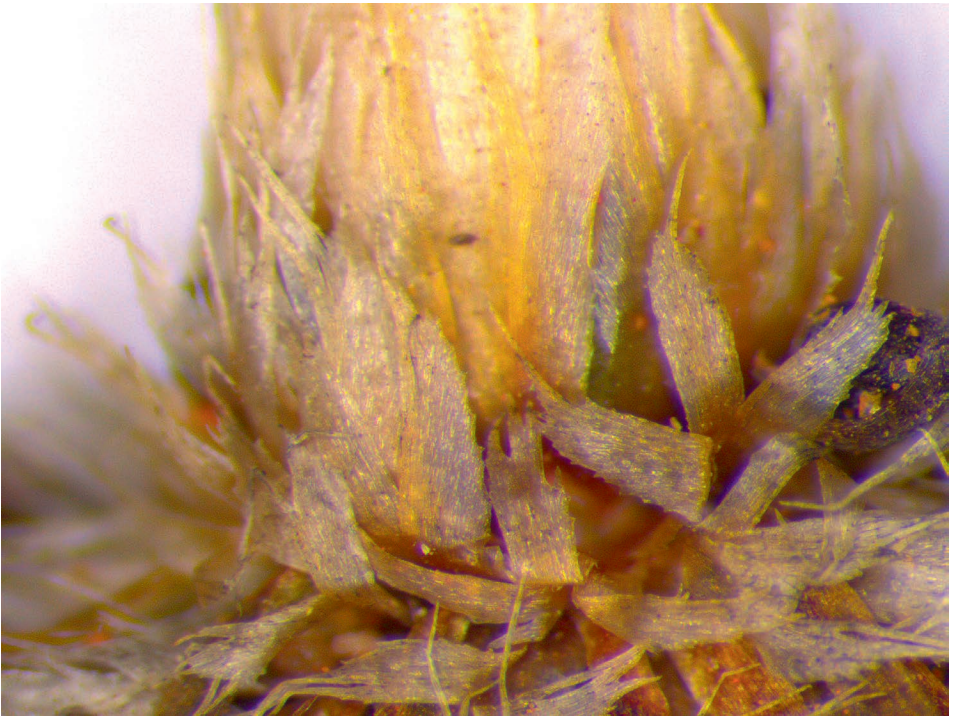


Figure 7: Close-up of the stipules from the type material of *D. coalara* (MEL2425943; isotype). Photo: Alastair Robinson.

(identical to those of the other two species) were observed in all populations of *D. coalara* studied (including at the *locus classicus*), and such are also pictured on the majority of habitat photographs of the species in Lowrie (2014: 373 figs. A, C & F). Only a single photograph in Lowrie (2014: 373 fig. D) depicts upward-curved styles. The first author occasionally observed upward-curved styles in a few individuals in any population of *D. coalara*, *D. citrina*, or *D. nivea* visited, often in freshly opened or senescent flowers. Hence this might not represent a stable feature, but rather a transitional stage during anthesis (see Back Cover).

The shape of the dome-shaped stipule bud (especially during dormancy) has been used by Lowrie (2014) as a further character to delimitate *D. citrina* from *D. nivea* (and *D. coalara*). Indeed, *D. citrina* usually has a much broader, smoother stipule bud compared to the more narrow, ovoid and bristly appearance of the stipule buds of *D. coalara* and *D. nivea*. However, this feature was not observed to be consistent as within each population of *D. citrina* some individuals produced the same type of stipule bud as the other two taxa. Likewise, some plants of *D. coalara* (even at its type locality) possessed a broad and smooth stipule bud extremely similar to *D. citrina*.

Lowrie (2014) highlighted the stipules of *D. coalara* to be notably different from those of *D. citrina* and *D. nivea*, with the former having stipules with very short apical laciniae, while those of the other two species are long-laciniate. However, the present authors have found stipules of *D. coalara*, including those from the type material (Fig. 7), not to match those illustrated in Lowrie (2014: 370-373). Instead they are identical to those of *D. citrina* and *D. nivea* – these three taxa cannot be distinguished based on stipule characters (Fig. 8), in contrast to the diagnosis given by



Lowrie (2014). Additionally, the shape and size of the stipules in most pygmy *Drosera* varies with the seasonal growth cycle, with stipules of dormant stipule buds or during gemmae production often being notably different from those produced during active growth (pers. obs.) – hence it is critical to document the stipules of the entire growth cycle, and compare among different populations of the same species, to get a clear picture of the individual ontogenetic and the intraspecific variation. Finally, the characters of petiole shape in section and lamina outline as mentioned by Lowrie (2014: petiole in section lenticulate and lamina more or less orbicular in *D. coalara*; petiole in section oblong with longitudinal ridges and lamina orbicular or elliptic in *D. citrina*; petiole in section depressed obovoid and lamina elliptic in *D. nivea*) were found to be variable within a population and even a given individual depending on the respective leaves and time observed (pers. obs.), and generally identical in all three taxa at the same developmental stage of the seasonal growth cycle. This leaves no reliable vegetative character to tell apart *D. citrina* from *D. nivea* in sterile specimens, both can only be distinguished with certainty based on flower characters (see above and Table 1).

As all major morphological characters of *D. coalara* fall within the observed variation of *D. citrina* (see Table 1), we consider both taxa to be conspecific, with *D. coalara* representing a heterotypic synonym of *D. citrina*. There is also significant morphological overlap with *D. nivea*, but that species can be distinguished from *D. citrina* (including *D. coalara* and regardless of color morph) by its orange pollen (vs. yellow pollen in *D. citrina/D. coalara*), usually longer peduncles and a mostly pale red ovary (vs. ovary always greenish-yellow; see Table 1 and Figs. 1, 3). In cultivation, if kept under identical growing conditions, *D. nivea* (plants from near Coorow are most frequently grown) also flowers notably earlier than *D. citrina*, usually 1-2 months ahead, leaving little or no overlap in flowering time, with *D. citrina* usually opening its first flowers when all those on the scapes of *D. nivea* are already spent (pers. obs.). However, their phenology in the wild does not differ as much as in cultivation, and all three taxa have been observed in full bloom in Western Australia by the first author in mid-September 2019. *Drosera nivea* from near the type locality and *D. citrina* from Moora both had opened their third or fourth (on average) sequential flower on the scape at the time (T. Krueger, pers. obs.). However, at least the more southern populations of *D. citrina* (e.g. those near Gingin) appear to exhibit a more extended anthesis time, flowering at least until mid-October and also bear considerably more flowers per inflorescence (pers. obs.).

Figure 8: (facing page): Comparative close-up images of stipules from different populations of *D. citrina* (A-F), *D. nivea* (G-L), and *D. coalara* (M-X). Stipule shape is very variable in all three taxa and it is thus impossible to delineate species based on this feature. A: *D. citrina*, Gingin, October 2014; B: *D. citrina*, Gingin, October 2014; C: *D. citrina*, Mogumber, September 2019; D: *D. citrina*, Moora, June 2019; E: *D. citrina*, Moora, September 2019; F: *D. citrina*, Moora, September 2019; G: *D. nivea*, Coorow 1, October 2014; H: *D. nivea*, Coorow 1, October 2014; I: *D. nivea*, Coorow 2, September 2019; J: *D. nivea*, Coorow 2, September 2019; K: *D. nivea*, SW of Coorow, September 2019; L: *D. nivea*, SW of Coorow, September 2019; M: *D. coalara*, locus classicus, June 2019; N: *D. coalara*, locus classicus, June 2019; O: *D. coalara*, locus classicus, September 2019; P: *D. coalara*, locus classicus, September 2019; Q: *D. coalara*, Locality 1, September 2019; R: *D. coalara*, Locality 1, September 2019; S: *D. coalara*, Locality 1, September 2019; T: *D. coalara*, Locality 1, September 2019; U: *D. coalara*, Locality 2, September 2019; V: *D. coalara*, Locality 3, September 2019; W: *D. coalara*, Locality 4, September 2019; X: *D. coalara*, Locality 5, September 2019. All photos by Thilo Krueger.

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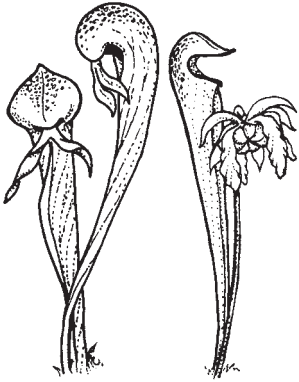


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Front Cover: Traps of *Genlisea hispidula* growing through a plastic mesh. Photo by Rita Corino. Article on page 39.

Back Cover: *Drosera coalara* growing in yellow sand northeast of Badgingarra, Western Australia. Note the variability of style positions in the different flowers (left individual with upward-curved styles, middle with horizontal styles, right one somewhat in-between). Photo by Thilo Krueger. Article on page 6.

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