

Article



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A new species of *Drosera* section *Arachnopus* (Droseraceae) from the western Kimberley, Australia, and amendments to the range and circumscription of *Drosera finlaysoniana*

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Abstract

A new annual species of *Drosera* section *Arachnopus*, *Drosera margaritacea*, from the western Kimberley region (Western Australia) is described and illustrated, including detailed comparisons with the morphologically most similar species, *D. finlaysoniana*. The latter name is lectotypified here. The global range of *D. finlaysoniana* is provided, including a doubtful first record for Thailand, while the species, in contrast with statements made in some published references, does not occur in India, Laos, Cambodia and the Philippines. Additionally, the first record from Indonesia of the frequently misidentified *D. aquatica* is reported.

Keywords: carnivorous plants, Indochina, lectotypification, non-core Caryophyllales, Nepenthales, taxonomy

Introduction

Drosera Linnaeus (1753: 281) is a genus of herbaceous carnivorous plants of the family Droseraceae Salisbury (Nepenthales or non-core Caryophyllales). It is the largest carnivorous plant genus with ca. 250 species known worldwide, 147 of which are endemic to Australia (Lowrie 2014, Fleischmann et al. 2018). The majority of Drosera species are perennial herbs, only 16 of them are annual therophytes (Fleischmann et al. 2018), including all eleven currently recognised species of Drosera section Arachnopus Planchon (1848: 93; which sits within D. subgenus Drosera per the infrageneric classification of Fleischmann et al. 2018). In addition to their annual life cycle, most species of this section, sometimes referred to as the "D. indica Linnaeus (1753: 282) species complex", are characterised by their relatively large, erect habit and narrowly linear-lanceolate, carnivorous leaves (Lowrie 2014, Krueger et al. 2020). Additionally, some species exhibit complex non-carnivorous glands or trichomes on their leaves, stems and inflorescences (Schlauer 2001, Lowrie et al. 2017a) or produce a strong, honey-like scent from their leaves which may play a role in prey attraction (Lowrie 2014, Fleischmann 2016, Krueger et al. 2020).

Drosera section Arachnopus was long considered a monotypic section containing only a highly variable species, D. indica, that is widely distributed in tropical Africa, Asia and Australia (e.g., Diels 1906, Marchant et al. 1982, Lowrie 1998, 2001; the latter three publications even denoting syntopic occurrence of different "variants"). However, this affinity has recently been subject to significant taxonomic revision, including new taxonomic delimitations and species descriptions (Schlauer 2001, Barrett & Lowrie 2013, Lowrie 2014). In separating D. hartmeyerorum Schlauer (2001: 104) from the Kimberley region of northern Western Australia, Schlauer (2001) recognised the importance of peduncle disposition and types and indumentum of non-carnivorous glands and trichomes as reliable taxonomic characters in this section. Three additional, clearly defined morphotypes were found in an analysis of the morphological variation of herbarium material from the Kimberley (Susandarini et al. 2002), with the presence/absence of petioles, stamen shape/colour and seed morphology found to be key characters. Consequently, Barrett and Lowrie (2013) resurrected the names D. finlaysoniana Wallich (1831: n. 3752) ex Arnott in Hooker (1837: 314) and D. serpens Planchon (1848:

204), which were previously considered as synonyms of *D. indica*. Both resurrected species are distributed across Indochina and Australia. Lowrie (2014) described an additional seven species, all of which were considered endemic to northern Australia, bringing the total number of currently recognised species in *D.* section *Arachnopus* to eleven.

Drosera finlaysoniana was separated from *D. indica* by Wallich (1831), Arnott (1837) and Planchon (1848) mainly by its larger size and more robust habit. Barrett and Lowrie (2013) revealed the importance of additional characters to distinguish it from the remainder of species from *D.* section *Arachnopus*, namely its sessile leaves (i.e., the carnivorous tentacles extend all the way to the stem), the presence of only a few simple non-carnivorous "hairs" (i.e., the absence of more complex glands or trichomes such as those found in *D. hartmeyerorum*; although Schlauer *et al.* (2018) since reported more complex T-or Y-shaped trichomes on its leaves), "normal" shaped stamens (i.e., stamens which are not hooded or dilated) and its relatively small seeds exhibiting a strongly reticulate surface.

Observations of *Drosera* section *Arachnopus* from the Kimberley region in 2012 and 2014 by the first author indicated the possible presence of an additional taxon morphologically similar to *D. finlaysoniana*, prompting studies of herbarium material and additional fieldwork during 2020. Following careful examination of the previously recognised morphological characters in *D.* section *Arachnopus* (Schlauer 2001, Susandarini *et al.* 2002, Barrett & Lowrie 2013, Lowrie 2014), it was found that plants from the western Kimberley constantly differ from *D. finlaysoniana* by floral and indumentum characters, as well as breeding mode. This distinctive taxon is described here as a species new to science.

In addition, the name *Drosera finlaysoniana* is here lectotypified, following the rules of ICN (Turland *et al.* 2018), as the assumption of Barrett and Lowrie (2013) that a sterile specimen at G (or G-DC) represents the holotype seen by Arnott is incorrect. Barrett and Lowrie (2013) provided no lectotypification for the name from the syntypes, which is required following ICN Art. 9.17 (Turland *et al.* 2018), as no type specimen was designated by Arnott (1837).

Materials and Methods

Herbarium specimens and live populations were studied by both authors, including careful microscopic examination of indumentum and seed characters. All measurements and morphological characters were taken from herbarium material and plants in situ. Herbarium studies were based on material from B, CNS, G, K, L, M, P, and PERTH. For the distribution map of *Drosera finlaysoniana*, additional digitised herbarium specimens were consulted or obtained from AU, BM, BRI, CANB, CBG, DNA, E, FJID, FJSI, HIMC, HUH, IBK, IBSC, MEL, MO, NAS, NY, P, PE, TAIF, and WAG (herbarium acronyms following Index Herbariorum; Thiers 2020+). Fresh herbarium material of both D. finlaysoniana and the new species was collected in Western Australia by TK under flora taking licence FT61000504, and seeds from this material were examined and imaged under a macroscope (Leica Z6 APO with objective Leica Planapo 2.0×, Leica, Germany) and by SEM (LEO, Germany). SEM studies of gland and trichome micromorphology were conducted with fresh leaves of D. finlaysoniana and the new species collected in situ in Western Australia (flora taking licence FT61000038-2 and export permit PWS2020-AU-001342). Leaves were preserved in 96% denatured ethanol, fully dehydrated in acetone and critical point dried with liquid carbon dioxide. For SEM analyses, seeds and critical point dried leaf petioles were mounted on carbon sticker-covered SEM stubs and coated with platinum in a vacuum sputter coater (SCD 050, Bal-Tec, Germany) for 240 s, and then imaged under SEM at 25 mm working distance and 15 kV operating voltage. The distribution maps were prepared with DIVA-GIS v.7.5 (Hijmanns et al. 2012).

Results

1. Drosera margaritacea T.Krueger & A.Fleischm., sp. nov. (Figs. 1–3 + 6–9)

Type:—AUSTRALIA. Western Australia: Kimberley. 60 m N of Great Northern Hwy., 80.4 km ESE of intersection with Derby Hwy., 123 km WNW of Fitzroy Crossing, narrow drainage channel, reddish-brown sandy clay, 18 July 2020, *T. Krueger* 7 (holotype PERTH!, isotype MEL!).

Diagnosis:—*Drosera margaritacea* is morphologically similar to *Drosera finlaysoniana* Wall. ex Arn. in Hook. from which it differs (contrasting characters in parentheses) by its petiolate leaves, borne on a 1.5–3.5 mm long petiole (leaves sessile), petiole covered with 20–50 stalked secretive glands 0.10–0.40 mm long with a multicellular stalk

and translucent milky white, hemispherical to depressed ovoid gland head 0.10-0.30 mm in diameter that remains present even in dried material (petiole absent), stem, leaves, peduncle, pedicels and sepals covered with 0.05-0.30 mm long stalked capitate trichomes with uniseriate stalk and yellow, spherical, non-secretory gland head ca. 0.05 mm in diameter (stem, abaxial leaf surface, peduncle, pedicels and sepals covered with 0.1-0.3 mm long secretory capitate trichomes with uniseriate stalk and flattened gland head secreting a translucent mucilage droplet 0.1-0.2 mm in diameter), T-or Y-shaped trichomes absent (adaxial leaf bases and margins covered with 0.05-0.40 mm long T-or Y-shaped trichomes), inflorescence (20-)30-55(-65) cm long, with at least 30-50 flowers, its peduncle held upright, \pm parallel to stem and much exceeding the carnivorous leaves (inflorescence (3-)6-18(-26) cm long, (2-)6-20(-26)-flowered, peduncle usually horizontal [this character is typically very obvious in live specimens, but sometimes not easily discerned in pressed herbarium material], shorter than or at most equalling the leaves in length), flowers 18-24 mm in diameter (7-14(-20) mm in diameter), stamen connective longer than filament, shorter than thecae and with rounded yellow tip ca. 0.2-0.4 mm in diameter (stamen connective usually much shorter than filament, as long as the thecae, lacking a rounded yellow tip).

Description:—Annual herb, 25–50(–90) cm tall including inflorescence. *Roots* simple, short, slightly succulent, terete, poorly branched. Stem upright or ascending, 8-16(-20) cm long, simple (unbranched), terete, 1.2-2.5 mm in diameter, green, turning reddish with age, internodes (1.5–)2.0–3.0(–8.0) mm long in flowering specimens; stem with indumentum consisting of two different types of trichomes: 0.05–0.15 mm long translucent, biseriate (double-tipped) trichomes (= type 5 sensu Länger et al. 1995) and 0.05-0.30 mm long stalked capitate trichomes with uniseriate stalk and yellow, spherical, non-secretory gland head ca. 0.05 mm in diameter. Leaves filiform, (40-)50-100(-130) mm long in flowering-sized specimens, straight, vernation circinate, sometimes emitting a strong honey-like scent; freshly developed leaves held erect or patent and with slightly curved lamina, leaves held horizontal and lamina straight with age, senescent leaves persistent, patent or reflexed towards the stem; stipules absent; petiole linear, 1.5–3.5 mm long, 1.5–2.4(-3.0) mm wide at its greatest width (at transition to the lamina), green, in section depressed narrowly reniform with slightly reflexed lateral margins; petiole adaxial surface and margins with 20-50 distinctive, stalked secretive glands with multicellular stalk (0.1-0.4 mm long) and translucent milky white, hemispherical to depressed ovoid gland head, 0.1–0.3 mm in diameter, turgescent and adhesive in living specimens, maintaining its shape but losing stickiness in dried material; petiole adaxial surface additionally very sparsely covered with 0.05–0.15 mm long, translucent, biseriate, double-tipped trichomes like those present on the stem (but yellow-headed capitate trichomes absent on adaxial petiole surface); abaxial petiole surface indumentum identical to the stem indumentum; lamina narrowly linear-lanceolate with long acuminate tip, (38–)48–100(–120) mm long (excluding tentacles), 1.5–2.4(–3.0) mm wide (excluding tentacles) at its greatest width; lamina yellowish-green, its adaxial surface covered with stalked, carnivorous, secretive capitate glands (tentacles) 1-5 mm long, tentacle stalk translucent white or tinged reddishpink, with regular, hemispherical microscopic projections, tentacle gland head red or orange-yellow, all tentacles with radially symmetric gland head; additionally, lamina adaxial surface and margins sparsely covered with stalked milkywhite glands of the same type as present on the petiole adaxial surface (slightly smaller on the lamina: gland stalk 0.10– 0.30 mm, hemispherical gland head 0.15–0.20 mm in diameter) and with 0.05–0.15 mm long, biseriate, double-tipped trichomes and 0.05-0.30 mm long yellow-headed capitate trichomes; indumentum of lamina abaxial surface identical to stem indumentum. Inflorescences (1)3-6, each forming a many-flowered (at least 30-50 flowers per peduncle), bracteate scorpioid cyme; inflorescence indumentum (covering peduncle, rhachis, bracts, pedicels, calyx and sepals) identical to stem indumentum; young inflorescences yellowish-green or bronze, turning reddish with age; scape (200–)300-550(-650) mm tall including peduncle; peduncle (80-)90-160(-190) mm long, much exceeding the leaves in length, terete, 1.1-1.5 mm in diameter, ascending vertically (± parallel to the stem axis in young inflorescences, mostly held at an angle <45° from the stem in older inflorescences and at fruit, rarely diverging up to 90° from stem); fruiting pedicels spaced by 5-18(-30) mm; pedicels terete, 0.2-0.6 mm in diameter, 9-25(-35) mm long in fruit; pedicels straight upright at anthesis becoming more or less arcuated or reflexed in fruit (arcuated horizontal/slightly downwards from the inflorescence axis, then sharply curving upright at the apex, so that the seed capsule is held upright). Bracts subulate, $1.0-2.5(-3.0) \times 0.05-0.20$ mm, persistent, margins entire, apex acute, shallowly truncate or bifid, often ending in a glandular trichome, adaxial surface glabrous, abaxial surface indumentum identical to the stem indumentum. Flowers 18-24 mm in diameter. Sepals 5, basally adnate (usually not overlapping in developing buds), lanceolate-elliptical, margins serrate or entire, 2.0–3.5 mm long, 0.9–1.4 mm at their greatest width, abaxial surface with indumentum identical to the stem indumentum. Petals 5, obovate to broadly obovate, 9–12 mm long, 7–9 mm at their widest point, apical margin slightly irregularly crenulate to undulate, petals overlapping near their base, petals bright pink. Stamens 5, narrowly lanceolate, $2.5-3.0 \text{ mm} \times 0.7-0.9 \text{ mm}$; filaments linear, $0.9-1.5 \times 0.2-0.5 \text{ mm}$, white; anthers bithecate, exceeding (or at least equalling) the filament in length, 1.4–2.0 mm long, connective dilated,

narrowly triangular, 0.5–0.6 mm wide, slightly shorter than the thecae, with rounded, swollen yellow apex ca. 0.2–0.4 mm in diameter; thecae pale yellowish-white; pollen pale yellowish-white. *Ovary* 3-carpellate, fused, subglobose, 1.0–1.5 mm in diameter, glabrous, pale green. *Styles* 3, each basally divided into 2 entire style-arms; style-arms translucent white, 1.5–3.0 mm long (excluding stigmatic portion), flagelliform, terete, ca. 0.1–0.2 mm in diameter, glabrous, positioned horizontally, graduating into stigmatic part; stigmas 1.2–2.2 mm long, translucent white, apex slightly (rarely strongly) curved upwards, stigmatic surface papillate. *Seeds* numerous, $(350-)400-500 \times (200-)250-300 \mu m$, ellipsoid to broadly ellipsoid or ovoid, testa black or grey, testa surface more or less isodiametrically reticulate, with anticlines comparatively thick and raised, periclinal walls tabular, covered with microscopic, bladed wax crystals.

Etymology:—The species' epithet (from Latin *margaritaceus* = pearly, pearl-bearing) refers to the indumentum of unique, stalked secretive glands with translucent milky white, hemispherical to depressed ovoid (pearl-like) gland heads, as well as to the characteristic swollen, roundish (pearl-like) apical dilatation of the anther connective.

Taxonomic notes:—*Drosera margaritacea* is morphologically most similar to *D. finlaysoniana* as both species share a similar habit (at least of the vegetative parts) with leaves that appear glandular to the very base (no petioles apparent), similar seed shape and scent production. However, in *D. finlaysoniana* [as well as in *D. aquatica* Lowrie (2014: 1268) which is frequently confused with *D. finlaysoniana*, see Discussion: Taxonomy] it is the carnivorous tentacles that reach the leaf base, hence that species is lacking a petiole, while in *D. margaritacea*, the petiole is short but clearly apparent upon close examination and covered by distinctive glands with multicellular stalks and translucent to milky-white, depressed heads. This gland type/trichome type is not paralleled in any other member of *D. section Arachnopus*, nor any other *Drosera* species. *Drosera aquatica* is additionally separated from *D. margaritacea* and *D. finlaysoniana* by its stem and inflorescence indumentum which consists of long, patent, simple, translucent eglandular hairs (Lowrie 2014).

The comparatively long and many-flowered, vertically arising inflorescence readily allows identification of *Drosera margaritacea in situ* as well as in herbarium material, and even in low-resolution scans of herbarium specimens. A similar inflorescence habit is found only in *D. barrettiorum* Lowrie (2014: 1269) and in large "variants" of *D. hartmeyerorum* and *D. serpens* from the Kimberley (T. Krueger pers. obs.). Indeed, *D. hartmeyerorum* is the only other species in *D.* section *Arachnopus* whose anthers exhibit similar, swollen, apical connective dilatations. However, in *D. hartmeyerorum* this apical connective swelling of the anthers is white (rarely yellow) and much exceeding the thecae (Barrett & Lowrie 2013, Lowrie 2014, T. Krueger & A. Fleischmann pers. obs.), while in *D. margaritacea* the yellow, swollen part of the connective is subequal to the thecae in length. In the anthers of *D. barrettiorum*, the deltoid connective is much dilated and curved to the ventral side, resulting in a yellow, dorsal swelling, the anthers of this species are subequal to (slightly exceeding) the connective. While *D. serpens* is readily distinguished from *D. margaritacea* by its well-expressed petioles, *D. barrettiorum* and *D. hartmeyerorum* always produce groups of relatively large and conspicuous yellow emergences on their adaxial petiole surfaces, and thus can readily be told apart from all remaining members of *D. section Arachnopus* (Lowrie 2014).

Distribution and habitat:—*Drosera margaritacea* is endemic to the western part of the Kimberley region of tropical northern Western Australia, apparently limited to lowlands of the Canning Basin, with records made at elevations of 10–70(–180) m above sea level (Fig. 3A). It is known from the base of the Dampier Peninsula in the west to Christmas Creek Homestead (ca. 95 km SE of Fitzroy Crossing) ca. 400 km to the east, extending northwards to Derby and throughout the Yampi Peninsula (Fig. 3A). Although not reported from there yet, it is likely that *D. margaritacea* also occurs in central or northern parts of the Dampier Peninsula, as this area is in close geographic proximity to the Yampi Peninsula and features suitable habitat as well as similar climate and geomorphology. A single PERTH record with geocoordinates given for near Kununurra in the eastern Kimberley (*A. Lowrie 2461*) has been determined to originate from the Yampi Peninsula, as it was evidently collected by Allen Lowrie during his 2000 expedition to that area (Lowrie 2001).

The morphologically similar (and putatively closely related) *D. finlaysoniana*, while abundantly recorded in southern, eastern, and central parts of the Kimberley, is not known to occur within the distribution range of *D. margaritacea*, indicating that the two species may be allopatric (Fig. 3A). In the Christmas Creek area, however, both species apparently occur within a distance of less than 40 km from each other. Additionally, *D. finlaysoniana* is apparently limited to higher elevations (above ca. 200 m) in the central and western parts of the Kimberley, i.e. the area of parapatry of the two species (Fig. 3A).

Drosera margaritacea grows in sandy soils near the edges of seasonally wet swamps, creeks, and seepage areas, usually amongst dense grassy vegetation. Associated flora includes Fuirena ciliaris (L.) Roxb. (Cyperaceae; pers. obs. and mentioned on specimen label of R. Jensen & J.E. Kemp RJ 3983), Cyperus spp. (Cyperaceae; pers. obs. and also mentioned on L. Wallis LW 97A/112), Schoenoplectiella dissachantha (S.T.Blake) Lye (Cyperaceae; mentioned as

"Schoenoplectus dissachanthus" on L. Wallis LW 97A/112), Eriachne festucacea F.Muell. (Poaceae; mentioned on R. Jensen & J.E. Kemp RJ 3983), Calandrinia sp. (Montiaceae; pers. obs.) and Melaleuca sp. (Myrtaceae; pers. obs. and mentioned on L. Wallis LW 97A/112).

Ecology and Phenology:—Annual. Flowering has been recorded from May to August, i.e. during the northern Australian dry season. However, the phenology of some examined herbarium specimens collected in early May (*K. Coate 406, A. Lowrie 2216, A. Lowrie 2219*), and of individuals studied *in situ* in mid-August (T. Krueger pers. obs. 2014), indicates that flowering can occur from April to at least early September. Following particularly dry wet seasons, this species has been observed to be completely absent from known locations even at anthesis time (T. Krueger pers. obs. 2020). Therefore, it is possible that seed germination in this species strongly depends on the amount of wet-season flooding.

Conservation status:—Least Concern (LC) according to IUCN Red List Criteria (IUCN 2012). *Drosera margaritacea* is known from at least 15 locations as defined by IUCN Red List guidelines (IUCN 2012), covering a wide area of the Kimberley. None of these sites are situated on conservation managed lands (CALM Act lands). While commonly localised and occurring in rather small populations (two populations, one with 5 and one with ca. 100 individuals, were observed by the first author in 2012, 2014 and 2020), very large populations are known to exist at some sites (e.g., at Lanlacatta Swamp, where it is the "most abundant insectivorous plant in the area" according to specimen label data of *L. Wallis LW 97A/131*). At present, the species does not meet any criteria for conservation code listing in Western Australia, but further surveys to assess its wider distribution and potential threats (such as cattle farming and altered fire regimes) are recommended.

Additional specimens examined (paratypes):—AUSTRALIA. Western Australia: [Kimberley region], Christmas Creek, May 1927, A.J. Ewart s.n. (PERTH 3289516!, PERTH 3289095!); W.A. Kimberleys [sic. l], 3 km E of Stuart River, Oobagooma Road, between Stuart and Robinson Rivers, c. 74 km NNE of Derby, 14 June 1976, A.C. Beauglehole 52915 (DNA D0269214 photo!); Prior's Bore, ca 10 km N of Great Northern Highway, at a point 135 km E of Broome along Broome-Derby Road, damp soil, 04 July 1982, K.F. Kenneally 8538 (PERTH 3289451!, CANB); Deep Creek, 55 km E of Broome on Great Northern Highway, Kimberley, in damp sand, 29 June 1993, K.F. Kenneally 11379 (PERTH 3048292!, CANB); W Kimberley coast, Jinunga River off The Graveyard, seepage areas beside pool, 02 July 1996, K.F. Kenneally 11667 (PERTH 4410521!); W Kimberley coast, Kyulgam River, a freshwater creek off Strickland Bay, on creek edge in damp soil, 03 July 1996, K.F. Kenneally 11686 (PERTH 4410742!); Dugong Falls, Talbot Bay, top of falls, 08 July 1996, K.F. Kenneally 11758 (PERTH 4411404!); Near Blina on Great Northern Highway, Kimberley, 13 May 1997, K. Coate 406 (PERTH 4942795!, MEL); c. 1 km from Taylors Lagoon, Broome, growing in sandy soil, 26 June 1997, A. Lowrie s.n. (PERTH 6440355!); Blina Swamp on Blina Station, edge of Blina Swamp, 23 July 1997, L. Wallis LW 97A/112 (PERTH 5025540!); Lanlacatta Swamp on Camballin Station, Kimberley, Edge of Lanlacatta Swamp, 27 July 1997, L. Wallis LW 97A/131 (PERTH 5025745!); c. 129 km W of Fitzroy Crossing, Kimberley, 09 May 1999, A. Lowrie 2216 (PERTH 6440576!); c. 129 km W of Fitzroy Crossing, Kimberley, 09 May 1999, A. Lowrie 2219 (PERTH 6440568!); Crossing Falls [Yampi Peninsula], Kimberley, 30 July 2000, A. Lowrie 2461 (PERTH 6440274!); Sand pit, 11.2 km E on the Gibb River Road from the Broome/Derby junction outside Derby townsite, flat, red sand, freshwater ponds, 12 June 2006, L.S.J. Sweedman 6853 (PERTH 7640277!); Stewart River where Kimbolton Road crosses, c. 9.4 km ESE of Kimbolton homestead, Yampi Training Area, on sand and cobble in river channel, 14 July 2018, R. Jensen & J.E. Kemp RJ 3983 (PERTH 9201726!).

Georeferenced photographs:—AUSTRALIA. Western Australia: Fitzroy Crossing Road, Kimberleys [sic.!], Western Australia, 23 June 2017, R. Fryer & J. Newland 6177 (northqueenslandplants.com); Taylor's Lagoon, Willare, Western Australia, 24 June 2017, R. Fryer & J. Newland 6190 (northqueenslandplants.com).

Additional localities reported by Lowrie (2001):—AUSTRALIA. Western Australia: 8 km NE of Karriwell Yard [Yampi Peninsula], open grassy plain, July 2000; 11 km NE of Karriwell Yard [Yampi Peninsula], near minor seepage area, July 2000.

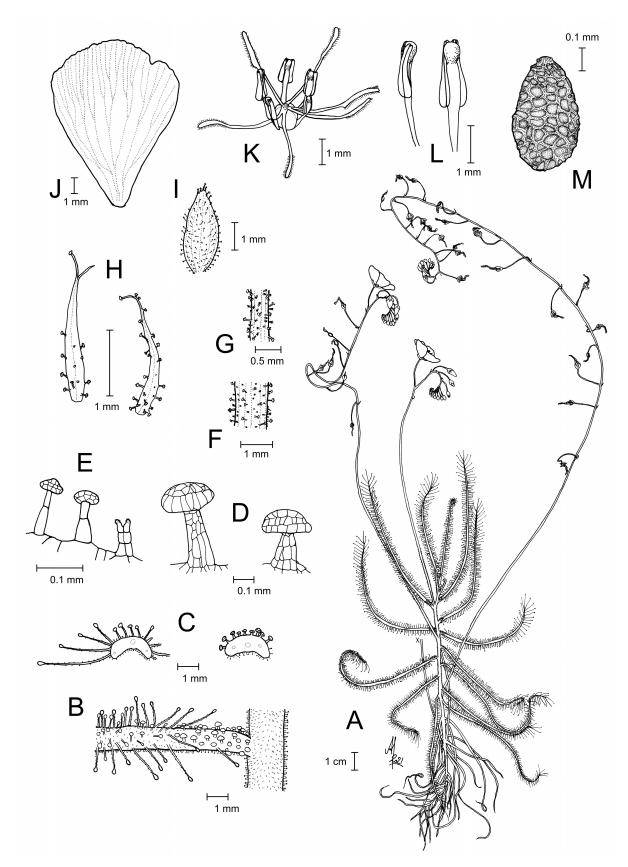


FIGURE 1. Drosera margaritacea T.Krueger & A.Fleischm. A. habit. B. stem and leaf base. C. transection of lamina (left) and petiole (right). D. stalked milky-white glands from petiole adaxial surface. E. yellow-headed capitate trichomes (two on left) and biseriate double-tipped trichome (right) from leaf abaxial surface (identical indumentum present on stem, peduncle, pedicels and calyx). F. peduncle, detail of indumentum. G. pedicel, detail of indumentum. H. bracts, left: from lower part of the rhachis, right: from upper part. I. sepal. J. petal. K. gynoecium and anthers. L. anthers, left: lateral view, right: dorsal view. M. seed. All from the type collection (*T. Krueger 7*), B–E from alcohol preserved leaves, the rest from herbarium material. Drawing by A. Fleischmann.

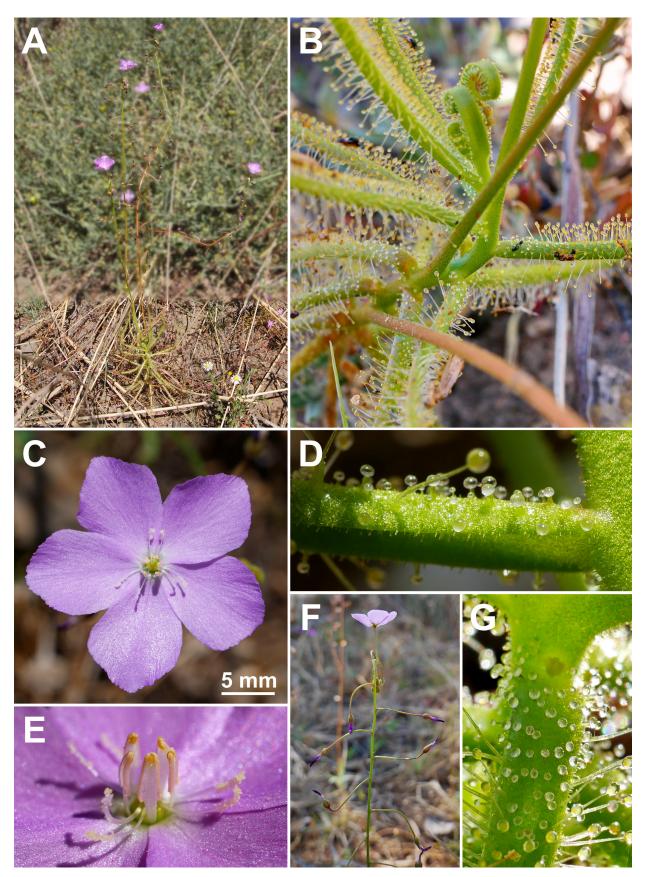


FIGURE 2. *Drosera margaritacea.* **A.** habit; note the very tall, many-flowered inflorescences. **B.** stem, with peduncle and leaf bases, showing the stalked milky-white glands on the adaxial petiole surfaces. **C.** flower. **D.** close-up of petiole covered with stalked milky-white glands, lateral view. **E.** close-up of stamens; note the rounded yellow connective tips around which the thecae protrude. **F.** inflorescence. **G.** close-up of petiole covered with stalked milky-white glands, adaxial view. All photographs taken at the type locality on 18 July 2020 by T. Krueger.

2. Drosera finlaysoniana Wall. ex Arn. in Hook. [as "finlaysoni"] (Figs. 3–9)

Lectotype (designated here):—[VIETNAM. Municipality Đà Nẵng], Hb. Finl. [Herbarium Finlayson], Turun Bay [Turon Bay = Da Nang Bay] E.I.C. [East Indian Company], without date [collected 15–19 September 1822], Wallich Cat. no. 3752 [= G. Finlayson 507] (E00206577 photo!; isolectotype K000217501! [from Wallich's herbarium K-W]; isolectotype K000659132! [from Herbarium Hookerianum via the East Indian Company Herbarium]; isolectotype G00414356 photo!). (Fig. 4)—for notes on lectotypification see section below.

- ≡ Drosera finlaysoniana Wallich (1831: n. 3752), nomen nudum (Art. 38.2 Ex.1 of ICN).
- = Drosera angustifolia Mueller (1855: 7).

Lectotype (designated by Barrett & Lowrie 2013: 531):—[AUSTRALIA. Victoria]: Ad ripam glareosam humidam tingiore imbuis inundatam lacus Yualb prope fl.[umen] Murray [at gravelly soaking moist inundated banks of a lake on the Victorian side of the Murray River near Euston, see Mueller (1855: 7; 1862: 58)], Dec [18]53, *F. Mueller s.n.* (MEL 96369 photo!; isolectotype LD; probable isolectotype MEL 96386 photo!).

= Drosera indica f. robusta Bailey (1913: 115).

Type:—[AUSTRALIA]. Queensland: Mill Stream Falls, Ravenshoe, Jun 1913, E.W. Bick s.n. (holotype BRI AQ0183206, isotype K!).

Description:—Annual herb, (5–)7–30(–90) cm tall. *Roots* simple, short, slightly succulent, terete, poorly branched. Stem upright or ascending, (3-)7-25(-75) cm long, simple (unbranched), terete, (0.9-)1.3-3.0 mm in diameter, green to bronze, turning reddish with age, internodes 1–3(–15) mm long in flowering specimens; stem covered with indumentum consisting of two different types of trichome: 0.05-0.15 mm long, translucent, biseriate, double-tipped trichomes (= type 5 sensu Länger et al. 1995) and 0.1–0.3 mm long, secretory capitate trichomes with uniseriate, translucent stalk (base often reddish) and flattened gland head secreting a translucent mucilage droplet ca. 0.1 mm in diameter. Leaves filiform, (30–)50–150(–220) mm long in flowering-sized specimens, straight, transversely elliptic to depressed transversely reniform in cross-section, lateral margins slightly reflexed, vernation circinate; freshly developed leaves held erect or patent and with slightly curved lamina, leaves held horizontal and lamina straight with age, senescent leaves persistent, patent or reflexed towards the stem; stipules absent; petiole absent (leaves sessile: tentacle-bearing part of the leaf reaching all the way to the stem/leaf axil); lamina comprising the entire leaf length, narrowly linear-lanceolate with long acuminate tip, (30-)50-150(-220) mm long (excluding tentacles), (1.6-)2.0-4.0(-4.5) mm wide (excluding tentacles) near the leaf base, gradually tapering towards the apex; lamina yellowish-green, often emitting a honey-like scent, its adaxial surface covered with stalked, carnivorous, secretive capitate glands (tentacles) 1-4 mm long, tentacle stalk translucent white or yellowish-white, with regular, hemispherical microscopic projections, tentacle gland head translucent white, orange-vellow or red, all tentacles with radially symmetric gland head; additionally, lamina adaxial surface and margins covered with 0.05–0.15 mm long, translucent, biseriate, double-tipped trichomes (= type 5 sensu Länger et al. 1995) and T-or Y-shaped trichomes (= type 14 sensu Länger et al. 1995; found in highest numbers at the leaf base) with translucent uniseriate stalk (0.05-0.40 mm long) and bifurcated, yellowish or pale pink head 0.2-0.3 mm wide; lamina abaxial surface and leaf margin indumentum identical to stem indumentum). *Inflorescences* (1–)2– 7(-10), each forming a (2-)6-20(-26)-flowered scorpioid cyme with persistent bracts; inflorescence indumentum (covering peduncle, rhachis, bracts, pedicels, calyx and sepals) identical to stem indumentum; young inflorescences yellowish-green or bronze-green, turning reddish with age; scape (30-)60-180(-260) mm tall including peduncle; peduncle (15–)20–80(–110) mm long, shorter than the leaves in length or at most equalling them, terete, 1.0–2.0 mm in diameter, usually ascending ± horizontally, even young inflorescences often diverging at an angle >45° from the stem, fruiting inflorescences often slightly curving downwards from their middle; fruiting pedicels spaced by (2–)3–15(–27) mm; pedicels terete, 0.5–1.0 mm in diameter, (2–)4–12(–20) mm long in fruit; pedicels straight or just gently arcuated upwards, held upright at anthesis and spreading horizontally from the rhachis in fruit (sometimes pedicels sharply bent upwards at the apex so that the fruiting seed capsules are held upright). Bracts persistent, $1.5-4.0(-4.5) \times 0.2-0.8$ mm, subulate, margins entire, apex acute to shallowly truncate, adaxial surface glabrous, abaxial surface indumentum identical to stem indumentum. Flowers (6-)7-14(-20) mm in diameter. Sepals 5, basally adnate, slightly imbricate in bud, especially at their apices, lanceolate-elliptical, margins serrate or entire, (2.0–)2.5–6.0 mm long, (0.8–)1.2– 2.3 mm at their greatest width, abaxial surface with indumentum identical to stem indumentum. Petals 5, narrowly obovate to obovate, (3.0–)4.5–7.0(–9.0) mm long, 2.5–5.0 mm wide at widest point, apical margin slightly irregularly crenulate, petals not overlapping, pale pink or white (rarely bright pink). Stamens 5, narrowly lanceolate, 2.0-2.5 mm long, 0.3–0.5 mm wide; filaments linear, ca. 1 mm long, ca. 0.3 mm wide, white; anthers bithecate, much shorter than the filament in length, 0.6–1.0 mm long, connective only slightly dilated, narrowly triangular, 0.2–0.4 mm wide, subequal to the thecae; thecae pale yellowish-white; pollen yellow or rarely pale yellowish-white. Ovary 3-carpellate, fused, subglobose, 1.0–1.5 mm in diameter, glabrous, pale green. Styles 3, each basally divided into 2 entire style-arms;

style-arms translucent white, 1.2-1.5(-2.0) mm long (excluding stigmatic portion), flagelliform, terete, 0.1-0.2 mm in diameter, glabrous, positioned horizontally, graduating into stigmatic part; stigmas ca.1 mm long, translucent white, apex strongly curved upwards, stigmatic surface papillate. *Seeds* numerous, $(350-)400-500 \times (250-)290-350 \mu m$ in Australian specimens, $300-400 \times 200-280 \mu m$ in Indochinese specimens, ovoid to broadly ellipsoidal, testa black with grey wax cover, testa surface very regularly foveate-reticulate, with anticlines pronounced and raised, periclinal walls tabular, occasionally with iridescent shine underneath wax cover, periclines and anticlines covered with microscopic, dendritic, bladed wax crystals.

Etymology:—The species epithet commemorates Scottish surgeon and naturalist George Finlayson (1790–1823), who explored and botanised Thailand and southern Vietnam as accompanying medical officer to John Crawfurd's Mission in 1821–1822 (Finlayson & Raffles 1826, Watson 2013). During this expedition, Finlayson made the first collection of the *Drosera* taxon that was named posthumously in his honour as *Drosera finlaysoniana* by Wallich (1831), however lacking a description or diagnosis like most of the names published in Wallich's Catalogue, rendering the name a *nomen nudum*. The name was later nomenclaturally validated by Arnott *in* Hooker (1837) as "*D. finlaysoni*", however Wallich's original spelling of the epithet has to be retained, see ICN Arts. 60.1 and 45.6 (Turland *et al.* 2018).

Distribution:—Drosera finlaysoniana occurs in Australia (Western Australia, Northern Territory, Queensland, New South Wales, South Australia, Victoria), southern China (Provinces Fujian, Guangdong, Guangxi, Hainan), northeastern Taiwan (Counties Hsinchu, Miaoli, Taichung, Taipei, as well as Kinmen Island) and Vietnam (Northeast, North Central Coast, South Central Coast and South East regions: Provinces Nghệ An, Khánh Hòa, Quảng Trị, Quảng Ninh, Thừa Thiên Huế, Bà Ria-Vũng Tàu, Bình Thuân, and Municipalities Đà Nẵng and Hanoi) (Fig. 3B). In Australia, the species is widespread in the northern and central parts, where it occurs from ca. 10 m to well above 1000 m elevation (it has been collected from "near summit of Mt Zeil" [J.H. Willis s.n.] in the Northern Territory, which is the highest mountain on the Australian mainland outside the Great Dividing Range with an elevation of 1531 m). The Indochinese records of D. finlaysoniana are all situated along the coast of the South China Sea (Fig. 3B), while the species does not seem to cross the Mekong River to the Gulf of Thailand. All Indochinese populations are found in coastal regions, some even at offshore beaches and lagoons; the most inland record is ca. 80 km from the coast (Vietnam, surroundings of Hanoi, C. d'Alleizette s.n., P04583159), and all are at lowland elevations, from sea level to 100 m, reaching the species' highest localities in Taiwan at 80-100 m elevation and on Hainan island, China, at 100 m a.s.l. Not a single occurrence could be confirmed from Cambodia, neither from herbarium records nor from field observations in suitable habitats along coastal seepage habitats (F. Mey, pers. comm.), where the related species D. indica and D. serpens are abundant. Despite earlier (erroneous) mentions of D. finlaysoniana from Laos (Barrett & Lowrie 2013; who do not cite any vouchers from the country), India (Lowrie 2014, Lowrie et al. 2017b), southern Japan (Lowrie et al. 2017b) and the Philippines (Lowrie et al. 2017b), no herbarium specimens or observation data of that species could be traced from any of these four countries. We therefore conclude that D. finlaysoniana is absent from India, Cambodia, Laos and Japan, although its presence in the Philippines cannot be excluded considering the rather poor botanical exploration of some remote Philippine islands, and in the light of recent *Drosera* range extensions following floristic surveys (Fleischmann & Coritico 2016, Robinson in Lowrie et al. 2017b). A single questionable herbarium record exists from Thailand, from today's Prachuap Khiri Khan Province (a duplicate of Collins 1621 at P), however the collection site does not match typical habitat for the species, and no further records of D. finlaysoniana exist from any nearby area in Thailand, nor the same site, which is a touristic and frequently visited spot today. Therefore, we cannot exclude the possibility that the locality has been mixed up in the herbarium record, yet the specimen is clearly D. finlaysoniana.

Records and depictions of "Drosera indica" from New South Wales (FINSW 1990, Harden 2000, Gibson 1999, 2002), Victoria (Conn 1996), central Australia (Marchant 1981, Latz 1995), mainland China (Ruan 1984, 1991, Lu & Kondo 2001, excluding Hong Kong) and Taiwan (Liu 1976, 1996) exclusively refer to D. finlaysoniana, which is the only representative of D. section Arachnopus occurring there. Reports and illustrations of "Drosera indica" from Hainan (Merrill 1927, Chen 1964, Lu & Kondo 2001) and Vietnam (Gagnepain 1908–1923, Lecompte 1965) may refer to either D. finlaysoniana, D. indica s.str. or D. serpens, as all three species occur in these regions, sometimes two of them syntopically (see Notes under Specimens Examined: Electronic Appendix). Reports of D. indica from Hong Kong (Lu & Kondo 2001) and Thailand (Larsen 1987) indeed refer to D. indica s.str., which is the sole member of D. section Arachnopus recorded there. At the northernmost limit of its range in north-western Taiwan, Drosera finlaysoniana reaches a latitude of ca. 25.07° North, at its southernmost outpost in Victoria, Australia, it reaches 34.72° South (Fig 3B). An observation record from Adelaide, South Australia (Atlas of Living Australia 2020) could not be confirmed and is excluded from the species' range here.

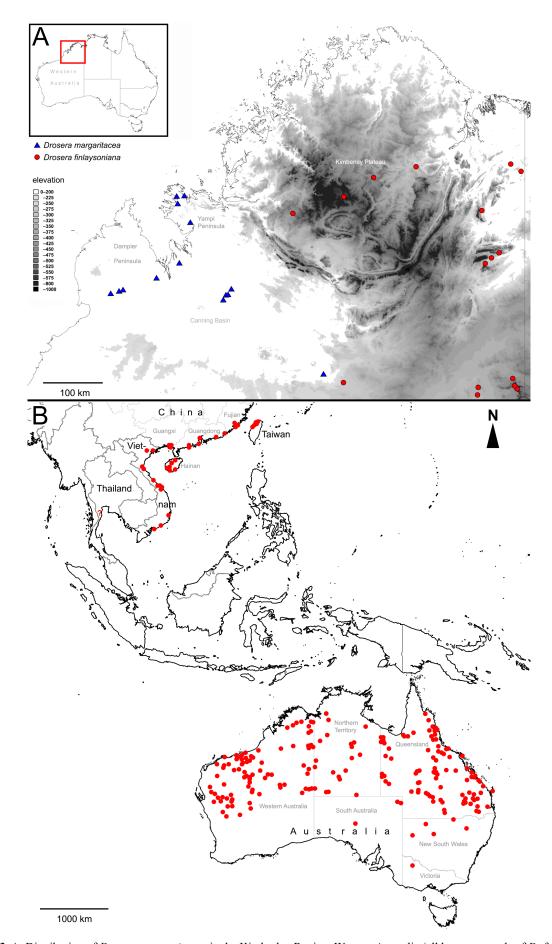


FIGURE 3. A. Distribution of *Drosera margaritacea* in the Kimberley Region, Western Australia (all known records of *D. finlaysoniana* in that range also indicated). **B.** Global range of *D. finlaysoniana*. Maps drawn by A. Fleischmann.

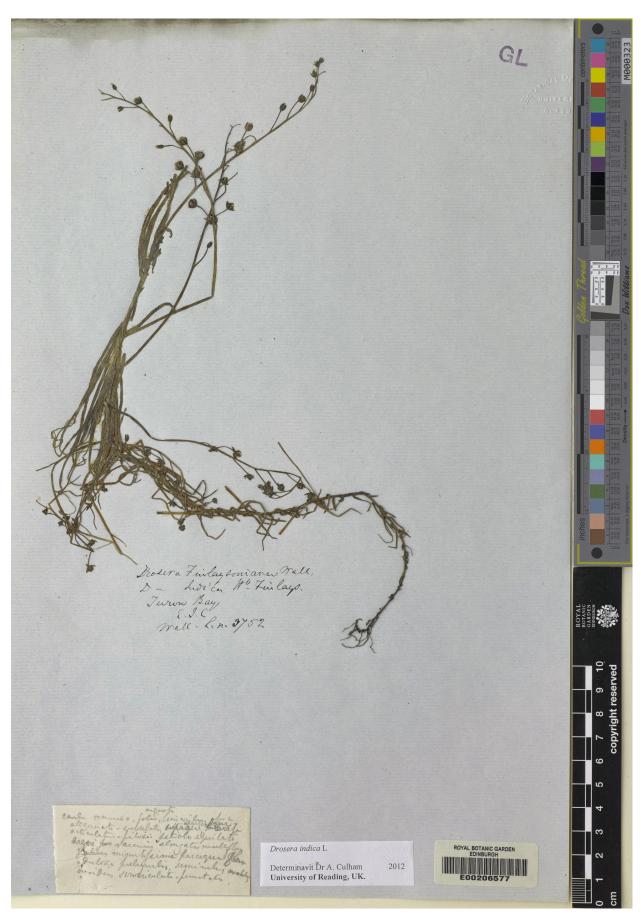


FIGURE 4. Lectotype of *Drosera finlaysoniana*, *Wallich Cat. No. 3752* [= *G. Finlayson 507*, collector denoted only on the duplicate at K-W] (E-00206577). Image kindly provided by the Royal Botanic Garden Edinburgh and available online at: http://data.rbge.org.uk/herb/ E00206577

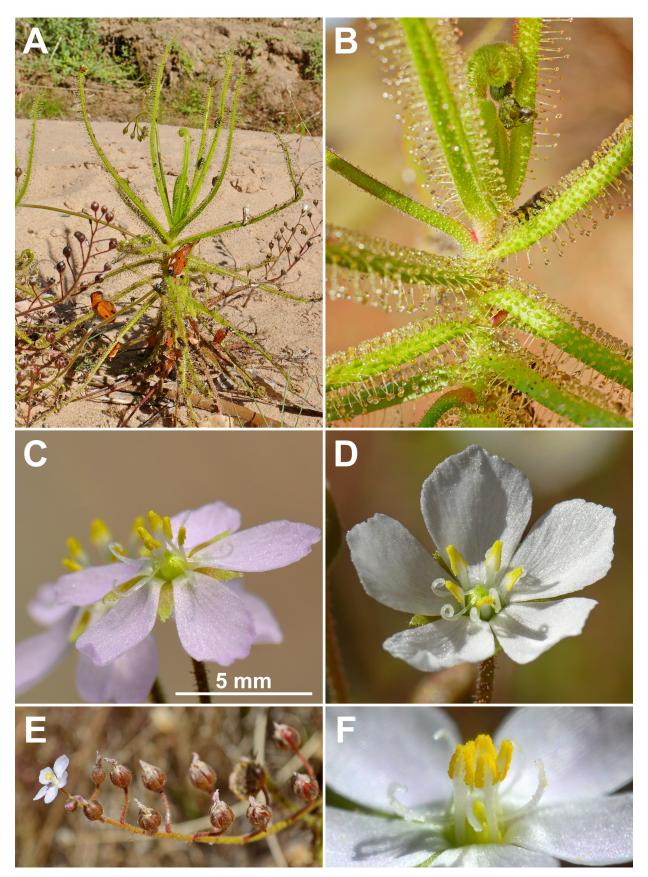


FIGURE 5. *Drosera finlaysoniana*. **A.** habit; note the relatively short, few-flowered inflorescences. **B.** stem with peduncle and leaf bases; note the sessile leaves lacking any obvious petiole, i.e. the carnivorous tentacles are emergent all the way to the stem. **C.** pink-petalled flower. **D.** white-petalled flower. **E.** inflorescence. **F.** close-up of stamens. **A, C, D** from Keep River National Park, Northern Territory, 09 July 2014, photographs by A. Fleischmann. **B** from Cue, Western Australia, 13 July 2020, photograph by T. Krueger. **E, F** from near Indee Station, Western Australia, 20 August 2014, photographs by T. Krueger.



FIGURE 6. Comparison of herbarium specimens of *Drosera margaritacea* (left) and *D. finlaysoniana* (two plants on the right). Note the differences in inflorescence size, peduncle length and numbers of flowers per inflorescence. These features allow quick identification of herbarium material without microscopic indumentum inspections. Inset shows macro-photograph of stalked-milky white glands on petiole of *D. margaritacea*. Note that these glands retain their shape in dried material but lose stickiness (as tested with steel needle visible on right edge of this inset). Left specimen *T. Krueger* 7 (holotype; PERTH), right specimens *T. Krueger* 6 (PERTH, MIN). Photographs by T. Krueger.

Drosera finlaysoniana is absent from Japan, the Indian subcontinent and the Malesian biogeographical region (Indonesia, Malaysia, Brunei, Singapore, the Philippines, East Timor, and New Guinea), and most likely also from Thailand. This results in a disjunct Indochinese-Australian range (Fig. 3B; by no means a "more or less continuous distribution between Australia and Vietnam", as concluded by Barrett & Lowrie 2013), a rare biogeographic pattern, which is shared by the likewise carnivorous *Utricularia odorata* Pellegr. (Lentibulariaceae Rich.) (Taylor 1989; however, that species is much more localised in northern Australia and absent from southern China), as well as—with a few additional occurrences in Malesia and one in Sri Lanka—by the genus Stylidium Sw. (Stylidiaceae R.Br.) (van Slooten 1954). In addition, D. finlaysoniana occurs in very different climatic areas on either side of the equator. While the Indochinese populations experience humid subtropical or tropical savanna climates (Köppen climate types Cwa, Cfa and Aw), almost all Australian populations are found in hot arid or semi-arid climates (BWh and BSh), with only few occurrences in tropical savannah climate (Aw, these occur in the central Kimberley, southern Top End and Cape York regions; Fig. 3B). Interestingly, seeds of D. finlaysoniana from Indochinese provenances are ca. 25–30% smaller in size than those of Australian specimens (Fig. 9; Barrett & Lowrie 2013). This could be related to a more pronounced dry seed dormancy of the more arid Australian habitats, while the Indochinese populations do not need to survive a prolonged dry seed dormancy (e.g., Chinese populations are reported to grow more or less continuously year-round; Ruan 1991). Drosera finlaysoniana is the only Australian species of D. section Arachnopus which is largely absent from the area of tropical savanna climate (Köppen climate type Aw) in northern Australia.

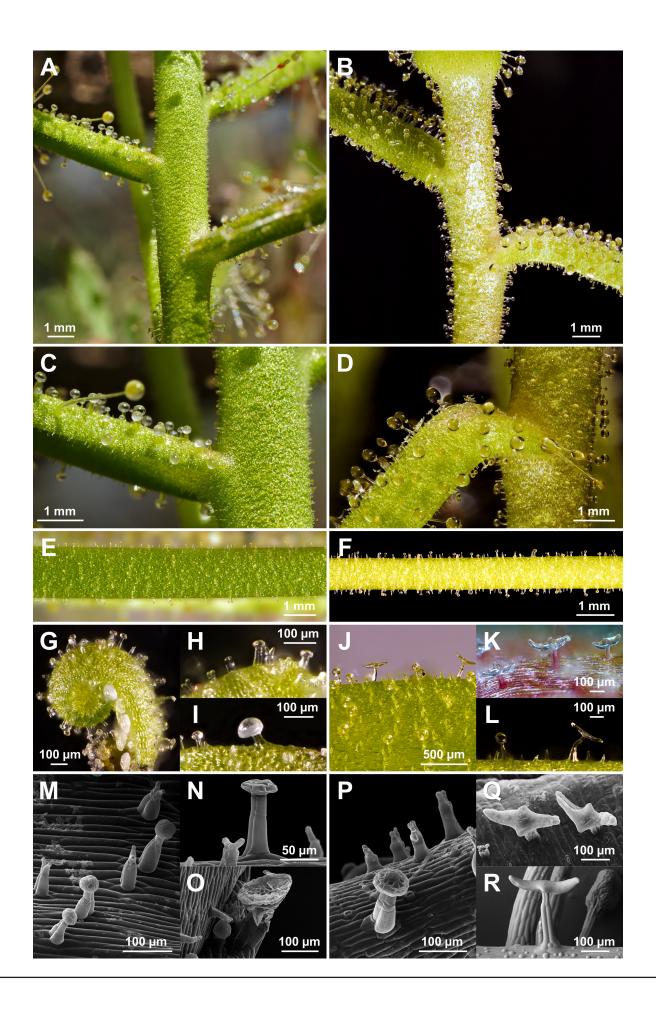


FIGURE 7. Indumentum comparison of *Drosera margaritacea* (left row) and *D. finlaysoniana* (right row). A, C. stem and petioles of *D.* margaritacea. Note the stalked milky-white glands on the adaxial petiole surface and the small, yellow-headed capitate trichomes on the stem and abaxial lamina surface. B, D. stem and leaf bases of D. finlaysoniana. Note the T-or Y-shaped trichomes on the adaxial lamina surface/margins and the stalked capitate secretory trichomes on the stem and abaxial lamina surface. E. peduncle of D. margaritacea. Indumentum is identical to its stem indumentum. F. peduncle of D. finlaysoniana. Indumentum is identical to its stem indumentum. G. juvenile developing leaf of D. margaritacea, showing the relatively large stalked milky-white glands on the adaxial petiole surface as well as the smaller biseriate double-tipped and yellow-headed capitate trichomes. H. close-up of biseriate double-tipped and yellow-headed capitate trichomes of D. margaritacea. I. close-up of a stalked milky-white gland of D. margaritacea. J. abaxial lamina indumentum of D. finlaysoniana, showing biseriate double-tipped and stalked capitate secretory trichomes. Two T-or Y-shaped trichomes are also visible on the lamina margin. K. T-or Y-shaped trichomes on the adaxial lamina surface near the leaf axil of D. finlaysoniana. L. stalked capitate secretory trichome (left) and T-or Y-shaped trichome (right) on the lamina margin of D. finlaysoniana. M. SEM image of abaxial lamina indumentum of D. margaritacea, showing biseriate double-tipped and yellow-headed capitate trichomes. N. SEM image of a yellow-headed capitate trichome of D. margaritacea. O. SEM image of a stalked milky-white gland of D. margaritacea, CP-dried alcohol material, gland head disrupted. Note the multicellular stalk and much larger size compared to the biseriate double-tipped and yellowheaded capitate trichomes also visible in this image. P. SEM image of abaxial lamina base indumentum of D. finlaysoniana, showing biseriate double-tipped and a stalked capitate secretory trichome. Q. SEM image of large T-or Y-shaped trichomes on the adaxial lamina surface near the leaf axil of D. finlaysoniana. R. SEM image of a T-or Y-shaped trichome on the lamina margin of D. finlaysoniana, living plant tissue under low pressure vacuum. Carnivorous tentacles (including a tentacle head) can be seen in the background. A, C, E photographed in-situ at the type locality of D. margaritacea by T. Krueger. G, H, I cultivated material originating from the type locality of D. margaritacea. Photographs by A. Fleischmann. M, N, O alcohol-preserved leaf material collected from the type location. P from Cue, W.A. SEM-image by A. Fleischmann. B, D, F, J, K, L, Q, R from cultivated material originating from Northern Territory, Australia. Photographs and SEM images by A. Fleischmann.

Ecology, habitat and phenology:—Annual. In Australia, *Drosera finlaysoniana* grows in a wide range of seasonally wet or inundated habitats. It has been recorded from sandy or rocky areas in or adjacent to freshwater lakes, swamps, creeks, riverbeds, sandstone or granite outcrops (inselbergs), dunes, claypans, soaks, springs and seepage areas. Flowering occurs from late March to October, which are typically the drier months of the Australian desert climates. In Indochina, *D. finlaysoniana* has been collected in flower and fruit year-round (Ruan 1991; see also Specimens Examined: Electronic Appendix), and the species occurs in perennial or seasonal open wetlands, seepage areas, at the margins of rivers, ponds, dams and lagoons, on wet rock, wet oligotrophic sands, but it is also frequently reported from rice fields and—at least historically—even in urban areas (see Specimens Examined: Electronic Appendix).

Conservation status:—Least Concern (LC) regarding the species' global range (IUCN 2012, Bourke 2018). Drosera finlaysoniana is widespread and common throughout many parts of its range. Within Australia, it is currently not listed as threatened by any state except Victoria where it is only known from a single locality (Hattah-Kulkyne National Park) and thus is listed as Vulnerable (vicflora.rbg.vic.gov.au). The species may also be threatened in some regions of China and Vietnam, as most records were made in the 1930's and earlier. Many of these historical localities are now urbanised or have become developed, thus some of the populations shown for Indochina in Fig. 3B might have been lost by now.

Notes on the lectotypification:—Wallich's exsiccate series was distributed to several herbaria, however the Finlayson collections included in that series comprise only few duplicates (Candolle & Radcliffe-Smith 1981, Watson 2013). Of Wallich Cat. No. 3752 we could only trace four duplicates (i.e., syntypes of Drosera finlaysoniana), of which two are deposited at K in Wallich's and Hooker's Herbaria (K000217501! and K000659132!, respectively). Indeed, most of Wallich's types and his main set are housed at K (Stafleu & Cowan 1979). A further duplicate is housed at the Herbarium of the Royal Botanic Garden Edinburgh (E), to where Arnott's herbarium was finally transferred (Stafleu & Cowan 1976). Barrett and Lowrie (2013) mention the duplicate from G as the "holotype" of D. finlaysoniana, indicating that the original material consulted by Arnott has to have been a sterile specimen. Indeed, Arnott himself noted that he had only seen a single specimen of Wallich's D. finlaysoniana, "and that an imperfect one" (Arnott 1837: 314). However, as Arnott (1837) describes details of the inflorescence ("racemis elongatis multifloris"; the plural might indicate that he examined a specimen with more than one inflorescence present), including its indumentum and seed characters, it cannot be a sterile specimen that he consulted. Furthermore, the syntype at G does not bear any indication that it had been consulted by Arnott. The specimen examined by Arnott would have had to have been a fertile specimen, and an "imperfect" one lacking (open) flowers, but with infructescence(s) present. K000217501 comprises a) two individuals with b) some flowers present thus can be excluded as having been seen by Arnott. K000659132 contains a single, rather incomplete specimen with one infructescence (and some detached seed capsules which apparently had

been dissected for examination), and E00206577 is a single large specimen with six infructescences. Hence one of these two specimens very likely represents the single specimen examined personally by Arnott, i.e. the holotype. The E duplicate is accompanied by a handwritten diagnosis of the plant (likely of Arnott's hand, at least not in conflict with the typography of his handwritten correspondence) that almost literally agrees with Arnott's published description in Hooker (Arnott 1837). Therefore, it is reasonable to assume that the E duplicate of *Wallich Cat. No. 3752* is the specimen which Arnott examined for the description of *D. finlaysoniana* and hence that gathering is selected as the lectotype here. As duplicates of *Wallich Cat. No. 3752* are found in different herbaria (syntypes according to the Art. 9.6 of ICN; Turland *et al.* 2018), a lectotypification is required (ICN Art. 9.17; Turland *et al.* 2018), which thus far has not been done for the name *Drosera finlaysoniana*. The mention of a "holotype" by Barrett and Lowrie (2013) and Lowrie (2014) does not constitute an inadvertent lectotypification (see ICN Art. 7.11; Turland *et al.* 2018).

Notes on the collector:—The specimen from Wallich's Herbarium (K000217501) is the only duplicate of *No.* 3752 containing a note (possibly from Wallich's hand) on the original collector's collection number ("*G. Finlayson* 507, Turon Bay") in addition to the lithographed original labels cut from Wallich's Catalogue that are present on all specimens of the exsiccate series (except the lectotype in E, which has that information transcribed directly on the sheet, including the typo "Turun Bay"). Wallich's Catalogue labels only state "Hb. Finl. e sinu Turon" [Herbarium Finlayson, from the Bay of Turon] as source, but additionally mention "(Coet. spec. 1242-44)", i.e. an internal cross-reference to the other ("coeterae") three *Drosera* species mentioned in previous entries in Wallich's catalogue (*Wallich Cat. Nos. 1242, 1243* and *1244*).

	D. margaritacea			D. finlaysoniana		
Live image	10 <u>u</u> m	10 <u>um</u>	100 pm.	10 <u>u</u> m	10 <u>µm</u>	50 μm
SEM image	10 μm.	10 <u>um</u>	50 µm	10 μm	10 <u>u</u> m	50 μm
Gland description	0.05–0.15 mm long translucent, biseriate, double- tipped, trichomes (= type 5 sensu Länger et al. 1995).	0.05–0.3 mm stalked capitate trichomes with uniseriate stalk and yellow, spherical, non-secretory gland head ca. 0.05 mm in diameter.	stalked secretive glands with multicellular stalk (0.1–0.4 mm long) and translucent milky white, hemispherical to depressed ovoid gland head 0.1–0.3 mm in diameter.	0.05–0.15 mm long translucent, biseriate, double- tipped, trichomes (= type 5 sensu Länger et al. 1995).	0.1–0.3 mm long, secretory capitate trichomes with uniseriate, translucent stalk (base often reddish) and flattened gland head secreting a translucent mucilage droplet 0.05–0.2 mm in diameter.	
Stem	✓	✓	×	✓	✓	×
Adaxial petiole	✓	×	✓	N/A	N/A	N/A
Abaxial petiole	√	✓	×	N/A	N/A	N/A
Adaxial lamina/margins	✓	✓	✓	✓	✓	✓
Abaxial lamina	✓	✓	×	✓	√	×
Inflorescence	√	√	×	√	√	×

FIGURE 8. Distribution of non-carnivorous trichome and gland types on *D. margaritacea* and *D. finlaysoniana*. Close-up photographs, SEM-images and descriptions are given for each trichome/gland type. The presence of each trichome/gland type on various parts of the plant is indicated by check marks.

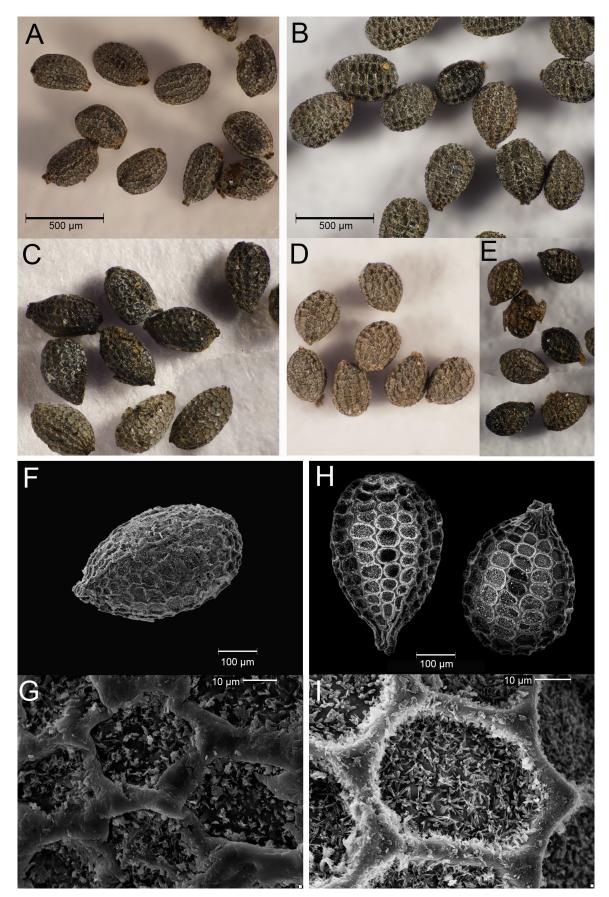


FIGURE 9. Seed comparison of *Drosera margaritacea* (left: A, C, F, G) and *D. finlaysoniana* (right: B, D, E, H, I). A Trent River Valley, Yampi Peninsula, Kimberley, Western Australia (*A. Lowrie s.n.*). C, F, G Type locality of *D. margaritacea*, Kimberley, Western Australia (*T. Krueger 7*) B, H, I Keep River, Northern Territory, Australia (*A. Lowrie s.n.*). D Fujian, China (*P.E. Chen 2491*). E Hsinchu, Taiwan (from cultivated plant). Photographs and SEM-images by A. Fleischmann.

Notes on the collection date:—The collection date of the type material is not evident from the herbarium specimens of *Wallich Cat. No. 3752*, but can be concluded from Finlayson's expedition journal (Finlayson & Raffles 1826): the expedition landed at Turon Bay on 15th September 1822. On p. 331, Finlayson mentions "[t]he daily excursions of our party [that] were the means of adding many valuable plants to my collection", before they re-embarked from the bay of Turon for the village of Turon on September 20th (Finlayson & Raffles 1826). Hence Finlayson's plant collections at the bay of Da Nang (the former Turon) during which the type gatherings of *D. finlaysoniana* were made took place 15–19 September 1822.

Notes on the type locality of *Drosera angustifolia*:—The exact location of the locus classicus of *Drosera angustifolia* is not evident from the type label, but was given by Mueller (1855), and later under the entry of *D. indica* by Mueller (1862: 58), as "[...]around the fresh-water lakes near Eustone on the Murray River, rare". Strangely, Barrett & Lowrie (2013) locate the locus classicus in New South Wales, although Mueller (1855, 1862) clearly denoted that he collected the plant in the state of Victoria. The most likely locality of Mueller's collection is within Hattah-Kulkyne National Park, possibly near Lake Mournpall or Lake Lockie (ca. 38 km WSW of Euston) which is the only known locality of *D. finlaysoniana* within Victoria, based on more recent herbarium records (*J.H. Browne 851, T. Mitchell s.n.*). The area around Lake Mournpall was botanised by Mueller, denoted by him as "Moornpool" (e.g., on *F. Mueller s.n., Acacia anthoclada,* MEL 0026133A photo!). Mueller (1855: 7) already recognised his *D. angustifolia* as very close to *D. finlaysoniana* and highlighted it to be "one of the many tropical forms of plants, which, transgressing the torrid zone, advance so far southerly as the Murray desert".

Specimens Examined:—Drosera finlaysoniana (oldest known and most recent records are listed for each state/ country of occurrence, for full specimens list see Electronic Appendix). AUSTRALIA. Western Australia: Between Barrow's [=Barrow] & Rawlinson's [=Rawlinson] Range, 1873, W.E.P. Giles s.n. (MEL 0096394A photo!); Nallan Lake, 30 m E of Great Northern Hwy., 20 km NNE of Cue, Western Australia, lake margin, reddish-brown sand, 13 July 2020, T. Krueger 6 (PERTH!, MIN!). Northern Territory: Between the Finke River and Charlotte Waters, 1885, F.A.H. Kempe 26 (MEL 0096436A photo!); 1.2 km West of Attack Creek crossing of Stuart Highway, occasional in seepage area on plain near creek, sandy loan, herb-rich Hummock grassland, 11 Jun 2006, D.E. Albrecht 12001 (K!, DNA—voucher for Millenium Seed Bank, as "Drosera indica"). Queensland: Normantown [=Normanton], 1875, A. Henry s.n. (MEL 0096359A photo!); Adjacent culvert crossing of the Barron River, upstream and 3 km NW of Kurand, sand and silt deposits over and about exposed geology forming rapids at this point in the river, 09 August 2009, G.W. Wilson 588 (CANB 723361.1 photo!, CNS). Victoria: Hattah Lakes National Park, ca 2km NNW Hattah Camping Ground, close to water after flood recession, 14 December 1981, T. Mitchell s.n. (MEL 0595758A photo!); Hattah-Kulkyne National Park, E side of Mournpall Track, ca 1.4km S of Lake Mournpall, growing on the edge of a flood plain depression recently filled by river flood, in open area protected from winds by Callistemon brachyandrus, sandy clay soil, 04 March 1993, J.H. Browne 851 (MEL 2014399A photo!). South Australia: Central Australia, 1883, C.G.A. Winnecke 27 (MEL 0096435A photo!); 6 km ESE of Bloodwood Bore, Cordillo Downs Station, sandplain, brown loam soil, 19 August 1991, F.J. Badman 4942 (MEL 1617508A photo!).

CHINA. Guangdong: Swatow [Shantou], 180 miles N.E. of Hong Kong, 1901, *J.M. Dalziel s.n.* (HUH photo!, IBSC-117088 photo!, P-04583188 photo!); Guangwei, Zhuhai County, Sanzao, wetland, 16 August 1992, *Z.M. Wu 84975* (MO photo!). Guangxi: Hepu County, Zhongshan, 1952, *J. Zhong 809459* (IBK photo!); Hepu, Yin field water, 13 April 1956, *Plant Investigation Team of Hepu District 2011* (IBSC photo!, PE photo!). Fujian: Prov. Fohien [Fujian], 1861, *Hance 1425* (P photo!); Bantou Reservoir, wet grass, 21 October 1980, *G. Ye 1763* (FJSI photo! PE photo!). Hainan: Ching Mai District [Chengmai County], Tai Wong Ling and vicinity, Tung Pin Tin Village, moist, level land, sandy soil, meadow, cult. field, abundant, 19 February 1933, *C.I. Lei 385* (IBSC photo!, NAS photo!, P!, PE photo!); Dan County, on the way from Paipu to Shatao, 24 March 1982, *G. Fu 2780* (IBSC photo!).

TAIWAN. Taoyuan County, Luchu, 10 September 1908, S. Sasaki s.n. (TAIF-11100 photo!); Yangming Lake, 0–50 m, 20 October 2018, S.W. Chung 13593 (TAIF photo!).

VIETNAM. [Nghệ An Province]: Annam, Vinh, in ricefield, 23 January 1909, *W. Micholitz s.n.* (K!). [Khánh Hòa Province]: Annam, Nha-trang [Nha Trang] and vicinity, 11–26 March 1911, *C.B. Robinson 1054* (K!, NY photo!, P photo!, WAG photo!), Annam, Nhatrang [Nha Trang] et enviros, 04–05 February 1914, *A. Chevalier 30427* (P photo!). Thua-thien [Thừa Thiên Huế Province]: Cau-hai [Cầu Hai lagoon], dans les sables des dunes [in the sand of the dunes], without date, *P. Eberhardt 1362* (P photo!); Hui [Huế], citadelle, champ du Boi (rare), March–May without year, *P. Couderc s.n.* (P-04583197 photo!, P-04583197 photo!). [Quảng Ninh Province]: Quang-Yen [Quảng Yên], ricières [rice fields], December 1908, *Rotereau s.n.* (P-04581087 photo!); Tonkin, Quang Yen, rizières, October 1909, C. *d'Alleizette s.n.* (P-04583151 photo!). [Bình Thuận Province]: Phanthiết [Phan Thiết], route de Phui-hài, sables humides [wet sands], 05 November 1924, *F. Evrard 1715* (P photo!). [Đà Nẵng municipality]: Tourane [Đà

Nẵng], January 1837, *M. Gaudichaud 170* (P photo!); Annam, Tourane [Da Nang], common in the dunes near the sea, May–July 1927, *J. & M.S. Clemens 3032* (IBSC photo!, MO photo!, P photo!, WAG photo!). [Bà Rịa-Vũng Tàu Province]: Cap St. Jacques [Vũng Tàu], 19 October 1919, *M. Poilane 616* (P photo!). [Hanoi municipality]: Jongkin [Tonkin], Env.[irons] de Hanoï [surroundings of Hanoi], rizière [rice field], July 1908, *C. d'Alleizette s.n.* (P-04583159 photo!). [Phú Yên Province]: Tonkin (NB), Yên Môi (Vung), 17 November 1889, *R.P. Bon 144* (P photo!). [Quảng Trị Province]: Annam, Province de Quang Trị, Village de An Nha [today a quarter of Gio Linh city], bonds d'une rizière (margins of a rice field), 17 April 1936, *Pételot 5718* (P photo!).

THAILAND. [Prachuap Khiri Khan Province]: Rachaburi [not corresponding to today's Ratchaburi Province], Nawng Kae [Hua Hin District], Kao Ta Kiep [Khao Takiap], c. 5 m, 26 September 1927, *Mrs. D.J.* [=*E.E.*] *Collins* 1621 (P photo!).

Discussion

Non-carnivorous indumentum

The stalked milky-white glands on the adaxial petiole and lamina surface of *Drosera margaritacea* are not paralleled in any other *Drosera* species. Their depressed ovoid to hemispherical adhesive gland heads are also very different from the common, mucilage-secreting *Drosera* tentacles or the stalked trichomes that cover glandular stems and inflorescence parts of certain species. In contrast to the clear, translucent mucilage secreted from *Drosera* tentacles (a highly viscous, acidic, aqueous polysaccharide solution; Rost & Schauer 1977, Gowda *et al.* 1982, Kokubun 2017), the secreted droplets from the stalked petiole glands of *D. margaritacea* often appear milky white and, despite being adhesive as well, are of much lower viscosity. Notably, in contrast to *Drosera* tentacles, their gland heads do not desiccate on dried leaves, but persist and maintain their spherical shape (Fig. 6 inset), even in 94-year-old herbarium material (*A.J. Ewart s.n.*). The secretion droplets are adhesive in fresh material but lose their stickiness in dried material. Further functional-morphological and ecological studies on these adhesive glands and their secretions, whether it is mucilage or resin, are necessary to evaluate their possible function. At present, it is not known whether they play a role in prey attraction or carnivory or whether they might rather be related to herbivore and kleptoparasite defence.

Apart from the unique stalked milky-white glands of the petiole and lamina adaxial surface, all green parts of *D. margaritacea* except the petiole upper surface are covered by identical microscopic indumentum: the stem, petiole lower surface, upper and lower surface of the lamina, peduncle, bracts, pedicels and sepals are lined with 0.05–0.15 mm long biseriate double-tipped trichomes and 0.05–0.30 mm long yellow-headed capitate trichomes (Figs. 7 and 8).

Trap scent

While the leaves of most *Drosera margaritacea* individuals are unscented, a small percentage (ca. 10–20% of the type population) emit a sweet, honey-like odour, similar to the presumably related *D. finlaysoniana* (Fleischmann 2016, Gibson 2002, in the latter as "*D. indica*"). As observed by Fleischmann (2016) for *D. finlaysoniana*, not every individual in a given population of *D. margaritacea* is scented (at least to the human nose), and some have a stronger scent than others (T. Krueger, pers. obs.).

Taxonomy

In herbarium material, *Drosera aquatica* can be mistaken for *D. finlaysoniana* upon casual examination, as this species shares sessile leaves (with no discernible petiole, i.e., the carnivorous tentacles emerge all the way down the lamina to the stem) and a similar size range. However, *D. aquatica* is easily distinguished from *D. finlaysoniana* by a) its shaggy stem and inflorescence indumentum consisting of long, patent, simple, translucent eglandular hairs and scattered intermixed glandular hairs, b) upright ascending peduncles, and c) somewhat narrower leaves [1.1–1.3 mm wide (Lowrie 2014), as opposed to (1.6–)2.0–4.0(–4.5) mm lamina width in *D. finlaysoniana*]. *In vivo*, both species often can be readily distinguished by the vividly red stems and inflorescences of *D. aquatica* contrasting with the species' greenish leaves (all parts, stem, leaves and inflorescences are typically yellowish-green in *D. finlaysoniana*, although bronze-red stems and inflorescences have been recorded in some populations). *Drosera aquatica* is most common in northern parts of the Northern Territory's Top End region (especially around Darwin, where *D. finlaysoniana* is absent), but both species do co-occur in the Victoria River (Northern Territory) and Kununurra (Western Australia) areas (Lowrie 2014, Lowrie *et al.* 2017a). Additionally, we here document the first record outside Australia, from the

Lesser Sunda Islands, Indonesia (specimen listed below). This makes *D. aquatica* the fourth species from *D.* section *Arachnopus* to occur outside Australia, together with *D. finlaysoniana*, *D. serpens*, and the entirely non-Australian *D. indica*.

Drosera aquatica (only new records representing range extension given):—INDONESIA. [Lesser Sunda Islands]: Kl. Soenda Eil. Flores, West-; Rekas-Orong, padang, 450–600 m, 27 Mar 1967, *E. Schmutz 1360* (L!).

Breeding mode

Drosera finlaysoniana is self-fertile and (facultatively) autogamous (A. Fleischmann pers. obs., Gibson 2002), usually every pedicel of an infructescence will bear a fertile capsule (herbivore damage notwithstanding). Occasionally, unisexual flowers can be observed in that species, usually in the terminal flowers of an inflorescence: functionally female flowers lacking stamens (Gibson 2002), but also functionally male flowers with reduced styles (A. Fleischmann pers. obs., see also Fig. 5E). In contrast, the much larger-flowered *D. margaritacea* is self-incompatible and therefore requires xenogamy, which means that only cross-pollinated flowers will develop into ripe capsules, while pedicels of unpollinated flowers will carry undeveloped, empty capsules on the infructescence. This can easily be observed in herbarium specimens and is also visible on photographs (Figs. 2F and 6), as pedicels of successfully pollinated flowers will arcuately curve upwards after pollination (so that the developing capsule is facing the sky), while pedicels of unpollinated flowers remain straight, patent from the rhachis or bend downwards at their base (A. Fleischmann pers. obs.).

TABLE 1. Morphological comparison of *Drosera margaritacea* and the morphologically similar *D. finlaysoniana*. All data are based on own measurements and personal observations (see Material and Methods).

	Drosera margaritacea	Drosera finlaysoniana		
indumentum of stem and peduncle	biseriate, double-tipped trichomes (type 5 sensu Länger et al. 1995) + yellow-headed capitate trichomes)	biseriate, double-tipped trichomes (type 5 sensu Länger et al. 1995) + stalked capitate secretory trichomes		
petiole length (= part of the leaf not covered with carnivorous tentacles)	1.5–3.5 mm	petiole absent (<1 mm), leaves sessile		
glands of petiole adaxial surface	20-50 stalked milky-white glands	n/a		
non-carnivorous lamina indumentum	adaxial surface and margins sparsely covered with same stalked milky-white glands as on petiole (but slightly smaller) + biseriate double-tipped trichomes (type 5 sensu Länger et al. 1995) + yellow-headed capitate trichomes	adaxial surface (especially near stem and lamina margins) with T-or Y-shaped trichomes (type 14 sensu Länger et al. 1995) + biseriate double-tipped trichomes (type 5 sensu Länger et al. 1995)		
peduncle insertion	ascending vertically (± parallel to stem in young inflorescences; mostly <45° but rarely diverging up to 90° from stem in older inflorescences)	ascending ± horizontally, even young inflorescences mostly held at >45° from the stem		
peduncle length total inflorescence length	(8-)9-16(-19) cm, much exceeding the leaves in length $30-55(-65)$ cm	(1.5-)2.0-8.0(-11.0) cm, shorter than or at most equalling the leaves in length $(3-)6-18(-26)$ cm		
total innorescence length	30–33(–63) CIII	(3–)0–18(–20) CIII		
flowers per scape	at least 30-50	(2–)6–20(–26)		
pedicel length in fruit	9–25(–35) mm	(2–)4–12(–20) mm		
pedicel disposition in fruit	horizontal or gently bent downwards from the rhachis then sharply arcuated upright near seed capsule (S-shape)	horizontal and straight or gently curved upwards from the rhachis (I-or C-shape, rarely slightly S-shaped)		
flower diameter	18–24 mm	(6–)7–14(–20) mm		
anther shape	anthers longer than the filament, connective shorter than the thecae, white with swollen, rounded yellow tip	anther much shorter than the filament, connective as long as the thecae, white, apex plain, not dilated		
pollen colour	pale yellowish-white	yellow, rarely pale yellowish-white		
breeding mode	self-incompatible	self-compatible, facultatively autogamous		

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Specimens examined:

Drosera finlaysoniana:

AUSTRALIA. Western Australia: Murchison River, without date, A.F. Oldfield s.n. (MEL 0096391A photo!); Near Mount Hale, without date, Carr s.n. (MEL 0096427A photo!); Murchison River, ante Oolinyarrah [not found], without date, A.F. Oldfield 870 (MEL 0096375A photo!); Between Barrow's [=Barrow] & Rawlinson's [=Rawlinson] Range, 1873, W.E.P. Giles s.n. (MEL 0096394A photo!); Fortescue River, 01 June 1878, J. Forrest s.n. (MEL 0096431A photo!); Yule River, 1878, J. Forrest s.n. (MEL 0096420A photo!); Champion Bay, 1890, L. Gould s.n. (MEL 0096367A photo!); Mt Narryer, Murchison River, grows about the rock holes, 1893, I. Tyson 11 (MEL 0096408A photo!); Near Nickol Bay, 1895, W.D. Cussack s.n. (MEL 1518898A photo!); Muccan Station, De Grey Station, in damp sand near pool, 05 June 1941, N.T. Burbidge 907 (PERTH 657980!, PERTH 657484!); Eginbah Station, damp ground in small drainage channel, 08 June 1941, N.T. Burbidge 1007 (PERTH 657476!, PERTH 657425!); Mount Edgar Station, SE from Marble Bar, in damp soil near creek pool, 11 June 1941, N.T. Burbidge 1125 (PERTH 3289028!); Sandy Creek, 12 miles N of Jigalong, sandy soil along No 1 Rabbit Proof Fence, 14 May 1947, R.D. Royce 1607 (PERTH 658022!); Yakabindie, Mount Sir Samuel, in argillaceis ad margine paludosis, 06 September 1963, F. Lullfitz 1606 (PERTH 657468!); 1.5 km W of Chesterfield Mine, Belele Station 56 km WNW of Meekatharra, on bank of temporary pool, 16 August 1965, D.W. Goodall 3186 (PERTH 657441!, PERTH 5863120!); Manderry Pool Robe River between Onslow and Roebourne, 27 August 1966, R. Butler 45 (PERTH 657492!); Glen Helen, Rawlinson Range, damp creek bed, 20 July 1967, A.S. George 8793 (PERTH 657506!); Glen Cumming, Rawlinson Range, Damp soil in gorge, 21 July 1967, A.S. George 8838 (PERTH 657433!); Yarra-Yarra Creek, creek banks, 14 October 1971, H. Demarz 3440 (PERTH 657948!); Glen Cumming, 24 July 1974, S. Carlquist 5176 (PERTH 657921!); Entrance to Glen Cumming, damp sand among rocks in creek bed, 24 July 1974, A.S. George s.n. (PERTH 658006!); Kimberleys [sic!], Durack River, +/-80 km S.S.W. of Wyndham, 6 km by Road from Gibb River-El Questo Road, 40 km by Road from Bindoola Creek to turn-off, small creek entering river, 28 May 1976, A.C. Beauglehole 51439 (CBG 8004798.1 photo!, DNA); Rudall River National Park, Little Sandy Desert, Central Australia, bed of river, 30 April 1979, A.S. Mitchell 861 (PERTH 657956!); Little Sandy Desert, Central Australia, drainage line in grassy sand plain, 02 May 1979, A.S. Mitchell 929 (PERTH 657913!); Paterson Range-Lake Waukarlycarly area, edge of shallow claypan, June 1979, J.S. Reeve s.n. (PERTH 657964!); Newman, 07 August 1980, K. Walker KW/MNM 159 (PERTH 2580802!); Margin of Lake Cohen Gibson Desert, on damp soil near freshwater lake, 01 August 1983, R.P. McMillan & T.F. Houston s.n. (PERTH 658014!); 23 km N of Cue, claypan, 26 September 1984, H. Demarz 10204 (PERTH 5863422!); Mount Gould Police Station (abandoned), on river bank, red clayey sand, 01 May 1986, R.J. Cranfield 5411 (PERTH 5811538!); Wade Creek, Osmond Range, damp sand beside creek, sandstone substrate, 19 July 1991, I.D. Cowie 1884 (PERTH 5862361!, MEL 1603443A photo!); Hamersley Ranges, in the bed of Kumina Creek eight kilometres east-south-east of Mt Elvire, in damp patches on a loamy bank next to a pool in the bed of a moderate sized creek running through a hilly area; the creek bed has a mosaic of pools, open loamy areas and pebbly banks Soil: Mid-brown loam, 13 August 1991, M.E. Trudgen & D. True MET 10274 (PERTH 4310462!); Site 21, Honeymoon Well Project Area, 40 km S of Wiluna, in and around low-lying clayey flat prone to flooding, 12 June 1992, R.P. Hart & D. Corbyn RPH 3175 (PERTH 4216164!); Between Piccanniny carpark and western creek, Bungle Bungle National Park, white/yellow washed sand over sandstone, 14 June 1993, I. Solomon 796 (PERTH 3759210!); Victoria Highway, 2.3 km NW of the Ord Dam turnoff, SE of Kununurra, 16 June 1993, A. Lowrie 713 (PERTH 3178749!); Russ Creek, Gibb River Road, Mitchell Plateau, Kimberley, sandy soil on banks of the creek, 25 June 1993, A. Lowrie 772 (PERTH 3143562!); At Plain Creek crossing, ca 30 km N of Beverley Springs Station Homestead, growing in sand, 30 June 1993, M. Barrett MDB 214 (PERTH 6294138!); Trugallenden Pool, 22.4 km NNE of Newman, 16.2 km W of Shovelanna Hill, adjacent to small rock pool in damp situations, low in landscape, westerly aspect, skeletal red soil over massive rock, 10 July 1993, S. van Leeuwen 1341 (PERTH 5864070!); Above Harrys Hole, Doon Doon-Glenhill Station, 26 July 1993, K.H. Coate 280 (PERTH 3281868!); Edge of Kennedy Range, soak on margin of Kennedy Range Rocky outwash over clay, 17 August 1994, G.J. Keighery & N. Gibson 1640 (PERTH 5018579!); Yakabinda Lake (Yakabindie Station), lake edge (below high water mark, above present water mark) Yakabinda Lake is a freshwater claypan, 03 May 1995, R.T. I (PERTH 4135342!); 5.0 km NNW of Mileura Hill, Mileura Station, red clay over hardpan, 10 May 1995, R.J. Cranfield 9775 (PERTH 4349490!); Paynes Find-Sandstone Road, ca 26 km S of the Atley Station turn off SW of Sandstone, small fresh water lake on W side of road, 23 June 1995, A.P. Brown 1057 (PERTH 7518552!); 61 km from Sandstone on Paynes Find Road, small lake W side of road, Shallow lake, red brown sandy clay, 23 June 1995, S. Patrick 2288 (PERTH 5070465!); Next to Mount Brophy Springs at N end of Gardner Range, 190 km SE of Halls Creek, SE

Kimberley, red brown sandy clay, 02 July 1995, K. Coate 361 (PERTH 4231252!; exceptionally large specimen); Barlee Range Nature Reserve, 15.2 km WSW of Jarrabuduundy Bore, 18.3 km N of Mount Palgrave, 18.9 km SW of Wongajerra Well, growing alongside pool at base of gorge, in gritty brown clay loam with lots of silt and organic material, 06 July 1995, S. van Leeuwen 1863 (PERTH 4969022!); Barlee Range Nature Reserve, 16 km WSW of Jarrabuduundy Bore, 17.2 km N of Mount Palgrave, 20.2 km SW of Wongajerra Well, Ashburton Botanical District, growing alongside pool at base of gorge, in gritty brown clay loam with lots of silt and organic material, 06 July 1995, S. van Leeuwen 1872 (PERTH 5223490!); Within 1 km of campsite, Gardner Range, 190 km SE of Halls Creek, SE Kimberley, 07 July 1995, K. Coate 378C (PERTH 4231104!); Talbot Springs, Sturt Creek Station, 13 July 1995, K. Coate 380 (PERTH 4231090!); 1.5 km W of Bidiganning Bore, Burnerbinmah Station, Small soil pocket on granite dome, pale brown sandy loam, 01 August 1995, S. Patrick SP 2365 (PERTH 4284666!); Cardilya Pool, Cardilya Creek, Carey Downs Station, 7 km E of Homestead by track. (Site: Adjacent, cb93c), river pool River sand, 31 August 1995, G.J. Keighery & N. Gibson 552 (PERTH 4950992!); Cardilya Pool, Cardilya Creek, Carey Downs Station, 7 km E of Homestead by track. (Site: Adjacent, cb93), river pool, with rocky areas and sandy banks River sand, 31 August 1995, G.J. Keighery & N. Gibson 568 (PERTH 4952804!); Cardilya Pool, Bidgelang Pool, Pell Creek, Carey Downs Station. (Site: cb93a), river pool, with sandy banks River sand, 31 August 1995, G.J. Keigherv & N. Gibson 676 (PERTH 4973631!); Nallan Dam, 19 km N of Cue, growing in sandy loam on upper section of Lake Margin, 10 October 1995, A. Lowrie 1352 (PERTH 6440673!); Jigalong Station, 60 km E of Newman, wide river bed with sandy bedload, 21 June 1996, A.L. Payne PRP 1361 (PERTH 4859871!); Little Sandy Desert, 7.3 km ENE of Cooma Well, 44 km N of Yanneri Lake, 41.2 km ESE of Weelarrana Homestead, 30.3 km S of Burranbar Pool on Savory Creek, proterozoic medium-grained sandstone (Spearhole Formation) breakaway and gorge terrain, high in landscape, skeletal red gritty sand, 15 April 1997, S. van Leeuwen 3065 (PERTH 7014236!); Site number: 157. Erallinya Pool, Hamersley Range, Fortescue Botanical District, semi-permanent pool, soil: Banks brown clayey-loam Some of the bank was cracking clay, 20 April 1997, M.E. Trudgen MET 15298 (PERTH 6657028!); Joffre Creek, just above Joffre Falls, Karijini National Park, 10.2 km SSW of Drillers Ridge, 11.5 km NNE of Mount Vigors, 23 km SE of Mount King, Hamersley Range, moist red-brown alluvial soil, low in landscape, creekline and wash area, 20 April 1997, S. van Leeuwen s.n (PERTH 6275370!); Near Lake Willson, 25 km SSE of Sturt Creek Station, SE Kimberley, 15 May 1997, K. Coate 424 (PERTH 4941810!, MEL 0266628A photo!); 3 km NE of Mount Brophy, SE Kimberley, 17 May 1997, K. Coate 431 A (PERTH 4941896!); West Strelley River on Marble Bar Road, 77 km SE of Port Hedland, Pilbara, in damp river bed, 30 July 1997, D.J. Edinger & G. Marsh P.2 (PERTH 5536944!); Above Talbot Springs in Denison Range, N Tanami Desert, on sandstone escarpment, 04 May 1998, K.F. Kenneally 11938 (PERTH 5088518!); Mount Brophy Spring in Gardner Range, N Tanami Desert, in shallow pool of seepage area, 11 May 1998, K.F. Kenneally 12044 (PERTH 5090334!; exceptionally large specimen); Virgin Spring, Carnarvon Range, Little Sandy Desert, seepage area at base of spring, 19 August 1998, K. Coate 487 A (PERTH 5252881!); Virgin Spring, 1 km SE of Kadyara Rockhole in Carnarvon Range, Little Sandy Desert, in dark red Calyie sandstone, 28 August 1998, B. & B. Backhouse & D. Edinger BEMJ 130 (PERTH 5241928!); Camp 3, Fowl House, Red Rock Creek near junction with Osmond Creek, E Kimberley, in damp spot at base hill, 05 May 1999, D.J. Edinger BEMJ 1318 [A] (PERTH 5370132!); Carnarvon Ranges, creek line E of M6, creekline, on damp edge, 21 May 1999, M. French 848 (PERTH 5791898!); On old Rabbit Proof Fence, 4 km S of Pardoo Roadhouse, Pilbara, in red sandy soil, 14 June 1999, K. Coate 487 A (PERTH 5469252!); Mount Augustus, Kotka Trail, brown clayey sand Waddi dry water, 21 June 1999, R. Davis 8887 (PERTH 5371376!); Site 3, 1 km N of Site 2 which was 2.5 km SW of Silver Grass Peak, 30 km NNE of Mount Farquhar, West Hamersley Range, 23 July 1999, B. Backhouse, D. Edinger & G. Marsh BEM 49 (PERTH 5463076!); Muggon Station, claypan 5.5 km SW of homestead close to track Yallawell Paddock, claypan, on surrounding slopes, red brown clayey sand, 05 September 1999, S. Patrick et al. SP 3173 (PERTH 5759641!); Coolibah Claypan. Mandora Marsh area, large ephemeral claypan on S side of linear sand dune, 18 October 1999, T. Start ANS 1149 (PERTH 8592721!); Gibson Desert Nature Reserve, flat laterite plain, wet claypan, moist cryptogamic red sandy clay loam, 16 May 2000, T.B. Bragg 47 (PERTH 5346541!); Meentheena Station Conservation Reserve, 2.3 km SSW of Bullgarina Hill, 5.5 km NW of King Rock Hole, 18.4 km ENE of Mt Edgar, 33.6 km NNW of Baroona Hill (Survey Site 4). Nullagine, 25 May 2000, S. van Leeuwen 4485 (PERTH 6414354!); Near Duck Hole, Christmas Creek Station, S Kimberley, in seepage areas at base of dunes, 03 July 2001, K. Coate 644 (PERTH 5927951!); Gorge below Trig point on M6, SE of camp at Serpents Glen, Carnarvon Range, Little Sandy Desert, in damp soil beside creek, 06 August 2001, K.F. Kenneally & D.J. Edinger K 12221 E 2686 (PERTH 5849675!); Little Sandy Desert, Willie Soak, northwestern side of soak, 9.1 km NNE of Kulonoski East Well on Beyondie Station, 27.6 km SE of Canning Well on Ilgarari Creek, 27.7 km SW of Yanneri Lake, 23.2 km NNW of Ten Mile Lake, edge of reasonably fresh claypan, fringing apron, low in landscape, flat terrain, damp red sand, 20 August 2001, S. van Leeuwen 5011 (PERTH 6538339!,

CANB photo!, AD, MEL); Drill site named Missing, northern Great Sandy Desert, salty area between sand dunes, damp at 5 cm Red sand-laterite, 01 October 2001, C.P. Campbell 3923 (PERTH 6142788!); Pope's Claypan, 9 km SSE of Earaheedy Homestead, near waterline of wet claypan, 15 April 2002, D.J. Edinger, B. & B. Backhouse & G. Marsh DJE 2994 (PERTH 6117139!); Barlee Range Nature Reserve, 5.2 km WNW of Wadgawaranna Pool, 3.8 km SSW of Pamprunnah Pool, 24.9 km NE of Padbury, 17.4 km N of Mount Palgrave, along drainage line at base of steep side gorge, numerous pools and seepages, skeletal red gritty alluvial soil amongst cobbles, boulders and rocky screes, low in landscape, 26 July 2002, S. van Leeuwen 5070 (PERTH 7506406!); Lake Nallan, Nallan Station, Cue, lake shore Freshwater Rangeland Brown dry sand, 26 July 2002, G. Byrne 354 (PERTH 7254938!); Kimberley Region, Mornington Wildlife Sanctuary, 250 km E of Derby, Sir John Gorge, rocky sandstone shelf of gorge, 04 May 2004, S. Legge & S. Murphy 32 (CANB 668930.1 photo!); Kimberley Region, Mornington Wildlife Sanctuary, 250 km E of Derby, [The 'Dag'], growing in damp soil beside river, 24 April 2005, S. Legge & S. Murphy 511 (CANB 678792.1 photo!); Caramulla Creek, towards 'Jigalong', E of Newman, coarse orange sandy soil, 03 May 2006, A.R. Bean 25272 (PERTH 8041091!); Road into [Kutjurntari] Rockhole, below Gill Pinnacle, N of Docker River-Warakuna (Giles) Road (Great Central Road), soakage area near creekline, recently burnt, 24 September 2006, H.P. Vonow, V.T. Clarke, W.A. Thompson HPV 3164 (PERTH 8128723!); A soak on the track south of Desert Bore. Warrawagine Homestead, dry sandy clay above the dry soak, recently burnt, 03 September 2007, G. Byrne 2902 (PERTH 7991630!); Port Hedland Outer Harbour Development, SW of Port Hedland, sand plain, red brown sandy loam, 28 May 2008, K. Chuk QN 75-13 (PERTH 9067469!); Kotka Trail, behind carpark Mount Augustus, limestone fringed creek bed Small steam full of algae Light brown sandy loam, very damp, wet, 15 August 2008, S.C. Coffey 85 (PERTH 7991150!); Kotka Trail, behind carpark Mount Augustus, limestone fringed creek bed Small steam full of algae Light brown sandy loam, very damp, wet, 15 August 2008, S.C. Coffey 86 (PERTH 7991169!); N of carpark to Edney's Lookou, Mount Augustus National Park, gully with winter creek Granitic boulders, 16 August 2008, S.C. Coffey 87 (PERTH 7991118!); Gorge above Serpents Glen, Carnarvon Range, ca. 1 km S of Good Camp Rockhole, in deep gorge on sandy soils derived from massive red sandstones, 20 August 2008, N. Gibson 4615 (PERTH 8176612!); Yalgoo North Road, Yalgoo, 5.2 km N from Dalgaranga Road then E for 0.5 km to the granite outcrop, Flat, outcrop Moist-dry brown loam-sand over granite-boulders, 18 September 2008, F. Hort, J. Hort & F. Obbens 3264 (PERTH 8117985!); Nallan Lake, ca 19 km of Cue, near Great Northern Highway, grows in red sandy soils on the shores and margins of seasonally flooded soak in semi arid zones of inland Australia, 18 July 2009, A. Lowrie 4005 (PERTH 8691649!); Virgin Springs, N of the Carnarvon Range, near the edge of rock pools, in shallow sand, 13 September 2010, D. Pickles 2010-2 (PERTH 8322538!); Serpents Glen, ca 3.7 km on a bearing of 296 degrees from Trig Point M6, Carnarvon Range, Birriliburu Indigenous Protected Area [plot C006], flat outwash fan from gorge Soil variable porportions of sand and gravel, 08 August 2012, N. Gibson, S. van Leeuwen, M.A. Langley & K. Brown NG 6817 (PERTH 8793832!); S side of Carnarvon Range, ca 3.1 km on a bearing of 71 degrees from Trig Point M6, Birriliburu Indigenous Protected Area [plot C022], rocky dolerite creek line mid way up open gorge, 12 August 2012, N. Gibson, S. van Leeuwen, M.A. Langley & K. Brown NG 6818 (PERTH 8793824!); Mackay Creek within the Little Sandy Desert bioregion, 140 km N of Telfer, 280 km W of Newman, creek banks Loose red sand with slightly cobble surface, 24 May 2013, J. Williams WP 13 (PERTH 8531501!); Pasture Monitoring Site 7, Milly Milly Station, Murchison catchment, open hardpan plain, 19 May 2015, J. Stretch 10668 (PERTH 8880751!); Mulga Downs Station, Pilbara Region. 20 km ENE of intersection of Great Northern Highway and Nanutarra-Munjina Road. 3.5 km SSW of Puncher Bore (FV011A), flat beside inflow channel to large claypan Edge of drainage channel on eastern edge of dune, 01 August 2015, M.N. Lyons & S.D. Lyons FV 0381 (PERTH 9071385!); C. 85 km due NE of Kiwirrkurra, flat area grading to freshwater lake edge Pale pinkish brown sandy loam, swampy, 10 September 2015, R. Butcher & D. Albrecht RB 2029 (PERTH 8894329!); 10.5 km N of Mount Webb, rangeland Watercourse Dry red rocky sand Area burnt c 1 + years ago, 27 July 2016, T. Blake DD 1375 (PERTH 8897379!); 11 km N of Bibarrd, rangeland Dry watercourse Red rocky sand, 01 August 2016, M. Goods DD 1176 (PERTH 8875707!); Unallocated Crown Land Exclusion, Pilbara Region. 71 km N of Newman, 33 km SW of Roy Hill homestead, W side of Coondiner Pool 170m SSW of quadrat FV034A, damp edge of turbid creek pool, 22 August 2016, M.N. Lyons & R.A. Coppen FV 0556 (PERTH 9066608!); 15.93 km NE of Hussar Bore, off Eagle Highway, rangeland Wetland, floodplain, fresh water lake bank, grey brown wet sandy clay, 31 July 2018, M. Goods DD 1538 (PERTH 9125531!); Panorama pastoral lease, ca. 50 km NW of Marble Bar, drainage line, red sand, 18 May 2019, B. Loudon MC 53-17 (PERTH 9125531!); Nallan Lake, 30 m E of Great Northern Hwy., 20 km NNE of Cue, Western Australia, lake margin, reddish-brown sand, 13 July 2020, T. Krueger 6 (PERTH!, MIN!).

Northern Territory: Attack Creek, waterhouse, without date, *J.McD. Stuart s.n.* (MEL 0096361A photo!); Sturts [=Sturt] Creek [could also be Western Australia], 01 February 1856, *F. Mueller s.n.* (MEL 0096360A photo!); Between the Finke River and Charlotte Waters, 1885, *F.A.H. Kempe 26* (MEL 0096436A photo!); McArthur River, 1886, *D. Lindsay*

s.n. (MEL 0096400A photo!); W of McDonnells [=MacDonnell] Ranges, 24 May 1889, W.H. Tietkens s.n. (MEL 0096410A photo!); Finke River, S.A. [See notes on sheet], 1889, W.F. Schwarz s.n. (MEL 0096383A photo!); Near Haast's [Haast] Bluff, Macdonnell Ranges, 22 May 1911, G.F. Hill 201 (MEL 0096387A photo!); Banka Banka, S of Powells Creek, Aug 1922, C.E.F. Allen 670 (K!, DNA); Wycliffe Well, 01 June 1924, A.J. Ewart s.n. (MEL 0096365A photo!); 32 mls SW Hookers [=Hooker] Creek, 12 July 1956, G.M. Chippendale s.n. (MEL 0096352A photo!); 7 mls N of Aileron, in small sandy sheltered area by rocky hill, 02 June 1962, D.J. Nelson 410 (MEL 0096354A photo!); Mount Olga, March 1967, W.H. Butler s.n. (PERTH 658480!); Learmonth Park, Livingstone Pass, March 1967, W.H. Butler s.n. (PERTH 658472!); Ayers Rock, 28 August 1967, H.A. Morrison s.n. (MEL 0096385A photo!); Gibson Creek, 35 miles N Tennant Creek, Stuart Highway, 19 July 1968, J. Must 219 (PERTH 658502!); Frew River, 3 miles ENE Epenarra Homestead, rather rare in sandy gravel on gently sloping bank of river, 25 March 1970, P.K. Latz 555 (PERTH 658464!, K!, DNA, MEL); Near False Mount Russell, 01 August 1970, S. Parker 273 (PERTH 658510!); Little Creek crossing, 162 km E. Stuart Hwy. on Borroloola Rd., growing in heavy clay soil, damp area near river, 04 Jun 1971, C. Dunlop 2184 (K!, NY photo!, DNA, HO; specimens with exceptionally large floral bracts); Wartupunya Rockhole, moist earth in watercourse, 19 January 1972, C. Dunlop 2447 (MEL 0096366A photo!); Near summit of Mt Zeil, 13 June 1974, J.H. Willis s.n. (MEL 2111395A photo!); 80 km N of Tennant Creek on old Highway, in creek with some water, 10 July 1993, D.E. Murfet 1812 (PERTH 6440762!); Fitzmaurice River, on edge of stream with Utricularia and Eriocaulon, in deep sandstone gorge, M.J.A. Barritt 1242 (MEL 0278798A photo!); NE corner of Lake Mackay, damp (non-saline) sand between dune and saltlake, 05 October 2001, P.K. Latz 18057 (PERTH 8305226!); 1.2 km West of Attack Creek crossing of Stuart Highway, occasional in seepage area on plain near creek, sandy loan, herb-rich Hummock grassland, 11 Jun 2006, D.E. Albrecht 12001 (K!, DNA—voucher for Millenium Seed Bank, as "Drosera indica").

Queensland: Broadsound [=Broad Sound], without date, without collector (MEL 0096371A photo!); Rockhampton, without date, without collector (MEL 0096357A photo!); Rockhampton, no date, E. Bowman s.n. (MEL 0096373A photo!); Rockhampton, no date, A. Thozet s.n. (MEL 0096390A photo!); Brawl C[ree]k, no date, E. Bowman 121 (MEL 0096358A photo!); From the Flinders [River], no date, W. Woolls s.n. (MEL 0096432A photo!); Gainsford, no date, E. Bowman s.n. (MEL 0096362A photo!); East Coast [Port 1—between Curtis and Facing Islands], no date, R. Brown s.n. (MEL 0096395A photo!); Normantown [=Normanton], 1875, A. Henry s.n. (MEL 0096359A photo!); Trinity Bay, 1882, E.F.A. Fitzalan s.n. (MEL 0096422A photo!); Mitchell [River], 1882, E. Palmer 63 (MEL 0096445A photo!); Barron Falls, Trinity Bay, 1886, W.A. Sayer s.n. (MEL 0096404A photo!); Barron River, 1886, W.A. Sayer s.n. (MEL 0096444A photo!); Near Port Curtis, 1888, J.S. Edgar s.n. (MEL 0096447A photo!); Herbert River, 1889, E.F. Lamont s.n. (MEL 0096381A photo!); Upper Barcoo [River], 1890, M. Walker s.n. (MEL 0097035A photo!); Mill Stream Falls, Ravenshoe, Jun 1913, E.W. Bick s.n. (BRI AQ0183206 photo!, K!; type of Drosera indica f. robusta); Near sand mining operation, Chewko, near Mareeba, grows in sandy soils in wet ground, 08 June 1981, A. Lowrie 261 (PERTH 6440738!); Road 151, 2.3km S of Milmerran-Goondiwindi road, sandy watercourse dominated by Leptospermum polygalifolium, 28 February 1996, A.R. Bean 10037 (MEL 0286906A photo!); Ca 1km S of 'Glen Harding' turnoff, S of Mt Garnet, spring-fed creek with Cyperus, Eleocharis, Fimbristylis spp., sandy soil, 31 July 1997, A.R. Bean 12134 (MEL 0257681A photo!); Adjacent culvert crossing of the Barron River, upstream and 3 km NW of Kurand, sand and silt deposits over and about exposed geology forming rapids at this point in the river, 09 August 2009, G.W. Wilson 588 (CANB 723361.1 photo!, CNS).

New South Wales: Pulpulla, 1885, *H. Andrae s.n.* (MEL 0096421A photo!); Mootwingee, drainage tract near rock lease, sand, 21 September 1973, *G.M. Cunningham 1208* (CANB 00828355 photo!, NSW).

Victoria: Hattah Lakes National Park, ca 2km NNW Hattah Camping Ground, close to water after flood recession, 14 December 1981, *T. Mitchell s.n.* (MEL 0595758A photo!); Hattah/Kulkyne National Park, E side of Mournpall Track, ca 1.4km S of Lake Mournpall, growing on the edge of a flood plain depression recently filled by river flood, in open area protected from winds by Callistemon brachyandrus, sandy clay soil, 04 March 1993, *J.H. Browne 851* (MEL 2014399A photo!).

South Australia: Central Australia, 1883, C.G.A. Winnecke 27 (MEL 0096435A photo!); 6 km ESE of Bloodwood Bore, Cordillo Downs Station, sandplain, brown loam soil, 19 August 1991, F.J. Badman 4942 (MEL 1617508A photo!).

CHINA.

Guangdong: Swatow [Shantou], 180 miles N.E. of Hong Kong, 1901, *J.M. Dalziel s.n.* (HUH photo!, IBSC-117088 photo!, P-04583188 photo!); Yangjiang, Hailing Island, June 1956, *Z. Huang 41690* (IBSC photo!); Yangjiang Xian,

in plain, 30 June 1956, *C. Wang 41690* (IBK photo!, MO photo!); Lufeng, Touqing, beachside, waterside, barren sandy wet soil, 13 August 1958, *Z. Wei 121231* (IBK photo!, PE photo!); Sanzao, 26 October 1973, *Guangdong-73-Team 02921* (MO photo!); Huilai County, Banmei, 20 December 1982, *Z.X. Li 732* (MO photo!); Guangwei, Zhuhai County, Sanzao, wetland, 16 August 1992, *Z.M. Wu 84975* (MO photo!).

Guangxi: Hepu County, Zhongshan, 1952, *J. Zhong 809459* (IBK photo!); Guangxi, Hepu, 26 March 1971, *Y. Chen 405424* (IBK photo!); Hepu District, Yingpan, 18 September 1973, *C.F. Liang 33372* (IBSC photo!, PE photo!); Hepu, Yin field water, 13 April 1956, *Plant Investigation Team of Hepu District 2011* (IBSC photo!, PE photo!).

Fujian: Prov. Fohien [Fujian], 1861, *Hance 1425* (P photo!); Sung-A., Diongloh [Changle District, Fuzhou] and vicinity, growing on the sand, near stream, 28 July 1925, *P.E. Chen 2491* (AU photo!, M!); Amoy I.[sland], wet slope, along a watercorse, 08 October 1922, *H.H. Chung 277* (AU photo!); Amoy [Xiamen], hill slope, growing in bed of a stream, 15 May 1923, *H.H. Chung 5632* (AU photo!); Amoy, I.[sland], Naput hill, in bed of a stream, 22 April 1923, *H.H. Chung 1485* (AU photo!); Amoy, Nanputuo [South Putuo], 19 April 1926, *H.H. Chung 4842* (IBSC photo!); Amoy, near the university, in the swamp place by a bolder, 18 October 1926, *H.H. Chung 4734* (AU photo!); Amoy, Nanputo [Nanputao], 07 January 1927, *H.H. Chung 5896* (AU photo!); Amoy Island, on springy bank near the shore, 17 July 1933, *A.N. Stewart 3070* (AU photo!); Amoy, Nanputao, A.U. campus vicinity, 30 November 1934, *C.K. Tseng 515* (AU photo!); Amoy, university campus, 01 July 1936, H.H. Chao 485 (AU photo!); Xiamen, Xiamen University, water pool, 01 July 1955, *R. Lin 1* (IBSC photo!); Xiamen University, 31 October 1978, *K. Cai 19* (IBSC photo!); 16 May 1958, *without collector, s.n.* (FJIDC photo!); Xiamen, Bantou Reservoir, waterside on wetland, 27 August 1980, *Y. Chen et al. 228* (PE photo!); Bantou Reservoir, wetland at the stone wall, 20 m, 21 October 1980, *G. Ye 1711* (PE photo!); Bantou Reservoir, wet grass, 21 October 1980, *G. Ye 1763* (FJSI photo!) PE photo!).

Hainan: Ching Mai District [Chengmai County], Tai Wong Ling and vicinity, Tung Pin Tin Village, moist, level land, sandy soil, meadow, cult. field, abundant, 19 February 1933, *C.I. Lei 385* (IBSC photo!, NAS photo!, P!, PE photo!); [Danzhou, Dan County], Nodoa [Nada] and Tai Wan, San Hu, in sand near and in the water along river, 10 April 1922, *F.A. McClure 8939* (MO photo!, P); Huangliu, 31 January 1933, *X. Liang 63965* (IBK photo!—the duplicate at MO is *D. serpens*); Yaichow [Yacheng], Na[a]m Shan Lang, 06 January 1933, *N.Q. Chen 44798* (MO photo!); Yazhou, Nanshanling, 100 m, 06 January 1933, *J. Zuo & N. Chen 44798* (IBSC photo!); Gan'en County [today part of Dongfang City], 31 October 1933, *X. Liang 63965* (IBK photo!); Changjian Xian, empty sand, 11 March 1934, *X. Liang 65407* (IBK photo!, MO photo!); Kan-en District [Ledong County], Chim Fung Ling [Jianfeng Ling mountain] near Sam Mo Watt village, moist, level land, sandy soil, retain.[ing] wall, fairly common, 19 March 1934, *S.K. Lau 3489* (IBSC photo!); On the way from Ya County to Jiusuo, December 1954, *H.Y. Liang 69358* (IBSC photo!); Xinglong, on the way from Liji to Chang'an, 15 m, 22 August 1960, *Hainan Workstation 2529* (IBSC photo!); Dan County, on the way from Paipu to Shatao, 24 March 1982, *G. Fu 2780* (IBSC photo!).

TAIWAN.

not localized: Biyositsu [on duplum: Bijoritsu], in habidis collinum, 27 May 1903, U. Faurie 186 (P photo!).

Taoyuan County, Luchu, 10 September 1908, *S. Sasaki s.n.* (TAIF-11100 photo!); Taoyuan County, Kuanyin, 10 May 1909, *S. Sasaki s.n.* (TAIF-11102 photo!); Taoyuan City, Sule, 11 May 1909, *T. Kawakami & S. Sasaki s.n.* (TAIF-11096 photo!); Taoyuan County, Tahsi, 01 August 1910, *T. Kawakami s.n.* (TAIF-11101 photo!); Taoyuan County, Chungli, 01 August 1914, *T. Kawakami s.n.* (TAIF-11104 photo!); Taoyuan County, Taoyuan, 01 September 1916, *Y. Shimada s.n.* (TAIF-11097 photo!); Taoyuan County, Dayuan, 01 November 1923, *S. Sasaki s.n.* (TAIF-11099 photo!); Tooen et Nankan, 05 May 1929, *Y. Yamamoto s.n.* (IBSC photo!); Nankan, Xinzhuzhou, 06 July 1930, *H. Takahide 1230* (NAS photo!); Nankan, Xinzhuzhou, 23 November 1931, *S. Suzuki-Tokio 5869* (IBSC photo!).

Hsinchu County, Tamaopu, 15 December 1915, *Y. Shimada s.s.* (TAIF-11103 photo!); Lienhuashih, on the bank, moist place, ca. 100 m, 06 October 1991, *C.C. Wang & C.H. Chen 649* (HUH photo! MO photo!); Then, 25 May 1930, *S. Suzuki 4624* (MO photo!); 23 November 1931, *S. Suzuki-Tokio 5869* (IBSC photo!, PE photo!); Hsinchu County, Lienhua temple, mountain slope, marsh, sand soil, 50-100 m, 30 August 1996, *K.C. Yang et al. 4971* (TAIF photo!); Lienhua Temple, coastal hill, marsh, 70 m, 16 January 1997, *Y.C. Kao & C.N Wang 100* (TAIF photo!); Lienhuasyh, marsh, very rare, 18 December 2000, *C.C. Lin 67* (TAIF photo!); Lienhuasyh, wetland, open place, sandy soil, 20-50 m, 12 July 2002, *C.Y. Kuo 147* (TAIF photo!); Lienhua Temple, 100 m, 04 July 2003, *Y.P. Cheng 4164 & 4165* (TAIF photo!); Lienhua Temple, open, wet places, 0-100 m, 18 August 2003, *C.C. Chen 835* (TAIF photo!); Jhubei Lianhua Temple wetland, 50-80 m, 23 November 2008, *W.Y. Wang 137* (TAIF photo!).

Taipei County, Mt. Hsin & Meng pond, 03 March 2010, *H.L. Chang s.n.* (TAIF-462470 photo!). Taichung County, Mt. Tiehchen [Tiehchan Shan], 12 October 1997, *S.Y. Lu s.n.* (TAIF-236218 photo!).

Miaoli County, Tunghsiao Twon Fifth Cemetery, 05 July 2007, *M.J. Jung z070503* (TAIF photo!); County Highway 121, Tungshiau, open grassland, near rice field, 65 m, 01 October 2009, *Y.S. Liang 2711* (TAIF photo!); Chengpei Neighbourhood, 80 m, 27 June 2017, *T.C. Hsu 9313* (TAIF photo!).

Kinmen County, Kinmen, 01 June 1997, without collector 8440 (TAIF photo!); Kinmen, Chuehshan, 40-80 m, 25 August 2010, T.C. Hsu 3104 (TAIF photo!); Chinmen [Kinmen] County, Tienpu, 17 July 2007, G.S. Tung s.n. (TAIF-286760 photo!); Chinmen [Kinmen] County, Houlung, 20-50 m, 25 August 2010, T.C. Hsu 3095 (TAIF photo!); Houlung, 10 m, 25 May 2017, T.C. Hsu 9236 (TAIF photo!); Yangming Lake, 0-50 m, 20 October 2018, S.W. Chung 13593 (TAIF photo!).

VIETNAM.

not localized: Tonkin méridional, Phuong Mai, in arenosis agris, 12 November 1881, H. Bon 1036 (P photo!, P).

[Nghệ An Province]: Annam, Vinh, in ricefield, 23 January 1909, W. Micholitz s.n. (K!);

[Khánh Hòa Province]: Annam, Nha-trang [Nha Trang] and vicinity, 11-26 March 1911, *C.B. Robinson 1054* (K!, NY photo!, P photo!, WAG photo!), Annam, Nhatrang [Nha Trang] et enviros, 04-05 February 1914, *A. Chevalier 30427* (P photo!).

Thua-thien [Thừa Thiên Huế Province]: Cau-hai [Cầu Hai lagoon], dans les sables des dunes [in the sand of the dunes], without date, *P. Eberhardt 1362* (P photo!); Thua Lum, without date, [*P.*] *Eberhardt 2616* (K!, P![the P specimen comprises 2 individuals of *D. finlaysoniana* and 3 *D. serpens*]); Hui [Huế], citadelle, champ du Boi (rare), March-May without year, *P. Couderc s.n.* (P-04583197 photo!, P-04583197 photo!).

[Quảng Ninh Province]: Quang-Yen [Quảng Yên], ricières [rice fields], December 1908, *Rotereau s.n.* (P-04581087 photo!); Tonkin, Quang Yen, 1908, *C. d'Alleizette 218* (P photo!); Tonkin, Quang Yen, rizières, October 1909, *C. d'Alleizette s.n.* (P-04583151 photo!).

[Bình Thuận Province]: Phanthiết [Phan Thiết], route de Phui-hài, sables humides [wet sands], 05 November 1924, *F. Evrard 1715* (P photo!).

[Da Nang municipality]: Tourane [Da Nang], January 1837, *M. Gaudichaud 170* (P photo!); Tourane [Da Nang], 20 February 1908, *C. d'Alleizette s.n.* (P-04583160 photo!); Annam, Tourane [Da Nang], common in the dunes near the sea, May-July 1927, *J. & M.S. Clemens 3032* (IBSC photo!, MO photo!, P photo!, WAG photo!); Tourane [Da Nang], March-April without year, *P. Couderc s.n.* (P photo!).

[Bà Rịa-Vũng Tàu Province]: Cap St. Jacques [Vũng Tàu], 19 October 1919, M. Poilane 616 (P photo!).

[Hanoi municipality]: Jongkin [Tonkin], Env.[irons] de Hanoï [surroundings of Hanoi], rizière [rice field], July 1908, *C. d'Alleizette s.n.* (P-04583159 photo!)

[Phu Yen Province]: Tonkin (NB), Yên Môi (Vung), 17 November 1889, R.P. Bon 144 (P photo!).

[Quang Tri Province]: Annam, Province de Quang Tri, Village de An Nha [today a quarter of Gio Linh city], bonds d'une rizière (margins of a rice field), 17 April 1936, *Pételot 5718* (P photo!).

THAILAND.

[Prachuap Khiri Khan Province]: Rachaburi [not corresponding to today's Ratchaburi Province], Hawng Kae [Hua Hin District], Kao Ta Kiep [Khao Takiap], c. 5 m, 26 September 1927, *Mrs. D.J.* [=*E.E.*] *Collins 1612* (P photo!).

Georeferenced photographs for localities not covered by a herbarium voucher (from iNaturalist.org): AUSTRALIA. Western Australia: Hann River, in creek bed, in sand above water line, 15 July 2019, *G. Krygsman* ("overlander") (inaturalist.org)

Queensland: Laglan, 25 June 2019, B. McLennan ("bmac111") (inaturalist.org)