

A new and endemic species of *Drosera* (Droseraceae) from Madagascar

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Background and aims – This study is part of an ongoing revision of the world *Drosera* species. During herbarium revisions of *Drosera* from Madagascar, a new species was identified and is here described.

Methods – The species' morphology is described based on herbarium studies and observation of living plants *in situ*, and ecological notes from field observations are provided. The species is compared and contextualized within the current subgeneric classification of *Drosera*.

Key results – The new species, *Drosera arachnoides*, is recognized as most closely related to another Malagasy-endemic, *D. humbertii*, from which it is morphologically and ecologically distinct. The new species is placed within *D.* subg. *Drosera* sect. *Ptycnostigma*. Based on the restricted occurrence, the species is assessed as Vulnerable, following IUCN categories and criteria. A key to the *Drosera* species from Madagascar is provided.

Conclusion – *Drosera arachnoides* is the second endemic *Drosera* species in Madagascar and raises the total number of species on the island to six.

Keywords – Non-core Caryophyllales; *Drosera* subgenus *Drosera*; taxonomy; carnivorous plants.

INTRODUCTION

The genus *Drosera* L. (Droseraceae, non-core Caryophyllales) comprises approximately 250 species of herbaceous carnivorous plants. The diversity centers of the genus lie in the Southern Hemisphere in South-West and Northern Australia, the Cape Region of South Africa and central-eastern Brazil (Fleischmann et al. 2018a). So far, five *Drosera* species have been recorded from Madagascar, one of them, *Drosera humbertii* Exell & J.R.Laundon, endemic to the island (Exell & Laundon 1956; Keraudren-Aymonin 1982; Robinson et al. 2017). The other species, *D. madagascariensis* DC.,

D. natalensis Diels, *D. burkeana* Planch., and *D. indica* L., are widespread in tropical and subtropical Southern Africa, the first and the last extending into tropical East and West-Africa, *D. indica* even further into (sub)tropical Asia (Hutchinson & Dalziel 1954; Laundon 1959; Robinson et al. 2017).

The Forêt de Vohibe (Vohibe Forest) is a low to mid-elevational (326–1008 m a.s.l.), moist evergreen tropical rainforest covering 3117 ha in northwestern Vatondromy District, Eastern Madagascar (Rakotoarivony & Rasoaviety 2007; Rabearivony et al. 2015). It hosts a rich fauna and flora (Rakotoarivony & Rasoaviety 2007; Rakotoarivony et al. 2013), including at least 672 plant species with an aston-

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ishing endemism rate of 76% (Rakotoarivelo et al. 2013). The homonymous “Vohibe low-altitude rainforest fragment” mentioned by Andrianandrasana et al. (2013) west of the confluence of the Mangoro and Nosivolo rivers is a different area of lower elevation and ca. 80 km to the south of the present study site.

During expeditions for floristic inventories to Vohibe Forest in 2010, 2015 and 2016, an unknown species of *Drosera* was collected by N.H. Rakotoarivelo and co-workers, tentatively identified as “*D. aff. indica*” or “*Drosera sp.*”, respectively. Photographs of these herbarium specimens in the MO database were immediately identified as distinctive new species by A. Fleischmann, A. Rocca, and P.M. Gonella (as well as independently also by Jan Schlauer and Thilo Krueger). A herbarium revision of *Drosera* species from Madagascar by A. Fleischmann revealed a further collection of this new taxon made at Mont Taolana (Sud Betsileo) in 1941 (P04582299!; erroneously cited as “*D. humbertii*” by Keraudren-Aymonin 1982). This species is described as new to science here.

MATERIAL AND METHODS

The description of the new taxon is based on examination of herbarium specimens of this species and related taxa held at BM, G, MO, P and TAN (herbarium acronyms following Thiers 2019) by A. Fleischmann, P.M. Gonella and N.H. Rakotoarivelo, as well as on field observations and *in situ* photographs by N.H. Rakotoarivelo, F. Rakotoarivony, A. Razanatsima and L.R. Andriamiarisoa. The distribution map was drawn by A. Fleischmann based on herbarium specimen records using DIVA-GIS (Hijmans et al. 2005) and its free spatial georeferenced data.

RESULTS AND DISCUSSION

Drosera arachnoides Rakotoar. & A.Fleischm., sp. nov.

Figs 1–4

Diagnosis – Species similar to *Drosera humbertii* Exell & J.R.Laundon, from which it differs by shorter, condensed stems, (6–)10–20(–25) active leaves per rosette (*D. humbertii*: (2–)3–7 active leaves), linear-lanceolate leaves (15–)22–40 mm long and (1.0–)1.5–3.0 mm wide (*D. humbertii*: leaves 5–20 mm long, 1.0–1.5 mm wide), petiole adaxial surface densely covered with pubescent indumentum of white eglandular hairs (*D. humbertii*: petiole adaxial surface (sub)glabrous, only few white eglandular hairs present), and old leaves patent and persistent on the stem (*D. humbertii*: old leaves reflexed or deciduous).

Type – Madagascar: Prov. Toamasina, Atsinanana. Vatoman-dry, Ambalabe, Sahanonaka. Forêt de Vohibe, en haut du chute Tsitondroina, site n°2, 724 m, 27 Oct. 2016, *Nivo H. Rakotoarivelo, F. Rakotoarivony, C. Zafindrafeno & Y.J. Lezafy 789* (holotype: TAN; isotypes: MO (herbarium sheet and flowers preserved in alcohol), P[MNHN-P-P01046876, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p01046876>]).

Description – Perennial herbs, rosetted, with upright or prostrate stems (10–)25–45(–60) mm tall in flowering specimens (juvenile plants acaulescent). **Stems** terete, ca. 1.5 mm

in diameter, condensed (internodes short), densely covered by persistent dead leaves. **Roots** slightly succulent, terete, up to 0.5 mm wide, unbranched and densely covered with root hairs when young, glabrous and sparsely branched with age, up to 50 mm long in the specimens studied. **Leaves** (15–)22–40 mm long, with circinate vernation, active leaves semi-erect, patent when old (persistent on the stem), linear-lanceolate, pale red in colour (dull green when growing in shaded conditions); **petioles** (6–)10–15(–17) mm long, (1.0–)1.5–2.0 mm wide, linear to linear-cuneate, narrowly transversely ellipsoid in cross section, petiole margins, adaxial and abaxial surfaces with pubescent to pilose indumentum of patent to antrorse, simple, eglandular white hairs 0.50–1.25 mm long (hairs drying pale brownish), and scattered microscopic short-stalked to subsessile, capitate glands; petiole passing continuously into the lamina; **lamina** (7–)12–22(–30) mm long, (1.0–)1.5–3.0 mm wide at its greatest width, linear-lanceolate to narrowly lanceolate, gradually tapering into an obtuse to slightly acute apex, adaxial surface covered with numerous red, carnivorous, capitate tentacles up to 3 mm long, abaxial surface subglabrous, covered with minute short-stalked to subsessile glands; **stipules** intrapetiolar, 4–5 mm long, ca. 2.0 mm wide at the base, gradually widening, narrowly cuneiform to rectangular in outline, membranaceous, translucent white (drying pale brown), only the lowermost part (ca. 1 mm) entire, the rest divided into 3 long lacinate segments, which are each further divided into very narrowly triangular lacinae; the central segment 4–6-lacinate, 3.0–3.5 mm long, the two lateral segments exceeding the central segment in length, up to 4.5 mm long, 2–3-lacinate (length of the marginal lacinae increasing towards the tip). **Scapes** 1–2(–4), peduncle (85–)100–220(–300) mm tall (including floriferous part), terete, thin, (0.8–)1.0–1.3 mm in diameter at the base, peduncle ascending from arcuated base, sparsely covered with eglandular white hairs at the very base, becoming glabrous in the middle and upper part, floriferous part sparsely microscopically glandular (minute short-stalked to subsessile capitate glands), green to greenish-red in colour; inflorescence a scorpioid cyme, simple, bearing (2–)4–8 flowers. **Bracts** 1.8–2.5(–3.0) mm long, up to 0.35 mm wide, narrowly lanceolate to subulate, persistent (first flower of the cyme not subtended by a bract), abaxially sparsely covered with minute short-stalked to subsessile capitate glands. **Pedicels** (1–)2–5(–6) mm long, terete, filiform, ca. 0.15–0.30 mm in diameter, sparsely covered with minute short-stalked capitate glands, upright at anthesis and in fruit. **Sepals** 5, (3.0–)4.0–5.5 mm long, (0.8–)1.3–2.0 mm wide, lanceolate to narrowly obovate, apex acute, margins entire, adaxially glabrous, abaxial surface sparsely covered with minute short-stalk capitate glands in the basal half, upper half glabrous; sepals basally adnate to form a bell-shaped calyx; sepals persistent, spreading and usually with recurved apex in fruit. **Petals** 5, 6.0–7.5(–8.0) mm long, 5.0–6.5 mm wide, obovate to broadly obovate or broadly spatulate, apical margin entire, slightly truncate or minutely undulate, pale pink. **Stamens** 5, alternipetal, 2.0–2.5 mm long; **filaments** translucent white; **anthers** ca. 1 mm long, bithecate, connective slightly dilated, thecae yellow. **Ovary** 3-carpellate, fused, ca. 1.5 mm in diameter, subglobose, slightly 3-lobed in outline, glabrous, yellowish-green; **styles** 3, forked at the

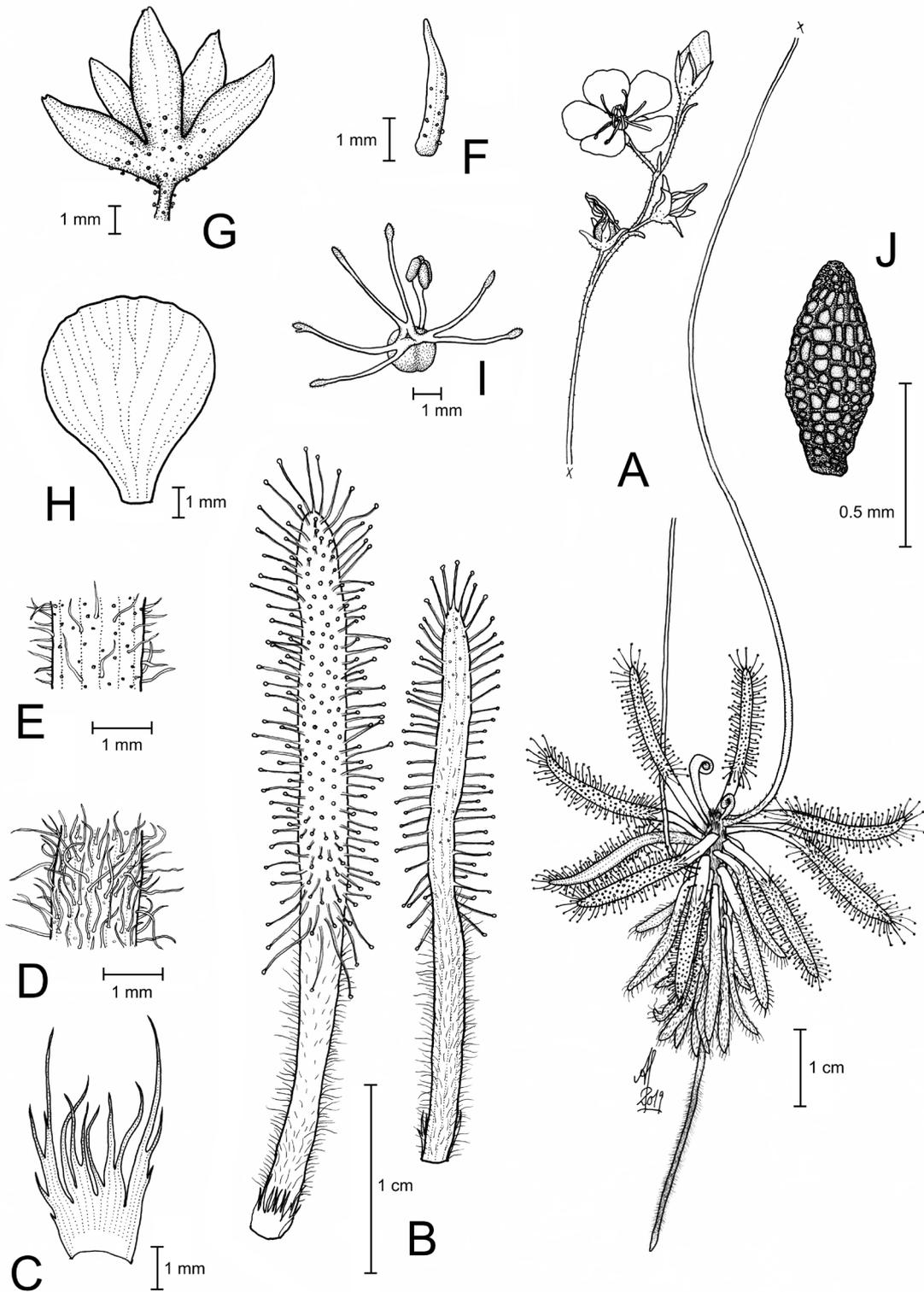


Figure 1 – *Drosera arachnoides*. **A.** Habit. **B.** Leaves: left showing adaxial (upper) surface, right showing abaxial (lower) surface. **C.** Stipule. **D.** Petiole abaxial (lower) surface. **E.** Petiole adaxial (upper) surface. **F.** Bract. **G.** Calyx. **H.** Petal. **I.** Gynoecium and one anther. **J.** Seed. A–I from Nivo H. Rakotoarivelo, F. Rakotoarivony, C. Zafindrafeno & Y.J. Lezafy 789 (P, isotype), flower details of A added from habitat photographs, J from N.H. Rakotoarivelo, F. Rakotoarivony, C. Zafindrafeno & Y.J. Lezafy 788 (P). Illustration by A. Fleischmann.

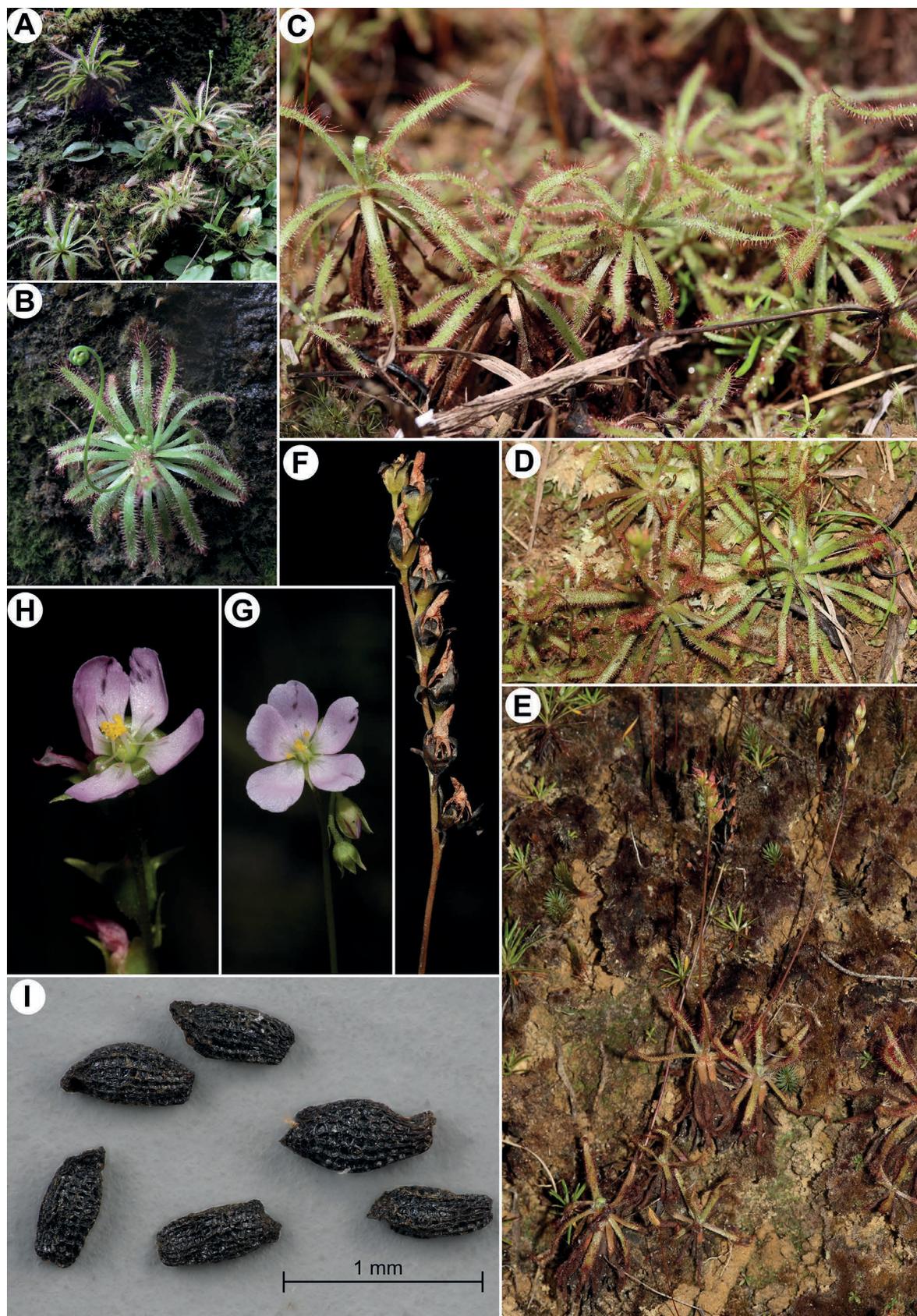


Figure 2 – *Drosera arachnoides*. A–E. Habit and habitat. A, B. Plants growing in partial shade. C, D. Plants growing in exposed area. E. Fruiting individuals. F. Inflorescence. G, H. Flower. I. Seeds. Photographs: A, B by N.H. Rakotoarivelo, C, E–H by F. Rakotoarivony, D by A. Razanatsima, I by A. Fleischmann.

base, 3.0–3.5 mm long (including stigmata), style arms terete to transversely elliptical in cross-section, straight to slightly ascending, translucent white; stigmata rhomboidal to linear or very narrowly cuneate, apex obtuse, entire, rarely shallowly bifurcate, microscopically papillate, translucent white or pale pink. Fruit a dry dehiscent capsule, 2.0–2.5 mm long, ellipsoid, 3-valvate. Seeds angulate-ellipsoid to rectangular, apiculate, black, 0.64–0.80 mm long, 0.28–0.35 mm wide, testa reticulate, testa cells rectangular to isodiametric.

Additional material examined

Drosera arachnoides (paratypes)

Madagascar: Prov. Toamasina, Atsinanana. Vatomaniry, Ambalabe, Sahanianaka. Forêt de Vohibe, côté droite du chute Tsitondroina. Forêt dense humide sempervirente de basse altitude, 634 m, 17 Sept. 2010, *N.H. Rakotoarivelo, A. Razanatsima, L.J. Razafitsalama, L.R. Andriamiarisoa, L. Raboto, L. Dedesy & C. Zafindrafeno* 358 (MO[MO-2973047, <http://tropicos.org/Specimen/100379685>], P[MNHN-P-P06805807, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p06805807>], TAN); en haut du chute Tsitondroina, près du campement Ambatovaky. Forêt dense humide de basse altitude, 729 m, 16 Sept. 2010, *N.H. Rakotoarivelo, L.J. Razafitsalama, A. Razanatsima, L.R. Andriamiarisoa, L. Raboto & L. Dedesy* 356 (MO[MO-2973048, <http://tropicos.org/Specimen/100379679>], TAN); en haut du chute Tsitondroina, site n°1, 654 m, 27 Oct. 2016, *N.H. Rakotoarivelo, F. Rakotoarivony, C. Zafindrafeno & Y.J. Lezafy* 788 (MO, P[MNHN-P-P01046877, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p01046877>], TAN); en haut du chute Tsitondroina, site n°3, 722 m, 27 Oct. 2016, *N.H. Rakotoarivelo, F. Rakotoarivony, C. Zafindrafeno & Y.J. Lezafy* 790 (MO[MO-2973884, <http://tropicos.org/Specimen/100950639>], P[MNHN-P-P01046885, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p01046885>], TAN); Village de Vodiriana. Forêt de Vohibe, côté Sud du chute Tsitondroina, 719 m, 12 Nov. 2015, *A. Razanatsima* 1423 (MO, P[MNHN-P-P01199716, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p01199716>], TAN); [Prov. Fianarantsoa], Mont Taolana C. [Mont Itaolana, central part; 21°56'S, 47°14'E], rochers humides vers 1500 m, 9 Apr. 1941, *Herb.Jard.Bot.Tan. [coll. P. Boiteau]* 4529 (P[MNHN-P-P04582299, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p04582299>]; identified as “*Drosera* cf. *Humbertii*” by J. Bosser, May 1971).

Drosera humbertii

Material of *Drosera humbertii* examined for morphological comparison and for the distribution map.

Madagascar: [Prov. Antsiranana], Nord-Est, sommet oriental du Massif de Marojejy, à l’Ouest de la haute Manantenina, affluent de la Lokoho, gneiss et quartzite, 1850–2137 m alt., 17–20 Dec. 1948, *Humbert* 22771 (type of *Drosera humbertii*; BM[BM000752944, <https://data.nhm.ac.uk/object/2ff77f73-f2ef-4c96-83f7-9ec-2c123b50e/1586822400000>], G, P[MNHN-P-P00374813, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p00374813>], P[MNHN-P-P00374814, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p00374814>], P[MNHN-P-P00374815,



Figure 3 – Habit of *Drosera arachnoides* growing on red clayish soil among tall Cyperaceae. Photograph by A. Razanatsima.

<http://coldb.mnhn.fr/catalognumber/mnhn/p/p00374815>], P[MNHN-P-P04582303, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p04582303>]); Sommet oriental du Massif de Marojejy (nord-est) à l'ouest de la haute Manantenina, affluent de la Lokoho, gneiss et quartzite (dépressions tourbeuses), 1850–2137 m, 26 Mar.–2 Apr. 1949, *H. Humbert & G. Cours* 23855 (P[MNHN-P-P04582296, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p04582296>]); Vallée de la Lokoho, Mont Beondroka au Nord de Maroambihy, rochers de la crête (gneiss et quartzite), 1400–1450 m, 17–22 Mar. 1949, *Humbert* 23619 (P[MNHN-P-P04582256, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p04582256>], P[MNHN-P-P04582297, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p04582297>]); Partie occidentale du Massif de Marojejy, de la vallée de l'Ambatoharanana au bassin supérieur de l'Antsahaberoka, sylve à Lichens et végétation éricoïde des sommets sur gneiss et granite, 1600–1700 m, 15–25 Nov.

1959, *Humbert & Saboureau* 31780 (MO[MO-2973051, <http://tropicos.org/Specimen/100988170>], P[MNHN-P-P04582298, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p04582298>], P[MNHN-P-P04582300, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p04582300>]); Sommet du massif du Marojejy, très fréquent, existant au bord des marais et tourbiers, et sur les pentes les mieux drainées, 2000–2100 m, Dec. 1972, *Morat* 4036 (P[MNHN-P-P04582301, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p04582301>]); Masif du Marojejy, tourbiers du sommet ou sur rochers humide, 2000–2137 m, Dec. 1972, *Morat* 4090 (P[MNHN-P-P04582302, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p04582302>]); Réserve Naturelle de Marojejy, along the trail to the summit of Marojejy Est, NW of Mandena, steep upper slopes and summit, low ericoid vegetation with small trees and shrubs only in protected areas, 1900–2133 m, 15 Feb. 1989, *Miller & Lowry II* 4173 (MO[MO-2973052,

Figure 4 – Distribution of the two endemic Malagasy species *Drosera arachnoides* and *D. humbertii*.

Key to the *Drosera* species of Madagascar

All *Drosera* species of Madagascar are members of *D.* subgenus *Drosera*, in which the annual *D. indica* belongs to *D.* sect. *Archnopus* and is only distantly related to the remaining five species, all of which belong to *D.* sect. *Ptycnostigma* (infrageneric classification following Fleischmann et al. 2018a, 2018b).

1. Plants stem-forming 2
 - 1'. Plants rosulate, acaulescent 5
 2. Stipules absent (but 2 fimbriate setae present laterally at the base of the petiole); leaves linear-filiform (thread-like); scapes (peduncles) not much exceeding the leaves in height [annuals] *D. indica* L.
 - 2'. Papery stipules (triangular with fringed apex; translucent white to reddish in living plants, drying pale to dark brown) adnate to each leaf base; leaves narrowly lanceolate, cuneate or spatulate; inflorescences on long peduncles [perennial plants] 3
 3. Leaves spatulate; leaf veneration involute-imbricate; seeds pale brown, fusiform *D. madagascariensis* DC.
 - 3'. Leaves linear-lanceolate to lanceolate; leaf veneration circinate; seeds black, angulate-ellipsoid to rectangular 4
 4. Active leaves (2–)3–7; leaves 5–20 mm long and up to 1.5 mm wide; petiole upper surface glabrous or only sparsely covered with white eglandular hairs; old leaves reflexed towards the stem or deciduous (patent in juvenile and stunted specimens); stems elongate, upright, 30–70(–200) mm tall; plant of montane habitats above (1400–)1800 m elevation *D. humbertii* Exell & J.R.Laundon
 - 4'. Active leaves (6–)10–20(–25); leaves (15–)22–40 mm long, (1.0–)1.5–3.0 mm wide; petiole upper surface densely covered with white eglandular hairs; old leaves patent, persistent on the stem; stems condensed, upright or prostrate (10–)25–45(–60) mm tall; plant of lowland and mid-elevation rainforest habitats at 630–730(–1500) m elevation *D. arachnoides* Rakotoar. & A.Fleischm.
 5. Leaves spatulate, petioles linear; seeds ovoid, black *D. burkeana* Planch.
 - 5'. Leaves cuneiform with rounded apex to broadly spatulate, petioles narrowly cuneiform to cuneiform; seeds fusiform, dark brown *D. natalensis* Diels (erroneous records of *D. dielsiana* Exell & J.R.Laundon from Madagascar refer to *D. natalensis*).
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tropicos.org/Specimen/61757]); province d'Antsiranana, Marombihy, Mandena, Parc National de Marojejy, 11 km de Manantenina, à la source de la rivière Andranomifotatra, campement 5, sur le sommet du Marojejy, 2100 m, 15 Nov. 1996, Messmer, Rakotomalaza & Ravelonarivo NM 363 (G, MO[MO-2973053, <http://tropicos.org/Specimen/100988158>).

Distribution – Endemic to Madagascar. So far only known from Eastern Madagascar, from one locality (comprising four populations) in Toamasina Province, and from one collection from Fianarantsoa Province (fig. 4). The four populations in Toamasina are all around the Tsitondroina waterfall in the Forêt de Vohibe rainforest in northwestern Vatoman-dry District of the Atsinanana Region; the single collection from Fianarantsoa was made at Mont Taolana [Itaolana], Haute Matsiatra Region, which is more than 335 km to the south-southwest of Vohibe Forest (fig. 4).

Habitat – On wet rocks and clayish soils overlying metamorphic rock along a waterfall in more open areas of dense, evergreen mid-elevation forest (at ca. 630–730 m elevation) at Vohibe (figs 2, 3). At Mont Taolana collected on wet rocks at 1500 m elevation. At Vohibe Forest, *Drosera arachnoides* has been found growing at the top of the waterfall and its sur-

roundings in four different places. The plants grew on perennially wet to humid vertical rock and soil in dappled shade, but also in apparently periodically less wet places, more exposed to full sun. Accompanied by mosses (e.g., *Polytrichum commune* Hedw. (Polytrichaceae), *Sphagnum* sp. (Sphagnaceae), *Jensenia spinosa* (Lindenb. & Gottsche) Grolle (Pal-laviciniaceae), *Amazoopsis diplopoda* (Pócs) J.J.Engel & G.L.Merr. (Lepidocziaceae), *Campylopus* sp., and *Pilopogon* sp. (Dicranaceae)), liverworts, *Utricularia livida* E.Mey. (Lentibulariaceae) and *Gravesia* sp. (Melastomataceae).

Phenology and ecology – Specimens have been collected in flower and fruit in September and October, which is during the cool and dry season. *Drosera arachnoides* is a perennial tropical lowland to mid-elevation species. At Vohibe Forest it experiences a wet tropical climate (average annual precipitation ca. 1773 mm, average annual temperature 24°C; Cornet 1974) with two pronounced seasons influenced by the Indian monsoon (hot and humid season November–April, average temperature 26.7°C, cool season May–October, lowest average temperature 20.8°C; Rabearivony et al. 2015). On some *in situ* photographs, characteristic feeding damage and frass could be observed on the leaves of *D. arachnoides* (see e.g., the two middle individuals on fig. 2C), which very

likely result from caterpillars of the pterophorid moth *Buckleria* Tutt, 1905 which are oligophages on the genus *Drosera* (Gielis 2014). The Malagasy endemic *Buckleria madecassea* Gibeaux, 1994 has been described from Ambatolampy, Antananarivo Province (Gibeaux 1994, host species and larval stages unknown), which is just 117 km distant from Vohibe Forest, thus this moth could probably also occur there, using *D. arachnoides* as a host plant there.

Etymology – The specific epithet “*arachnoides*” (Greek “*arachne*” = spider, “*-oides*” = resembling) refers to the spider-like appearance of the plant, both in terms of its numerous long, linear-lanceolate leaves covered with a pubescent indumentum as well as its habit clinging to vertical rock.

Conservation assessment – Vulnerable (VU criterion D1 and D2; IUCN 2012). The four populations at Tsitondroina waterfall are situated within the borders of the NAP de Vohibe (Vohibe Forest New Protected Area, part of the conservation unit Ankeniheny-Zahamena corridor, which is protected as a key biodiversity area MDG-96; CEPF 2014), but lie outside the strict conservation zone of the NAP (Rakotoarivelo 2015). The populations at sites 1 and 4 comprise fewer than 50 individuals, at site 2 several hundred plants of *D. arachnoides* were found, at site 3 fewer than 20 individuals. Therefore, the total known population size is fewer than 1000 individuals (IUCN criterion VU D1). Even if no direct threat is observed to influence the known populations to date, the species is restricted and currently known from only four sites, covering a very small EOO and AOO, hence it could be prone to human interference or stochastic events that would make it extinct or endangered/critically endangered in a short time (IUCN criterion VU D2). The single collection from Mont Taolana [Itaolana] dates from 1941, and no recent records are known from this area, hence the current population size or presence of the species in Fianarantsoa Province remains unknown. Given that both known collection localities lie more than 300 km apart in a rather poorly botanically explored region, it is likely that further occurrences of *Drosera arachnoides* might exist in Eastern Madagascar.

Taxonomic remarks – *Drosera arachnoides* is a new and distinctive species, morphologically well distinguishable from all *Drosera* species known from Madagascar. Additionally, it is geographically and ecologically isolated from the morphologically closest species, *D. humbertii*. Its morphological diagnosability (and occupation of a different ecological adaptive zone) supports our hypothesis that this new species forms a separately evolving metapopulation that is not conspecific with any other named species of *Drosera* known to date.

Affinity – *Drosera arachnoides* belongs to *Drosera* subgenus *Drosera* section *Ptycnostigma* Planch. (*sensu* Fleischmann et al. 2018a, 2018b). It is most similar to and apparently closely related to *D. humbertii*, a montane species from North-eastern Madagascar, where it is restricted to the summits of the Marojejy Massif and Upper Manantenina (Antsiranana Province; fig. 4), where it grows in open areas of ericoid vegetation and montane scrub among sclerophyllous (high-) montane forest at elevations of (1400–)1800–2137 m (Excell & Laundon 1956; Schlosser 2005; Robinson et al. 2017). While *D. humbertii* is a highland species found at montane

to subalpine elevations, *D. arachnoides* is a lowland species that grows in small open areas of mid-elevation tropical evergreen forests.

Drosera arachnoides superficially resembles some Brazilian species of *D.* section *Brasilianae* Rivadavia, Gonella & A.Fleischm. (like *D. humbertii* also does), such as *D. latifolia* (Eichler) Gonella & Rivadavia, *D. riparia* Gonella & Rivadavia or *D. villosa* A.St.-Hil., with which it shares a similar habit, circinate leaf vernation and similar habitat on vertical wet walls and slopes (Gonella et al. 2014). However, *D. arachnoides* and *D. humbertii* do not possess the characteristic yellow-translucent short-stalked glands (TSG trichomes) on their leaves, which represent an apomorphy for *D.* sect. *Brasilianae* (Fleischmann et al. 2018b; however, these glands are lacking in members of the *D. villosa* complex, see Gonella et al. 2014). The arcuate, ascending base of the peduncle also distinguishes the two species from Madagascar from all superficially similar species of *D.* section *Brasilianae* (with the exception of *D. ascendens* A.St.-Hil.). Additionally, *D. arachnoides* (like all other tropical African/Malagasy species) differs from the aforementioned Brazilian species in having flowers with entire stigmata (very rarely shortly bifid; figs II and 2G & H), while all species of *D.* sect. *Brasilianae* have flabellate to bilobed stigmata (never entire; Gonella et al. 2014). Hence the morphological similarity of *D. arachnoides* and *D. humbertii* with their New World congeners is convergent and merely superficial, but not based on phylogenetic affinity.

Morphology – The circinate leaf vernation of *D. arachnoides* and *D. humbertii* is rare among African *Drosera*, but a typical feature in the Brazilian *D.* sect. *Brasilianae* (Fleischmann et al. 2018b); hence the superficial similarity to some New World species. Among the African *D.* sect. *Ptycnostigma*, *D. arachnoides* and *D. humbertii* are the sole hemicyptophyte members with circinate leaf vernation, the remainder of species have geniculate-involute vernation (with the rare exception of one clone of the South African *D. capensis* L. that is only known from cultivation). Only some of the geophyte species of *D.* sect. *Ptycnostigma* from the Western Cape of South Africa share involute leaf vernation (i.e., the affinity of *D. cistiflora* L. and *D. trinervia* Spreng., with the notable exception of *D. pauciflora* Banks ex DC.). Circinate leaves among African *Drosera* are further found only in the unique species *D. regia* Stephens (*D.* subgenus *Regiae*; sister to all remaining species of *Drosera*) from the Western Cape of South Africa, as well as in the widespread tropical annual *D. indica* (*D.* subgenus *Drosera* sect. *Arachnopus*). Overall, circinate vernation is a homoplastic character connected to linear leaf shape in the genus *Drosera*, having evolved in several lineages but not mirroring phylogenetic affinity.

Drosera humbertii has been described by Excell & Laundon (1956) as having adaxially glabrous petioles, but this is not the case in all specimens studied by A. Fleischmann (including type material), and this is also not evident from the *in situ* photographs of the species from Marojejy summit published in Robinson et al. (2017). In fact, *D. humbertii* shares an identical leaf indumentum of eglandular white hairs with *D. arachnoides*, but the hair cover on the petiole upper surface is sparser in *D. humbertii*, so that the petioles appear subglabrous. The pubescence of white eglandular hairs on

the petioles of *D. arachnoides* also slightly varies depending on growing conditions (as is the case in many species of *Drosera*), with specimens growing in more shaded conditions (fig. 2A & B and e.g., *N.H. Rakotoarivelo*, *A. Razanatsima*, *L.J. Razafitsalama*, *L.R. Andriamiarisoa*, *L. Raboto*, *L. Dedesy* & *C. Zafindrafeno* 358) displaying a less dense indumentum compared to specimens growing in more exposed, sunnier habitats (fig. 2C–E and e.g., *N.H. Rakotoarivelo*, *F. Rakotoarivony*, *C. Zafindrafeno* & *Y.J. Lezafy* 788, *Nivo H. Rakotoarivelo*, *F. Rakotoarivony*, *C. Zafindrafeno* & *Y.J. Lezafy* 789). However, in all specimens the petioles are more pubescent than in the related *D. humbertii*.

Further, Exell & Laundon (1956) described the (immature) seeds of *D. humbertii* as “likely fusiform” (a seed shape which would link it to *D. madagascariensis*). However, in the scarce fruiting material among the specimens examined by A. Fleischmann the seeds were angulate-ellipsoidal, hence identical in shape to those of *D. arachnoides*.

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