A NEW SECTIONAL NAME FOR THE BRAZILIAN TETRAPLOID CLADE OF DROSERA SUBGENUS DROSERA

ANDREAS FLEISCHMANN • Botanische Staatssammlung München • Menzinger Strasse 67 • D-80638 Munich • Germany • fleischmann@lrz.uni-muenchen.de
PAULO MINATEL GONELLA • R. Cid Silva Cesar, 1039 • São Carlos • SP • 13562-400 • Brazil • paulogonella@uol.com.br
FERNANDO RIVADAVIA • 185 SW 7th St • Miami • Florida 33130 • USA • fe_riva@uol.com.br

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Historical infrageneric classifications of the genus Drosera L. (De Candolle 1824; Planchon 1848a, b; Diels 1906; Seine & Barthlott 1994; Schlauer 1996) took into account the external morphology of its species, especially style division, but also data from palynology (Takahashi & Sohma 1982), trichome morphology (Seine & Barthlott 1993; Länger et al. 1995) and chromosome numbers (e.g., Kondo 1976). Nevertheless, when confronted with the molecular phylogenetic reconstructions (Rivadavia et al. 2003, 2012), all existing classifications were unsuccessful in circumscribing a monophyletic D. section Drosera, due to the high homoplasy of morphological traits in that section. Hence, a new classification congruent with the phylogeny and based on monophyletic groups became necessary (Fleischmann et al. 2018).

The phylogenetic reconstructions of Rivadavia et al. (2003, 2012), based on the plastid marker rbcL, showed that all Drosera species, except for D. regia Stephens and D. arcturi Hook., belong to two large sister clades more or less geographically defined, an “Australian Clade” (D. subgen Ergaleium, comprising D. sections Coelophylla, Lasioccephala, Bryastrum, Erythrorhiza, Stolonifera and Ergaleium), and another clade representing an “out of Australia” movement. The latter has to be referred to as D. subgen. Drosera (as it contains the generic type, D. rotundifolia L.), with clades connected to basal nodes centered in Australia (D. sections Arachnopus, Stelogyne, Prolifera, Psychophila, Thelocalyx), and clades connected to more apical nodes of Neotropical and African distribution (D. sections Ptycnostigma, and Drosera sensu Seine & Barthlott 1994). In this topology, D. sect. Drosera (sensu Seine & Barthlott 1994) appears as paraphyletic with D. sect. Ptycnostigma nested within.

To better reflect the phylogenetic, geographical, and morphological groups, we adopted the topology of Rivadavia et al. (2012) for a new classification of the taxa hitherto placed in D. sect. Drosera. Therefore, D. sect. Drosera is here redefined as the clade containing D. rotundifolia (the type species of the genus), along with other temperate and diploid Neotropical taxa, as well as D. spatulata Labill and allied taxa. This clade is sister to two clades, the “African clade” (which contains D. sect. Ptycnostigma) and the “Brazilian Tetraploid clade” (Rivadavia et al. 2003, 2012; Gonella 2012). Consequently, D. sect. Ptycnostigma (whose type is D. pauciflora Banks ex DC.) is here expanded to include all taxa that fall within the “African clade”. Finally, the “Brazilian Tetraploid clade” remains unnamed, and a new sectional name is here proposed.

Drosera section Brasiliae Rivadavia, Gonella & A.Fleischm., sect. nov.

This section comprises the species of the “Brazilian Tetraploid clade”, a monophyletic group that emerged in the phylogenetic reconstructions of Rivadavia et al. (2003, 2012). The sectional name
refers to the predominantly Brazilian distribution and the likely Brazilian origin of this evolutionary lineage.

Of the 18 species belonging to this section (Table 1), chromosome numbers are known for nine, which are consistently 2n = 40 (Futagawa et al. 2002; Rivadavia et al. 2003; Rivadavia 2005). The species are also recognized by morphological characters such as an indumentum of translucent-yellow, short-stalked globose non-carnivorous trichomes in most species (Fig. 1; Gonella 2012; Gonella et al. 2014; Rivadavia et al. 2014; however, they are not an apomorphy for this section, these glands are also found in other species, e.g. D. meris-tocaulis Maguire & Wurdack, see Rivadavia et al. 2012), scapes often covered by a woolly indumentum of long, patent eglandular hairs and, most notably, circinate leaf vernation (Fig. 2; all except D. tentaculata, which is uniquely simple-geniculate among Brazilian sundews; Rivadavia et al. 2014). All sympatric members of other sections display geniculate-involute vernation (D. sects. Bryastrum and Drosera) or entire-involute vernation (D. sect. The-localyx) (Gonella 2012; Rivadavia et al. 2014).

Circinate leaf vernation is homoplastic in Drosera, as this characteristic appears independently in several lineages, including in three members of D. sect. Drosera (see below), and may be generally connected to more elongated leaf and lamina shapes (this is paralleled in the unrelated genus Pinguicula L. of Lamiales, where species with filiform leaves show circinate vernation). Such characteristic is also present in the three Andean species revised by Gonella et al. (2016), however, due to the unique combination of characters and the fact that these taxa were not sampled in any published molecular phylogenetic studies so far, these species remain unplaced for now.

**Drosera section Drosera**

*Type:* Drosera rotundifolia L.


*Type:* Drosera intermedia Hayne

*Drosera* sect. *Drosera*, as here redefined, includes all taxa belonging to the clade containing *D. rotundifolia* in the phylogeny of Rivadavia et al. (2012). Species of this section present chromo-
some numbers of $2n = 20$ (except for *D. anglica* Huds., a species of amphiploid hybrid origin, with $2n = 40$; Rivadavia *et al.* 2003, and perhaps a few taxa of recent genome duplication). The species of the section are also characterized by spatulate leaves with geniculate-involute leaf vernation or, more rarely, circinate vernation in the species with linear leaves (*D. filiformis* Raf., *D. tracyi* (Diels) Macfarl. and *D. linearis* Goldie).

*Drosera* section *Oosperma* Schlauer (1996), was segregated from *D*. sect. *Drosera* based on the ovoid seed shape (vs. fusiform) and has as type-species *D. intermedia* Hayne. According to the topology found in the phylogenetic reconstruction of Rivadavia *et al.* (2012), ovoid seed shape is homoplastic, and taxa that would be classified as belonging to *D*. sect. *Oosperma* based on the section description provided by Schlauer (1996), can be found spread in *D*. sections *Drosera*, *Brasiliae* and *Ptycnostigma*. Hence, *Drosera* section *Oosperma* as circumscribed by Rivadavia (2003) is polyphyletic, as it additionally included four of the tetraploid Brazilian taxa, which belong to a different clade herewith classified as *D*. section *Brasiliae*. As the type of *D*. section *Oosperma*, *D. intermedia*, is part of the clade that is also comprising the generic type, *D. rotundifolia* (and hence the type of *D*. sect. *Drosera*), *D*. section *Oosperma* (*sensu* Schlauer 1996) is here placed under synonymy of *D*. sect. *Drosera*.

*Drosera* sect. *Brasiliae* is sister to a more widely circumscribed *D*. sect. *Ptycnostigma*, i.e. the clade comprising *D. pauciflora* and all other African sundews except *D. regia* and *D. indica* (Fleischmann *et al.* 2018):
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Type: Drosera pauciflora Banks ex DC., Prodr. 1: 317 (1824).
Type: Drosera hilaris Cham. & Schldl.
Type: Drosera capensis L.

This section, as here redefined, includes all species belonging to the “African clade” in the phylogeny of Rivadavia et al. (2012), which comprises all Drosera species occurring on the African continent, with the exception of D. regia (D. subgen. Regiae) and D. indica L. (D. sect. Arachnopus). Regarding chromosome number, this section is quite heterogeneous, with variable numbers (2n = 20, 40, 60 or 80; Rivadavia et al. 2003). Most common leaf vernation pattern is geniculate-involute, but circinate is also present in some taxa (D. pauciflora, D. alba E.Phillips, and allied taxa).

Figure 2: Circinate leaf vernation of Drosera villosa: the leaf in bud of most members of D. sect. Brasiliae is enrolled like a mainspring or crozier – which distinguishes this affinity from other Neotropical Drosera. Photo: Paulo M. Gonella.
In the original circumscription, Planchon (1848a, b) defined *D. sect. Ptycnostigma* as plants with flowers with multi-flabellate stigmata, succulent roots, and lacking stipules, containing only *D. cistiflora* L. and *D. pauciflora*. In the current expanded circumscription, all these three traits are not present in all taxa.

The summer-dormant, South African species with succulent roots (*D. cistiflora*, *D. pauciflora*, and allied taxa), which were segregated in *D. sect. Ptycnostigma* by Planchon (1848a, b; elevated to subgeneric rank by Diels 1906 and adopted by Schlauer 1996) are nested within a clade of African *Drosera* species (belonging to *D. section Drosera sensu* Diels 1906). The discrete classification of the summer-dormant species was reasoned by Planchon (1848a) based on the distinctive multifid-flabellate stigmata, a concept followed by Diels (1906), who even gave further weight to the stigma shape in his *D. subgenus Ptycnostigma*. However, this proved to be inconsistent, as the doubtlessly related *D. trinervia* (summer-dormant, stipules reduced) was not included in this affinity, but treated by Diels (1906) and subsequent authors in *D. subgen. Drosera*. Moreover, a grade of morphological characters connects the summer-dormant species of *D. subgen. Ptycnostigma* with the perennially growing species of *D. subgen. Drosera* (sensu Diels 1906). A clear example is the stipule reduction observed in *D. hilaris*, which connects to the stipule-lacking summer-dormant species circumscribed by Diels in his *D. subgen. Ptycnostigma*. *Drosera hilaris* was even placed in its own section, *Crypterisma*, by Planchon (1848a, b; spelled “Cripterisma” in the former source), based on its peculiar morphology. However, it is morphologically connected to the other South African *Drosera* species — both the perennially growing and the summer-dormant, hemicryptophyte species, to the former by overall flower morphology and to the latter by absence of stipules (Fleischmann et al. 2018). Further support is gained from molecular phylogenetic data, which show *D. hilaris* nested within a clade of South African *Drosera* species (Rivadavia et al. 2003), including those of *Ptycnostigma* (sensu Diels 1906).

Additionally, a similar type of non-carnivorous glandular trichomes was observed in all African *Drosera* species (except *D. regia* and *D. indica*) by Länger et al. (1995). Thus Seine & Barthlott (1994) correctly merged Planchon’s section/Diels’ subgenus *Ptycnostigma* with *D. subgenus Drosera*. However, as *D. section Drosera* proved to be paraphyletic (Rivadavia et al. 2003; Fleischmann et al. 2018), and as the clade comprising the African members does not contain the generic type, *D. rotundifolia*, Planchon’s sectional name *Ptycnostigma* is here re-elevated in a larger circumscription to classify all *Drosera* species of the African clade (viz. all species of *Drosera* that occur in Africa, excluding *D. indica* and *D. regia*).

The stigma shape of the summer-dormant species *D. cistiflora*, *D. pauciflora*, and allies is not a reliable taxonomic character for infrageneric classification, and rather seems to mirror adaptations to certain pollinator groups in these large-flowered species. The doubtlessly closely related *D. trinervia* (support comes from life strategy, morphology, and molecular data) does not share flabellate stigmata, but has simple spatulate-bifid stigmatic apices; in contrast, the only distantly related *D. regia* of *D. subgenus Regiae* also flabellate stigmata with multiple divisions.

References


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International Carnivorous Plant Society, Inc.
2121 N. California Blvd., Suite 290
Walnut Creek, CA 94596-7351, USA
icps@carnivorousplants.org

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