New Chromosome Numbers for *Drosera* L.(Droseraceae)

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Introduction

Out of nearly 150 known *Drosera* species, chromosome numbers are known for approximately 50 (Bennett & Cheek, 1989; Behre, 1929; Beuzenberg & Hair, 1983; Debbert, 1987; Heitz, 1926; Hoshi & Kondo, 1998a, 1998b; Kondo, 1969, 1971, 1973, 1976, 1984; Kondo & Lavarack, 1984; Kondo & Olivier, 1979; Kondo & Segawa, 1988; Kondo & Whitehead, 1971; Kress, 1970; Peng *et al.*, 1986; Rothfels & Heimburger, 1968; Schlauer, 1987; Sheikh & Kondo, 1995; Venkatasubban, 1950; Wood, 1955) in almost all subgenera and sections *sensu* Schlauer (1996). A summary of chromosome numbers previously published for *Drosera* taxa is presented in Table 1.

Most of the New World *Drosera* species belong in subgen. *Drosera* (sections *Drosera*, *Oosperma*, and *Ptycnostigma*) except *D. meristocaulis* Maguire & Wurdack and *D. sessilifolia* A.Saint-Hilaire which belong respectively in the subgenera *Meristocaulis* and *Thelocalyx* (Schlauer, 1996). All chromosome numbers known for subgen. *Drosera* are multiples of the basic number x=10, including 2n=20, 30, 40, 60, and 80 (Bennett & Cheek, 1989; Behre, 1929; Beuzenberg & Hair, 1983; Debbert, 1987; Futagawa, *et al.*, 2002; Hoshi & Kondo, 1998a, 1998b; Kondo, 1969, 1971, 1976; Kondo & Lavarack, 1984; Kondo & Olivier, 1979; Kondo & Segawa, 1988; Kress, 1970; Peng *et al.*, 1986; Rothfels & Heimburger, 1968; Venkatasubban, 1950; Wood, 1955). The only exceptions are *D. adelae* F.Muell., *D. cuneifolia* L.f., and *D. indica* L. (see Table 1).

All of the taxa native to North America (excluding simple hybrids) have 2n=20 (Futagawa, *et al.*, 2002; Hoshi & Kondo, 1998a, 1998b; Kondo & Segawa, 1988; Rothfels & Heimburger, 1968; Wood, 1955), except *D. anglica* Huds. which has 2n=40 (Kondo & Segawa, 1988; Wood, 1955). Among these, three species also occur in Europe and temperate Asia (*D. anglica* Huds., *D. intermedia* Hayne, and *D. rotundifolia* L.) and three in South America (*D. brevifolia* Pursh, *D. capillaris* Poir., and *D. intermedia*) (Diels 1906; Schlauer 1987).

New chromosome numbers for *Drosera* species are reported below and the karyology of the genus is discussed and compared to recent molecular data.

Materials and Methods

Only meristematic tissue from live root tips (collected from plants in the wild or in cultivation) were used for chromosome counts. Mitotic arrests were acomplished with 8-hydroxyquinoline (0.002M for 3-5h in the refrigerator) and methanol/glacial acetic acid (3:1) was used for fixation. Root tips collected in the field were fixed directly in methanol/acetic acid (3:1). Standard chromosome preparations (HCl/ Giemsa) followed Guerra (1983).

A list is given in Table 2 of the taxa native to areas south of the Amazon Basin in Brazil that were karyologically analyzed, as well as their chromosome numbers, and respective herbarium voucher specimens. In Table 3 are the chromosome numbers and origins of the taxa analyzed which were grown from seed or vegetatively propagated.

Results and Discussion

Chromosome numbers for all taxa in Table 3 have been previously reported by other authors, the only exception being *Drosera roraimae*, which has been found to have 2n=20. The chromosome counts carried out for *D. capensis* L., *D. intermedia*, and *D. filiformis* Raf. var. *tracyi* (Macf.) Diels (respectively 2n=40, 2n=20, and 2n=20) agree with those published by other authors (Behre, 1929; Heitz, 1926; Hoshi & Kondo, 1998a; Kondo & Segawa, 1988; Rothfels & Heimburger, 1968; Wood,

Subgenus / Section	Approximate # of species	Distribution	Chromosome numbers
Thelocalyx	2	S Asia, N Australia, S America	20
Arcturia	2	SE Australia, N.Zealand	20
Stelogyne	1	SW Australia	28
Meristocaulis	1	N Brazil, S Venezuela	unknown
Regiae	1	South Africa	34
Coelophylla	1	S Australia	22
Lasiocephala	13	N Australia, N.Guinea	12, 13, 14, 19, 24
Drosera / Prolifera	3	NE Australia	28, 30
Drosera / Arachnopus	1	Africa, Asia, Australia	28
Drosera / Ptycnostygma	7	South Africa, New World	20, 40, 60, 80
Drosera / Oosperma	24	Worldwide	20, 40, 60, 80
Drosera / Drosera	20	Africa, Asia, Europe, New World	20, 32, 40
Bryastrum / Bryastrum	1	S Australia, N.Zealand	*c.*28
Bryastrum / Lamprolepis	29	SW Australia	6, 10, 12, 14, 16, 18, 20, 28
Phycopsis	1	E Australia, N.Zealand	32, 46, 64
Ergaleium / Ergaleium	23	S & E Asia, Australia, N.Zealand	14, 26, 28, 30, 32, 40
Ergaleium / Stolonifera	4	SW Australia	20, 26

Table 1: Chromosome numbers for the genus *Drosera* (Bennett & Cheek, 1989; Behre, 1929; Beuzenberg & Hair, 1983; Debbert, 1987; Futagawa, *et al.*, 2002; Heitz, 1926; Hoshi & Kondo, 1998a, 1998b; Kondo, 1969, 1971, 1973, 1976, 1984; Kondo & Lavarack, 1984; Kondo & Olivier, 1979; Kondo & Segawa, 1988; Kress, 1970; Peng *et al.*, 1986; Sheikh & Kondo, 1995; Venkatasubban, 1950; Wood, 1955) with the distribution (Diels, 1906; Schlauer, 1987) and number of species in each subgenus and section *sensu* Schlauer (1996).

1955). *D. cistiflora* L. has been reported to have 2n=40 (Kondo & Olivier, 1979) and 2n=60 (Behre, 1929), this variation not being a surprise considering it is one of the most morphologically polymorphic species in the genus. For this study, a purple-flowered form of *D. cistiflora* was found to have 2n=60.

Both Rothfels & Heimburger (1968) and Behre (1929) published 2n=80 and Heitz (1926) 2n=*c.*72 for *D. spatulata* Labill., the highest chromosome numbers known in the genus *Drosera*. These specimens were later considered synonymous of *D. aliciae* Hamet (Kondo, 1971). The number reported by Heitz was most likely obtained from 2n=80 specimens, the confusion arising from the difficulty of counting the tiny chromosomes found in polyploid species of subgen. *Drosera*. Bennett & Cheek (1989) published 2n=40 for *D. aliciae*, a number confirmed in the present work. The question stands whether *D. aliciae* comprises both a tetraploid and an octoploid race, or whether two different taxa are involved (a very likely scenario, considering the taxonomic confusion involving small rosetted African sundews).

Among the rosetted African species is *D. cuneifolia*, which belongs to sect. *Drosera* (Schlauer, 1996) and is native to the Cape Town region of South Africa (Diels, 1906; Schlauer, 1987). Kondo & Olivier (1979) reported 2n=32 for this species, although Debbert (1987) found 2n=40 for *D. admirabilis* P.Debbert, which is considered a synonym of *D. cuneifolia* by Schlauer (1987). A new chromosome count for *D. cuneifolia* would be of interest to confirm (or refute) the above number.

For *D. spatulata* the chromosome numbers of 2n=20, 40, 50, and 60 have been reported (Beuzenberg & Hair, 1983; Hoshi & Kondo, 1998a, 1969, 1971; Rattenbury, 1957), excluding the above-mentioned 2n=*c*.72 and 80 which pertain to *D. aliciae*. The *D. spatulata* specimens reported to have 2n=60 belong to what was later described as *D. tokaiensis*, the amphiploid hybrid between *D. spatulata* and *D. rotundifolia*. The specimens reported to have 2n=50 are most likely hybrids between *D. tokaiensis* and tetraploid *D. spatulata*. Thus the only chromosome numbers confirmed for true *D. spatulata* are 2n=20 in New Zealand and 2n=40 in Australia and Japan.

The odd 2n=30 obtained in this work for *D. spatulata* from Beerwah (near Brisbane, Queensland, Australia collected by Mr. Ivan Snyder) is a new number never before reported for *D. spatulata* and the specimens used are almost certainly hybrids between a tetraploid and a diploid race. Seeds obtained from these cultivated specimens did not germinate, suggesting that the plants were sterile. However it is uncertain whether the hybridization occurred accidentally in cultivation or naturally in the wild, since it is not known if diploid races of *D. spatulata* exist in Australia. The chromosome number 2n=30 is also known from other sterile hybrids between diploid and tetraploid *Drosera* species. (Kondo & Segawa, 1988), including the recently described *D. tokaiensis* subsp. *hyugaensis* J.Seno, a simple cross between *D. spatulata* and *D. rotundifolia* (Seno, 2003).

As with the majority of the North American taxa, several of the South American taxa have been found to be diploids with 2n=20. These are *D. cayennensis* Sagot ex Diels (here including *D. pumila* Santos and *D. colombiana* Fernandez-Perez as synonyms), *D. communis* A.Saint-Hilaire, *D. hirtella* A.Saint-Hilaire var. *hirtella*, *D. hirtella* var. *lutescens* A.Saint-Hilaire, *D. roraimae* (Klotzsch ex Diels) Maguire & Laudon, *D. sessilifolia*, and *D. viridis* F.Rivadavia. The South American *D. brevifolia* and *D. intermedia* here analyzed, similarly to other specimens studied (Futagawa, *et al.*, 2002; Hoshi & Kondo, 1998a; Kondo & Segawa, 1988; Wood, 1955), also have 2n=20 (Tables 2 and 3). Interestingly, *D. ascendens* A.Saint-Hilaire, *D. camporupestris* F.Rivadavia, *D. chrysolepis* Taubert, *D. grantsaui* F.Rivadavia, *D. graomogolensis* T.Silva, *D. tomentosa* A.Saint-Hilaire, and *D. tentaculata* F.Rivadavia were discovered to be tetraploids with 2n=40. The natural hybrid *D. grantsaui* × *D. tomentosa* was also found to have 2n=40, as in both parent species (Table 2). In agreement with Futagawa, *et al.* (2002), *D. graminifolia* A.Saint-Hilaire and *D. villosa* A.Saint-Hilaire were found to have 2n=40.

Drosera sessilifolia is here reported to have 2n=20 (Table 2), as does the only other member of subgen. *Thelocalyx*, *D. burmannii* Vahl. (Hoshi & Kondo, 1998b; Kondo & Lavarack, 1984; Peng *et al.*, 1986; Venkatasubban, 1950) (Table 1). *Drosera sessilifolia* is known to occur in Brazil, Venezuela, and Guyana (Schlauer, 1987) whilst *D. burmannii* occurs from Northern Australia to Southern and Eastern Asia (Diels, 1906; Schlauer, 1987) (a collection of *D. burmannii* from West Africa is cited in Diels, yet this has never been confirmed). Although geographically distant, *D. burmannii* and *D. sessilifolia* are very similar morphologically, differing in that the former has cuneate leaves, ascending scapes, and white flowers whilst the latter has cuneate-spathulate leaves, erect scapes, and pink-lilac flowers. Interestingly, fertile offsprings between these two species have been obtained through artificial hybridization in cultivation (Ivan Snyder, pers. comm.).

The chromosome number for *D. sessilifolia* has been reported as 2n=80 (Hoshi & Kondo, 1998b) and as 2n=20 (Futagawa, *et al.*, 2002). Seeds labelled as *D. sessilifolia* have been circulating in cultivation for a few years, yet the resulting plants are almost always *D. aliciae*, which also has 2n=80. Considering that *D. sessilifolia* crosses with *D. burmannii* (2n=20) and that these hybrids are fertile, the conclusion reached is that the plants used by Hoshi & Kondo were in fact *D. aliciae* and not *D. sessilifolia*.

Among the Brazilian *Drosera* taxa here analyzed no significant differences in chromosome lengths were observed for any one species, although the chromosomes of the tetraploid taxa were always relatively smaller than those of the diploid taxa. The only exception was *D. sessilifolia* which, like the tetraploid taxa, was found to posses relatively small chromosomes. Futagawa *et al.* (2002) describe chromosomes varying between 1.02-2.95μm in length for the diploid species *D. filiformis*, *D. capillaris*, and *D. brevifolia* while the tetraploids *D. graminifolia*, *D. montana*, and *D. villosa* plus the diploid *D. sessilifolia* have chromosomes varying between 0.43-1.56μm in length.

The relatively smaller size of the chromosomes observed among the Brazilian tetraploid species suggests that there has been chromosome reduction subsequent to the polyploidization event. This is a frequent occurrence in polyploid taxa, where the doubling (or more) of the whole genome permits the subsequent loss over time of repeated sections (coding and non-coding regions) without compromising functionality of the chromosomes (Degreef, 1990; Rothfels & Heimburger, 1968).

Taxa Examined	2n	Herbarium Vouchers (deposited at SPF)
D. ascendens A.Saint-Hilaire	40	São Paulo. São Bernardo do Campo: ao lado da rodovia dos Imigrantes, 12/Nov./1992, *Rivadavia 153*.
D. brevifolia Pursh	20	Paraná. São Luís do Purunã: estrada Curitiba - Ponta Grossa (BR 376), 21/Apr./1995, *Rivadavia et al. 393*.
D. camporupestris F.Rivadavia	40	Minas Gerais. Jaboticatubas: Serra do Cipó, Fazenda da Serra do Cipó, 6/Jul./1995, *Rivadavia 447*.
D. chrysolepis Taubert	40	Minas Gerais. Santana do Riacho: Serra do Cipó, bifurcação da estr. Conceição do Mato Dentro-Morro do Pilar, 5/Jun./1994, *Rivadavia 288*.
D. cayennensis Sagot ex Diels	20	Mato Grosso. Chapada dos Guimarães: nascente ao lado do córr. da Mata Fria, 23/Feb./1994, *Rivadavia & Cardoso 255*.
D. cayennensis Sagot ex Diels	20	Mato Grosso. Chapada dos Guimarães: descendo a encosta do Mirante, 30/Apr./1995, *Rivadavia & Cardoso 425*.
D. communis A.Saint-Hilaire	20	Mato Grosso. Chapada dos Guimarães: nascente brejosa do córr. Mata Fria, 23/Feb./1994, *Rivadavia & Cardoso 257*.
D. communis A.Saint-Hilaire	20	Minas Gerais. Grão Mogol: Morro do Jambeiro, 3/Jun./1994, *Rivadavia 284*.
D. communis A.Saint-Hilaire	20	São Paulo. Cotia: após Vargem Grande, estrada p/ Ibiúna, 13/Feb./1996, *Rivadavia et al. 512*.
D. grantsaui F.Rivadavia	40	Minas Gerais. Grão Mogol: Morro do Jambeiro, 8/Sep./1994, *Rivadavia 299*.
D. grantsaui F.Rivadavia	40	Minas Gerais. Botumirim: Serra da Canastra, 21/Dec./1994, *Rivadavia 339*.
D. grantsaui F.Rivadavia × *D. tomentosa* A.Saint-Hilaire	40	Minas Gerais. Grão Mogol: Morro do Jambeiro, 3/Jun./1994, *Rivadavia 286*.
D. graminifolia A.Saint-Hilaire	40	Minas Gerais. Grão Mogol: Trilha da Tropa, 7/Sep./1994, *Rivadavia 295*.
D. graminifolia A.Saint-Hilaire	40	Minas Gerais. Diamantina: metade do caminho para Biri-Biri, 7/Jul./1995, *Rivadavia et al. 453*.
D. graomogolensis T.Silva	40	Minas Gerais. Grão Mogol: Morro do Jambeiro, 8/Sep./1994, *Rivadavia 297*.
D. hirtella A.Saint-Hilaire var. *hirtella*	20	Minas Gerais. Jaboticatubas: trilha p/ o mirante do canyon, 6/Jul./1995, *Rivadavia 445*.
D. hirtella A.Saint-Hilaire var. *lutescens* A.Saint-Hilaire	20	Mato Grosso. Chapada dos Guimarães: arredores da cachoeira Véu de Noiva, 30/Apr./1995, *Rivadavia & Cardoso 424*.
D. tomentosa A.Saint-Hilaire	40	Minas Gerais. Jaboticatubas: Serra do Cipó, morro entre sede do IBAMA e estátua do Juquinha, 4/Jul./1995, *Rivadavia 439*.
D. tomentosa A.Saint-Hilaire	40	Minas Gerais. Jaboticatubas: Serra do Cipó, Fazenda da Serra do Cipó, 6/Jul./1995, *Rivadavia 449*.
D. tomentosa A.Saint-Hilaire	40	Minas Gerais. Grão Mogol: Morro do Jambeiro, nascente brejosa, 8/Sep./1994, *Rivadavia 298*.
D. sessilifolia A.Saint-Hilaire	20	Mato Grosso. Chapada dos Guimarães: Salgadeira, 15/Feb./1992, *Cardoso s/n*.
D. tentaculata F.Rivadavia	40	Minas Gerais. Jaboticatubas: trilha p/o mirante do canyon da Bocaina, 23/Feb./1996, *Rivadavia & Mullins 541*.
D. villosa A.Saint-Hilaire	40	Minas Gerais. Lima Duarte: Parque Estadual Florestal de Ibitipoca, Morro da Lombada, 30/Oct./1995, *Rivadavia & Padovese 507*.
D. viridis F.Rivadavia	20	São Paulo. Paranapiacaba: *c.*2km antes da cidade, 21/Apr./1995, *Rivadavia & Cardoso 393*.

Table 2: List of the *Drosera* L. (Droseraceae) taxa collected in Brazil, their chromosome numbers, and voucher specimens. All plants were collected and cultivated by the author at the Botany Department of the University of São Paulo and the herbarium vouchers are deposited at SPF.

Taxa Examined	2n	Place of Origin
D. aliciae Hamet	40	South Africa, Cape Province
D. capensis L.	40	South Africa, Cape Province
D. cistiflora L. — purple flowers	60	South Africa, Cape Province
D. filiformis Raf. var. *tracyi* (Macf.) Diels	20	Southeastern USA
D. intermedia Hayne	20	Mt.Roraima, Venezuela
D. roraimae (Klotzsch ex Diels) Maguire & Laudon	20	Mt.Roraima, Venezuela
D. spatulata Labill. — pink flowers	30	Beerwah, Queensland, Australia

Table 3: List of the *Drosera* L. (Droseraceae) taxa obtained as seeds or from vegetative propagation, their chromosome numbers, and their place of origin. All plants were cultivated by the author at the Botany Department of the University of São Paulo.

The difference in chromosome length observed between the diploid and tetraploid taxa suggests that the polyploidization event may be ancient and therefore any obvious signs of hybrid origin, such as bimodal karyotypes, may already have been erased. Bimodal karyotypes (when two sets of chromosomes are clearly visible due to differences in size) have been used as evidence of recent hybridogenic origin through amphiploidy (hybridization followed by duplication of the whole genome, allowing sterile crosses to become fertile) for *D. anglica* and *D. tokaiensis* (Komiya & Shibata) T.Nakamura & Ueda, with the probable crosses being *D. rotundifolia* with *D. linearis* Goldie for the former (Kondo & Segawa, 1988; Wood, 1955) and *D. rotundifolia* with a tetraploid *D. spatulata* Labill. for the latter (T.Nakamura & Ueda, 1991).

Drosera adelae is included by Schlauer (1996) in sect. *Prolifera* together with *D. prolifera* C.T.White and *D. schizandra* Diels, all of which are native to Northeastern Australia (Diels, 1906; Schlauer, 1987) and have been reported to have 2n=30 (Kondo, 1976; Kondo & Lavarack, 1984; Kondo & Olivier, 1979). Yet 2n=28 has also been reported for a cultivated cytotype of *D. adelae* (Kondo, 1976). The two chromosome numbers recorded for *D. adelae* may represent different forms of this taxon known to cultivation, such as the red and the salmon-pink flower forms.

Drosera indica is the sole member of sect. *Arachnopus* (Schlauer, 1996) and is native to the tropics and subtropics of Africa, Asia, and Australia (Diels, 1906; Schlauer, 1987). The chromosome number of 2n=28 has been recorded more than once for this species (Kondo & Lavarack, 1984; Peng *et al.*, 1986; Venkatasubban, 1950), although if one considers how morphologically variable and geographically widespread *D. indica* is, it is not unlikely that populations with different chromosome numbers exist, possibly even 2n=30.

Centromeres were not observed in any of the taxa in this study and are probably diffused along the entire length of the chromosomes, as has been suggested by Sheikh *et al.* (1995).

Conclusions

Previously published chromosome numbers are here confirmed for some taxa and several new counts are reported, including a few tetraploid South American taxa and the first triploid *Drosera spatulata*.

Chromosome numbers for Droseraceae are remarkably consistent with phylogeny inferred from recent molecular data (Rivadavia *et al.*, 2003). The phylogenetic tree inferred from the DNA sequences of chloroplast rbcL gene show the pygmy sundews of subgen. *Bryastrum* as a sister group to subgen. *Lasiocephala*, and curiously both have relatively low chromosome numbers, varying from 2n=6 to 28 in the former and 2n=12-24 in the latter. The tuberous sundews of subgen. *Ergaleium* are shown to form a sister clade to subgen. *Phycopsis*, and the chromosome numbers known for both are relatively high, varying from 14-40 in the former and 32-64 in the latter. Basal to these four subgenera is *D. glanduligera* Lehm. Which surprisingly has an intermediate chromosome number of 2n=22.

On another branch of this phylogenetic tree one finds African sundews towards the apex, including species from subgen. *Drosera* sect. *Drosera*, sect. *Oosperma* and sect. *Ptycnostygma*, suggesting these sections are not monophyletic. Chromosome numbers in this branch include 2n=20, 40, 60, and 80, as well as the doubtful 2n=32. Sister to this group are the tetraploid Brazilian taxa of subgen. *Drosera* sect. *Drosera* and sect. *Oosperma* reported above. Just below these two branches is another branch that includes a majority of diploid taxa from subgen. *Drosera* sect. *Drosera* and sect. *Oosperma* native to the New World and the Northern Hemisphere.

An apparently unrelated group of species that branch together on the phylogenetic tree is also supported by chromosome numbers. *Drosera adelae*, *D. indica*, and *D. hamiltonii* are all reported to have 2n=28, a rather rare number in the genus. Furthermore *D. burmannii* and *D. sessilifolia* branch together, both having 2n=20. The two basal species in the genus *Drosera* are *D. arcturi* Hook and *D. regia* Stephens. The latter has 2n=34, a relatively high number, as with the closely related genera *Dionaea* (2n=30, 32 and 33) and *Aldrovanda* (2n=38 and 48) while the latter has 2n=20, a number that could be considered as basic for the genus.

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