



Chromosome studies in *Drosera* (Droseraceae)

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Abstract. Thirty-two species and one hybrid of *Drosera*, *Aldrovanda vesiculosa*, *Dionaea muscipula* and *Drosophyllum lusitanicum* were investigated for a chromosome analysis with sequentially fluorescent distamycin A and chromomycin A₃ (DMA-CMA), and actinomycin D and 4'-6-diamidino-2-phenylindole (AMD-DAPI) staining methods. In genus *Drosera*, no primary constriction was observed in the mitotic-metaphase chromosomes stained by orcein, DMA-CMA and AMD-DAPI. The hexaploid *D. spathulata* ($2n=60$) had 20 middle-size chromosomes stained positively by DMA-CMA and stained negatively by AMD-DAPI. Moreover, genomic *in situ* hybridization to mitotic chromosomes showed that 20 middle-size chromosomes of the hexaploid in *D. petiolaris* exhibited six bivalent and two univalent chromosomes at meiotic metaphase I. The bivalent chromosomes of *D. petiolaris* showed circular ring-shaped pairing and distinctively displayed four chromatids held together end-to-end association as a diffused-centromeric nature. In contrast, the bivalent chromosomes of *D. rotundifolia* showed ring-shaped pairing at end-to-end of two chromosomes as a behavior of the usual pairing of the localized-centromeric chromosome during meiosis I. Thus, respective, meiotic chromosomes of *D. rotundifolia* could perform a single active site out of multacentromeres or the diffused centromeres, although its mitotic chromosome has the active diffused-centromere throughout the length of the chromosome. Localization of active centromere in the meiotic chromosome might make the species of *Drosera* in the Northern Hemisphere very stable and promoted a polyploid speciation with the basic chromosome number of $x=10$.

Introduction

Drosera L. is a member of the Droseraceae and one of the largest genera among the carnivorous plants. *Drosera* is distributed throughout the world; more than 15 species are native to the Northern Hemisphere and more than 70 species are native to the Southern Hemisphere. It has the close relatives of the monotypic *Aldrovanda* L., *Dionaea* Ellis and *Drosophyllum* link. within the family (Diels 1906).

Most of the previous cytological investigation concentrated on a orcein karyomorphological study in *Drosera*. These studies of *Drosera* species were mostly of chromosome counts and karyotype analysis (e.g., Kondo 1973, 1976, Kondo *et al.* 1976). The chromosome analysis in these studies disclosed coexistence of polyploid and aneuploid complex in genus *Drosera*, common nature of mitotic chromosomes with unclear primary constriction, and intraspecific high-similarity of each chromosome morphology. Although chromosome data in *Drosera* were so much accumulated, the conventional karyotype analysis was not possible to obtain more useful information from *Drosera* chromosomes since the chromosomes of this genus could not be distinguished using primary constriction. Thus, more critical chromosome analysis with banding technique and cytomolecular methods are necessary for further *Drosera* cytological investigation.

In this study, DNA base specific banding and *in situ* hybridization were employed for providing detailed data of karyomorphological characterization, and for clarifying

chromosomal phylogenetic relationships in the Droseraceae. Moreover, to demonstrate the diffused centromeric nature of the *Drosera* chromosomes, induction of fragment chromosomes by radiation was carried out.

Materials and Methods

Thirty-two species and one natural hybrid (*D. filiformis* x *D. intermedia*) of *Drosera* and *Aldrovanda vesiculosa*, *Dionaea muscipula*, *Drosophyllum lusitanicum* of the Droseraceae used in this study are listed in Table 1.

To observe mitotic chromosomes, root tips were collected and pretreated with 0.002 M hydroxyquinoline for two hours at 18°C before fixation with 45 % acetic acid for five minutes. Then, these were hydrolyzed in a mixture of 1N hydrochloric acid and 45% acetic acid (2:1) at 60°C for seven seconds. For, orcein staining, root meristems were cut and stained with 1 % aceto-orcein for six hours and then squashed. To observe meiotic chromosomes, pollen mother cells were stained and prepared with the standard aceto-orcein smear method. For slide preparation before fluorescent staining and *in situ* hybridization, root tips were pretreated, fixed and hydrolysed by the procedure described above, then they were squashed in 45 % acetic acid. The preparations were air-dried for 24 hours at room temperature after removal of coverslips with dry ice. For Sequentially fluorescent staining with distamycin A and chromomycin A₃ (DMA-CMA) and with actinomycin D and 4'-6-diamidino-2-phenylindole (AMD-DAPI), the method of Schweizer (1981) and Schweizer (1976) was followed with slight modifications, respectively.

Hexadecyltrimethylammoniumbromide (CTAB)-based method was employed to isolate total genomic DNA of *Drosera rotundifolia*. Isolated DNA was treated with DNase-free RNase A (0.2 mg/ml) at 37 °C for one hour followed by extractions with phenol-chloroform and chloroform. Total genomic DNA was labeled with biotin-14-dATP by nick translation according to the supplier's instruction (BRL). Probe mixture (400 µl) contained 10 % dextran sulfate, 50 % formamide, 2xSSC (1xSSC; 0.15 M NaCl, 0.015 M sodium citrate, pH 7.0) and 1 µg biotin-labeled DNA.

For *in situ* hybridization to chromosomes, biotin-labeled probes were cytochemically detected using the avidine-horse radish peroxidase complex (Vector Lab.) and a diaminobenzidine-H₂O₂ solution. The chromosomes were counterstained with 2 % Giemsa in 2xSSC for two minutes and were, then, mounted with Eukitt. All *Drosera* chromosomes at mitotic metaphase could not be classified by the method using localized-centromeric position, since they do not have localized centromere and/or primary constriction (Kondo *et al.* 1976, Kondo and Segawa 1988). Thus, individual chromosome areas stained by AMD-DAPI at mitotic metaphase were measured by an image analyzer (IBAS: Kontron). The karyotype formulae are based on measurements of 30 metaphase cells with DAPI single staining. Chromosome size are defined as: Super large (LL) > 15.00 µm² in area, large (L) 6.00-14.99 µm², middle (M) 1.50-5.99 µm² and small (S) <1.49 µm². Relative area of average-sized individual chromosome was calculated by average individual chromosome area/total area of the chromosomes in the complement x 100. The ratio of the largest chromosome to the smallest chromosome was calculated by average area of the largest chromosome / average area of the smallest chromosome.

Plants of *Drosera petiolaris* and *D. rotundifolia* *in vitro* were exposed to Gamma radiation in the Facility of Faculty of Engineering, Hiroshima University. Doses were determined by time and distance from the source around a circular disc in the 'Gamma shine' (Co unit). Soon after exposed to Gamma radiation, the flasks were returned to the culture room of the Laboratory for continuous *in vitro* culture.

Results and Discussion

Chromosomal analysis of 32 species and one natural hybrid of *Drosera*, *Aldrovanda vesiculosa*, *Dionaea muscipula* and *Drosophyllum lusitanicum* are shown in Table 1 and Fig. 1.

In the squash method skipped pretreatment, the sister chromatids of the *Drosera* species laid parallel to each other at mitotic-prophase to metaphase. The configuration of a chromatid complement at late anaphase was dome-shape or flat when viewed from the lateral side. This configuration indicated parallel separation at mitotic anaphase. The metaphase chromosome morphology and anaphase chromatid behavior supported that *Drosera* species have diffused-centromeric chromosome. Diffused-centromeric nature of the chromosome in *Drosera* was previously reported (Kondo *et al.* 1976, Kondo and Lavarack 1984). The presence of diffused-centromeric chromosomes in *Drosera* (Kondo *et al.* 1976, Kondo and Lavarack 1984, Kondo and Segawa 1988) is only a case in the dicots. In contrast, the sister chromatids of *Dionaea muscipula* laid parallel to each other at mitotic-prophase to metaphase and were not observed to move apart parallel in separation at mitotic anaphase since the chromatids showed the end-to-end association and their CMA-negative or DAPI-positive sites separated at last at mitotic latemetaphase. Thus, *Dionaea muscipula* could have a localized-centromere at the CMA-negative or DAPI-positive site of the chromosome. *Drosophyllum lusitanicum* had well-differentiated and localized centromeres in the chromosome at mitotic metaphase. *Aldrovanda vesiculosa* did not obviously show any localized centromere due to difficulty in observing non-staining gap of small chromosome in this genus.

In genus *Drosera*, the sixteen species and one hybrid in sect. Rossolis, ser. Eurossolis studied exhibited karyomorphologically the gradient type of the mitotic chromosome, while five species in section Rossolis, ser. Lasiocephala exhibited the interstitial type of the mitotic chromosome. These two series showed karyomorphologically different properties each other. In chromosome number, the basic chromosome number of $x=10$ was directly connected to the species of ser. Eurossolis divided into three groups: The first group is characterized by the chromosome number of $2n=20$, the second group is characterized by the chromosome number of $2n=40$, and the third group is characterized by the chromosome number of $2n=80$. In contrast, aneuploid chromosome numbers were characteristic in ser. Lasiocephala. Moreover, ser. Eurossolis has small and middle-size chromosomes, while ser. Lasiocephala has large-size chromosomes. From these cytogenetic points, ser. Eurossolis and ser. Lasiocephala took evolutionally independent differentiation each other, and then ser. Eurossolis might not be closely related to ser. Lasiocephala.

Average chromosome size made it possible to divide the members to sect. Rossolis, ser. Eurossolis into two major groups: One group, which was characterized by middle-size chromosomes, consisted of *D. anglica*, *D. brevifolia*, *D. capillaris*, *D. filiformis*, *D. intermedia*, *D. rotundifolia* and *D. x hybrida*, distributed in the Northern Hemisphere (Fig. 1). The other group, which was characterized by small-size chromosomes, consisted of *D. aliciae*, *D. capensis*, *D. dielsiana*, *D. hilaris*, *D. madagascariensis*, *D. montana*, the diploid and the tetraploid *D. spathulata*, *D. trinervia* and *D. villosa*, distributed mainly in the Southern Hemisphere (Fig. 1). Thus, correlation between average area of respective complement and distribution pattern seemed to be found in *Drosera*, sect. Rossolis, ser. Eurossolis.

The karyotype formulae and fluorescent staining in South African and South American species with the chromosome number of $2n=40$ of *Drosera* suggested two possibilities of the basic chromosome number: One basic chromosome number might be $x=10$ because average area of respective chromosome complement of South African and South American species

were as small as those of the diploid *D. spathulata*. The other possible basic chromosome number might be $x=20$, because all species distributed in South Africa and South America studied displayed the chromosome number of $2n=40$, exhibited up to two sat-chromosomes and did not have four sat-chromosomes in fluorescent staining. Moreover, the meiotic configuration of 20_{II} was observed in *D. madagascariensis* from South Africa. The phenomena of spontaneous hybridization and chromosome doubling for amphiploid speciation supported the species relationship with the basic chromosome number of $x=10$ (Kondo 1971, 1973). Thus, these results speculated that the species with chromosome number of $2n=40$ in South Africa and South America might be arisen from diploid species with the basic chromosome number of $x=10$ by spontaneous hybridization to produce amphidiploid.

Among six populations of *Drosera spathulata* complex investigated, the chromosome numbers of $2n=20, 40$ were counted from the Southern Hemisphere populations, while the chromosome numbers of $2n=40, 60$ were counted from the Northern Hemisphere populations. Rattenbury (1957) observed the somatic chromosome number of $2n=20$ in *D. spathulata* in a New Zealand population. Kondo (1971) observed a somatic chromosome number of $2n=40$ in the same species in an Australian population. Migration trend of the *D. spathulata* complex was speculated by Kondo (1971) that the tetraploid *D. spathulata* seemed to be originated from the diploid *D. spathulata* in New Zealand and might be shown the northward distribution. Thus, the present result supported Kondo's explanation (1971).

Drosera petiolaris complex of sect. Rossolis, ser. Lasiocephala, displayed large total chromosome area more than $80.00 \mu\text{m}^2$, and large average area of chromosome complement more than $7.00 \mu\text{m}^2$ (Fig. 1). the *D. petiolaris* complex displayed both an aneuploid and polyploid nature since it showed chromosome numbers of $2n=12-14$ in *D. petiolaris* and $2n=24$ in *D. ordensis*. Kondo (1976) and Kondo and Lavarack (1984) reported the chromosome number of $2n=12$ in *D. dilatato-petiolaris*, *D. falconeri* and *D. petiolaris* and $2n=19$ [hypertriploid as Kondo (1984) said] in *D. lanata*. Kondo (1976) suggested that primitive basic chromosome number of $x=6$ for *Drosera* was *D. petiolaris*. Moreover, Sheikh and Kondo (1995) reported that species of sect. Lamprolepis possessed large-sized chromosomes with aneuploid series. Thus, cytological studies suggest that *D. petiolaris* complex and species of sect. Lamprolepis had common karyomorphological features with low basic chromosome number.

Drosera x hybrida is a natural hybrid between *D. filiformis* and *D. intermedia*. In florescent staining investigation at metaphase, *D. filiformis* had four chromosomes with CMA faintly-positive or DAPI-positive distal bands and 16 chromosomes with CMA faintly-positive or DAPI-positive interstitial bands, while *D. x hybrida* had two chromosome with CMA faintly-positive or DAPI-positive distal bands, eight CMA-faintly positive or DAPI-positive interstitial bands, and ten chromosomes with neither CMA nor DAPI band. Moreover, *D. intermedia* displayed no CMA-negative or DAPI-positive band in all chromosomes. Thus, DNA fluorescent banding technique had an ability to distinguish between two parental chromosomes in *D. x hybrida*.

Total genomic DNA from *Drosera rotundifolia* hybridized 20 middle-size chromosomes of the hexaploid *D. spathulata* ($2n=60$) by genomic *in situ* hybridization (GISH). Thus, the hexaploid *D. spathulata* could be arisen from an amphidiploid hybrid origin between the sympatric species of the diploid *D. rotundifolia* ($2n=20$) and the tetraploid *D. spathulata* ($2n=40$). Moreover, the hexaploid *D. spathulata* had 20 CMA-positive or DAPI-positive middle-size chromosomes and 40 CMA faintly-positive or DAPI-positive small-size chromosomes. The tetraploid and the hexaploid *D. spathulata* and the diploid *D. rotundifolia* are sympatric in some areas in Shizuoka Prefecture in Japan (Kondo 1971).

The hexaploid *D. spathulata* 'Kansai type' has been hypothesized to be derived from a hybrid between *D. rotundifolia* and the tetraploid *D. spathulata*, since it is morphologically intermediate and shows a bimodal karyotype (Kondo 1971, Kondo and Segawa 1988). The GISH with total DNA of *D. rotundifolia* supported the Kondo's hypothesis of hybrid-origin of the hexaploid *D. spathulata* 'Kansai type' (Kondo 1971, Kondo and Segawa 1988). Further molecular phylogenetic investigation is expected to identify a parent involved in a maternal or cytoplasmic inheritance of the hexaploid *D. spathulata*.

Drosera petiolaris and *D. rotundifolia* both *in vitro* exposed to different doses of Gamma radiation showed fragmented and fused chromosomes. Different types of the chromosome fragmentation could be observed in root tip cells of the exposed plants. Simple breakages occurred frequently in most of the metaphase cells exposed to 50 Gy produce chromosome fragments with various length. Long chromosomes made by fusion of two or more chromosomes were also found in some metaphase cells radiated. The plant materials *in vitro* exposed to above 1000 Gy were completely died 120 days after the exposure. Separation of the fragment chromosomes at mitotic anaphase and telophase was quite normal. The localized-centromeric chromosomes always displayed lagging chromosomes and/or chromosome bridges at mitotic anaphase and micronuclei at mitotic telophase after irradiation. Most of the fragment chromosomes in the somatic cells of *Drosera* did not lose kinetic activity and thus, might have multi- or diffused-centromeres, since the behaviour and appearance of the chromosomes are quite in agreement with some of the features of holocentric and/or diffused-centromeric chromosomes reported previously (Tanaka and Tanaka 1977, Sheikh *et al.* 1995).

The $2n=14$ plant from the intraspecific aneuploid series in *D. petiolaris* ($2n=12-14$) exhibited six bivalent and two univalent chromosomes at meiotic metaphase I. In contrast, *D. rotundifolia* ($2n=20$) in a polyploid series with the basic chromosome number of $x=10$ in the Northern Hemisphere exhibited ten bivalent chromosomes at metaphase I of meiosis. The bivalent chromosomes of *D. petiolaris* showed circular ring-shaped pairing and distinctively displayed four chromatids held together end-to-end association. In contrast, the bivalent chromosomes of *D. rotundifolia* showed ring-shaped pairing at end-to-end of two chromosomes as a behavior of the usual pairing of the localized-centromeric chromosome during meiosis I. Thus, respective, meiotic chromosomes of *D. rotundifolia* could perform a single active site out of multicentromeres or the diffused centromeres, although its mitotic chromosome has the active diffused-centromere throughout the length of the chromosome. Localization of active centromere in the meiotic chromosome might make the species of *Drosera* very stable and promoted a polyploid speciation with the basic chromosome number of $x=10$. Bivalent chromosomes at meiotic metaphase I in some species of *Luzula* (Malheiros and Castro 1947, Nordenskiöld 1951) and *Elocharis* (Strandhede 1965) were equatorially oriented with regard to the spindle at meiotic metaphase I and separate equatorially at anaphase I. This type of orientation of the holocentric chromosomes at meiotic metaphase I (White 1973). Speciation accompanied by orderly and stable polyploidization in *Drosera* seen in the Northern Hemisphere could be an unexpected phenomenon and could be due to localized-centromeric behavior function and formation during the meiosis I instead of diffused-centromeric nature seen during the mitosis. The species of *Drosera* in the Northern Hemisphere might obtain a character of the most active centromere among the multi- or poly-centromeres or along the entire lengths of the chromosomes to maintain the stable meiotic division for the stable sexual reproduction after the ancestor species might choose rarely the basic chromosome number of $x=10$ under certain natural selective pressure.

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Table 1. Comparison in karyotypes of 32 species and one natural hybrid of *Drosera*, *Aldrovanda vesiculosa*, *Dionaea muscipula* and *Drosophyllum lusitanicum* investigated

Species	Chromosome number	Total chromosome area (μm^2) (mean \pm SD)	Chromosome area from the largest to the smallest chromosomes (μm^2)	Average area of chromosome complement (μm^2) (mean \pm SD)	Largest / smallest chromosome	inter-chromosomal asymmetry index	Karyotype formula ^a	Number of CMA- positive or DAPI- negative sat-chromosomes in metaphase complements
Genus <i>Drosera</i>								
Subgenus <i>Roella</i>								
Section <i>Thelocalyx</i>								
<i>D. burmanni</i>	20	15.36 \pm 3.12	1.02 - 0.57	0.77 \pm 0.12	1.84	0.16	20S	2
<i>D. sessilifolia</i>	80	48.15 \pm 6.94	0.92 - 0.35	0.62 \pm 0.14	2.67	0.24	80S	2
Section <i>Arachnopus</i>								
<i>D. adetae</i>	30	16.59 \pm 2.92	0.95 - 0.22	0.55 \pm 0.17	4.87	0.32	30S	2
<i>D. indica</i>	28	47.18 \pm 9.04	2.36 - 0.45	1.69 \pm 0.44	5.97	0.26	22M + 6S	4
<i>D. prolifera</i>	30	19.94 \pm 5.02	1.04 - 0.24	0.66 \pm 0.18	4.72	0.27	30S	2
Section <i>Rosolis</i>								
Series <i>Eurosolis</i>								
<i>D. aliciae</i>	80	75.96 \pm 10.26						
<i>D. anglica</i>	40	93.59 \pm 29.56	1.49 - 0.41	0.95 \pm 0.23	4.02	0.25	80S	2
<i>D. brevifolia</i>	20	38.15 \pm 5.09	3.19 - 1.71	2.34 \pm 0.34	1.95	0.15	40M	0
<i>D. capensis</i>	40	21.50 \pm 5.73	2.48 - 1.52	1.91 \pm 0.25	1.65	0.14	20M	2
<i>D. capillaris</i>	20	68.50 \pm 12.90	0.82 - 0.34	0.53 \pm 0.10	2.56	0.20	40S	2
<i>D. collinsiae</i>	40	38.11 \pm 7.01	4.80 - 2.33	3.43 \pm 0.66	2.08	0.20	20M	0
<i>D. dielsiana</i>	40	37.52 \pm 10.10	1.06 - 0.43	0.70 \pm 0.14	2.52	0.21	40S	0
<i>D. filiformis</i>	20	88.03 \pm 19.07	1.35 - 0.59	0.94 \pm 0.19	2.38	0.21	40S	4
<i>D. hilaris</i>	40	28.91 \pm 8.95	5.87 - 2.97	4.40 \pm 0.82	2.01	0.19	20M	2
<i>D. intermedia</i>	20	47.33 \pm 13.82	1.13-0.39	0.72 \pm 0.16	3.04	0.23	40S	2
<i>D. madagascariensis</i>	40	20.60 \pm 5.72	3.26-1.63	2.37 \pm 0.44	2.02	0.19	20M	2
<i>D. montana</i>	40	50.01 \pm 11.99	0.80 - 0.29	0.51 \pm 0.12	2.93	0.25	40S	2
<i>D. rotundifolia</i>	20	46.28 \pm 9.19	1.95 - 0.59	1.25 \pm 0.34	3.37	0.27	10M + 30S	2
<i>D. spathulata</i>	20	17.79 \pm 4.79	3.18-1.52	2.31 \pm 0.42	2.19	0.19	20M	0
	40	36.74 \pm 6.71	1.25 - 0.59	0.89 \pm 0.16	2.17	0.19	20S	2
	60	92.49 \pm 13.68	1.40 - 0.52	0.92 \pm 0.21	2.78	0.23	40S	0
<i>D. trinervia</i>	40	35.39 \pm 8.71	3.73-0.52	1.54 \pm 1.05	7.64	0.68	20M + 40S	0
<i>D. villosa</i>	40	27.99 \pm 6.14	1.90 - 0.48	0.88 \pm 0.27	4.60	0.32	2M + 38S	2
<i>D. x hybrida</i>	20	62.88 \pm 8.59	1.14 - 0.33	0.70 \pm 0.19	3.60	0.27	40S	2
			5.50 - 1.50	3.14 \pm 1.27	3.70	0.41	20M	2
Series <i>Lasiocephala</i>								
<i>D. dilatato-petiolaris</i>	12	98.07 \pm 18.65						
<i>D. falconeri</i>	12	89.12 \pm 19.33	9.77 - 6.24	8.17 \pm 0.98	1.57	0.12	12L	0
	13	95.12 \pm 12.34	8.87 - 6.34	7.43 \pm 0.70	1.40	0.10	12L	0
<i>D. lanata</i>	12	89.63 \pm 15.62	9.13 - 3.02	7.32 \pm 1.52	3.22	0.21	12L + 1M	0
	14	100.80 \pm 14.88	8.94 - 6.10	7.47 \pm 0.83	1.48	0.12	12L	0
<i>D. ordensis</i>	24	181.79 \pm 35.24	9.15 - 3.05	7.20 \pm 1.81	3.06	0.25	12L + 2M	0
<i>D. petiolaris</i>	12	90.52 \pm 19.42	9.86 - 6.06	7.57 \pm 1.04	1.64	0.14	24L	0
	13	93.34 \pm 17.62	9.01 - 6.00	7.54 \pm 0.89	1.52	0.12	12L	0
	14	102.66 \pm 15.08	9.04 - 2.96	7.18 \pm 1.45	3.22	0.21	12L + 1M	0
			9.34 - 3.09	7.33 \pm 1.88	3.14	0.26	12L + 2M	0
Section <i>Stelogyne</i>								
<i>D. hamiltonii</i>	28	18.88 \pm 5.19						
			1.00 - 0.42	0.67 \pm 0.14	2.42	0.21	28S	2
Section								
<i>D. binata</i>	32	41.06 \pm 10.02						
			1.89 - 0.75	1.28 \pm 0.28	2.67	0.22	8M + 24S	2
Subgenus <i>Ptycnostigma</i>								
Section <i>Ptycnostigma</i>								
<i>D. cistiflora</i>	60	34.10 \pm 6.63						
<i>D. pauciflora</i>	40	23.42 \pm 5.33	0.83 - 0.28	0.57 \pm 0.11	5.63	0.21	60S	4
Subgenus <i>Ergaleium</i>								
Section <i>Polypeltes</i>								
<i>D. auriculata</i>	32	30.24 \pm 5.56						
<i>D. peltata</i>	32	28.03 \pm 9.68	1.49 - 0.48	0.95 \pm 0.26	4.28	0.30	32S	0
Genus <i>Aldrovanda</i>								
<i>Aldrovanda vesiculosa</i>	48	43.25 \pm 7.50	1.40 - 0.39	0.88 \pm 0.27	4.39	0.32	32S	4
Genus <i>Dionaea</i>								
<i>Dionaea muscipula</i>	33	96.96 \pm 19.03	1.48 - 0.33	0.90 \pm 0.26	6.37	0.30	48S	2
Genus <i>Drosophyllum</i>								
<i>Drosophyllum lusitanicum</i>	12	377.28 \pm 29.15	3.82 - 0.53	2.94 \pm 0.53	9.20	0.20	32M + 1S	0
			40.02 - 26.28	31.44 \pm 5.20	1.32	0.18	12LL	0

^aS = small-size chromosome ($< 1.49 \mu\text{m}^2$), M = middle-size chromosome ($1.50 - 5.99 \mu\text{m}^2$), L = large-size chromosome ($6.00 - 14.99 \mu\text{m}^2$), LL = super large-size chromosome ($> 15.00 \mu\text{m}^2$)
SD = standard deviation of the mean

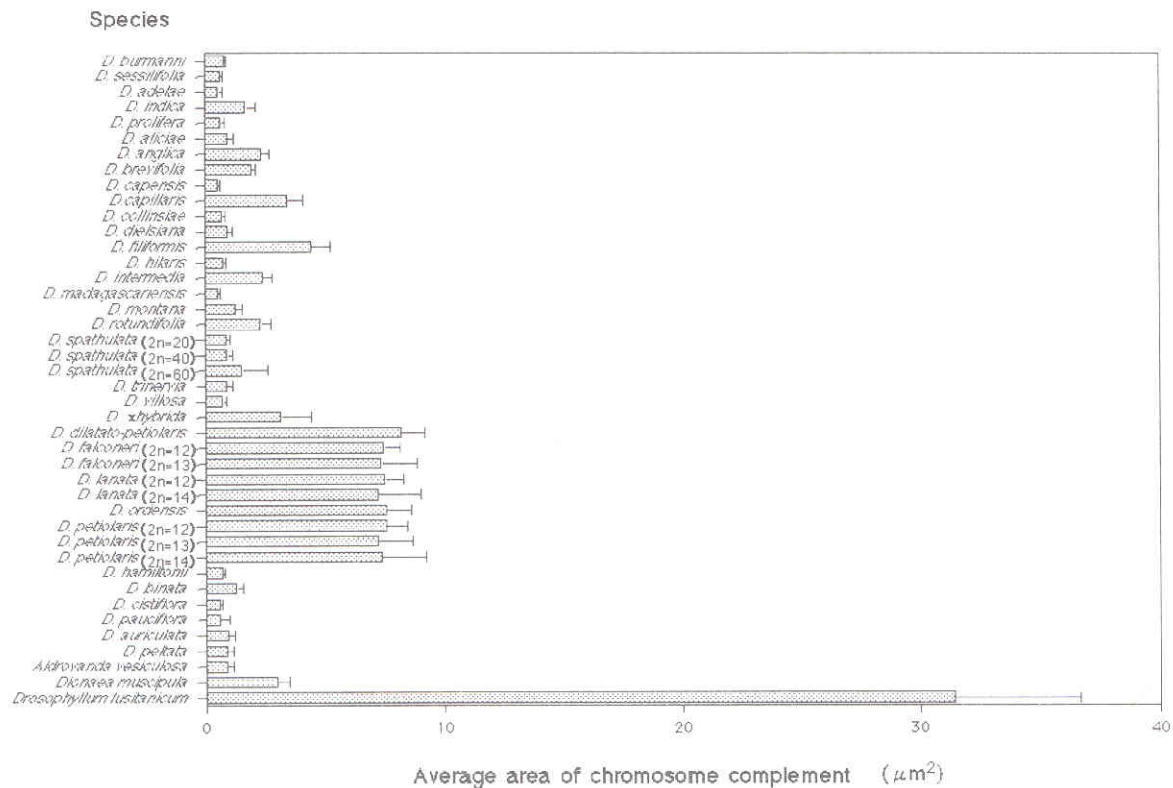


Figure 1. Histograms of average chromosome size measured in the members of the Droseraceae studied. Average chromosome size made it possible to divide the members to sect. *Rossolis*, ser. *Eurossolis* into two major groups: One group, which was characterized by middle-size chromosomes, consisted of *D. anglica*, *D. brevifolia*, *D. capillaris*, *D. filiformis*, *D. intermedia*, *D. rotundifolia* and *D. x hybrida*, distributed in the Northern Hemisphere. The other group, which was characterized by small-size chromosomes, consisted of *D. aliciae*, *D. capensis*, *D. dielsiana*, *D. hilaris*, *D. madagascariensis*, *D. montana*, the diploid and the tetraploid *D. trinervia* and *D. villosa*, distributed mainly in the Southern Hemisphere. In the species of *Drosera* studied, *D. petiolaris* complex had more than $7.00 \mu\text{m}^2$ of large-size chromosomes.