Research Article

Karyomorphological Studies in Some Species of *Parnassia* L. (Saxifragaceae *s.l.*) in East Asia and Intraspecific Polyploidy of *P. palustris* L.

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Karyomorphological information is one of the most important characters for cytotaxonomy. We described karyomorphology of 14 species of *Parnassia* in East Asia. They had commonly the resting chromosomes of the simple chromocenter type and the mitotic prophase chromosomes of the proximal type. The somatic chromosome number of 2n = 14 was shown in three species, that of 2n = 18 was shown in six species, that of 2n = 18 or 36 was shown in two species, that of 2n = 32 was shown in one species, that of 2n = 36 or $36+1 \sim 8$ s was shown in one species, and that of 2n = 18, 27, 36 or 45 was shown in one species. They were commonly monomodal (gradual) decrease in length from the largest to the smallest chromosomes. However, their absolute chromosome sizes were different from each other. Average chromosome sizes were recognized as three types small (1.21μ m), medium ($1.7-2.36 \mu$ m), and large ($3.1-3.75 \mu$ m). *Parnassia palustris* showed four cytotypes that could be likely cytogeographically correlated with habitats, polyploidy, and sizes of pollen grains.

1. Introduction

The genus *Parnassia* L., traditionally classified in the monotypic subfamily Parnassioideae, the family Saxifragaceae *sensu lato* [1], is currently placed in the family Parnassiaceae, closely related to Saxifragaceae in the order Celastrales [2, 3]. The genus *Parnassia* consists of approximately 70 species [4], that are perennial herbs and grow in wet grassy plains and forests in the temperate to arctic regions of the Northern Hemisphere. Among the species of this genus, 63 species are found in China [4], five species are distributed in Russia [5] of which four species are common to China and Russia, and three species grow in Japan [6].

The chromosome numbers of 33 species of *Parnassia* have been documented as 2n = 18, 27, 32, 33, 34, 35, 36, 37, 36 + 1~8s, 43, 44, 45, 48, and 54 including intraspecific polyploid and aneupoid (e.g., [24, 28–35]; Table 1).

The present study contributes cytological data for the species of *Parnassia*, mainly in its East Asian distribution

range, and based on karyomorphology with respect to resting nuclei, mitotic prophase chromosomes and the mitotic metaphase chromosomes, the distribution of intraspecific polyploidy and aneuploidy, and cytogeographic patterns.

2. Materials and Methods

Total 400 samples of 14 species of *Parnassia* were collected in 75 localities in Russia, Mongolia, China, and Japan (Figure 1; Table 2) and were brought and cultivated in pots in shade place in the experimental garden of Showa Pharmaceutical University. Somatic chromosome observations were made in meristematic cells of fresh root tips. They were pretreated in 2 mM 8-hydroxyquinoline at ca 20°C for 4 hours and then fixed in 45% acetic acid at ca 2°C for 10 minutes. They were macerated in a mixture of 45% acetic acid and 1 N hydrochloric acid (1:1) at ca 60°C for 20–23 seconds and were then stained with 2% aceto-orcein at room temperature

TABLE 1: Chromosome numbers of Parnassia previously reported.

Species	Chromosome number	Selected bibliography		
P. tenella Hook.f. et Thoms.	2n = 18	Ding et al. 2005 [7]		
P. yunnanensis Franch. var. longistipitata Jine	2n = 32	Funamoto et al. 1997 [8]		
P. esquirolii Lévl.	2n = 18	Ding et al. 2005 [7]		
P. faberi Oliv.	2n = 18	Ding et al. 2005 [7]		
P. chinensis Franch.	2n = 18	Ding et al. 2005 [7]		
P. epunctulata J.T. Pan	2n = 18	Ding et al. 2005 [7]		
P. venusta Jien	2n = 18	Ding et al. 2005 [7]		
P. mysorensis Heyne ex Wigjt et Arn.	2n = 18	Ding et al. 2005 [7]		
P. scaposa Mattf. var. yushuensis J.T. Pan	2n = 18	Funamoto et al. 1996 [9]		
P. aff. cacuminum HandMazz. f. yushuensis Ku	2n = 18	Funamoto et al. 2001 [10]		
P. pusilla Wall.	n = 9	Malla et al. 1979 [11]		
P. oreophylla Hance	2 <i>n</i> = 18, 36	Funamoto et al. 1994, 1996 [10, 12]		
P. nubicola Wall.	n = 9	Malla et al. 1979 [11]		
P. subscaposa C.Y. Wu ex Ku	2n = 18	Ding et al. 2005 [7]		
P. trinervis Drude	2n = 18	Funamoto et al. 1996 [9]; Ding et al. 2005 [7]		
P. viridiflora Batalin	2 <i>n</i> = 18, 36	Funamoto et al. 1998 [13], 2001 [10, 13]		
P. laxmannii Pall.	2 <i>n</i> = 18, 36	Funamoto et al. 2002 [14]; Murín et al. 1984 [15]		
P. brevistyla (Brieg) HandMazz.	2n = 14	Funamoto et al. 2001 [10]; Ding et al. 2005 [7]		
P. delavayi Franch.	2n = 14	Funamoto et al. 1998, 2001 [10, 13]; Ding et al. 2005 [7]		
P. alpicola Makino	2n = 18	Funamoto 1986 [16]		
P. bifolia Nekrass.	$2n = 36, 36 + 1 \sim 8s$	Funamoto et al. 2002 [14]; Ding et al. 2005 [7]		
P. wightiana Wall.	2n = 14,36	Funamoto et al. 1998 [13]; Malla et al. 1981 [17]		
P. monochorifolia Franch.	2n = 48	Ding et al. 2005 [7]		
P. foliosa Hook.f. et Thoms.	2n = 18	Funamoto 1986 [16]		
P. grandifolia D.C.	2n = 32	Gastony and Soltis 1977 [18]		
P. caroliniana Michaux	2n = 32	Gastony and Soltis 1977 [18]		
P. asarifolia Vent.	2n = 32	Gastony and Soltis 1977 [18]		
P. glauca Raf.	2n = 32, 36	Gastony and Soltis 1977 [18]; A. Löve and D. Löve 1980 [19]		
P. palustris L.	2n = 18, 27, 32, 33, 34, 35, 36, 37, 43, 44, 45, 54	Hultgård 1987 [20]; Lövkvist and Hultgård 1999 [21]; Funamoto et al. 2006, 2008 [22, 23]		
P. obtusiflora Rupr.	2n = 36	A. Löve and D. Löve 1982 [24]		
P. kotzebuei Cham.	2n = 18,36	Packer 1964 [25]; Löve and Ritchie 1966 [26]		
P. fimbriata Koenig.	2n = 36	Packer 1964 [25]		
P. townsendii Robinson	2n = 36	Bye and Soltis 1979 [27]		

in moist chamber with 45% acetic acid for ca 30 minutes and were prepared by the conventional squash method. Measurements of chromosomes in 14 species were made in each average length in several good metaphase cells.

Morphological types of the resting and the mitotic prophase chromosomes were classified for Tanaka [36, 37], and the classification of mitotic metaphase chromosomes followed Levan et al. [38]. Taxonomical treatment followed Czerepanov [5], Ku and Hultgård [4], and Akiyama [6]. The voucher specimens of the plants used in this study were deposited in Funamoto's Herbarium in Showa Pharmaceutical University.

3. Results and Discussion

3.1. Resting Nuclei and Mitotic Prophase Chromosomes. Fourteen species of *Parnassia* in East Asian (Table 2) had common karyomorphological characters in the resting and the mitotic prophase chromosomes: the resting chromosomes were classified as the simple chromocenter type which had several small heteropycnotic bodies per nucleus according to Tanaka [36, 37], and the mitotic prophase chromosomes were classified as the proximal type in which the early condensed segments were confined to the proximal regions of both short and long arms or short arm, showing clear condensation

Section	Species	Number of locality and samples	Chromosome number (2 <i>n</i>) 32	
Saxifragastrum	P. yunnanensis var. Franch. longistipitata Jien	2 localities 17 samples		
	P. scaposa Mattf. var. yushuensis J.T. Pan	5 localities 17 samples	18	
	P. aff. cacuminum HandMazz. f. yushuensis Ku	1 locality 5 samples	18	
	P. oreophila Hance	3 localities 24 samples 1 locality 2 samples	18 36	
	P. trinervis Drude	7 localities 28 samples	18	
Nectarotrilobos	P. viridiflora Batalin	1 locality 5 samples 1 locality 3 samples	18 36	
	P. laxmannii Pall.	2 localities 11 samples	18	
	P. brevistyla (Brieg) HandMazz	2 localities 7 samples	14	
	P. delavayi Franch.	2 localities 5 samples	14	
	P. alpicola Makino	1 locality 1 sample	18	
Nectarabilobos	P. bifolia Nekrass.	5 localities 39 samples 1 locality 5 samples	36 36 + 1s, 2s, 3s, 5s, 7s, 8s*	
Allolobos	P. wightiana Wall.	1 locality 4 samples	14	
Fimbripetalum	P. foliosa Hook.et Thoms.	4 localities 25 samples	18	
Parnassia (Nectarodroson)		28 localities 153 samples	18	
	P. palustris L.	3 localities 12 samples	27	
	<i>г. ранизн из</i> L.	11 localities 35 samples	36	
		1 locality 2 samples	45	

TABLE 2: Chromosome numbers in 14 species of Parnassia studied here.

 * s: supernumerary chromosome.

Species	Chromosome	Chromosome length (μ m)				Form
	number $(2n)$	$Longest \pm SD$	Shortest \pm SD	Total \pm SD	Average \pm SD	TOTIL
P. yunnanensis var. longistipitata	32	1.6 ± 0.1	1.0 ± 0	38.6 ± 1.1	1.21 ± 0.08	m
P. scaposa var. yushuensis	18	2.8 ± 0.3	1.9 ± 0.2	41.2 ± 3.8	2.29 ± 0.21	m + sm
P. aff. cacuminum f.yushuensis	18	2.3 ± 0.1	1.5 ± 0	33.0 ± 0.9	1.83 ± 0.07	m
P. oreophyla	18	2.8 ± 0.2	1.8 ± 0.2	40.6 ± 3.2	2.26 ± 0.27	m + sm
	36	2.8 ± 0.3	1.8 ± 0.2	78.5 ± 4.1	2.13 ± 0.16	m + sm
P. trinervis	18	2.7 ± 0.2	2.1 ± 0.1	42.5 ± 2.9	2.36 ± 0.19	m + sm
P. viridiflora	18	2.0 ± 0.1	1.6 ± 0.1	30.7 ± 1.2	1.71 ± 0.11	m + sm
	36	2.1 ± 0.2	1.4 ± 0.1	61.1 ± 1.8	1.70 ± 0.09	m + sm
P. laxmannii	18	2.3 ± 0.3	1.6 ± 0.1	34.9 ± 1.7	1.94 ± 0.1	m
P. brevistyla	14	3.6 ± 0.7	2.7 ± 0.4	43.4 ± 3.3	3.10 ± 0.25	m + sm
P. delavayi	14	4.3 ± 0.8	3.2 ± 0.4	52.5 ± 3.6	3.75 ± 0.31	m + sm
P. alpicola	18	2.6 ± 0.1	1.9 ± 0.1	39.7 ± 0.9	2.21 ± 0.18	m + sm
P. bifolia	36	2.5 ± 0.2	1.6 ± 0.1	71.4 ± 2.8	1.98 ± 0.08	m + sm
P. wightiana	14	2.3 ± 0.2	1.4 ± 0.1	26.7 ± 1.0	1.91 ± 0.11	m + sm + st
P. foliosa	18	2.8 ± 0.3	1.9 ± 0.2	39.5 ± 2.8	2.19 ± 0.13	m + sm
P. palustris	18	2.7 ± 0.2	1.9 ± 0.1	41.8 ± 3.4	2.32 ± 0.18	m + sm
	27	2.8 ± 0.2	1.9 ± 0.1	61.2 ± 3.9	2.27 ± 0.15	m + sm
	36	2.8 ± 0.2	1.9 ± 0.1	81.4 ± 5.3	2.27 ± 0.13	m + sm
	45	2.7 ± 0.1	1.8 ± 0	99.4 ± 2.5	2.21 ± 0.07	m + sm

TABLE 3: Karyotype characters in 14 species of Parnassia observed here.

SD: standard deviation; m: median-centromeric chromosome; sm: submedian-centromeric chromosome; st: subterminal-centromeric chromosome.

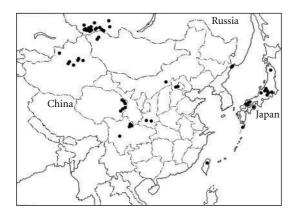


FIGURE 1: Collection sites of 14 species of *Parnassia* in China, South Siberia and Far East in Russia, Mongolian Altai, and Japan.

transition from the proximal to the distal regions (Tanaka [36, 37]; Figure 2). There was no difference in the resting and the mitotic prophase chromosome types among in these 14 species, thus it was concluded that the genus *Parnassia* had the simple chromocenter types at the resting nucleus and the proximal types at the mitotic prophase chromosomes.

3.2. The Mitotic Metaphase Chromosomes. Chromosome numbers in 33 species of Parnassia were from 2n = 14 to 2n = 54 (Table 1). Three species had the somatic chromosome number of 2n = 14, five species had that of 2n = 32, one species had that of 2n = 48, and the other 24 species had that of 2n = 18. Intraspecific polyploids were found in P. oreophylla, P. viridiflora, P. laxmannii, P. palustris, and P. obtusiflora, while intraspecific aneuploids were found in P. bifolia, P. wightiana, P. glauca, and P. palustris (Table 1). Particularly, Parnassia palustris had various chromosome numbers from 2n = 18 to 54 (e.g., [34, 35]; Table 1). Parnassia brevistyla (Figure 3(j)), P. delavayi (Figure 3(k)), and *P. wightiana* (Figure 3(n)) had 2n = 14, P. scaposa var. yushuensis (Figure 3(b)), P. aff. cacuminum f. yushuensis (Figure 3(c)), P. trinervis (Figure 3(f)), P. laxmannii (Figure 3(i)), P. alpicola (Figure 3(l)), and P. foliosa (Figure 3(o)) had 2n = 18, *P. oreophylla* (Figures 3(d)) and 3(e)) and P. viridiflora (Figures 3(g) and 3(h)) had 2n = 18 and 36, *P. palustris* had 2n = 18, 27, 36, and 45 (Figures 3(p)–3(s)), P. yunnanensis var. longistipitata had 2n = 32 (Figure 3(a)), and *P. bifolia* had 2n = 36 and $36 + 1 \sim 8s$ (Figures 3(m) and 4). Parnassia palustris in a plant collected in Scandinavia by Hultgård [20] and Lövkvist and Hultgård [21] was very rarely documented to have the chromosome numbers of 2n = 27 and 45. The chromosome number of 2n = 14 for *P. wightiana* [13] was different from the previous counts of 2n = 36 [17] and 2n = 32[18], while that of P. glauca was also different from the previous count of 2n = 36 [19]. Thus, these two species are necessary to have more cytological studies. A peculiar chromosome number of 2n = 14 for Chinese species of Parnassia was reported by Funamoto et al. [10, 13] and Ding et al. [7]. The chromosome number of 2n = 32was previously reported in four North American species of

Parnassia such as *P. gandifolia*, *P. caroliniana*, *P. asarifolia*, and *P. glauca* by Gastony and Soltis [18] and that was also found in Chinese species [8].

An euploid chromosome numbers of $2n = 36 + 1 \sim 8s$ for *P. bifolia* could include supernumerary chromosomes since these an euploid plants had high pollen stainabilities (87.5– 98.6%).

3.3. Chromosome Sizes and Basic Chromosome Numbers. Morphological characters of chromosomes in chromosome numbers, chromosome sizes, chromosome complements in centromeric positions, and chromosome alignment from the longest to the shortest one are important information for cytotaxonomy. The chromosome number of 2n = 14 was considered diploid x = 7, that of 2n = 32 was considered tetraploid x = 8, and that of 2n = 18 and 36 was considered diploid and tetraploid x = 9, respectively, if these basic chromosome numbers of x = 7, 8, and 9 were accepted. Plants of the basic chromosome number of x = 7 are found in China, those of x = 8 are found in China and North America, and those of x = 9 are commonly found in the world. Their karyotypes had commonly monomodal gradation in chromosome length from the longest to the shortest chromosomes and had median and submedian centromeric chromosomes, rarely median, submedian, and subterminal centromeric chromosomes (Table 3; Figure 5). Thus, Parnassia could be divided by four groups at least from chromosome characters mentioned above. (1) Smallsized and median-centromeric chromosomes ranged from 1.6 to 1.0 μ m long with average 1.21 μ m long, and had the base number of x = 8. (2) Medium-sized and medianand submedian-centromeric chromosomes ranged from 2.8 to $1.9\,\mu\text{m}$ long with average $2.29\,\mu\text{m}$ long and had the base number of x = 9. (3) Large-sized and medianand submedian-centromeric chromosomes ranged from 3.6 to 2.7 μ m long with average 3.10 μ m long and had the base number of x = 7. (4) Medium-sized and median-, submedian-, and subterminal-centromeric chromosomes ranged from 2.3 to $1.4 \,\mu m$ long with average $1.91 \,\mu m$ long, and had the base number of x = 7. These cytotaxonomical groupings were not agreed with the taxonomical treatment by Ku [39]. More cytological information and another new technique are necessary to clarify and justify the cytosystematic relationships of Parnassia.

3.4. Intraspecific Polyploid and Aneuploid. Intraspecific polyploid of 2n = 18 and 36 for *P. oreophylla*, *P. viridiflora*, and *P. laxmannii*, and that of 2n = 18, 27, 36, 45, and 54 for *P. palustris* were reported, especially this polyploidy for *P. palustris* was found in Scandinavia [20, 21] and Great Britain [34, 35], and 2n = 27 and 45 chromosomes were also found in Russia [22, 23]. For example, 156 samples of this species were collected in 23 localities in Altai Mountains, Tuva and Krasunoyarsk region in Russia, of which 113 samples (72.4%) in 18 sites had 2n = 18 chromosomes, 29 samples (18.6%) in five sites had 2n = 36 chromosomes, and two samples (1.3%) in one site had 2n = 45 chromosomes (Figure 6; [22, 23]; Funamoto and Smirnov unpublished).

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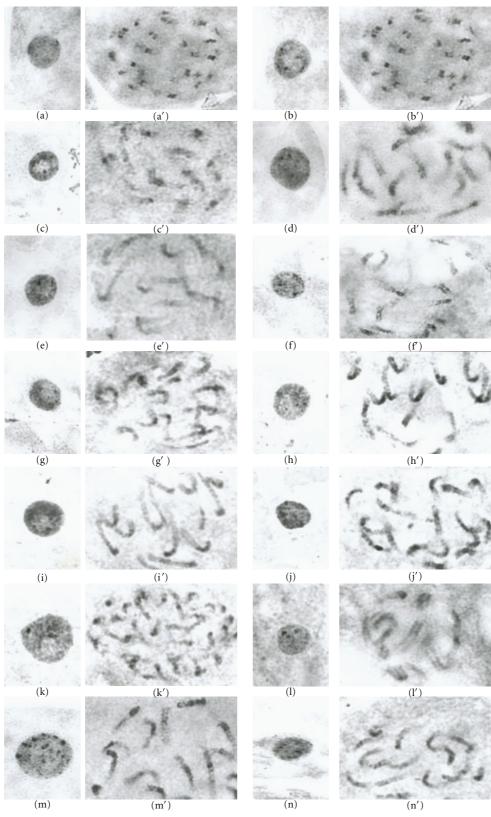


FIGURE 2: Karyomorphological comparisons of resting and mitotic prophase chromosomes in 14 species of *Parnassia*. (a)–(n) The resting chromosomes; (a')–(n') the mitotic prophase chromosomes. (a) and (a') *P. yunnanensis* var. *longistipitata*; (b) and (b') *P. scaposa* var. *yushuensis*; (c) and (c') *P. aff. cacuminum* f. *yushuensis*; (d) and (d') *P. oreophylla*; (e) and (e') *P. trinervis*; (f) and (f') *P. viridiflora*; (g) and (g') *P. laxmannii*; (h) and (h') *P. brevistyla*; (i) and (i') *P. delavayi*; (j) and (j') *P. alpicola*; (k) and (k') *P. bifolia*; (l) and (l') *P. wrightiana*; (m) and (m') *P. foliosa*; (n) and (n') *P. palustris*. Scale bar = 5 μ m.

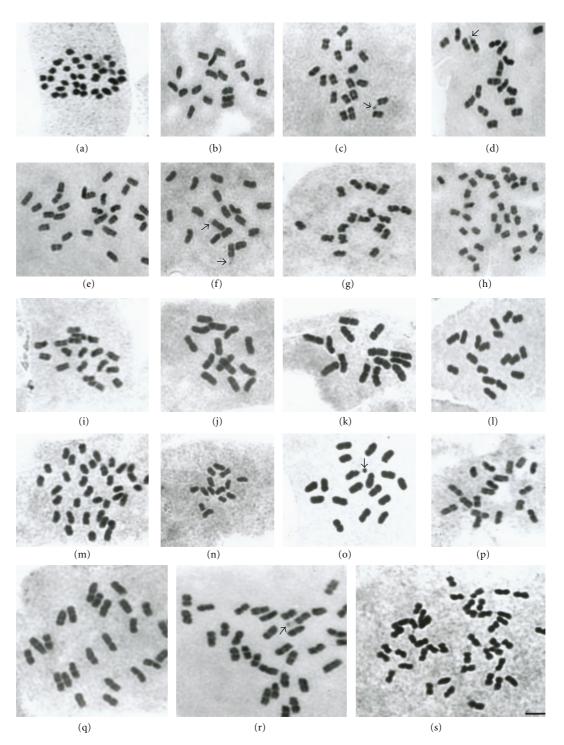
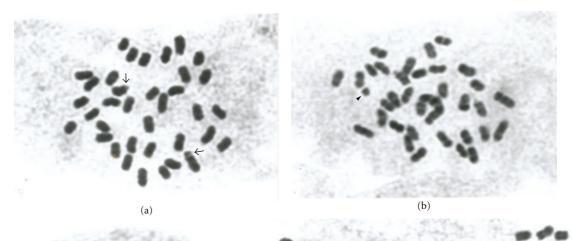
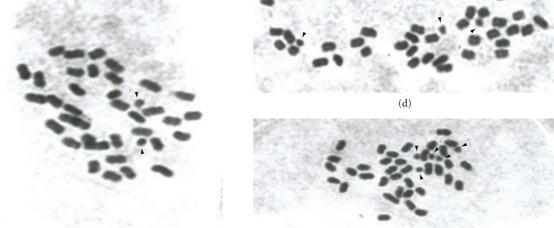


FIGURE 3: Somatic metaphase chromosomes in 14 species of *Parnassia*. (a) *P. yunnanensis* var. *longistipitata* (2n = 32); (b) *P. scaposa* var. *yushuensis* (2n = 18); (c) *P. aff. cacuminum f. yushuensis* (2n = 18); (d) and (e) *P. oreophylla* ((d) 2n = 18; (e) 2n = 36); (f) *P. trinervis* (2n = 18); (g) and (h) *P. viridiflora* ((g) 2n = 18; (h) 2n = 36); (i) *P. laxmannii* (2n = 18); (j) *P. brevistyla* (2n = 14); (k) *P. delavayi* (2n = 14); (l) *P. alpicola* (2n = 18); (m) *P. bifolia* (2n = 36); (n) *P. wrightiana* (2n = 14); (o) *P. foliosa* (2n = 18); (p) to (s) *P. palustris* ((p) 2n = 18; (q) 2n = 27; (r) 2n = 36; (s) 2n = 45). Arrow points satellite. Scale bar = $5 \mu m$.

According to pollen stainability and sizes of pollen grains of *Parnassia palustris*, plants of 2n = 18 and 36 had high pollen stainabilities (81.4–98.2%), while those of 2n = 27 and 45 had very low pollen stainabilities (0.74–0.85%). Sizes

of pollen grains of the species were 27.3–30.3 μ m × 25.8–28.1 μ m in plants of 2n=18, 30.1–32.5 μ m × 27.6–30.2 μ m in plants of 2n = 27, and 31.8–33.6 μ m × 30.1–31.3 μ m in plants of 2n = 36, respectively. Significant *t*-test in sizes





(c)



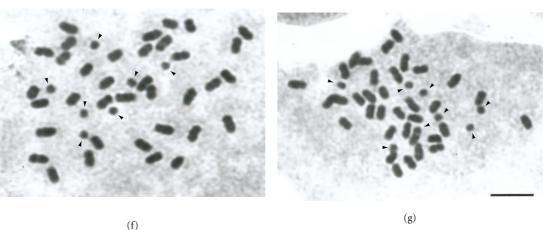


FIGURE 4: Variations of supernumerary chromosomes of *Parnassia bifolia*. Arrow indicates satellites and arrows head indicates supernumerary chromosomes. (a) 2n = 36. (b) 2n = 36 + 1s; (c) 2n = 36 + 2s; (d) 2n = 36 + 3s; (e) 2n = 36 + 5s; (f) 2n = 36 + 7s; (g) 2n = 36 + 8s. (s) supernumerary chromosomes. Scale bar = $5 \mu m$.

of pollen grains showed significant difference between the plants of 2n = 18 and 2n = 36 with P < 0.05 and P < 0.01 levels, respectively. Sizes of pollen grains could be correlated with polyploid levels [22, 23]. Similar results were reported with Japanese *Deutzia crenata* [40–42] and Japanese *Hydrangea paniculata* [43].

The plants with the chromosome number of 2n = 18 were commonly found along the vegetation edges such as in the disturbed riverine, forest meadows and tundra in Russian and Mongolian Altai, and Tuva in Russia, those with the chromosome number of 2n = 27 were found in placid lake side and together with the plants of the chromosome number

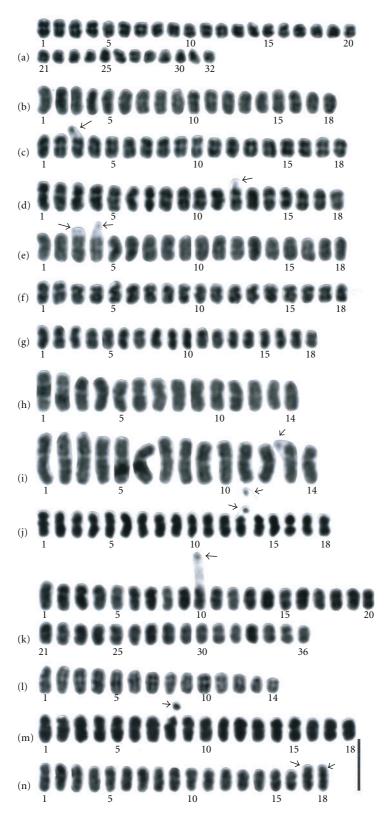


FIGURE 5: Karyotype comparisons in 14 species of *Parnassia*. (a) *P. yunnanensis* var. *longistipitata*; (b) *P. scaposa* var. *yushuensis*; (c) *P. aff. cacuminum* f. *yushuensis*; (d) *P. oreophylla*; (e) *P. trinervis*; (f) *P. viridiflora*; (g) *P. laxmannii*; (h) *P. brevistyla*; (i) *P. delavayi*; (j) *P. alpicola*; (k) *P. bifolia*; (l) *P. wightiana*; (m) *P. foliosa*; (n) *P. palustris*. Arrows indicate satellites. Scale bar = $5 \mu m$.

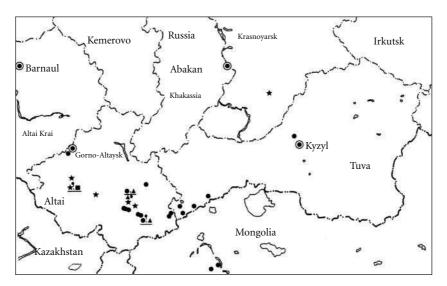


FIGURE 6: Map of collection sites and polyploidy of *Parnassia palustris* in Altai Mountains and the adjacent regions. Chromosome numbers of 2n = 18 (\bigcirc), 2n = 27 (\blacktriangle), 2n = 36 (\star), and 2n = 45 (\blacksquare).

2n = 18 in Russian Altai, while those with the chromosome number of 2n = 36 were commonly found in narrow stream in mountain slope and mountain meadows in Russian Altai and Krasnoyarsk Region in Russia, and those with the chromosome number of 2n = 45 were rarely found together with the plants with the chromosome number of 2n = 36 in Russian Altai. Thus, Parnassia palustris in Altai Mountains and adjacent regions in Russia seemed one of the welldiversified species with respect to chromosome characters. These cytological phenomena speculated that the two plant strains with the chromosome numbers of 2n = 27 and 2n =45 might be isolated by pollination between nondisjunction diploid gametes producing diploid and tetraploid ovules (2x and 4x) and normal male gamete for diploid pollen (x), since any plant with the chromosome number of 2n = 27 has never been found within the populations of the plants with the chromosome number of 2n = 36. This factor might be caused by various geographical conditions and extremes of climate temperature [22, 23].

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