

Cytological Evolution in the Genus *Lycoris* (Amaryllidaceae)

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Cytological characters of ten taxa of the genus *Lycoris* were investigated to illustrate their chromosomal evolution. The fusion theory was more appropriate than the fission theory. From the viewpoint of the fusion theory *L. sanguinea* group, diploids with R-shaped chromosomes was the most primitive and they might have diverged into two directions, the diploids with V+R shaped chromosomes and the triploid with V+R shaped chromosomes via triploids with only R-shaped chromosomes.

Keywords : lycoris, chromosome, fusion, fission, evolution

The genus *Lycoris* (Amaryllidaceae) consists of about 20 species, which are limited to moist warm temperate woodlands of eastern Asia (Lawrence, 1951; Creech, 1952; Hutchinson, 1959; Melchior, 1964; Stebbins, 1971; Kurita, 1987a).

For *Lycoris* plants, cytological researches have been mainly concentrated on the chromosome number, shape and evolution by Nishiyama (1928), Takenake (1931), Inariyama (1931, 1953), Sato (1938), Mookerjee (1995), Bose (1960), Koyama (1962a, b), Takemura (1962), Bose and Flory (1963), Yoshida (1972), Khaleel (1978), Nakamura (1978), Fukuda *et al.* (1980), Kurita (1988a, b), Tae and Ko (1991, 1993) etc. Their chromosome evolution has been explained through two theories, fusion and fission, which are contradictory to each other. The fusion theory is supported by Inariyama (1931, 1932, 1937, 1951, 1953), Stebbins (1971), Jones (1978), Nishikawa *et al.* (1979) and Tae *et al.* (1987), while the fission theory by Darlington (1973), Flory (1977) and Kurita (1988b). According to the fusion theory in the evolution of chromosome number and shape two R-shaped (rod-shape) chromosomes evolved into one V-shaped chromosome by their fusion. On the other hand the fission theory asserts that one V-shaped chromosome evolved into two R-shaped chromosomes by its fission. In *Lycoris* plants only two shapes of chromosome described are observed.

The present study was focused on illustrating chromosome shape evolution of *Lycoris* plants, and cytological relationship between 10 taxa, in which

chromosomal features of 4 species and 2 varieties of the Korean plants, and 2 species and 2 varieties of the foreign ones were included. For the Korean plants, chromosome number, karyotype and polyploidy were observed from living materials, and the foreign plants were examined through literatures.

MATERIALS AND METHODS

L. radiata (L' Hérit.) Herb., *L. chinensis* Traub var. *sinuolata* K. Tae et S. Ko, *L. chejuensis* K. Tae et S. Ko, *L. flavescens* M. Kim et S. Lee, *L. squamigera* Maxim., *L. sanguinea* Maxim. var. *koreana* (Nakai) Koyama were collected from Korea from May 1990 to October 1994. *L. sanguinea* Maxim. var. *sanguinea*, *L. sanguinea* var. *kiushiana* Makino, *L. albiflora* Koidz. and *L. aurea* (L' Hérit.) Herb. were referred to literatures.

To examine the chromosome number and the shape, 20-25 individuals in each taxon were used. Somatic chromosomes from the root tip were observed following the method of Tae and Ko (1991). Well-dispersed chromosome sets of metaphase in mitosis were chosen for the analysis of chromosomal morphology, and their length were calculated with the standardized scale improvised for this purpose. Karyotypes were classified into V-shaped chromosome and R-shaped chromosome followed by Bose (1958). Arm ratio and centromeric indices were adopted from Leven *et al.* (1964)

RESULTS

The details of chromosome characters and karyotypes of 6 *Lycoris* plants from Korea are given in

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Table 1. Summarized karyo-morphological features of *Lycoris* plants from Korea. 1, Chromosome numbers (2n); 2, Karyotypes; 3, Number of metacentric chromosomes; 4, Number of submetacentric chromosomes; 5, Number of subacrocentric chromosomes; 6, Number of acrocentric chromosomes; 7, Size range in microns; 8, Average chromosome length in microns; 9, Total chromosome length in microns

Taxa	1	2	3	4	5	6	7	8	9
<i>L. radiata</i>	33	33R	-	-	-	33	7.3-10.9	8.8	292.0
	34	33R+1B	-	-	-	34	4.2- 9.7	8.1	277.7
<i>L. chinensis</i> var. <i>sinuolata</i>	16	6V+10R	6	2	-	8	7.1-20.3	12.0	192.4
<i>L. chejuensis</i>	30	3V+27R	3	-	-	27	7.5-19.2	9.6	260.6
<i>L. flavescens</i>	19	3V+16R	3	-	-	16	7.4-21.8	10.5	200.7
<i>L. squamigera</i>	27	6V+21R	6	-	-	21	6.0-21.6	10.8	292.4
<i>L. sanguinea</i> var. <i>koreana</i>	22	22R	-	-	6	16	5.3- 9.1	7.5	164.4

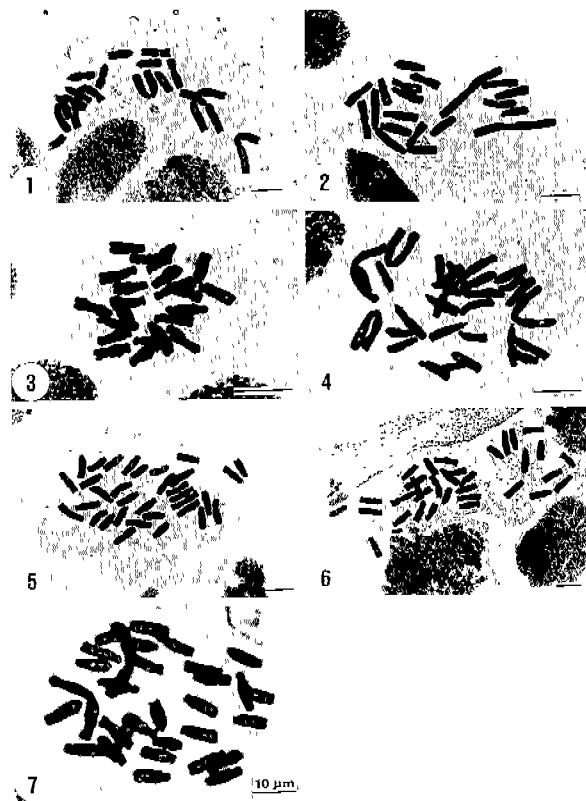


Plate 1.

Table 1 and Plate 1-4, respectively. Ten taxa including the foreign plants can be classified into 2 types in chromosome shape, and also into diploid and triploid in terms of polyploidy level (Table 2).

Chromosome shape

1. V+R type: Total chromosome complement is composed of V-shaped and R-shaped chromosomes. *L. flavescens*, *L. squamigera*, *L. chejuensis*, *L. albiflora*, *L. aurea* and *L. chinensis* var. *sinuolata* are

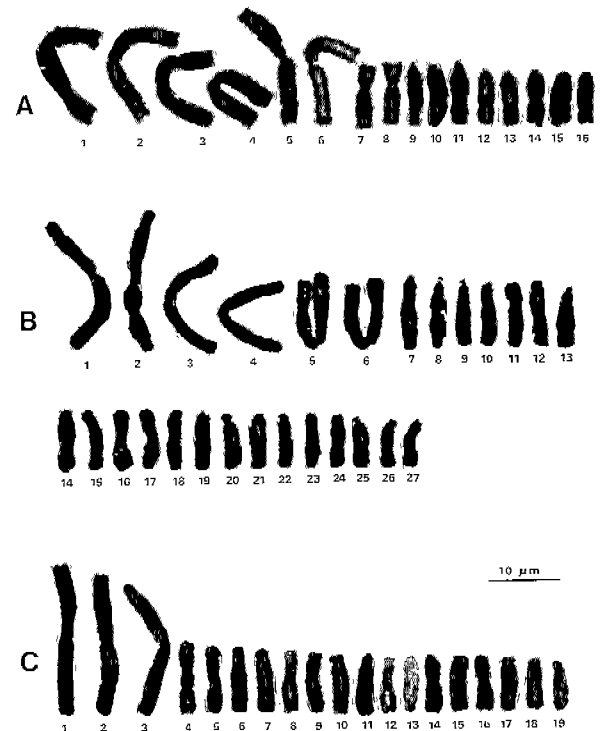


Plate 2.

this type.

2. All R type: All chromosomes in one cell are R-shaped. *L. radiata*, *L. sanguinea* var. *koreana*, *L. sanguinea* var. *sanguinea* and *L. sanguinea* var. *kiushiana* fall under this type.

Most of V-shaped chromosomes are metacentric except submetacentric chromosomes in *L. chinensis* var. *sinuolata* and *L. chejuensis*. Plants with all R type have only acrocentric chromosomes except 6 subacrocentric chromosomes in *L. sanguinea* var. *koreana* (Table 1).

Ploidy level

Table 2. Chromosome numbers of the genus *Lycoris*

Taxa	Present study		Previous study				Possible potentialities in rod chromosome
	2n	shape	2n	shape	author	and year	
<i>L. radiata</i>	33	33R	15	15R	Mookerjea (1955)		15
	34	33R+1B	22	22R	Mookerjea (1955)		22
			25	25R	Mookerjea (1955)		25
			28	28R	Lee (1967)		28
			32	32R	Mookerjea (1955)		32
			32	1V+31V	Kurita (1987b)		33
			33	33R	Bose (1963a), Bose and Flory (1963), Fukuda <i>et al.</i> (1980), Inariyama (1941, '37, '51, '53), Khaleel (1978), Kim and Seo (1979), Koyama (1976), Kurita (1978, '87b), Mookerjea (1955), Nakamura (1978), Nishikawa <i>et al.</i> (1979), Nishiyama (1928, '39), Tae <i>et al.</i> (1987), Park <i>et al.</i> (1989)		33
			33	1V+31R+1B	Bose (1963a)		33
<i>L. chinensis</i>	16	6V+10R	16	6V+10R	Tae <i>et al.</i> (1987), Tae and Ko(1993)		22
var. <i>sinuolata</i>							
<i>L. chejuensis</i>	30	3V+27R	30	3V+27R	Tae and Ko (1993)		33
<i>L. flavescens</i>	19	3V+16R	19	3V+16R	Park <i>et al.</i> (1989)		22
<i>L. squamigera</i>	27	6V+21R	27	6V+21R	Bose (1963b), Bose and Flory (1963), Inariyama (1931, '32, '37, '51, '53), Koyama (1962b, '78), Kurita (1978, '87b), Nakamura (1978), Nishikawa <i>et al.</i> (1979), Sato (1938, '41), Tae <i>et al.</i> (1987), Takenaka (1931)		33
<i>L. sanguinea</i>	22	22R	26		Khaleel (1978)		?
			21	21R	Tae and Ko (1991)		21
			22	22R	Kurita (1978, '88a), Tae <i>et al.</i> (1987), Tae and Ko (1991)		22
			33	33R	Tae and Ko (1991)		33
			43	1V+42R	Tae and Ko (1991)		44
<i>L. sanguinea</i> var. <i>sanguinea</i>	-		21	21R	Kurita (1989)		21
			22	22R	Inariyama (1931, '37, '51, '53), Kurita (1988a), Nakamura (1978), Nishiyama (1928, '39), Sato (1941) Tae and Ko (1991), Yoshida (1972)		22
<i>L. sanguinea</i> var. <i>kiushiana</i>	-		22	22+B	Kurita (1989)		22
			28	28R	Kurita (1989)		28
			32	1V+31R	Kurita (1989)		33
			22	22R	Kurita (1988a), Takemura (1962), Yoshida (1972)		22
			23	23R	Yoshida (1972)		
<i>L. albiflora</i>	-		16	6V+10R	Tae and Ko (1991)		23
			17	5V+12R	Inariyama (1931)		22
<i>L. aurea</i>	-				Bose (1960), Base and Flory (1963), Inariyama (1931, '37, '51, '53), Koyama (1962a, b), Kurita (1978, '87b), Nishikawa <i>et at.</i> (1979), Yoshida (1972)		22
			18	4V+14R	Inariyama (1931), Kurita (1978, '87b)		22
			12	10V+2R	Bose (1958), Bose and Flory (1963), Inariyama (1931, '37, '51, '53), Koyama (1962b), Yoshida (1972)		22
			13	9V+4R	Inariyama (1937, '51, '53), Koyama (1967), Nishikawa <i>et at.</i> (1979), Yoshida (1972)		22
			14	8V+6R	Bose (1963b), Inariyama (1937, '51, '53), Koyama (1967), Nishikawa <i>et at.</i> (1979), Yoshida (1972)		22
			15	7V+8R	Bose (1963b), Bose and Flory (1963), Kurita (1978, '87b)		22
			22	-	Khaleel (1978)		?

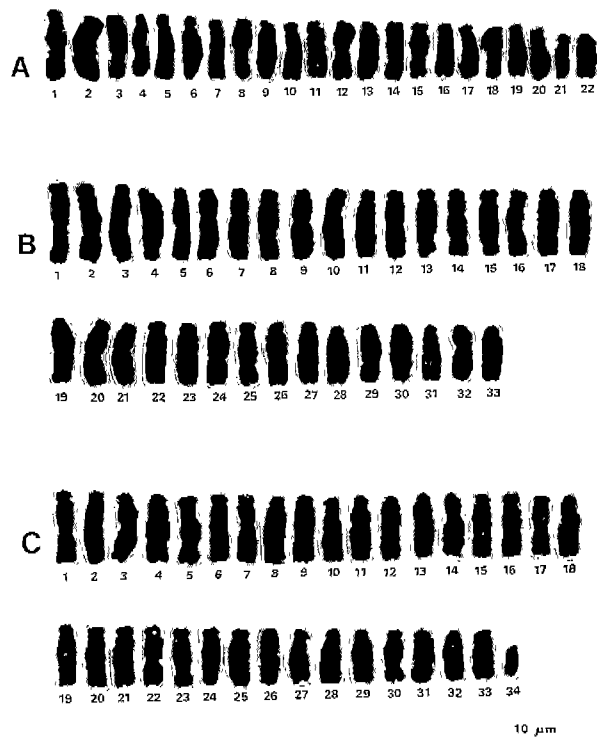


Plate 3.

If one V-shaped chromosome is regarded as two R-shaped chromosomes, ploidy levels of the genus *Lycoris* are classified into two types, diploidy and triploidy (Table 2).

1. Diploidy: basic chromosome number is $2n=22$ ($x=11$) and *L. chinensis* var. *sinuolata*, *L. albiflora*, *L. aurea*, *L. flavescens*, *L. sanguinea* var. *koreana*, *L. sanguinea* var. *sanguinea* and *L. sanguinea* var. *kiushiana* come under this type.

2. Triploidy: basic chromosome number is $2n=33$ ($x=11$) and *L. squamigera*, *L. radiata* and *L. chejuensis* come under this type.

Chromosome number, shape and polyploidy of 6 taxa examined from living materials were consistent with the previous reports. *L. radiata* cells with one accessory chromosome ($2n=34=33R+1B$) were also observed in the same individuals together with normal cells (Table 1).

DISCUSSION

From the chromosome number and the shape of 6 taxa examined in this study and the previous reports, an induction on the evolution of chromosome shape of the genus *Lycoris* was made.

First, the chromosome number and the shape are constant in each taxon except *L. radiata*, *L. san-*

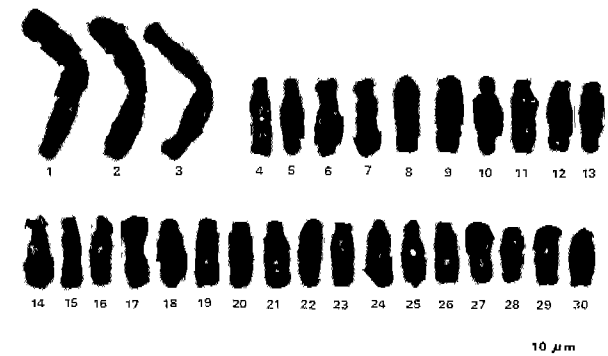


Plate 4.

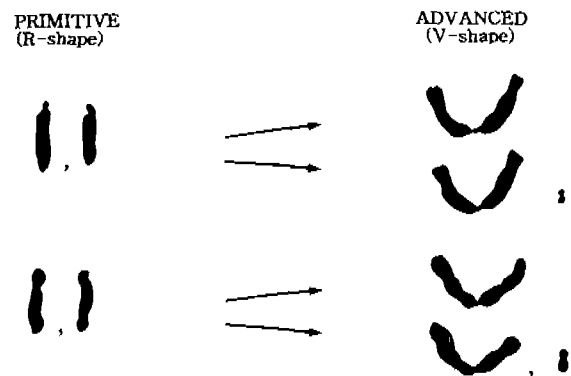


Fig. 1. Fusion from 2R-shaped chromosomes to 1 V-shaped chromosome and formation of accessory chromosome.

guinea var. *sanguinea*. and *L. sanguinea* var. *koreana*. This result was supported by Mookerjea (1995), Bose (1963a), Kurita (1987c, 1989), and Tae and Ko (1991). *L. radiata*, triploid has R-shaped chromosomes ($2n=33=33R$), but rarely a V-shaped chromosome ($2n=32=1V+31R$) or an accessory chromosome ($2n=34=33R+1B$). *L. sanguinea* var. *sanguinea* and *L. sanguinea* var. *koreana* carried R-shaped chromosomes in general ($2n=22=22R$) but often has accessory chromosome ($2n=23=22R+1B$), triploidy cells ($2n=33R$ and $2n=1V+31R$) or tetraploidy cells ($2n=43=1V+42R$) (Table 2). The cytological unstabilities, for example, formation of accessory and V-shaped chromosome, and increase of chromosome numbers showed cytological differentiation in the chromosomal evolution.

The increase in ploidy level seems to be related to the formation of V-shaped chromosome because the V-shaped chromosomes are mostly observed in triploids and tetraploids. Therefore, the V-shaped chromosomes are thought to be formed by the centromeric fusion of acrocentric R-shaped chro-

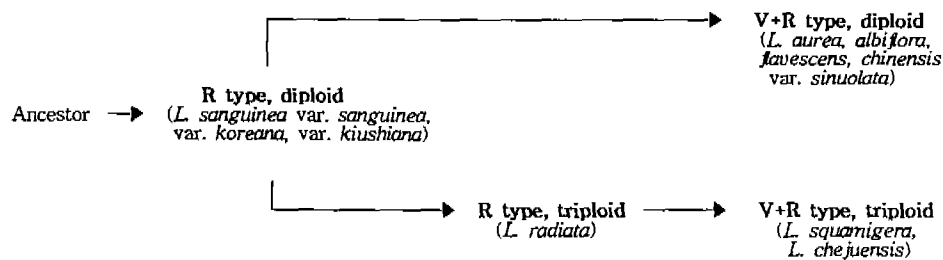


Fig. 2. Cytological evolution scheme of the treated taxa in this study.

mosomes. During this chromosomal behavior accessory chromosomes may be generated by deletion or duplication (Sharma, 1985).

Second, it was shown that there is a close proportionality between total chromosome length and relative DNA content of the nucleus during the chromosomal evolution (Stebbins, 1966; Bullen and Rees, 1972; Cheng and Grant, 1973; Nishikawa *et al.* 1979). Nishikawa *et al.* (1979) reported that longer the total length of chromosomes the larger was the DNA content and that there was much more V-shaped chromosomes in such nuclei. This study also found that one V-shaped chromosome length was longer than two R-shaped chromosomes and the total chromosome length of taxa with V+R shaped chromosomes was longer than that of taxa with all R-shaped chromosome (Table 1). According to these results, the fusion theory is more proper to explain the chromosomal evolution of the genus *Lycoris*, because the taxa with unstability in chromosome shape and number continue to increase in total chromosome length (Table 2). With respect to the fission theory, two R-shaped chromosomes are formed by the fission of a V-shaped chromosome and then contracted to a short length (Kurita, 1987a, Sivarajan, 1991). Since there exists no direct proof about the contraction of chromosomal length after the fission the authors' acceptance of the fission theory need to be waited. Consequently, in the chromosomal evolution of the genus *Lycoris*, V-shaped metacentric chromosome is thought to be formed by the centromeric fusion of acrocentric, subacrocentric and submetacentric chromosomes (Fig. 1). Cytologically, *L. sanguinea* var. *sanguinea*, *L. sanguinea* var. *koreana* and *L. sanguinea* var. *kiushiana* are the most primitive taxa among the taxa because they are diploids and have only R-shaped chromosomes ($2n=22=22R$). *L. sanguinea* var. *kiushiana*, especially, is the closest to an ancestor of the above three taxa owing to its cytological stability. It always has $2n=22R$ with one exception $2n=23R$ (Tae and Ko, 1991).

From the primitive taxa of diploids with R-shaped chromosomes like *L. sanguinea* group, chromosomal evolution of the genus *Lycoris* might have diverged into two directions, diploids with V+R shaped chromosomes, and triploids with R-shaped chromosomes and with V+R shaped chromosomes (Fig. 2). The possibility that triploid with V+R shaped chromosomes was derived from diploid with V+R shaped chromosomes seems very unlikely but can not be excluded.

LITERATURE CITED

- Bose, S. 1958. Cytological investigations in *Lycoris*. 2. Cytological similarities between *Lycoris aurea* and *L. traubii*. *Plant Life* 14: 33-37.
- Bose, S. 1960. Cytological investigation in the genus *Lycoris*. 4. Chromosome number and karyotypes in *Lycoris aurea*, "*L. sperryi*", *L. albiflora* and *L. elsiae*. *Plant Life* 16: 72-82.
- Bose, S. 1963a. Cytological studies in *Lycoris* VII. Chromosome number and karyotype from ovular tissues in *L. aurea* and *L. squamigera*. *Sci. Cult.* 29: 557-558.
- Bose, S. 1963b. A new chromosome number and karyotype in *L. radiata*. *Nature* 197: 1229-1230.
- Bose, S. and W.S. Flory. 1963. A study of phylogeny and karyotype evolution in *Lycoris*. *The Nucleus* 6: 141-156.
- Bullen, M.R. and H. Rees. 1972. Nuclear variation within *Avenae*. *Chromosoma* 39: 93-100.
- Cheng, R.I.-J., and W.F. Grant. 1973. Species relationship in the *Lotus corniculatus* group as determined by karyotype and cytophotometric analysis. *Can J. Genet. Cyto.* 15: 101-115.
- Creech, J.L. 1952. The genus *Lycoris* in the Mid-Atlantic States. *Nat. Hort. Mag* 31: 167-173.
- Darlington, C.D. 1973. Chromosome Botany and the Origins of Cultivated Plants. George Allen and Unwin Ltd., London, pp. 14-127.
- Flory, W.S. 1977. Overview of chromosome evolution in the Amaryllidaceae. *Nucleus* 20: 70-88.
- Fukuda, I., H. Kawafuchi, T. Kunai and K. Umehara. 1980. Chromosome analysis and ethnobotanical consideration of *Lycoris radiata* in Nepal. *Sci. Rep. Tokyo Women's Christ. Univ.* 48-52: 617-621.

- Hutchinson, J.** 1959. The families of flowering plants. II. Monocotyledons. Oxford Univ. Press, Oxford, pp. 645-646.
- Inariyama, S.** 1931. Cytological studies in the genus *Lycoris* (Preliminary notes). *Bot. Mag.* **45**: 11-24.
- Inariyama, S.** 1932. Cytological studies in the genus *Lycoris* I. Conjugation of chromosomes in meiosis of *L. albiflora*. *Bot. Mag.* **46**: 426-434.
- Inariyama, S.** 1937. Karyotype studied in Amaryllidaceae 1. *Sci. Rep. T.B.D. Sect. B.* **3**: 95-113.
- Inariyama, S.** 1951. Cytological studies in the genus *Lycoris* (I). *Sci. Rep. T.B.D. sect. B.* **6**: 74-100.
- Inariyama, S.** 1953. Cytological studies in *Lycoris*. *Rep. Kihara Inst. Biol. Res.* **6**: 5-10.
- Jones, K.** 1978. Aspects of chromosome evolution in higher plants. *Adv. Bot. Res.* **6**: 119-194.
- Khaleel, T.F.** 1978. IOPB chromosome number reports LXI. *Taxon* **27**: 375-392.
- Kim, J.H. and B.B. Seo.** 1979. Karyotype of *Lycoris radiata*. *Res. Rev. of Kyungpook Nat. Univ.* **28**: 375-377.
- Koyama, M.** 1962a. Meiosis in *L. albiflora*. *Ann. Rep. Doshisha Women's Coll.* **12**: 9-19.
- Koyama, M.** 1962b. Behavior of V-shaped and rod chromosomes in the genus *Lycoris*. *Ann. Rep. Doshisha Women's Coll.* **13**: 396-397.
- Koyama, M.** 1967. Chromosome pairing in genus *Lycoris*. *Ann. Rep. Doshisha Women's Coll.* **18**: 411-418.
- Koyama, M.** 1976. Interspecific hybrids in the genus *Lycoris*. *Ann. Rep. Doshisha Women's Coll.* **18**: 163-172.
- Koyama, M.** 1978. Chromosome pairing in the genus *Lycoris* II. *Ann. Rep. Doshisha Women's Coll.* **29**: 272-282.
- Kurita, S.** 1978. Chromosomal evolution in *Lycoris*. *Proc. Jap. Soc. Pl. Tax.* **4**: 8-9.
- Kurita, S.** 1987a. Variation and evolution on the karyotype of *Lycoris*, Amaryllidaceae II. Karyotype analysis of ten taxa among which seven are native in China. *Cytologia* **52**: 19-40.
- Kurita, S.** 1987b. Variation and evolution in the karyotype of *Lycoris*, Amaryllidaceae IV. Intraspecific variation in the karyotype of *L. radiata* (L' Herit.) Herb. and the origin of this triploid species. *Cytologia* **52**: 137-149.
- Kurita, S.** 1988a. Variation and evolution in the karyotype of *Lycoris*. Amaryllidaceae VI. Intrapopulationae and/or intraspecific variation in the karyotype of *L. sanguinea* Max. var. *Kiushiana* and *L. sanguinea* Max. var. *koreana* (Nakai) Koyama. *Cytologia* **53**: 307-321.
- Kurita, S.** 1988b. Variation and evolution in the karyotype of *Lycoris*. Amaryllidaceae VII. Modes of karyotype alteration within species and probable trend of karyotype evolution in the genus. *Cytologia* **53**: 323-335.
- Kurita, S.** 1989. Variation and evolution in the karyotype of *Lycoris* (Amaryllidaceae) V. Chromosomal variation in the *L. sanguinea* Maxim. *Pl. Sp. Biol.* **4**: 47-60.
- Lawrence, H.M.** 1951. Taxonomy of vascular plants. Oxford & IBH Publ. Co., pp. 419-420.
- Leven, A., K. Fredga and A.A. Sandberg.** 1964. Nomenclature for centromeric position on chromosomes. *Hereditas* **52**: 201-220.
- Melchior, H.** 1964. A Engler's Syllabus der Pflanzenfamilien II. Gebrüder Bortraeger, Berlin, pp. 529-530.
- Mookerjea, A.** 1955. Cytology of Amaryllida an aid to the understanding of evolution. *Cytologia* **7**: 1-71.
- Nakamura, T.** 1978. Cytological studies on medicinal plants. I. Chromosome numbers and karyotypes in some species of alkaloidal plants. *La Kromosomo* **10**: 271-281.
- Nishikawa, K., Y. Fukuta and H. Endo.** 1979. Consideration of the chromosome evolution on the basis of nuclear DNA content and total chromosome length in *Lycoris*. *Jap. J. Genet.* **54**: 387-396.
- Nishiyama, I.** 1928. Reduction division in *Lycoris*. *Bot. Mag.* **42**: 509-513.
- Nishiyama, I.** 1939. Chromosome number of a Chinese *Lycoris*. *Jap. J. Genet.* **15**: 83-85.
- Park, Y.J., E.H. Park, C.S. Kim, S.O. Yoo and B.T. Chung.** 1989. Cytological study on the genus *Lycoris* in Korea. II. Karyotype. *Abstracts, annual conference of J. Kor. Soc. Hort. Sci.* pp. 110-111.
- Sato, D.** 1938. Karyotype alteration and phylogeny IV. Karyotypes in Amaryllidaceae with special reference to the SAT-chromosome. *Cytologia* **9**: 203-243.
- Sato, D.** 1941. Karyotype alteration and Phylogeny in Liliaceae and allied families. *Jap. J. Bot* **12**: 57-161.
- Sharma, A.** 1985. Chromosomes. Oxford & IBH Publ. Co., Delhi, pp. 319-326.
- Sivarajan, V.V.** 1991. Introduction to the principles of plant taxonomy. Oxford & IBH Publ. Co. pp. 168-169.
- Stebbins, G.L.** 1966. Chromosomal variation and evolution. *Science* **3728**: 1463-1469.
- Stebbins, G.L.** 1971. Chromosomal Evolution in Higher Plants. Edward Arnold LTD, London, pp. 90-92.
- Tae, K.H. and S.C. Ko.** 1991. An investigation of taxonomic characters on the *Lycoris koreana* Nakai and *L. sanguinea* Maxim var. *sanguinea*. *Kor. J. Pl. Tax.* **21**: 105-115.
- Tae, K.H. and S.C. Ko.** 1993. New taxa of the genus *Lycoris*. *Kor. J. Pl. Tax.* **23**: 233-241.
- Tae, K.H., S.C. Ko and Y.S. Kim.** 1987. A cytotoxic study on genus *Lycoris* in Korea. *Kor. J. Pl. Tax.* **17**: 135-145.
- Takemura, E.** 1962. Morphological and cytological studies on artificial hybrids in the genus *Lycoris* III. An artificial hybrid having V-shaped chromosomes. *Bot. Mag.* **75**: 324-330.
- Takenaka, Y.** 1931. Further reports of the cytological investigations on the sterile plants. I On the chromosomes of *Lycoris squamigera* Maxim. *J. Chos. Nat. Hist. Inst.* **12**: 25-28.
- Yoshida, M.** 1972. Karyological studies on the genus *Lycoris* I. *Sand. Dunc. Res.* **18**: 20-36.

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