A taxonomic review of Korean Asparagales and Liliales (Liliopsida)

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A systematic review for Korean Liliopsida was carried out with rbcL and atpB sequence data. Congruent phylogenetic trees were obtained from two different data sets. Korean Liliopsida consists of the three orders, Asparagales, Liliales, and Dioscoreales sensu Dahlgren et al. Members of Dioscoreales were used as an outgroup for inferring relationships among Asparagales and Liliales in the molecular studies. Iridaceae showed close relationship to Asparagales both in the rbcL and atpB sequence trees rather than to Liliales. Family Nartheciaceae (previously included within Melanthiaceae s. lat.) appeared as a paraphyletic assemblage basal within Liliales, but did not show relationships to other orders. Genera of Ruscaceae (previously Convallariaceae) like Disporum, Clintonia, and Streptopus had to be transferred to Colchicaceae, Liliaceae, and Calochortaceae, respectively. A revised list of families for Korean members of Liliopsida is suggested.

Key words: Korean Liliopsida, molecular data, Asparagales, Liliales

In the traditional taxonomic systems of Bentham and Hooker (1883) and Engler and Prantl (1888), most Liliaceous plants with a superior ovary were placed in a broadly conceived family Liliaceae split into many tribes. Cronquist (1981) used a more traditional approach in his circumscription of monocot families and recognized 15 families within *Liliales*. Because their family concepts were very narrow, Dahlgren *et al.* (1985) classified the Liliaceous plants into 27

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different families comprising five orders.

The broad definition of Liliopsida by Dahlgren et al., (1985) who largely followed the concept of Huber (1969), divided this largest and most diverse superorder of monocotyledons into five orders: Dioscoreales, Asparagales, Melanthiales, Burmanniales and Liliales. Three orders of them, Dioscoreales, Asparagales, and Liliales were recognized in Korea.

The order Dioscoreales shows a number of features believed to be ancient and several of them associate this order with dicotyledoneous families. Therefore, this order could easily be discriminated from Asparagales and Liliales. The order Asparagales represents a monophyletic group characterized by a specialized seed coat containing phytomelan in most of its capsule-fruited taxa (Dahlgren et al., 1985). In addition to the phytomelaneous seeds, Dahlgren et al. (1985) listed 16 characters that differed between Asparagales and Liliales, although most of them did not occur in all taxa and several of them were plesiomorphic. Most of these characters are micromorphological characters, and thus no single field character was known that distinguishes the two orders with certainty. The largest of these orders is the order Asparagales and comprises 33 families (Kubitzki 1998). Dahlgren et al. (1985) used narrow family circumscriptions that were more likely to yield monophyletic families.

Recent DNA sequence data (Chase et al., 1995) in combination with non-molecular studies (Tamura, 1995; Chase et al., 1996; Fay and Chase, 1996; Rudall and Chase, 1996) have improved our understanding of family boundaries and affinities within Liliopsida. The most important synapomorphy for this order, first used by Huber (1969) as a unifying character, was the characteristic black seeds caused by phytomelan incrustation of the seed coat in most of the capsular and some berry-fruited taxa. The taxa now included in this order were relatively little known at the time of Krause (1930), who placed them into a broadly defined family Liliaceae.

Schlittler (1953) brought into focus the interesting phenomenon of articulation of flowers on the pedicels, which among monocots was concentrated within *Asparagales*. Both molecular and morphological data indicated that Asparagales comprises a paraphyletic lower asparagoid clade including early-branching families (including Orchidaceae, Iridaceae, and Tecophilaeaceae), and a higher asparagoid clade (including Agavaceae, Alliaceae, and Ruscaceae [Convallariaceae]). Simultaneous microsporogenesis and inferior ovaries were regarded as characteristic for lower asparagoids, whereas higher asparagoids

have successive microsporogenesis (Rudall *et al.*, 1997) and generally superior ovaries. The boundaries between *Asparagales* and *Liliales* are difficult to define using morphological data alone, as several characters are shared between some lilioids and lower asparagoids (Rudall *et al.*, 2000).

Although monocots usually have successive microsporogenesis, simultaneous microsporogenesis with inferior ovaries are characteristic of lower asparagoids with some exceptions. Otherwise, all higher asparagoids show successive microsporogenesis and generally superior ovaries (Rudall *et al.*, 1997).

Because traditional taxonomic systems (Krause 1930, Cronquist 1981) were applied for the classification of Korean Liliopsida, almost all Korean Liliopsida were placed into only a few families, especially into a broadly defined family Liliaceae. Although several systematic studies were performed at the generic level (Lee, 1985; Chung and Chung, 1988; Yu et al., 1981; Kim and Lee, 1990; Kim and Lee, 1991; Tae, 1995; Sim, 1988; Jang, 1998), studies at higher level taxonomy for Korean monocots are still scarce. Therefore, the application of a reasonable system for classification of Korean Liliopsida is still strongly required.

In the present study we used molecular data of the chloroplast rbcL and atpB genes to examine the relationship among families variously placed in the systematic treatments cited above. Although the Korean flora contains aonly a few families and genera of Liliopsida, and, therefore, the phylogenies are partly inflated by limited sampling, there is a necessity for arrangement of families and their generic members to facilitate future studies at the genus level.

Phylogenetic relationships among a wide array of seed plants have been intensively studied using the large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase (*rbc*L) including a number of relevant lilioid taxa (Chase *et al.*, 1993; 1995; Duvall *et al.*, 1993). Later, the atpB plastid gene was used for phylogenetic studies among monocot taxa. Both genes were regarded as strong tools to reveal relationships within Liliopsida (Fay *et al.*, 2000).

In this study, we will address the following topics:1) the applicability of Kubitzkis revised classification (1998) based on Dahlgren et al. (1995) for the taxonomy of Korean Liliopsida. 2) evaluation of relationships among Korean Liliopsida by conducting analyses of nucleotide sequence data from 18 families containing common members of the Korean monocot flora. 3) confirmation of the transfer of several genera like Disporum, Clintonia, and Streptopus from their affinity to Convallariaceae (Ruscaceae) to other families in Liliales. 4) elucidation of the position of Iridaceae and Nartheciaceae (previously included

within Melanthiaceae s. lat.) in the classification of Korean Liliopsida.

Material and Methods

We studied 18 families containing common members of the Korean flora using *rbc*L and *atp*B sequence data in phylogenetic analyses.

Family Dioscoreaceae was designated as outgroup for our molecular analyses. All data for plastid DNA sequences were taken from the EMBL gene bank (for accession numbers refer to Table 1). Sequence manipulations were performed on a Digital Alpha 1000A 5/400 server under the operating system Digital Unix V.4.0D. DNA sequences were pre-aligned using the PileUp program of the GCG software package (Genetic Computer Group, 1994). Final alignment of DNA sequences was done visually. The sequences have been trimmed on both ends to exclude ambiguous positions in close proximity to the sequencing primers. Phylogenetic analyses using the maximum parsimony (MP) method were performed with the computer program PAUP* version 4.0b10 (Swofford, 2000). MP analyses were performed with and without successive character weighting (rescaled consistency index) until tree lengths remained the same in two successive rounds. Most parsimonious trees were obtained by 1000 replicates of random sequence addition using tree bisection-reconnection (TBR) branch swapping under the Fitch criterion (Fitch, 1971). Ten thousand fast bootstrap replicates (Felsenstein, 1985) were used to assess confidence limits for the resulting tree topologies. Tree manipulations were performed using MacClade version 3.06 (Maddison and Maddison, 1993)

Results

Phylogenetic analysis of *rbcL* data: Maximum parsimony analysis of *rbcL* data yielded thirteen different strictconsensus trees with a weighted tree length of 336.51612, a consistency index (CI) of 0.797, a retention index (RI) of 0.904, a rescaled consistency index (RC) of 0.720, and a homoplasy index (HI) of 0.203. Differences in tree topologies among the trees were restricted to minor rearrangements within family Ruscaceae but did not change relationships among families and orders. Since tree topologies remained similar both in the unweighted and successively weighted trees, only successively weighted trees are shown, because bootstrap values tended to be higher in those trees. One of

Table 1. Taxa Examined for molecular analysis.

	Cronquist's System	Reference for System	Species	$\mathit{rbc}L$	at pB
Dioscoreales					
Dioscoreaceae	Dioscoreaceae	Dahlgren et al. 1985	Dioscorea bulbifera		AF187059
	*Dioscorea		Dioscorea japonica	AF307457	
			Dioscorea tenuipes	AB017340	
Liliales					
Liliaceae	Liliaceae	Huber 1969	Lilium superbum	AB034926	AF209618
	*Lilium	Dahlgren et al. 1985	Lilium japonicum		AB034921
	*Erythronium	Tamura 1995	Erythronium japonicum	D28156	
	*Tulipa		Tulipa kolpakowskiana		AJ235633
			Tulipa turkestanica	AB037378	
	${}^*\!Fritillaria$		Fritillaria koidzumiana	AB034939	
	*L loydia		Lloydia serotina	AJ235523	
	*Clintonia		Clintonia udensis	AB034750	
			Clintonia borealis	AB056856	
	*Gagea		Gagea lutea	AB034752	
Melanthiaceae	*Veratrum	Tamura 1995	Veratrum viride		AJ235638
		Chase et al. 1995	Veratrum maackii	AB018849	
	*Heloniopsis		Heloniopsis orientalis	AJ417894	AJ417583
Nartheciaceae	*Aletris	Ambrose 1980	Aletris farinosa		AF308040
	*Metanarthecium		Metanarthecium luteo-viride		AF308041
	$^*To fieldia$		Tofieldia calyculata		AJ235627
Calochortaceae	*Tricyrtis	Tamura 1995	Tricyrtis latifolia		AJ235630
		Chase et al. 1993, 1995	Tricyrtis macrantha	AB034749	
*					
	Streptopus		Streptopus amplexifolius	AF275992	
			Calochortus albus	AF275983	
Trilliaceae	*Trillium	Dahlgren et al. 1985	Trillium erectum		AF209692
		Chase et al. 1995	Trillium ovatum	AB018840	
*					
	Paris		Paris tetraphylla	D28159	AJ417584
Colchicaceae		Shinwari et al. 1994	Colchicum autumnale	AF168895	-
		Chase et al. 1995	Uvularia sessilifolia		AB009948
	*Disporum		Disporum sessile	D17376	
Smilacaceae	*Smilax	Cronquist 1981	Smilax glauca	AF206822	AF209677
Asparagales					
Hostaceae	*Hosta	Rudall et al. 1997	Hosta rectifolia	L10253	
Hemerocalli-	*Hemerocallis	Chase et al. 1993	Hemerocallis		AF168923
daceae			lilioasphodelus		
		Rudall et al. 1996	Hemerocallis fulva	L05036	
Alliaceae	*Allium	Dahlgren et al. 1985	-	AF206731	AF209525
			Allium cepa	AF479574	

Table 1. Continued.

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		Reference for System		rbcL	at pB				
Hyacinthaceae	*Hyacinthus	Speta 1980	Hyacinthus orientalis	AF116995	AF168925				
			Ornithogalum caudatum		AF168935				
	*Scilla		Scilla scilloides	D28161					
Asparagaceae	*Asparagus	Chase et al. 1995	Asparagus officinalis		AJ235400				
			Asparagus cochinchinensis	AB029849					
Ruscaceae	*Aspidistra	-	Aspidistra elatior		A J417575				
		Rudall et al. 2000	Tupistra albiflora	AB029837					
			Tricalistra ochreata	AB029839					
	*Rohdea		Rohdea japonica	AB029836					
			Campylandra sp.	AB029835					
	*Convallaria		Convallaria majalis		AF168897				
			Reineckea carnea	AB029834					
	*Liriope		Liriope muscari	AF168926					
*Ophiopogon			Ophipogon japonicus	AB029841					
			var. <i>japonicus</i>						
	*Smilacina		Smilacina racemosa		AF168945				
			Smilacina hondoensis	D17380					
			Calibanus hookeri		AJ417576				
	*Polygonatum		Polygonatum hookeri		AJ417578				
			Polygonatum humile	AB029828	}				
			Polygonatum involucratum	AB029829					
			Heteropolygonatum pendulum	AB029831					
			Disporopsis longifolia AB029833						
			Peliosanthes grandifolia	AB029845					
Anemarr-	Haemodoraceae	Chase et al. 1995	Anemarrhena		AJ417570				
henaceae	*Anemarrhena		asphodeloides						
Agavaceae	Agavaceae *Agave	Bogler & Simpson 1995	Agave ghiesbreghtii		AF209521				
Amarvllidaceae	_	Meerow et al. 2000	Hitteastrum sp.		AF168924				
Titte y Titte Coc	*Hippeastrum	1,1001011 07 08 2000	Hippeastrum papilio	AF206776					
	111ppeastr with		Hippeastrum papilio	111 200110	AF209598				
	*Crinum		Crinum yemenense	AF116951					
	*Clivia		Clivia nobilis		AF209566				
	*Lycoris		Lycoris sanguinea	AB034753					
	*Narcissus		Narcissus elegans	AF116972					
Iridaceae	Iridaceae	Dahlgren et al. 1985	_	L05037					
	*Iris		Iris forrestii	AJ307083					
	*Gladiolus		Gladiolus buckerveldii						
•	Giuaioius (Cl	·		A1 200772					

^{*}genera present in Korea (Chionographis, Zygadenus, Maianthemum, Yucca, Zephyranthes, Sisyrinchium, and Belamcanda were not analysed).

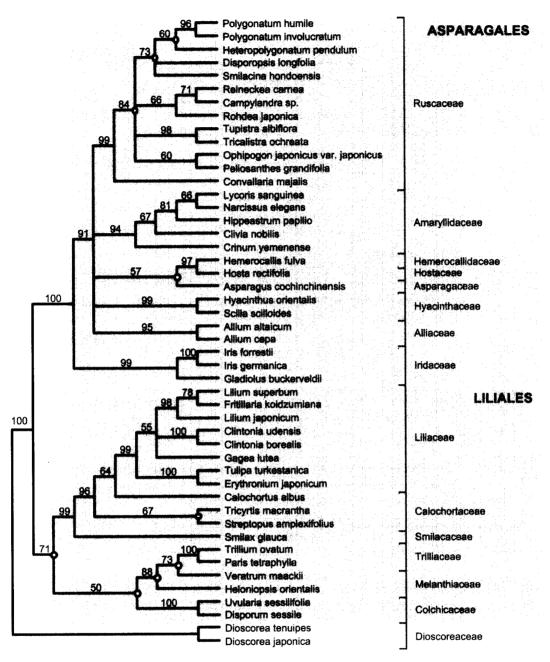


Fig. 1. One of thirteen equally most parsimonious strict consensus trees based on cladistic analysis of *rbc*L data for representative taxa of Liliopsida. Bootstrap values>50% after successive character weighting are indicated above branches. Nodes not present in the wnweighted trees are indicated by open circles.

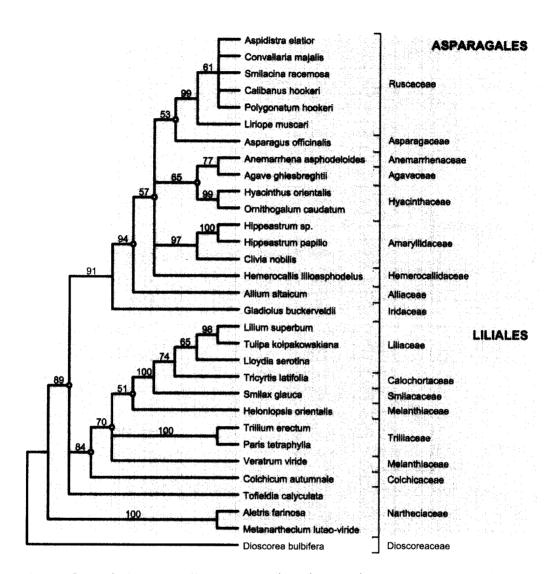


Fig. 2. One of three equally most parsimonious strict consensus trees based on cladistic analysis of *atp*B data for representative taxa of Liliopsida. Bootstrap values>50% after successive character weighting are indicated above branches. Nodes not present in the unweighted trees are indicated by open circles.

the equally parsimonious trees is shown in Fig. 1. Nodes not present in the unweighted trees are indicated by open circles.

In the rbcL tree the order Asparagales formed a highly supported monophyletic

group with the inclusion of Iridaceae (100% bootstrap support) and appeared to be well separated from *Liliales*. Within *Asparagales*, family Ruscaceae was monophyletic (99%). The genera *Disporum*, *Clintonia*, and *Streptopus* (previously included within Convallariaceae), however, were not included within *Asparagales* but formed a clade with members of *Liliales* (Colchicaceae, Liliaceae, and Calochortaceae, respectively).

Phylogenetic analysis of atpB data: Maximum parsimony analysis of atpB data yielded three strict consensus trees with a weighted tree length of 300. 14030, a consistency index (CI) of 0.828, a retention index (RI) of 0.834, a rescaled consistency index (RC) of 0.691, and a homoplasy index (HI) of 0.172. One of the equally most parsimonious trees is shown in Fig. 2. Like in the rbcL analysis, only minor intra-familial differences in topologies were encountered between weighted and unweighted trees in the atpB analysis.

Both Asparagales (91% bootstrap support value) and core Liliales (84% bootstrap support) yielded clearly separated clades. The genera Tofieldia, Aletris and Metanarthecium (Nartheciaceae) formed a paraphyletic assemblage at the base of Liliales. Within Asparagales, Ruscaceae appeared as a well-supported monophyletic group with a high bootstrap value (99%). The genus Gladiolus (family Iridaceae) nested within Asparagales (91% bootstrap support).

Discussion

Most recent treatments (Dahlgren et al. 1985; Takhtajan 1987; Thorne 1992; Kubitzki, 1998) tended to recognize more narrowly defined families. The classification into Liliopsida (instead of Liliflorae sensu Dahlgren et al. (1985); Thorne, 1992) represented an improvement over previous systems because a wide range of characters from many different types of data was considered, whereas earlier concepts often were based on single definitive characters. The broad classifications of Krause (1930), Hutchinson (1934) and Cronquist (1981) were not supported from our results, whereas that of Dahlgren et al. (1985), who recognized numerous smaller families, was reflected in our phylogenetic analyses.

The usage of Acorus (Acoraceae) as outgroup for Korean Liliopsida had been considered in our study, following the suggestion of Chase et al. (1995), but this result gave little resolution for the classification of Korean Liliopsida (data not shown). This might be caused by several big gaps in sampling of taxa for

analysis at higher taxonomical levels. To use family Dioscoreaceae as an outgroup, however, yielded satisfactory resolution for this study.

Although taxon sampling was not the same for both analyses, the tree topologies obtained were highly congruent. All members of *Liliales* and *Asparagales* formed clearly defined clades and most families in the sense of Kubitzki (1998) yielded monophyletic groups. This means that Kubitzkis system, which is characterized by narrow family concepts, should be applicable for the classification of Korean Liliopsida, too.

The results of our cpDNA study provided strong evidence that there were two major lineages in this group of Korean taxa. One lineage contained all Asparagales sensu Dahlgren et al. (1985) plus Iridaceae. Iridaceae were included by Dahlgren et al. (1985) on the basis of their extrose anthers, nonphytomelanous seeds, mottled tepals, and perigonal nectaries within Liliales. close to Colchicaceae. The presence of perigonal nectaries was, however, known to be the derived state in the family, whereas septal nectaries is the ancestral state. Mottled tepals are also derived in Iridaceae and helobial endosperm development appears to be characteristic for lower Iridaceae. Thus the placing on Iridaceae in a narrowly circumscribed Liliales appears to have little support. Molecular gene sequence similarities also support the latter relationship (Rudall et al. 2000). DNA sequences from the chloroplast gene rbcL placed Iridaceae close to, but outside the core taxa of Asparagales, which have phytomelan-incrusted seeds. Despite the absence of phytomelaneous seeds, assignment of Iridaceae to Asparagales must be given serious consideration even on morphological grounds, although overall morphology of Iridaceae appears superficially more similar to that of Liliales than that of Asparagales (Huber, 1969; Dahlgren et al., 1985).

The other major lineage consists of members from Liliales sensu Dahlgren et al. (1985) with the inclusion of Disporum, Clintonia, and Streptopus. In the cpDNA sequence data, family Nartheciaceae appeared paraphyletic and basal to Aspagagales and Liliales. Melanthiaceae s. lat. was suggested as a different order (Dahlgren et al., 1985) and a sister group for the remaining monocotyledons (Rudall et al., 2000). Some genera formerly included in Melanthiaceae s. lat., such as Tofieldia, Narthecium and Aletris, were shown to belong to other orders. This reclassification was largely based on the analysis of molecular data from rbcL sequences but was justified by morphological characters (Rudall et al., 2000). Melanthiaceae s. lat share common characters with Asparagales like the

tepals having perigonal nectaries. Tamura (1995) suggested a separation of some genera from Melanthiaceae s. lat. into Nartheciaceae which have large chromosomes in contrast to those of the core Melanthiaceae. Our data strongly support Tamuras (1995) suggestion and agree with Kubitzkis system that classifies members of Melanthiaceae s. lat. into two separate families, Melanthiaceae s. str. and Nartheciaceae. Whereas Melanthiaceae s. str. are clearly included within Liliales, no support for inclusion of Nartheciaceae within Liliales or Asparagales is found in the molecular analyses. This family lacks features typical for either Asparagales or Liliales. It differs from Asparagales in that the seeds are not phytomelanifereous, the tepals are inconspicuous, the stylodial branches are generally separate and the embryos are small. Unlike in Liliales, the endosperm formation is helobial in Nartheciaceae (Melanthiaceae s. lat.) and septal nectaries may be lacking. The tepals are less conspicuous and rarely spotted (characteristic for Liliales) and raphides are generally present (Dahlgren and Clifford, 1982).

According to our atpB sequence analysis, genus Tofieldia seems to be only distantly related to the other two genera Aletris and Metanarthecium. Therefore, Nartheciaceae could be subdivided into the two subfamilies Tofieldioideae and Narthecioideae as already suggested (Conran and Tamura, 1998). Ambrose (1980) undertook a numerical analysis of morphological characters of Melanthiaceae s. lat. and revealed three main clusters: (1) the Tofieldia group, (2) the Narthecium group, and (3) the Melanthium group. Chase et al. (1995) recognised similar groupings based on a parsimony analysis of rbcL sequences: (1) Pleea and Tofieldia, (2) Aletris (including Metanarthecium) and the Melanthiaceae s. str. including genera such as Heloniopsis, Zigadenus, and Veratrum. Nartheciaceae in the present circumscription contain group 1 and group 2 of Ambrose (1980) and Chase et al. (1995); group 1 corresponds to subfamily Tofieldioideae and group 2 to subfamily Narthecioideae in the classification of Conran and Tamura (1998).

One of the most consistent synapomorphies for *Liliales* is the presence of mainly three-traced tepals. It effectively distinguishes the net-veined lilioid taxa (e.g. *Disporum*, *Clintonia*, and *Streptopus*) from the net-veined asparagoids (e.g. *Convallaria*, *Polygonatum*, *Maianthemum*, and *Smilacina*), which have generally one-traced tepals (Vaikos *et al.*, 1989). Bjornstad (1970) pointed out that *Disporum* and *Clintonia* (previously referred to as members of Convallariaceae) show better agreement with Uvulariaceae, Colchiaceae, and Liliaceae. Dahlgren

et al. (1985) and Conran (1989) removed Disporum, Clintonia, and Streptopus from Convallariaceae and treated these genera as members of Colchicaceae, Liliaceae, and Calochortaceae, respectively. Although the rbcL studies of Shinwari et al. (1994) focused only on the berry-fruited taxa of Polygonatae including Disporum, Clintonia, and Streptopus, this transfer is supported by karyological data (Tamura, 1995) and molecular evidence (Chase et al., 1995; Wu et al., 2000).

Conclusions

The data suggest that the concept of Liliopsida as proposed by Cronquist (1981) is less accurate than that proposed by Dahlgren *et al.* (1985). According to this result, the revised Kubitzkis system based on Dahlgren *et al.* should be applied for the classification of Korean Liliopsida. Although the sampling of Korean taxa should be increased in future studies, we suggest the following list of families for Korean Liliopsida.

Liliales; Liliaceae (including Lilium, Erythronium, Tulipa, Fritillaria, Lloydia, Clintonia, and Gagea), Melanthiaceae s. str. (including Veratrum, Heloniopsis, Zygadenus, Chionographis), Nartheciaceae (Subfam. Narthecioideae (Aletris, Metanarthecium), Subfam. Tofieldioideae (Tofieldia), Calochortaceae (including Tricyrtis, Streptopus), Trilliaceae (including Trillium, Paris), Colchicaceae (including Disporum), Smilacaceae (including Smilax).

Asparagales; Hostaceae (including Hosta), Hemerocallidaceae (including Hemerocallis), Alliaceae (including Allium), Hyacinthaceae (including Hyacinthus, Scilla), Asparagaceae (including Asparagus), Ruscaceae (including Aspidistra, Rohdea, Convallaria, Liriope, Ophiopogon, Smilacina, Maianthemum, Polygonatum), Anemarrhenaceae (including Anemarrhena), Agavaceae (including Agave, Yucca), Amaryllidaceae (including Zephyranthes, Hippeastrum, Crinum, Clivia, Gladiolus, Lycoris, Narcissus), Iridaceae (including Iris, Sisyrinchium, Belamcanda, Gladiolus).

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한국산 비짜루목 및 백합목(백합강)에 대한 분류학적 재검토

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적 유

분자생물학적 자료에 의한 한국산 백합강 식물에 대한 분류학적 재검토를 시도하였다. 2가지의다른 자료, 즉 엽록체 DNA인 rbcL 및 atpB sequence 자료분석에서 대체적으로 일치하는 계통수를 얻었다. 즉, 한국산 백합강은 Dahlgren 등의 분류체계에 의한 비짜루목, 백합목, 마목의 3목으로 구분되었다. 이중 비짜루목과 백합목의 유연관계를 추론하는 분자생물학적 연구에서 마목의 분류군이 군외분류군으로 사용되었다. 두 엽록체 DNA인 rbcL 및 atpB sequence 분석에서 붓꽃과는 백합과 보다는 비짜루과에 더 가까운 유연관계를 보여주었다. 그러나, 넓은 의미의 Narthecaceae (종전의 Melanthiaceae [국명부재]에 속한 분류군)는 비짜루목이나 백합목에 속하는 분류군들과 가까운 유연관계를 보이지 않았다. 이전의 은방울꽃과 [Ruscaceae] 내에 취급되었던 애기나리속, 나도옥잠화속, 죽대아재비속 등은 각각 Colchiaceae, 백합과, Calochortaceae로 이전 되어야 한다는 결론이 내려졌다. 마지막으로 한국산 백합강에 속하는 과의 체계에 대해서 토의하였다.

주요어: 한국산 백합강, 분자생물학적 자료, 비짜루목, 백합목

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