

The cytogeography of *Aster ageratoides* var. *laticorymbus* (Asteraceae), a polyploid complex endemic to China

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Abstract. *Aster ageratoides* var. *laticorymbus* is distributed from southwestern China to eastern China. Population sampling across its whole distribution area was made in its twenty-six populations. Chromosome numbers of all the populations were investigated, and six populations, representative of various ploidy levels, were analyzed karyotypically for the first time. The results show that this variety is a polyploid complex comprised of 2x, 4x and 6x. The populations are mostly hexaploid ($2n = 6x = 54$) and occupy an extensive area from southwestern China to eastern China while the diploid ($2n = 2x = 18$) and the tetraploid ($2n = 4x = 36$) are less frequent and limited to narrower regions of the Yunnan-Guizhou Plateau and the transitional belts from the plateau to adjacent areas. Based on the cytogeographical distribution of the complex, the analysis of its karyotypes, its morphological variations related to geography and a previous report, some hypothesis are made: (1) the polyploids of the complex might be autopolyploids, and the tetraploid might have originated independently twice; (2) in terms of some karyotypical parameters, different ploidy levels of the complex evolved at different speeds; (3) the Yunnan-Guizhou Plateau is the diversity center and the origin center of the complex, and the place from which the hexaploid dispersed eastwards to eastern China; (4) the distribution pattern that the hexaploid is dominating might have been formed by the competitive exclusion and its high capability to disperse and occupy new habits; and (5) the variety is a relative young complex.

Keywords: *Aster ageratoides* var. *laticorymbus*; Dispersal route; Distribution pattern; Karyotype; Polyploid complex; Yunnan-Guizhou Plateau.

Introduction

Aster ageratoides Turcz., a perennial herb of Asteraceae (Compositae), is widely distributed from northeastern Asia to southeastern Asia, but with its major diversity center in China (Ling and Chen, 1985; Li, 2002). This species has a complex taxonomic history and is reputed to be a difficult taxonomical subject (Huziwara, 1957; Ling and Chen, 1985; Ito and Soejima, 1995; Soejima and Peng, 1998; Soejima et al., 1999; Li, 2002). According to Ling and Chen (1985), it comprises 11 varieties in China. However, the taxonomic status of these taxa is quite controversial, and some are very difficult to distinguish from each other (Ling and Chen, 1985; Soejima et al., 1999; Li, 2002). The taxonomic confusion in this difficult species comes from the fact that very little is known of its diversity and variation in morphology and cytology (Soejima et al., 1999; Li, 2002).

Aster ageratoides var. *laticorymbus* (Vant.) Hand.-Mazz. is endemic to China (Handel-Mazzetti, 1938; Ling and Chen, 1985; Li, 2002). It is characterized by poly-branched stem, oblong-lanceolate or ovate-lanceolate middle leaves, narrow phyllaries with green top, and white ray florets, the narrow phyllaries being the most important diagnostic character (Handel-Mazzetti, 1938; Ling and Chen, 1985; Soejima et al., 1999). This variety is of eco-

logical importance due to its participation in the revegetation of degraded or newly open habitats (Li, 2002). Chen et al. (1992a, 1992b) reported for the first time that the variety *laticorymbus* has two cytotypes ($4x = 36$; $6x = 54$) in Hunan Province and Guangxi Province. Unfortunately, mistakes in identifying specimens impaired the excellence of their work (Li, 2002). The only other report of cytology of the variety was from Soejima et al. (1999), who documented three cytotypes ($2x = 18$; $4x = 36$; $8x = 71, 72$) of this variety in the Zhaotong area, northeastern Yunnan.

While working on biosystematic studies on *Aster ageratoides*, the author made extensive field observations and sampling of 73 native populations in 20 provinces of China between 2000 and 2002. As a part of the work, *A. ageratoides* var. *laticorymbus* was investigated in cytogeography and morphology. This study reports the current distribution pattern of three cytotypes of var. *laticorymbus*, and then discusses its evolution of karyotype, its origin, dispersal route, the formation mechanism of current distribution pattern, and the age of the *A. ageratoides* var. *laticorymbus* complex.

Materials and Methods

Field observations and sampling were made in 73 populations of *Aster ageratoides*, of which 26 populations (Table 1; Figure 1) from 11 provinces belonged to *A. ageratoides* var. *laticorymbus* according to Li (2002). For each population, more than ten plants were transplanted to

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Hunan Normal University for cytological investigations, and the specimen were prepared and deposited as vouchers in the Herbarium of Hunan Normal University (HNNU).

Actively growing root tips were cut for chromosome observations from the living plants, and pretreated with 0.1% colchicine at 8-12°C for 4 h before being fixed in Carnoy I (glacial acetic acid: 95% ethanol = 1:3) at room temperature for 12 h. They were then macerated in 1 mol/L hydrochloric acid at 60°C for 8 min, stained in 5% $\text{NH}_4\text{Fe}(\text{SO}_4)_2$, an intermedia, at room temperature for 3 h, stained in 0.75% hematoxylin for 3 h, washed in distilled water for 30 min, and finally depigmented and squashed in 45% acetic acid. The chromosome number of each population was determined by counting the chromosomes in at least 10 metaphases of every sample. Six populations, representative of different ploidy levels, were analyzed karyotypically, with the karyotype parameters of each population being the average values of ten plants.

The karyotype parameters used in this study included: (1) index of the karyotype asymmetry, that is, $As.k$ (%) ($As.k = \text{the length of all long arms} / \text{the length of all chromosomes} \times 100$); (2) ratio of the longest chromosome to the shortest; (3) average arm radio for each population.

The symbols used to describe the karyotype followed Levan et al. (1964): m = median-centromeric chromosome (arm ratio: 1-1.70), sm = submedian-centromeric chromosome (arm ratio: 1.71-3.00). The karyotype symmetry was classified according to Stebbins (1971).

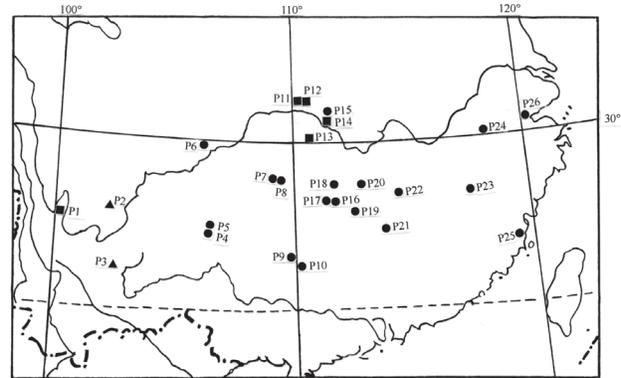


Figure 1. Map showing distribution of 26 sampling populations of the *Aster ageratoides* var. *laticorymbus* complex. Codes for populations correspond to those in Table 1. Triangles (▲) represent diploid populations, squares (■) tetraploid populations, and solid circles (●) hexaploid populations.

Table 1. Sampling locations and ploidy distribution of the *Aster ageratoides* var. *laticorymbus* complex.

Population	Location	Altitude (m)	Longitude	Latitude	Ploidy	Voucher
P1	Yulongxueshan, Lijiang, Yunan; at a deforested site	3,400	100°12'	27°03'	4x	Li00127
P2	Luojishan, Xichang, Sichuan; at forest margins	2,000	102°20'	27°28'	2x	Li00125
P3	Xishan, Kunming, Yunnan; at roadside	2,000-2,100	102°41'	24°50'	2x	Li00126
P4	Qingyan, Guiyang, Guizhou; on sidehill	1,100	106°41'	26°32'	6x	Li00117
P5	Qianlingshan, Guiyang, Guizhou; at roadside and in wood	1,100-1,300	106°42'	26°35'	6x	Li00118
P6	Jinyunshan, Chongqing; at forest margins	500-950	106°22'	29°49'	6x	Li00119
P7	Baiyunshan, Huayuan, Hunan; at top of mountain, and at roadside	1,200	109°18'	28°30'	6x	Li00114
P8	Dehan, Jishou, Hunan; on sidehill	500	109°43'	28°29'	6x	Li00111
P9	Taoshan, Lingui, Guangxi; at forest margins and roadside	800-1,200	109°54'	25°36'	6x	Li01123
P10	Yueyashan, Guilin, Guangxi; at roadside	200	110°11'	25°15'	6x	Li01122
P11	Banbiyan, Shennongjia, Hubei; at top of the mountain, and at roadside	2,100-2,900	110°12'	31°30'	4x	Li00075
P12	Muyu, Shennongjia, Hubei; at forest margins	1,100-1,600	110°23'	31°29'	4x	Li00077
P13	Hupingshan, Shimen, Hunan; at roadside	450	110°40'	30°02'	4x	Li01062
P14	Sanyoudong, Yichang, Hubei; at forest margins	200	111°17'	30°42'	4x	Li01112
P15	Yuanan, Hubei; at roadside	300	111°36'	31°06'	6x	Li01111
P16	Longshan, Lianyuan, Hunan; at top of mountain, and at forest margins	200-1,514	111°42'	27°30'	6x	Li00101
P17	Lianyuan, Hunan; at roadside	130	111°36'	27°42'	6x	Li00102
P18	Furongshan, Anhua, Hunan; at roadside and at forest margins	1,100	111°48'	28°12'	6x	Li01101
P19	Nanyue, Hunan; at forest margins	200-1,200	112°39'	27°15'	6x	Li01125
P20	Yuelushan, Changsha; at forest margins, in woods, and at roadside	100-150	112°46'	28°23'	6x	Li01012
P21	Huangyangjie, Jinggangshan, Jiangxi; at forest margins	1,400	113°50'	26°33'	6x	Li00116
P22	Yichun, Jiangxi; on sidehill	300-400	114°23'	27°49'	6x	Li02121
P23	Wuyishan, Fujian; at roadside	300	117°35'	27°43'	6x	Li01053
P24	Tangkou, Huangshan, Anhui; at forest margins, roadside, stream sides	300-500	118°11'	30°10'	6x	Li01035
P25	Gushan, Fuzhou; at forest margins	200	119°18'	26°05'	6x	Li01052
P26	Longjing, Hangzhou; sidehill, at roadside	50	120°09'	30°14'	6x	Li01032

Results

Presented in Figure 1 and Table 1 are the chromosome numbers of twenty-six populations, which can be divided into three cytotypes: diploid (two populations: P2 and P3) with $2n = 18$, tetraploid (five populations: P1 and P11-P14) with $2n = 36$, hexaploid (nineteen populations: P4-P10 and P15-P26) with $2n = 54$. The diploid was found in the west and the northwest of the distribution area, the tetraploid in the northwest and the middle, and the hexaploid from

106°41' E to the eastern end of the Chinese mainland. Note that elevations decline from the western portion of the range to the eastern (Table 1).

For the six populations (P1-P3, P12, P16, and P20) investigated karyotypically, the micrographs of somatic metaphase chromosomes, karyotypes, and the karyotype parameters are presented in Figure 2 and Table 2. The results show that the metaphase chromosomes vary gradually in length from the longest to the shortest without showing distinct bimodality, and the frequencies of me-

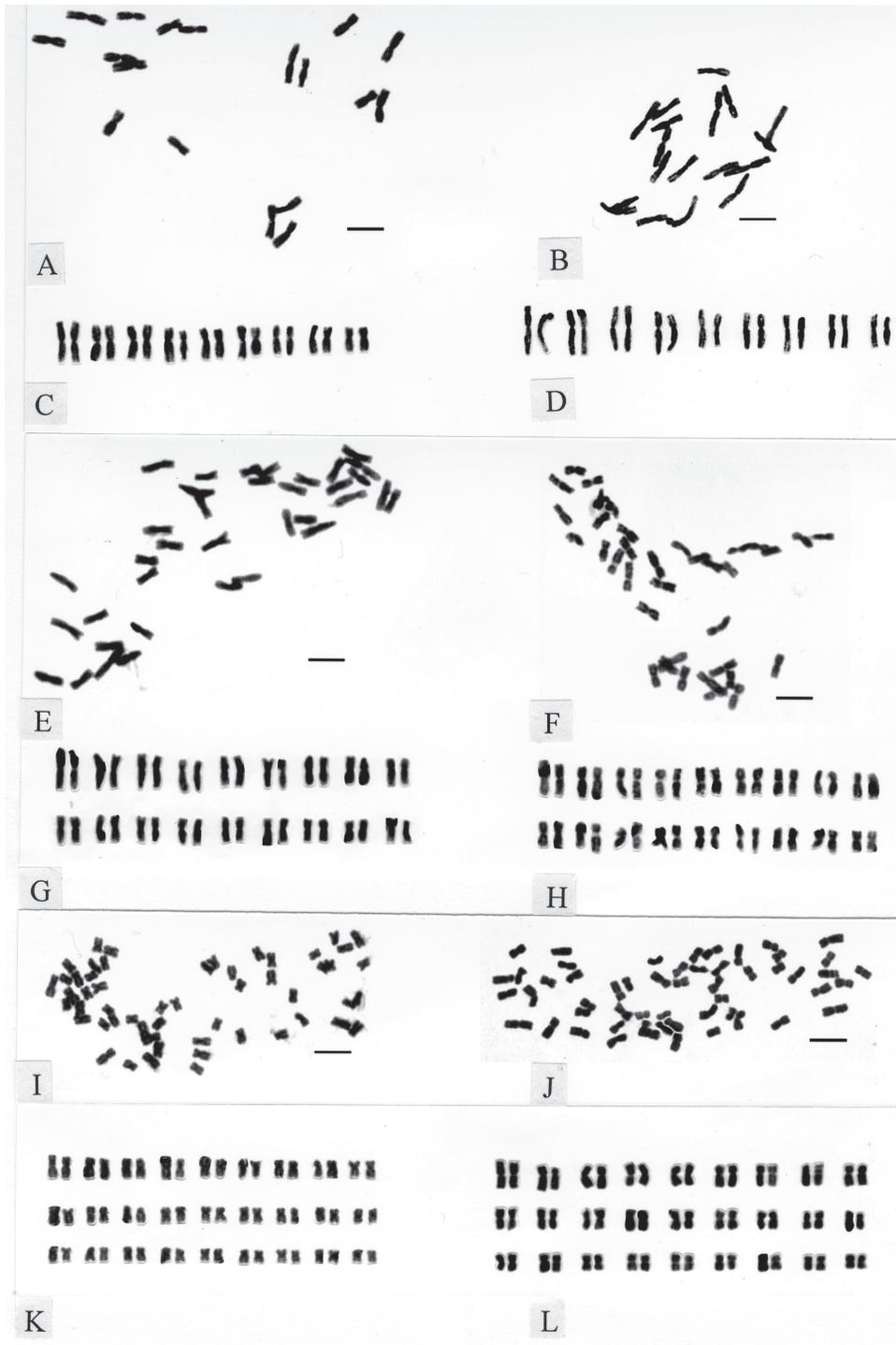


Figure 2. Micrographs of somatic metaphase chromosomes and the karyotypes of *Aster ageratoides* var. *laticorymbus* (Scale bar = 4 μ m). A, C. P2; B, D. P3; E, G. P1; F, H. P12; I, K. P16; J, L. P20 (Codes for populations correspond to those in Table 1).

dian-centromeric chromosomes are high, up to 88.9-100%. The karyotypes of all these six populations are categorized as Stebbin's 1A type because the ratios of the longest and the shortest chromosome are below 2, and no arm ratios are more than 2. Two populations of the same cytotype are largely identified in chromosome parameters while different ploidy levels are significantly different in two parameters (Lt/St and A.A.R) (Table 2). Satellites were found at the terminal region of the short arms of the first pairs only in the two diploid populations (P2, P3) (Figure 2A-D).

Discussion

Karyotype Evolution of the Complex

Since the chromosome base number of *Aster* s.s. is consistently $x = 9$ (Nesom, 1994; Li and Zhang, 2004), the results reveal that *Aster ageratoides* var. *laticorymbus* possesses three cytotypes: $2x$ (18), $4x$ (36), $6x$ (54) (Figure 1, 2; Table 1), suggesting that in the variety there is a polyploid series.

Although two karyotypically studied populations of each ploidy level have the same or similar karyotype formula and karyotype parameters (Table 2), there exist significant morphological differences between two diploid populations (P2 vs P3) and between two kinds of tetraploid populations (P1 vs P11-14). Especially, P2 ($2x$) is quite similar morphologically to P1 ($4x$) and P3 ($2x$) to P11-14 ($4x$). P2 and P1 have lanceolate leaves and relatively small heads with no more than 20 florets (including ray florets and disc florets) while the other populations studied here, including P3, P11-14 as well as all hexaploid populations, possess elliptic or oblong leaves and relatively large heads with usually more than 20 florets. Therefore, it is possible that these tetraploid and hexaploid are autopolyploids derived from ancestors with the same gross morphology but lower ploidy levels. In general, an autopolyploid is defined as a cytotype containing three or more sets of homologous chromosomes. However, neither in the tetraploid nor in the hexaploid, were four sets or six sets of morphologically similar chromosome complements observed, so the karyotype data do not support the hypothesis that they are of autopolyploid origin. This may be attributed to karyotype differentiation among populations of various ploidy levels, especially extensive and rapid chromosomal

restructuring and chromosomal diploidization after autopolyploidization (Soltis and Soltis, 1999; Yang, 2002) instead of an allopolyploid origin.

Soejima et al. (1999) studied var. *laticorymbus* in the Zhaotong area, which belongs to north the Yunnan-Guizhou Plateau and is near to P1 and P2. They found no significant morphological differences among the diploid, the tetraploid, or the octaploid of variety *laticorymbus* with narrower leaves and smaller heads (Soejima et al., 1999), similar to those of P1 and P2. Therefore, in the north Yunnan-Guizhou Plateau and the adjacent areas, tetraploid populations may originate from some diploid population like P2 whereas the other populations studied here, except P1 and P2, share the same morphological characters and may be on the same evolutionary lineage. If this is true, the tetraploid may have originated independently twice, and karyotype similarity between the two diploid populations and between the two tetraploid populations may have resulted from parallel evolution.

According to Table 2, diploid and polyploid demonstrate different evolutionary speeds in two karyotype parameters, Lt/St and A.A.R., which are directly proportional to karyotype asymmetry. Generally, the evolution of karyotype in the genus *Aster* is towards increasing asymmetry (Hong, 1990). The ratios of the longest chromosome to the shortest (Lt/St) are 1.63 and 1.57, respectively, in the two diploid populations (P2 and P3) while the values are 1.73 and 1.74 in the tetraploid, and up to 1.85 and 1.92 in the hexaploid, showing polyploidization may facilitate size differentiation among non-homologous chromosomes of a genome. In contrast, the average arm ratio is 1.38 in the two diploid populations, and it is 1.25 and 1.26 in the two tetraploid populations and 1.29 and 1.33 in the two hexaploid populations, showing higher length differentiation between the two arms of a chromosome in the diploid populations than in the polyploid populations (Table 2). However, no significant difference appears between the diploid and the tetraploid in As.k (%) or between the Ls/Lt values of *Mikania micrantha* H. B. K. (Asteraceae) and the Ls/Lt values of *Tripleurospermum caucasicum* (Willd.) Hayek (Asteraceae). Based on the data from Maffei et al. (1999) and Inceer and Beyazoglu (2004), I calculated the As.k (%) and Ls/Lt values of *M. micranthae* and the Ls/Lt values of *T. caucasicum* (Willd.) Hayek. I found that the values of As.k (%) were similar among the seven dip-

Table 2. The karyotype parameters of six populations of the *Aster ageratoides* var. *laticorymbus* complex.

Populations	Karyotype formula	As.K (%)	Lt / St	A. A. R	Type
P1	$2n = 4x = 36 = 34 m + 2 sm$	55.24	1.74	1.26	1A
P2	$2n = 2x = 18 = 16 m (2SAT) + 2 sm$	57.14	1.63	1.38	1A
P3	$2n = 2x = 18 = 16 m (2SAT) + 2 sm$	57.38	1.57	1.38	1A
P12	$2n = 4x = 36 = 36 m$	55.49	1.73	1.25	1A
P16	$2n = 6x = 54 = 48 m + 6 sm$	56.68	1.92	1.33	1A
P20	$2n = 6x = 54 = 50 m + 4 sm$	56.16	1.85	1.29	1A

As.k (%): Index of the karyotype asymmetry; Lt: Length of the longest chromosome; St: Length of the shortest chromosome; A. A. R.: Average arm ratio.

loid populations (ranging from 60.23 to 63.76) and the four tetraploid populations (ranging from 61.83 to 63.55) of *M. micranthae*. In *M. micrantha* the Ls/Lt values (3.1-3.9) of the four tetraploid populations were less than the variation range (3.2-5.0) of the seven diploid populations while the values were identical largely between the one diploid population (1.78) and two tetraploid populations (1.77 and 1.91, respectively) of *T. caucasicum*. Therefore, compared with these plants of Asteraceae, *A. ageratoides* var. *laticorymbus* is unique and notable in the karyotypical differences between the diploid and the polyploid.

In order to further test the above hypotheses, it is necessary to make karyotypic investigation and gather molecular evidence (including chloroplast DNA data) in more populations of the complex, especially in the Yunnan-Guizhou Plateau.

The Distribution Center and the Dispersal Route of the Complex

The Yunnan-Guizhou Plateau, belonging to southwestern China and covering 500,000 square km, comprises eastern Yunnan Province and most parts of Guizhou Province. It has an elevation of 1,000 to 2,000 meters and a terrain that descends from northwest to southeast. The plateau is covered with numerous mountain ridges, valleys and other rugged landforms. Yunnan-Guizhou Plateau plus Sichuan Province might have been an important center of development for angiosperms in the Northern Hemisphere during the Middle Cretaceous, and a strong evolutionary radiation might have taken place there, which resulted in the formation of many migration routes from this center to various regions in various directions (Wang, 1992a).

All ploidy levels of var. *laticorymbus* can be found in the Yunnan-Guizhou Plateau. The diploid occurs in the west (P3) and the north (P2; Soejima et al., 1999) of the plateau, the tetraploid and the octaploid in the north (Soejima et al., 1999), and the hexaploid in the center (P4 and P5). Moreover, the other tetraploid populations (P1 and P11-14) are located in the transitional zones from the plateau, the second step of Chinese topography, to the first step (P1) and to the third step (P11-P14). Only hexaploid extends far away from the plateau, arriving at eastern China. Therefore, the Yunnan-Guizhou Plateau can be regarded as the diversity center and the distribution center of the complex and might be its original center.

Because there is only one hexaploid in eastern China (Figure 1), it is reasonable to conclude that it originated in Yunnan-Guizhou Plateau and then from there dispersed eastwards to eastern China, forming a long and narrow distribution region (Figure 1). This conclusion is supported by morphology of the variety. The middle phyllary width of the hexaploid (P4-5) in Yunnan-Guizhou Plateau is 0.95-1.25 mm, identical with that of P1-P3, and the middle phyllaries of the hexaploid become wider and wider gradually from western populations (0.95-1.25 mm wide in P4-5) to middle longitude populations (e.g., 1.0-1.5 mm wide in P16 and P20) and to eastern populations (e.g., 1.35-1.60 mm wide in P24), showing a clinal variation along a longitudinal gra-

dent and a migration route of the hexaploid from Yunnan-Guizhou Plateau to eastern China. This migration route is consistent with "Pattern II" of migration routes described by Wang (1992a). Some taxa such as *Tetrastigma hemsleyanum* Dieks et Gilg (Vitaceae) were considered to have originated in southwestern China and then have migrated eastwards to eastern China, belonging to the "Pattern II" in migration routes (Wang, 1992a). However, Wang (1992b) divided the migration route of *Aster ageratoides* into "Pattern IIiv", that is, "From Southwest China to Siberia or /and adjacent regions." In fact, *Aster ageratoides* is so complex geographically that no simple pattern can be used to describe its migration. It is more useful to pay attention to the geography of each variety of this species.

Formation Mechanism of the Distribution Pattern

Figure 1 shows that in the whole distribution region of the complex, the diploid and the tetraploid seem to be on the decline while the hexaploid is dominant in distribution. Two factors might have contributed to shaping such a distribution pattern. First, competitive exclusion may explain the phenomenon that the hexaploid and the diploid or tetraploid are never sympatric. All ploidy levels usually occur in partially shaded places such as at forest margins and roadsides (Table 1), and are apt to form aggregative distribution owing to well-developed clonal growth via rhizomes (Li, 2002), indicating that different ploidy levels share very similar ecological needs. Thus, it is possible that an intensive competition rages among different ploidy plants of the complex if they are sympatric. Although autopolyploid evolution was viewed as maladaptive, molecular data have revealed three important genetic attributes of autopolyploids compared to their diploid progenitors: enzyme multiplicity, increased heterozygosity, and increased allelic diversity, leading to the potential success of autopolyploids in nature (Soltis and Soltis, 1995). Thus, autopolyploidization might have made the hexaploids of the complex more competitive so that the diploid populations and tetraploid populations went extinct when they were sympatric with the hexaploid. As a result, the diploid and the tetraploid gradually decreased when the hexaploid increased in population number. Secondly, it has long been held that a polyploid has the ability to colonize a wider range of habitats. Additionally, with a well-developed pappus the hexaploid of the variety *laticorymbus* disperses easily to a new habitat. It holds an advantage over many other sympatric species because of its vigorous clonal growth or vegetative reproduction with horizontal rhizomes. Furthermore, well-developed clonal growth facilitates the spread of the variety with self-incompatibility (Li, 2002) when only one or a small quantity of the plants arrive at a new site. In fact, the hexaploid usually dominates the herbaceous layer where it occurs (Li, 2002). In contrast, its two closely related taxa with no horizontal rhizomes, *Aster ageratoides* var. *micranthus* Ling and *A. shennongjiaensis* W. P. Li et Z. G. Zhang, are narrow taxa or even dangerous species (Li, 2002; Li and Zhang, 2004).

The Age of the Polyploid Complex

The present distribution pattern of the variety suggests that it represents a mature polyploid complex. In the 26 populations of var. *laticorymbus* sampled, only two are diploid, four are tetraploid, and the other twenty, representing 76.9% of all populations are hexaploid. The hexaploid occupies a large longitude range from 106°41' E to 120°09' E, especially exclusively from 111°36' E to 120°09' E while the diploid and the tetraploid occupy much narrower areas (Figure 1). The fact that the hexaploid dominates the distribution range of the complex seems to suggest that the complex has developed fully and arrived at a mature phase in the sense of Hong (1990).

The variety may remain a relatively young complex. First, in the Shonongjia area two populations were sampled, of which P12 was located at 1,100 m to 1,600 m alt, and P11 occurred at 2,100-2,990 m alt., occupying mainly the mountain summit where forests are similar to those of the other sites. The population P11 is characterized by consistently sessile, oblong leaves, and depending too much on the alpine conditions to live longer than a year in the garden of HNNU after they were transplanted three times while the plants from P12 and other populations can live longer after transplantation (Li, 2002). Such a unique population is distinguished morphologically and ecophysiologically from other populations and has not been found in other nearby mountains, suggesting this population differentiated in situ from P12 and has not begun to disperse. Therefore, the tetraploid is still in evolution.

Secondly, hexaploid is restricted within a relatively narrow middle latitude region from approximately 25° N to 31° N while there are no *Aster ageratoides* var. *laticorymbus* north of 31° N and south of 25° N according to my field sampling and my study of specimens in 14 herbaria (PE, WUK, SZ, CDBI, HNNU, KUN, IBSC, IBK, NAS, HGAS, CCNU, HIB, HIMC, and FUS) and *Flora Reipublicae Popularis Sinicae* (Ling and Chen, 1985). With well-developed pappus, the variety dispersed quickly eastward from Yunan-Gizhou Plateau along middle latitude because humidity and temperature conditions are similar at the similar latitude. It is very likely that the variety will continue expanding its latitudinal range.

Thirdly, in the Longshan, Furong and Nanyue Mountains, of Central China, the hexaploid populations (P16, P18 and P19) reach the mountain summits with altitudes of 1,514 m, 1,300 m, and 1,289 m, respectively, while the hexaploid population (P24) is restricted below 500 m alt. in Huangshan Mountain with the peak of 1,864 m, which is situated in East China. Such a difference may be interpreted as a possibility that the hexaploid arrived at Huangshan Mountain not long ago and has a potential to expand upwards in the future.

In a word, it is reasonable to conclude that *Aster ageratoides* var. *laticorymbus* is, though the hexaploid is dominated, a relatively young polyploid complex, for the tetraploid remains in evolution. The hexaploid has not

reached its greatest latitude extension and in eastern China has not reach its greatest altitude range.

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中國特有植物寬傘三脈紫菀的細胞地理學

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寬傘三脈紫菀分佈於華西南至華東地區。在其整個分佈範圍內，對 26 個野生居群進行取樣和染色體計數。本文還首次對分別代表 3 種細胞型的 6 個居群進行了核型分析。結果顯示，該變種是一個具有 3 種細胞型 ($2x$ ， $4x$ 和 $6x$) 的多倍體複合體，其中以六倍體 ($2n = 6x = 54$) 為主。六倍體廣布於華西南至華東地區，而二倍體 ($2n = 2x = 18$) 和四倍體 ($2n = 4x = 36$) 較為少見，分佈限於雲貴高原的局部地區及其臨近地區。基於該複合體的細胞地理分佈、核型分析、與地理分佈有關的形態變異以及先前的一則報導，作者提出以下建議：(1) 該複合體的多倍體可能是同源多倍體，並且四倍體兩次獨立起源；(2) 從某些核型參數來看，不同倍性的細胞型進化速度有差異；(3) 雲貴高原是該複合體的多樣性中心和起源中心。該複合體的擴散路線是從雲貴高原擴散到華東地區；(4) 以六倍體為主的分佈模式的形成可能歸因於競爭排斥和六倍體高度的擴散能力及佔領新生境的能力；(5) 該變種是一較為年輕的複合體。

關鍵詞：寬傘三脈紫菀；擴散路線；分佈模式；核型；多倍體複合體；雲貴高原。