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Distribution of Sexual and Agamospermous Populations of *Eupatorium* (Compositae) in Asia

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Abstract Examinations of chromosome number voucher specimens show that sexual diploid and agamospermous polyploid plants of *Eupatorium* in Asia can be distinguished by morphology, fertility, and stainability of pollen grains. Using these criteria, reproductive systems (sexual vs. agamospermous) were estimated for 558 herbarium specimens of *Eupatorium* in East Asia. Of 22 taxa examined, six included both sexual and agamospermous specimens; those of one taxon were all agamospermous; and those of 15 taxa were all sexual. This result shows that 21 taxa are not agamospermous microspecies but are differentiated at the diploid level. Sexual populations of most taxa had restricted geographical distributions. *Eupatorium chinense* var. *chinense* and var. *oppositifolium* consisted of both sexual and agamospermous populations. Sexual populations of these two varieties were allopatric and distinct in external morphology, suggesting differentiation at the species level. The specimens of *E. heterophyllum* s. str. were all agamospermous, while those of *E. mairei*, often treated as synonymous with *E. heterophyllum*, were sexual.

In comparing East Asian and North American *Eupatorium* for the distributional patterns of sexual and agamospermous populations, three differences can be pointed out: (1) Agamospermous plants of autopolyploid origin have evolved in eight species and are widespread in North America; while most agamospermous plants in East Asia may be of allopolyploid origin, have relatively restricted ranges, and are less frequent than the diploid plants with the exception of in *E. chinense* var. *oppositifolium*. (2) The number of sexual species with wide range is greater in North America than in East Asia. (3) The number of sexual species with restricted ranges is greater in East Asia than in North America. The results obtained suggest that speciation among the plants of *Eupatorium* has occurred more recently in East Asia than in North America.

The genus *Eupatorium* L. occurs in the northern hemisphere and has centers of diversity in eastern North America and in East Asia (King and Robinson, 1970, 1987). In both regions, several agamic complexes have evolved, in which agamospermy, polyploidy, and hybridization have contributed to taxonomic complexity (Sullivan, 1976, 1978; Watanabe, 1986). Consequently, to elucidate species taxonomy of *Eupatorium*, studies of ploidy level and reproductive system (sexual vs. agamospermous) for each species are of primary importance. For American species, Sullivan (1976, 1978) conducted extensive studies of chromosome number and reproductive systems, and her observations as well as previously reported cytological observations resulted in recognition of 23 species which are exclusively sexual diploids or include both sexual diploids and agamospermous polyploids (Watanabe, 1986). In contrast to American species, taxonomic delimitation of most Asian species still remains uncertain, partly due to the scarcity of cytological information. Recently, chromosome numbers and reproductive systems in certain Japanese species have been examined (Watanabe et al., 1982; Watanabe and Yahara, 1984; Watanabe, 1986) which have contributed to a revised taxonomic delimitation of certain Japanese species (Kawahara et al., 1989). In Taiwan and Thailand, chromosome counts have been made for some species (Peng and Hsu, 1978; Watanabe, 1986), but reproduction has not been examined. To revise Asian *Eupatorium*, it is necessary to examine chromosome numbers and reproductive systems throughout the entire region.

Reproductive systems can be determined from herbarium specimens because agamospermous plants of North American *Eupatorium* are polyploid and have been found to be male-sterile or to produce abnormal-appearing pollen grains (Sullivan, 1976). In contrast, sexual diploids are male-fertile. Except for very few angiosperms, agamospermous reproduction is correlated with polyploidy (Grant, 1981; Nogler, 1984). The differences in pollen quality between sexual and agamospermous *Eupatorium* have been successfully used to estimate the distribution of sexual and agamospermous populations in American *Eupatorium* (Sullivan, 1976, 1978), Asian *Taraxacum* (Morita, 1976, 1980), and Asian *Boehmeria* (Yahara, 1986) etc. This method is expected to be particularly useful for estimating reproductive systems for species of *Eupatorium* on the Asian Continent, including China where living materials for direct cytological observations are difficult to obtain.

As a step toward a full revision of Asian *Eupatorium*, this paper documents observations on reproductive systems and geographical distribution for a total of 558 herbarium specimens from *Eupatorium* in East Asia.

Materials and Methods

Plant materials used were (1) the chromosome number voucher specimens of *E. chinense* var. *oppositifolium*, *E. glehni*, and *E. lindleyanum* examined by Watanabe et al. (1982), Watanabe and Yahara (1984), Watanabe (1986, unpubl.), and Kawahara (unpubl.) housed in the Herbarium of the Faculty of General Education, Kobe University, and the Herbarium, Botanical Gardens, University of Tokyo (TI) and (2) specimens in the herbaria of A, E, GH, KUN, KYO, MAK, PE, TI, and TU, whose chromosome numbers are unknown.

In *Eupatorium*, sexual plants have always been found to be diploid whereas agamospermous specimens were polyploid (Sullivan, 1976, 1978; Watanabe, 1986). To establish criteria for distinguishing sexual and agamospermous plants, pollen morphology and its stainability were compared in diploid and polyploid vouchers. One or two flower buds were taken from each specimen and soaked in a 1% ethanol solution at 90°C for a few minutes. Subsequently pollen grains were dissected from the anthers on a glass slide under a binocular microscope and stained with 2% acetocarmine. The diameters of five pollen grains from each specimen were measured along the long axis under a light microscope. The mean, standard deviation, and coefficient of variation of pollen diameter were calculated. Differences in means, standard deviations, and coefficients of variation between diploid and polyploid voucher specimens were statistically examined using the modified *t*-test for unequal variance using t calculated by the formula

$$t=(x_1-x_2)/\sqrt{(s_1^2/n_1+s_2^2/n_2)},$$

where x_1 and x_2 are sample means, s_1^2 and s_2^2 are sample variances, and n_1 and n_2 are sample sizes of *Group 1* and *Group 2*, respectively; degrees of freedom were calculated by Satterthwaite's method (SAS Institute Inc., 1985). These calculations were done using the SAS package version 5 from the Computer Centre, University of Tokyo. Pollen stainability was calculated as percentage of more than 100 grains.

Reproductive system type (sexual vs. agamospermous) was estimated for 558 herbarium specimens based on the criteria obtained from the above observation. We excluded specimens obviously intermediate between two taxa and/or those difficult to identify. For controversial species, we adopted the narrowest taxonomic concepts; e.g., we consider the species *E. melanadenium*, *E. tozanense*, and *E. glehni* and not the complex species, *E. chinense*, which could include them.

Results and Taxonomical Notes

1. *Observations on Chromosome Number Vouchers*

Diploid specimens of all three species examined, *E. chinense* var. *oppositifolium*, *E. glehni*, and *E. lindleyanum*, had tricolporate pollen grains, but polyploid specimens had some (often numerous) irregularly shaped pollen grains (Fig. 1). Some polyploid specimens had no or only a few pollen grains. Diploids were significantly different from polyploids in mean, standard deviation, and coefficient of variation (Fig. 2). Means of mean pollen grain size are 20.3 μm for diploid specimens and 29.8 μm for polyploid specimens ($P<0.001$); means of standard deviation of pollen grain were significantly different, with 0.6 μm for diploids and 2.4 μm for polyploids ($P<0.001$); means of coefficient of variation are 0.030 for diploids and 0.080 for polyploids ($P<$

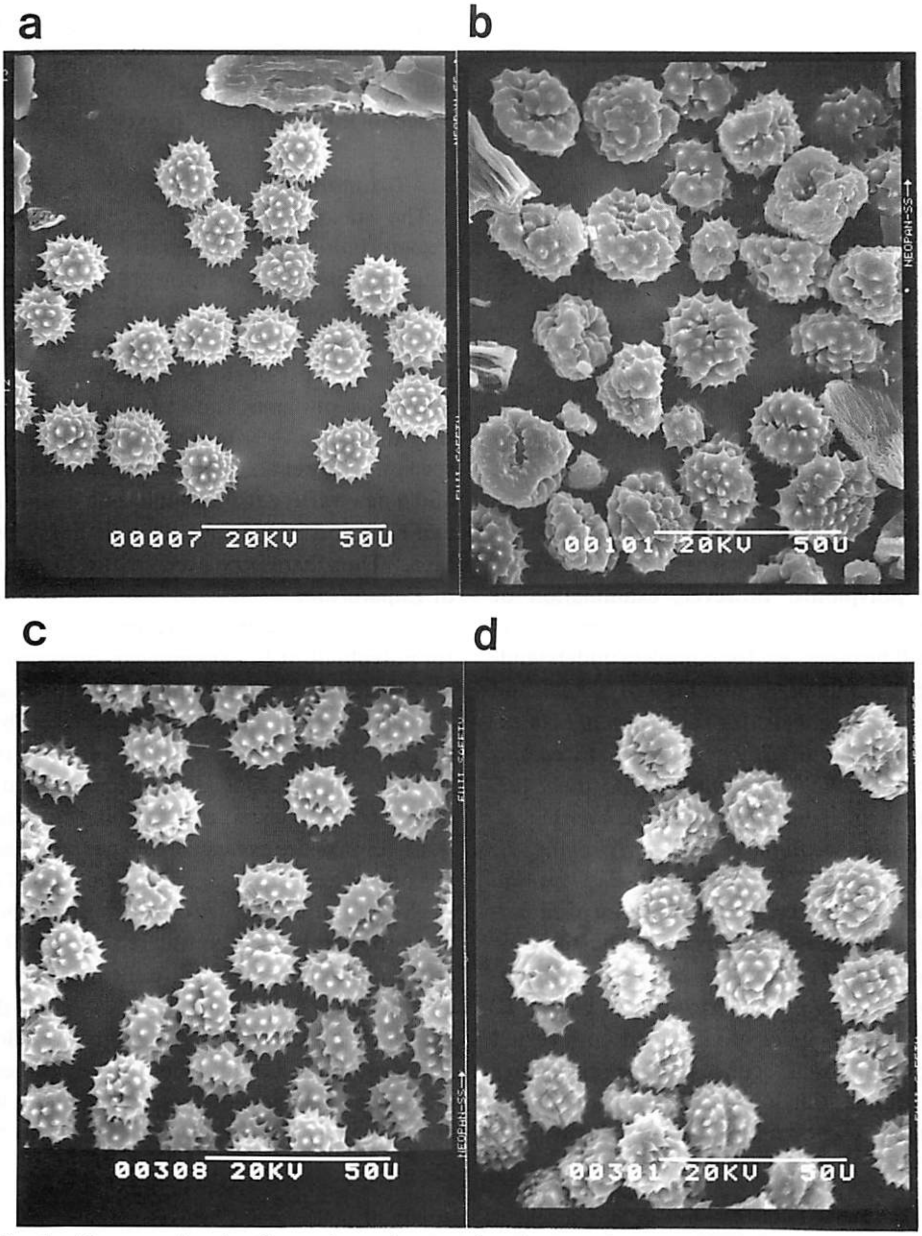

Fig. 1. Photographs of pollen grains under scanning electron microscopy. a, Diploid *E. chinense* var. *oppositifolium*; b, tetraploid *E. chinense* var. *oppositifolium*; c, diploid *E. lindleyanum*; d, triploid *E. lindleyanum*.

0.001). Pollen stainability for diploid specimens varied between 94.7% and 100.0% (mean, 99.1%), while that of polyploid specimens ranged from 5.5 to 99.8% (mean, 73.9%) but was mostly lower than 95%. The diagnostic differences between sexual diploids and agamospermous polyploids are presence or absence of unstained pollen grains smaller than 16 μm and presence of significantly larger grains in polyploid specimens.

These observations provided the criteria by which sexual diploids and agamospermous polyploids can be distinguished (Table 1).

2. *Estimated Distribution of Sexual and Agamospermous Populations*

The criteria in Table 1 enabled us to estimate the reproductive system for most specimens except 13 of *E. fortunei* var. *fortunei* from China. In these 13

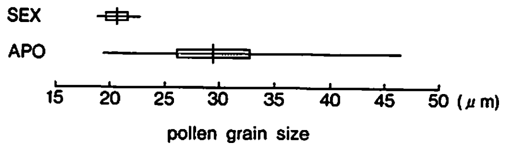

Fig. 2. Ranges, means and standard deviations of mean pollen size of each specimen for sexual diploids and agamospermous polyploids. Lateral slim bar shows range; vertical bar shows mean; and lateral thick bar shows standard deviation. SEX, sexual diploids; APO, agamospermous polyploids.

specimens, the pollen grains were significantly larger (mean, 23.1 μm) than those of the diploid vouchers, and the grains were well-shaped, well-stained, and nearly equal-sized and lacked unstained pollen grains smaller than 16 μm. These may be sexual, male-fertile polyploids; however, examination of chromosome numbers and breeding systems of living plants will be necessary for complete understanding. Table 2 summarizes numbers of sexual and agamospermous specimens for the 22 Asian taxa examined. Specimens of *E. benguetense, E. caespitosum, E. catense, E. formosanum, E. fortunei* var. *angustilobum, E. longicaule, E. luchuense, E. mairei, E. melanadenium, E. sambucifolium, E. shimadai, E. tashiroi, E. tozanense, E. variabile,* and *E. yakushimense* were all sexual; those of *E. heterophyllum* were all agamospermous; and those of *E. chinense* var. *chinense, E. chinense* var. *oppositifolium, E. fortunei* var. *fortunei, E. glehni, E. lindleyanum,* and *E. omeiense* included both sexual and agamospermous specimens. For the latter seven taxa, distribution of sexual and agamospermous specimens is shown in Figs. 3–8. Figure 9 illustrates ranges of sexual populations in 20 taxa; *E. fortunei* var. *fortunei*, which has often been cultivated in China, Korea, and Japan, and whose range might be artificial, is excluded.

3. *Taxonomic Notes*

The taxonomy of most Asian species of *Eupatorium* remains uncertain. Fifteen species are listed by King and Robinson (1970), 15 species and 2 varieties by Watanabe (1986), and 18 species by King and Robinson (1987). King and Robinson (1987) referred to most of the previously described species in their list of names known for the Eupatorieae, but they did not give criteria for their delimitations of species. Ling et al. (1985) described two new species and a new variety from China, but Watanabe (1986) and King and Robinson (1987) did not refer to these taxa. Thus there is no accepted list of Asian species of *Eupatorium.*

In Asian *Eupatorium*, agamospermy is reported for polyploids of *E. chinense* var. *oppositifolium, E. glehni,* and *E. lindleyanum* (Watanabe et al., 1982; Watanabe, 1986), but there are no extensive studies of the reproductive system of the remaining species. The present study demonstrated that six taxa consist of sexual and agamospermous populations, 15 taxa are exclusively sexual, and the remaining one is exclusively agamospermous. Therefore, 21 taxa are not so-called agamospermous microspecies, but are considered to be differentiated at the diploid level. This result provides a reasonable basis for taxonomic delimitation of the Asian species of *Eupatorium*. Although a revision of the Asian species will result from further studies of morphological variation of these 22 taxa, we will comment here on several species for which the results of

Table 1. Differences in morphology and fertility of pollen grains between sexual diploids and agamospermous polyploids.

Characters	diploid	polyploid
Range of mean size (μm)	18.9–22.8	19.4–43.0
Mean of means of pollen size within each plant (μm)***	20.3	29.8
Mean of standard deviation of pollen size (μm)***	0.6	2.4
Unstained pollen grains less than 16 μm	absent	present
Shape	normal	mal-formed
Stainability (%)	94.7–100.0 usually 99%<	5.5–99.8 usually 95%>

***, Significant at 0.1% by *t*-test.

Table 2. Number of sexual and agamospermous specimens of 22 taxa in Asian *Eupatorium*.

	Taxon	Sexual type	Agamospermous type	Locality
1.	*E. benguetense* C. B. Rob.	4		Philippines
2.	*E. caespitosum* Migo	14		E. of S. China
3.	*E. catense* Elm.	5*		Philippines
4.	*E. chinense* L. var. *chinense* L.	30	49	S. China, S. of N. China
5.	var. *oppositifolium* (Koidz.) Murata et H. Koyama	45	41	China, Korea, Japan
6.	*E. formosanum* Hayata	25		Taiwan, Ryukyu
7.	*E. fortunei* Turcz. var. *fortunei* Turcz.	13	20	China, Japan
8.	var. *angustilobum* Ling	3		S. China
9.	*E. glehni* Fr. Schem. ex Trautv.	30	20	Japan, Sachalin
10.	*E. heterophyllum* DC.		20	W. China
11.	*E. lindleyanum* DC.	44	20	China, Korea, Japan, Indochina, Philippines
12.	*E. longicaule* DC.	2		Himalaya
13.	*E. luchuense* Nakai	34		Taiwan, Ryukyu
14.	*E. mairei* Lévl.	40*		Himalaya, W. of S. China
15.	*E. melanadenium* Rob.	8*		S. China
16.	*E. omeiense* Ling et Shih	8	3	W. of S. China
17.	*E. sambucifolium* Elm.	5		Philippines
18.	*E. shimadai* Hayata	21		Taiwan
19.	*E. tashiroi* Hayata	22		Taiwan
20.	*E. tozanense* Hayata	13		Taiwan
21.	*E. variabile* Makino	12*		SW. Japan
22.	*E. yakushimense* Masam. et Kitam.	10		Yakushima Isl. in Japan

*, Including type specimens.

this study provide useful taxonomic information.

Eupatorium chinense L. is one of the species whose taxonomy is the most complicated and unclear. Several varieties have been recognized in this 'species'. Among them, two have wide ranges and are fairly distinct: *E. chinense* var. *chinense* occurs widely in South China, and var. *oppositifolium* (Koidz.) Murata et H. Koyama occurs widely in China, Korea, and Japan. In the eastern and central parts of China, plants morphologically intermediate between these two varieties are often found (Kitamura, 1949; Anonymous, 1975; Murata and Koyama, 1982), and occurrence of these plants is the major reason Kitamura (1949) gives for treating the two taxa as varieties. For *E. chinense* var. *oppositifolium* in Japan, Watanabe et al. (1982) and Watanabe and Yahara (1984) reported that the sexual diploids occur in southwestern Japan while the agamospermous polyploids occur throughout most of Japan except for the Ryukyu Islands. The present study clarified the distribution of sexual and agamospermous populations of these two varieties in China and/or Korea for the first time (Figs. 3–4). For var. *oppositifolium*, sexual populations were found on Mt. Lushan of Jiangxi Province and in Xiaowu of Fujian Province, China, while agamospermous populations were found widely in China and Korea. For var. *chinense*, sexual populations were found in Guangdong and Guangxi Provincies, China, while agamospermous populations were found widely in South China. Sexual populations of these two taxa are geographically isolated from each other. The two sexual races are morphologically distinct, and plants morphologically intermediate are all agamospermous (Kawahara, unpubl.). Therefore there is no positive reason to regard them as two conspecific varieties. *Eupatorium chinense* var. *oppositifolium* is separated from *E. chinense* and considered to a distinct species, *E. japonicum*, in the current Chinese literature (Anonymous, 1975; Ling et al., 1985). Our results support this treatment as a species for *E. chinense* var. *oppositifolium*. However, syntypes of *E. japonicum* do not include plants of *E. chinense* var. *op-*

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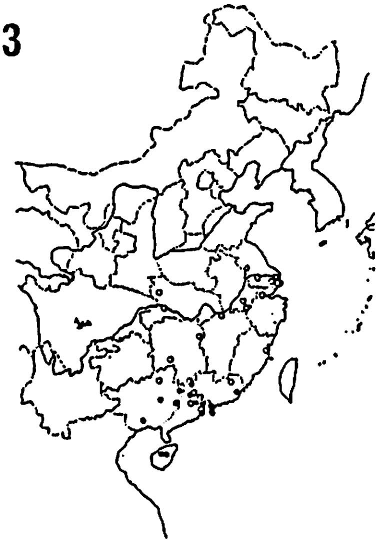

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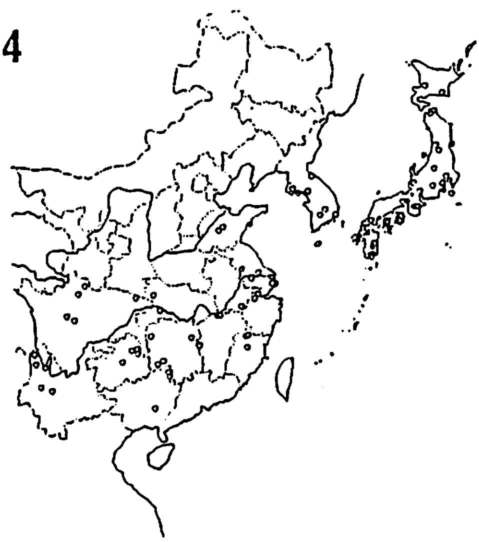

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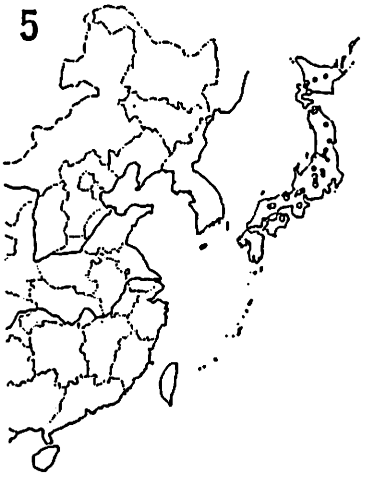

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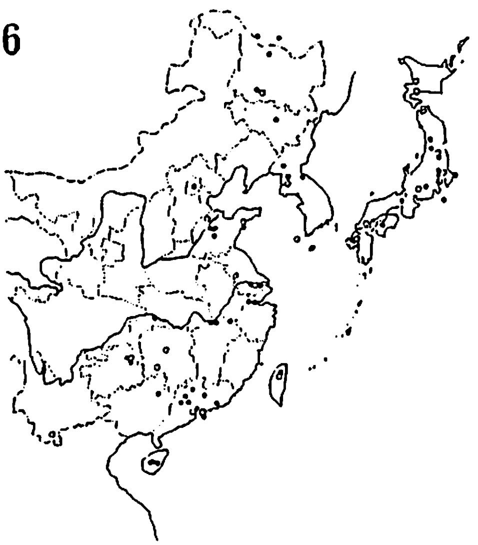
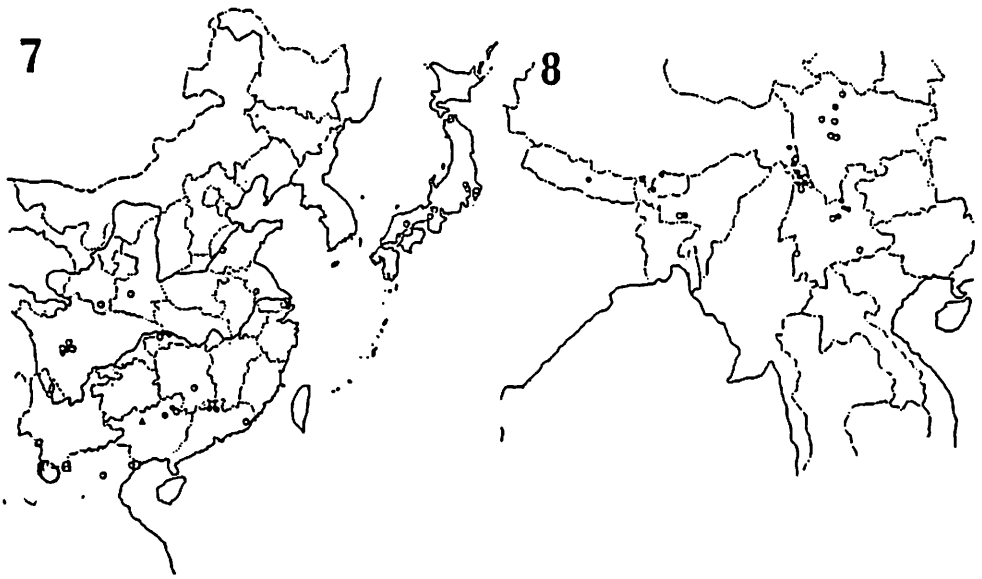


positifolium (Murata and Koyama, 1982). Nomenclature for *E. chinense* var. *oppositifolium* will be discussed in a forthcoming paper concerning the morphology of the entire *E. chinense* complex (Kawahara and Yahara, in prep.).

Eupatorium heterophyllum DC. is also a species, whose delimitation is uncertain. In this study, *E. mairei* Lévl., which has been reduced to *E. heterophyllum* (Kitamura, 1949; Lauener, 1976; Ling et al., 1985), is distinguished from *E. heterophyllum* s. str. by its deeply dissected and densely hairy leaves and compact inflorescences. The plants of *E. heterophyllum* s. str. which were examined were all agamospermous (Table 2), while those of *E. mairei*, including syntypes, were all sexual. *Eupatorium heterophyllum* s. str. occurs in Yunnan and Sichuan, China, while *E. mairei* occurs in Yunnan, Khasia, Bhutan, and Nepal (Fig. 8). *Eupatorium heterophyllum* s. str. is morphologically intermediate between *E. mairei* and *E. chinense* var. *oppositifolium* and occurs in areas where *E. mairei* occurs in contact with agamospermous populations of *E. chinense* var. *oppositifolium*. Thus, *E. heterophyllum* may be of hybrid origin between these two taxa.

Eupatorium fortunei Turcz. occurs in South and North China, Korea and Japan and consists of two



Figs. 3–8. Geographical distributions of the taxa which consist of sexual and agamospermous populations. Solid symbols, sexual populations; open symbols, agamospermous populations.
3: Circles, *E. chinense* var. *chinense*; triangles, *E. omeiense*. 4: *Eupatorium chinense* var. *oppositifolium*. 5: *Eupatorium glehni*. 6: *Eupatorium lindleyanum*. 7: Circles, *E. fortunei* var. *fortunei*; triangles, var. *angustilobum*. 8: Solid circle, *E. mairei* (all sexual populations); open circle, *E. heterophyllum* s. str. (all agamospermous populations).

varieties: var. *angustilobum* Ling and var. *fortunei*. Three specimens of var. *angustilobum* were all sexual and occur in Guangxi and Sichuan (the locality in Sichuan could not be determined) (Fig. 7); 20 specimens of var. *fortunei* were agamospermous and occur in China and Japan; and 13 Chinese specimens

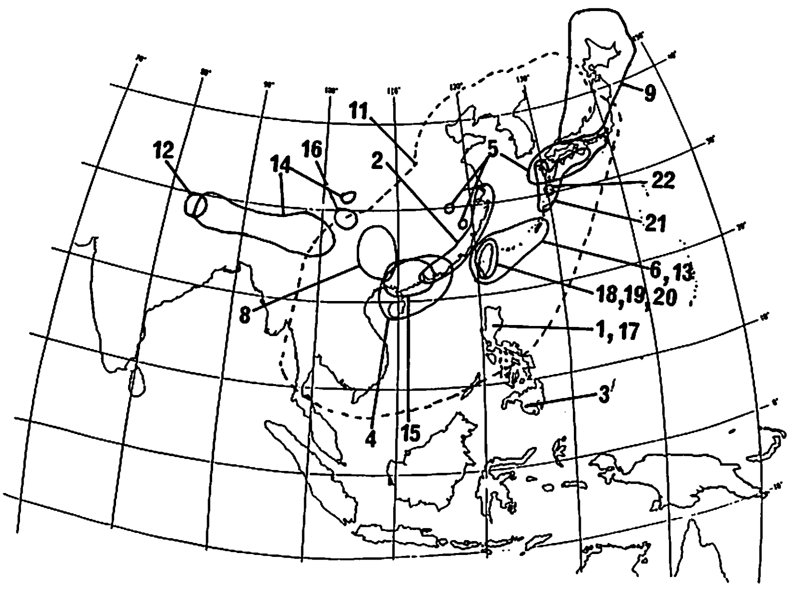


Fig. 9. Geographical distributions of sexual races except diploid *E. fortunei* var. *fortunei* (number 7 in Table 2). Numbers correspond to those of symbols of taxa in Table 2.

of var. *fortunei* with significantly larger pollen grains than other sexual specimens were regarded as sexual by our criteria. Thus *E. fortunei* seems to include two sexual types with distinct morphology. Further biological studies of these two types are needed. The sexuality and ploidy of Chinese plants with larger pollen grains should be reconfirmed by direct cytological observations of living plants.

Discussion

Criteria for Distinguishing Sexual and Agamospermous Specimens

In *Eupatorium* s. lat., Holmgren (1919) was the first to report deficient male function in *E. glandulosum* H.B.K., which is now treated as *Ageratina adenophora* (Sprengel) R. King et H. Robinson (King and Robinson, 1987). Sullivan (1976) examined microsporogenesis of North American species of *Eupatorium* s. str. and reported that meiosis of agamospermous polyploids failed to occur, resulting in failure of pollen grain production or less frequently, in production of malformed abortive pollen grains. Based on the observed positive correlation between polyploidy, agamospermy and pollen production, she could successfully estimate distributions of sexual and agamospermous populations in seven agamic complexes. However, in Asian *E. chinese* var. *oppositifolium*, microsporogenesis does occur frequently, although more or less irregularly, and results in production of pollen grains with stainability ranging from 5.6 to 99.6% (Watanabe et al., 1982). Thus, for Asian species of *Eupatorium*, agamospermous polyploids sometimes do not differ from sexual diploids in production and stainability of pollen grains. This study demonstrated that range of pollen size variation, particularly presence or absence of pollen grains smaller than 16 μm, is useful in determining whether the reproductive system is sexual or agamospermous (Table 1).

We successfully estimated reproductive systems and distributions for 22 Asian taxa of *Eupatorium*. Morita (1976, 1980) and Yahara (1986) used similar criteria to estimate the distributions of sexual diploid and agamospermous polyploid races of East Asian *Taraxacum* and *Boehmeria*, respectively. The criteria, shown in Table 1, could be widely applied to distinguish sexual and agamospermous plants of various amphi-agamic complexes in herbarium specimens.

Phytogeographical Comparison between East Asian and North American Eupatorium

Comparing the results of this study with those of Sullivan (1976) for North American species, three differences in patterns of geographical distribution of sexual and agamospermous populations can be pointed out. First, North America has a greater number of species with both sexual and agamospermous populations than does East Asia. In North America, agamospermous polyploids have evolved in nine species: *E. altissimum* L., *E. cuneifolium* Willd., *E. hyssopifolium* L., *E. leucolepis* (DC.) Torr. et A. Gray, *E. pilosum* Walter, *E. rotundifolium* Willd., *E. sessilifolium* L. (Sullivan, 1976), *E. recurvans* Small (Yahara and Sullivan, 1986), and *E. album* L. (Sullivan, pers. comm.). They have been regarded as autopolyploids (Sullivan, 1976; Yahara and Sullivan, 1986). In eight of these species (the exception is *E. album*), sexual diploids have restricted ranges but agamospermous polyploids occur widely in southeastern North America, and these polyploids are considered to have participated in developing secondary agamic complexes through hybridization between various species combinations (Sullivan, 1978). In East Asia, both sexual and agamospermous plants were found for *E. chinense* var. *chinense, E. chinense* var. *oppositifolium, E. fortunei, E. fortunei, E. glehni, E. lindleyanum*, and *E. omeiense*. However, it is uncertain whether all of these agamospermous plants are autopolyploids. Watanabe (1986) suggests on the basis of cytological evidence that the agamospermous polyploids of *E. glehni* and *E. lindleyanum* are not autopolyploids but are of hybrid origin between sexual diploids of these two species and agamospermous polyploids of *E. chinense* var. *oppositifolium*. Agamospermous plants of *E. chinense* var. *chinense, E. fortunei* var. *fortunei*, and *E. omeiense* might also be allopolyploids, because (1) they are similar morphologically to the agamospermous plants of *E. chinense* var. *oppositifolium* (Kawahara, unpubl.) and (2) agamospermous polyploids of *E. chinense* var. *oppositifolium* occur widely in Japan, Korea, and Northeast, North, and South China; agamospermous plants of *E. chinense* var. *chinense, E. fortunei* var. *fortunei, E. glehni, E. lindleyanum*, and *E. omeiense* are found around areas where sexual plants of these species occur in contact with agamospermous plants of *E. chinense* var. *oppositifolium*. As discussed above, exclusively agamospermous *E. heterophyllum* s. str. may be of hybrid origin between sexual *E. mairei* and agamospermous plants of *E. chinense* var. *op-*

positifolium. Thus, agamospermy seems to have evolved in fewer species in Asia than in North America. Indeed the agamospermous Asian populations may all be of hybrid origin.

Second, the number of sexual species with wide ranges is greater in North America than in East Asia. *Eupatorium lindleyanum* is the only Asian species whose sexual populations have a wide range. In contrast, there are six diploid species which occur widely in eastern North America: these are *E. capillifoium* (Lam.) Small, *E. fistulosum* Barrett, *E. macrantum* L., *E. perfoliatum* L., *E. purpureum* L., and *E. serotinum* Michx.

Third, in East Asia, the number of exclusively sexual species with restricted ranges is greater than in North America. The following are the 13 sexual species in East Asia with relatively restricted ranges: *E. longicaule* in the eastern Himalayas, *E. fortunei* var. *angustilobum* and *E. melanadenium* in South China, *E. benguetense, E. catense* and *E. sambucifolium* in the Philippines, *E. shimadai, E. tashiroi* and *E. tozanense* in Taiwan, *E. formosanum* and *E. luchuense* in Taiwan and the Ryukyu Islands, *E. yakushimense* in Yakushima Island, Japan, and *E. variabile* in southwestern Japan. Only eight totally sexual species with restricted ranges occur in North America: *E. dubium* Willd. and *E. resinosum* Torr. along the Atlantic coast, *E. compositifolium* Walter and *E. semiserratum* DC. in the coastal plain, *E. leptophyllum, E. mikanioides* Chapm., and *E. petaloideum* Britton in Florida, *E. lancifolium* (Torr. et A.Gray) Small in Arkansas and Louisiana.

King and Robinson (1970, 1987) speculated that *Eupatorium* originated in North America, where the greatest number of species and the nearest related genera occur, and then extended its range to the temperate regions of East Asia and Europe very late in the Tertiary. Watanabe et al. (1989) suggested on the basis of karyological evidence that Asian species are of monophyletic origin and in an earlier stage of differentiation than North American species. The results of the present study suggest that the number of Asian species is greater than considered previously, and is nearly equal to the number in North America. However, the second and third features of the phytogeographical pattern in Asian species support the hypothesis of King and Robinson (1970, 1987) and Watanabe et al. (1989). In particular, the fact that the larger numbers of Asian species have restricted ranges and are allopatric suggests that these differentiated rather shortly after geographical isolation from North America. Further studies of systematic relationships between these species are in progress and will provide evidence for or against this hypothesis.

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