

## Chrysanthemum genetic resources and related genera of *Chrysanthemum* collected in China

H. E. Zhao · Z. H. Liu · X. Hu · J. L. Yin ·  
W. Li · G. Y. Rao · X. H. Zhang · C. L. Huang ·  
N. Anderson · Q. X. Zhang · J. Y. Chen

Received: 26 July 2007 / Accepted: 2 February 2009 / Published online: 6 March 2009  
© Springer Science+Business Media B.V. 2009

**Abstract** Chrysanthemum is one of the most important and popular ornamentals over the world. Breeding of new pedigrees depends mainly on conventional crossing. Chrysanthemum genetic resources were categorized into three groups. Here we introduce the wild species and related genera of *Chrysanthemum* in order to extend the genetic resources that can be used for genetic improvement of chrysanthemums by hybridization. In the genus *Chrysanthemum* and closely related genera, there are many wild species

that are able to cross successfully with modern chrysanthemums. These represent important genetic resources for introducing new characters into florist's chrysanthemums. The genus *Chrysanthemum* consists of more than 40 species distributed mainly in East Asia. More than 20 species of *Chrysanthemum* are native to China. Unfortunately, little of this information has been published in western languages. In this paper, we also provide an overall review of the basic information of the wild species of we have collected in China in order to understand and exploit those genetic resources much better. We have collected about 17 wild species and studied their useful characters in the past several years. These species include *C. oreastrum* (Hance) Y. Ling, *C. hypargyrum* (Diels) Y. Ling et C. Shih, *C. zawadskii* (Herbert) Tzvelev, *C. chanetii* (H. Léveillé) C. Shih, *C. naktongense* (Nakai) Tzvelev, *C. mongolicum* (Y. Ling) Tzvelev, *C. argyrophyllum* (Y. Ling) Y. Ling et C. Shih, *C. rhombifolium* (Hemsley) Y. Ling, *C. vestitum* (Hemsley) Y. Ling, *C. dichrum* C. Shih, *C. glabriusculum* (W. W. Smith) C. Shih, *C. indicum* (Linnaeus) Des Moulin, *C. lavandulifolium* (Fischer ex Trautvetter) Kitamura, *C. foliaceum* G. F. Peng, Shih et S. Q. Zhang, *C. nankingense* (Handel-Mazzetti) X. D. Cui, *C. potentilloides* (Handel-Mazzetti) C. Shih and *C. maximowiczii* (Komarov) Tzvelev. In addition to this genus, we have collected some species of the related genera including *Brachanthemum mongolicum* Krascheninnikov, *B. pulvinatum* (Handel-Mazzetti) C. Shih, *B. gobicum* Krasch, *Ajania fastigiata* (C. Winkler) Poljakov, *A. achilleoides* (Turczaninow) Poljakov et

H. E. Zhao (✉) · X. Hu · J. L. Yin · W. Li ·  
Q. X. Zhang · J. Y. Chen

Department of Ornamental Horticulture, College of  
Landscape Architecture, Beijing Forestry University,  
Beijing 100083, People's Republic of China  
e-mail: zhaohuien@bjfu.edu.cn

Z. H. Liu  
College of Biology, China Agricultural University,  
Beijing 100094, People's Republic of China

G. Y. Rao  
College of Life Sciences, Peking University,  
Beijing 100871, People's Republic of China

X. H. Zhang · C. L. Huang  
Beijing Agro-Biotechnology Research Center, Beijing  
Academy of Agriculture and Forestry Sciences,  
Beijing 100089, People's Republic of China

N. Anderson  
Department of Horticultural Science, University of  
Minnesota, 1970 Folwell Avenue, St. Paul, MN 55108,  
USA

Grubov, *A. khartensis* (Dunn) C. Shih, *A. fruticososa* (Ledebour) Poljakov, *A. pallasiana* (Fischer ex Besser) Poljakov, *Phaeostigma salicifolia* (Mattf.) Muld., *Elachanthemum intricatum* (Franchet) Y. Ling et Y. R. Ling and two endemic species of *Opisthopappus* including *O. taihangensis* (Ling) Shih and *O. longilobus* Shih in China.

**Keywords** *Ajania* · *Brachanthemum* · China · *Chrysanthemum* · *Elachanthemum* · Genetic resources · *Opisthopappus* · *Phaeostigma*

Garden chrysanthemum has been cultivated for more than 1,600 years. By the eleventh century, there were 36 cultivars of mums in China. The most probable origin of garden chrysanthemum is a hybrid between *Chrysanthemum indicum* and *C. vestitum*, but the true origin is still unclear since most species are so close and very easily cross with each other (Dai 1994; Zhao 2000). There are many other important genetic resources and most of them are might be able to cross successfully with modern chrysanthemums though some of wild species have been transferred their important characters into the gene pool of modern chrysanthemums such as *Chrysanthemum zawadskii*, *C. weyrichii*, *Ajania pacifica* (Anderson 2006; Chen et al. 1995; Shibata et al. 1988). The current trend in the horticultural industry is focused on safer produces and environmentally friendly production systems. To achieve these goals and stay in front of the competition, further innovation is needed in both production techniques and plant improvement for floricultural crops. Genetic resources remain essential for all plant breeding programs including modern biotechnologies. Chrysanthemum genetic resources were categorized into three groups by Fukai (2003) according to the gene pool concept of Harlan and de Wet. Here we introduce the genetic resources according to the cross compatibility and biosystematics, respectively, and the primarily basic information that has been gathered on the genetic resources we collected in China in order to understand and exploit those genetic resources much better.

### Genetic resources according to the cross compatibility

The first group or primary genepool is the core species. *Chrysanthemum* species being cross

compatible with chrysanthemums are the constituents of this genepool. Commercial cultivars are also important genetic resources within the primary genepool (Fukai 2003). Ground cover chrysanthemums were bred from species (*C. vestitum*, *C. indicum*, *C. zawadskii*, *C. lavandulifolium*, *C. nankingense*, *C. chanetii*) and cultivars in the primary genepool (Chen et al. 1995). Reciprocal crosses between chrysanthemum and 10 wild chrysanthemum species (*C. articum* ssp. *maekawanum*, *C. lavandulifolium*, *C. crassum*, *C. indicum*, *C. japonicum*, *C. ornatum*, *C. occidentali-japonense* var. *ashizuriense*, *C. yoshinaganthum*, *C. chanetii*, *C. pacificum* (*A. pacifica*)) were possible when the appropriate parental genotypes were carefully chosen (Fukai et al. 2000). Though the investigation and sampling analysis is still fairly limited, some interspecific natural hybrids and intergeneric natural hybrids between *Chrysanthemum* and *Ajania* have been found (Ohashi and Yonekura 2004). Breeding programs for cut flowers have been reportedly using *Ajania* species, e.g., *A. pacifica* (Shibata et al. 1988; De Jong and Rademaker 1989) and *A. shiwogiku* (Douzono and Ikeda 1998). Cut flower production of the hybrids (pacific-mum: BC1 of *Chrysanthemum* × *A. pacifica*) was very successful in Okinawa, Japan in the 1990s (Fukai 2003). Hybrids between *C. lavandulifolium* (Fisch ex Trautv.) Ling et Shih and *Ajania remotipina* (Hand.-Mazz.) Ling et Shih were also reported (Kondo et al. 2003). There are so many natural and artificial intergeneric hybrids between *Chrysanthemum* and *Ajania* that Ohashi and Yonekura (2004) proposed that *Ajania*, *Arctanthemum* and *Phaeostigma* should be combined into this genus.

The secondary genepool consists of closely related species, which are partially compatible with chrysanthemums. Some species in the related genera of *Chrysanthemum* are included in this category (Fukai 2003). An interspecific hybrid between *Nipponanthemum nipponicum* and a genotype chrysanthemum has been reported through embryo rescuer culture (Ohishi et al. 1996). The hybrids are compatible with chrysanthemum but not with *Nipponanthemum nipponicum*. Species in the secondary genepools may be useful to increase crop genetic variation. The University of Minnesota herbaceous perennial breeding program focused on winter hardy chrysanthemums at its inception in 1926, using species from the primary and secondary genepools: *Chrysanthemum indicum*,

*C. sibiricum*, *C. koreanum*, *C. arcticum* (*Arctanthemum arcticum*), *C. rubellum* ‘Clara Curtis’, *C. uliginosum*, *C. weyrichii*, *C. zawadskii*, *C. nipponicum* (*Nipponanthemum nipponicum*), and *Leucanthemum maximum* (Anderson and Gesick 2003). Hybrid between *Argyranthemum frutescens* L. and chrysanthemums was attempted to improve marguerite by Furustai in 1978 (Fukai 2003). Hybrid between *C. japonicum* (Makino) Kitam. and *Tanacetum vulgare* L. was reported (Kondo et al. 1999). The crossability with chrysanthemums has been mentioned when *Tanacetum cinerariifolium* used be as the male (Anderson 2006). Even though the relationship between the genera is quite distant, they could still be cross compatible. The intergeneric hybrids have been reported between *Chrysanthemum* and the related species from the same subtribe Artemisiinae (*Crossostephium chinense*) and the close subtribes including Leucanthemeinae (*Nipponanthemum nipponicum*, *Leucanthemella linearis*) and Tanacetinae (*Tanacetum vulgare*, *T. parthenium*) (Kondo et al. 2003). These support the close related genera might be used for genetic improvement of chrysanthemums by hybridization.

### Genetic resources according to the phylogeny and classification

It was found that It almost could not provide any phylogenetic information analysing the sequences of ITS and *trnT–trnL*, *trnL–trnF* intergenic spacers of 11 wild species of *Chrysanthemum* native to China and related species for studying the origin of chrysanthemum and phylogenetics of *Chrysanthemum* though sequences of ITS could provide phylogenetic information on most other close species (Zhao et al. 2003). Yang et al. (2006) studied the relationship between *C. indicum* polyploidy complex and *C. lavandulifolium*, they found that the gene flow had occurred between *C. indicum* and *C. lavandulifolium*. Kim et al. (unpublished) sequenced ITS and *trnL–trnF* intergenic spacer of *Chrysanthemum* for studying the genetic diversity in the diploid populations of *Chrysanthemum zawadskii* and its related species in 2005. They found that the gene flow has occurred not only among *C. zawadskii* and its related species but also even between *Chrysanthemum* and *Ajania*. These indicate that all the species of *Chrysanthemum* might

the important genetic resources which could be hybridized successfully with modern chrysanthemums when the appropriate parental genotypes are careful chosen though the relationship and cross compatibility between chrysanthemums and wild species are not always consistent.

*Chrysanthemum* is very close to *Ajania* and *Arctanthemum* according to internal transcribed spacers (ITS) analysis on *A. pacifica*, *Arctanthemum arcticum*, *Artemisia canariensis*, *Leucanthemella serotina*, *Nipponanthemum nipponicum* and other species in Anthemideae (Franciso-Ortega et al. 1997). Ohashi and Yonekura (2004) proposed that *Ajania*, *Arctanthemum* (*Hulteniella* included) and *Phaeostigma* should be combined into *Chrysanthemum* since they are quite close. There is little support for monophyly of most of the subtribes of Bremer and Humphries (1993), and there is substantial disagreement with previously proposed sister-group relationships of genera and subtribes. A molecular phylogeny for the tribe based on the chloroplast gene *ndhF* (Watson et al. 2000) revealed a basal grade of Southern Hemisphere genera which are sister to a mostly Northern Hemisphere clade. Therefore, genera are arranged in a linear manner according to the results of Watson et al. (2000), i.e., in a primarily geographic representation of the members of the tribe, beginning with the southern African representatives, followed by the centra land eastern Asian ones, and ending with the Mediterranean genera (Oberprieler et al. 2007). Nine genera including *Ajania*, *Ajaniopsis*, *Arctanthemum*, *Brachanthemum*, *Chrysanthemum*, *Elachanthemum*, *Hulteniella*, *Phaeostigma*, *Tridactylina* are arranged in *Ajania* Group within Group B [Asian Grade] (Oberprieler et al. 2007). Zhao et al. (2007) found that *Opisthopappus* was closely related to *Ajania* Group based on the sequences of nrDNA ITS and *trnL–trnF* IGS. Reciprocal intergeneric hybrids between *Chrysanthemum lavadulifolium* and *Opisthopappus taihangensis* were also obtained after the intergeneric hybrids between *Ajania pacifica* and three species of *Chrysanthemum* with different ploidies (In the following papers). These suggest that some wild species in these related closed genera might be the primary or secondary genepools of chrysanthemums as well.

Group 3 are useful to extend a range of genetic variation of a crop according to the gene pool concept of Harlan and de Wet. However, there are some obstacles to their use in further breeding programs, such as the sterility of progeny. In the case of

chrysanthemum, the first and second groups are rather large and considerable genetic variation. Therefore, collection of *Chrysanthemum* species and related genera belong to the groups 1 and 2 becomes our main target.

### Wild species of *Chrysanthemum* and related genera collected in China

There are rich genetic resources of chrysanthemums in China. Since the middle-1980s, extensive collection has been conducted studying the origin of chrysanthemums and exploring genetic resources in China. This research has generated a wealth of cultivars of ground cover chrysanthemums and small chrysanthemums especially suitable for harsh growing conditions. Here we only provide the basic information that has been gathered on the wild related species collected by ourselves on Mainland China since 1998.

#### Morphological variation for horticulturally important traits

Phenotypic variations of the plant forms at the intergeneric, interspecific, and even intraspecific levels occur in both naturally in the wild and conserve in field repositories. Table 1 shows the species of the genetic resources we have collected in China. Each species shows a peculiar plant form due to unique leaves, branching pattern, plant height, and flowering habits as at least 50 plants in nature and more than 10 plants (*Phaeostigma* is an exception) introduced in our repository being observed (Fig. 1). From a horticultural point of view, some of the species we have collected have potential for potted plants and ground covers, which include *C. oreastrum* (Hance) Y. Ling, *C. hypargyrum* (Diels) Y. Ling et C. Shih, *C. argyrophyllum* (Y. Ling) Y. Ling et C. Shih, *C. naktongense* (Nakai) Tzvelev, *C. mongolicum* (Y. Ling) Tzvelev, *C. dichrum* C. Shih, and some of *C. chaneltii* (H. Léveillé) C. Shih and a few of *C. vestitum* (Hemsley) Y. Ling within *Chrysanthemum*, and *B. mongolicum* Krascheninnikov, *B. pulvinatum* (Handel-Mazzetti) C. Shih, *A. achilleoides* (Turczaninow) Poljakov ex Grubov, *A. khartensis* (Dunn) C. Shih, *A. fruticulosa* (Ledebour) Poljakov, *E. intricatum* (Franchet) Y. Ling et Y. R.

Ling, *O. taihangensis* (Ling) Shih and *O. longilobus* Shih. *C. oreastrum* (Hance) Y. Ling is a small alpine tuft. *C. hypargyrum* (Diels) Y. Ling et C. Shih and *C. argyrophyllum* (Y. Ling) Y. Ling et C. Shih are dwarf plants. *C. dichrum* C. Shih has great groundcover potential with densely branches and leaves. Its lobed leaves are covered with silver on the abaxial surface, creating a striking and distinctive effect, but at 50 cm and with soft branches this plant might be too tall for most groundcover demands especially growing in loamy soil with slender branches. *E. intricatum* (Franchet) Y. Ling et Y. R. Ling has many densely branches as well. *O. taihangensis* (Ling) Shih and *O. longilobus* Shih have great groundcover potential with very softy branches. An accession of *C. chaneltii* (H. Léveillé) C. Shih distributed in alpine meadow is a cushion plant. A few seedlings of *C. vestitum* (Hemsley) Y. Ling have a prostrate characteristic found in our friend's garden and our nursery. *B. mongolicum* Krascheninnikov and *B. pulvinatum* (Handel-Mazzetti) C. Shih are very small dwarf subshrubs. *A. khartensis* (Dunn) C. Shih is a small diffuse dwarf alpine plant. *A. achilleoides* (Turczaninow) Poljakov ex Grubov and *A. fruticulosa* (Ledebour) Poljakov are dwarf only in arid region.

#### Flowering dates

Table 1 shows the approximate flowering periods of the wild genetic resources we have collected in China according to Flora of China (Ling and Shih 1983). Flowering times are affected by a variety of factors, including habitat, elevation and species type. Generally at higher elevations plants will bloom earlier and possibly for longer periods of time. It was found that the flowering time of *C. naktongense* (Nakai) Tzvelev is very early in late May of 2008 new introduced in 2007.

#### Flower colors

It has not found that there is *C. hypargyrum* with yellow ray flowers in nature though it named by this characteristic. We have not collected *C. mongolicum* and *C. maximowiczii* with pink rays as though it has according to the description of Flora of China (Ling and Shih 1983). It is found that almost all ray flowers of *C. vestitum* will become pale purple in the very

**Table 1** Cytogenetic, floral coloration and flowering period of the wild species of *Chrysanthemum* and related closed genera we have collected in Mainland China

Species	Chromosome no. (2n)	Ray flower color	Flowering period (month)
<i>C. hypargyrum</i>		Yellow	8–9
<i>C. oreastrum</i>	2x = 18, 6x = 54	White, pink, pale purple	7–8
<i>C. zawadskii</i>	6x = 54, 8x = 72	White, pink, pale purple	7–9
<i>C. chanetii</i>	4x = 36, 6x = 54	White, pink, pale purple	7–10
<i>C. naktongense</i>	2x = 18, 4x = 36, 8x = 72	White, pink, pale purple	7–8
<i>C. maximowiczii</i>	6x = 54	White, pink	8–9
<i>C. mongolicum</i>	2x = 18, 8x = 72	White, pink	8–9
<i>C. argyrophyllum</i>	6x = 54	White	8–9
<i>C. rhombifolium</i>		White	10–11
<i>C. vestitum</i>	6x = 54	White	9–11
<i>C. dichrum</i>	2x = 18, 4x = 36	Yellow	8–10
<i>C. glabriusculum</i>	6x = 54	Yellow	9–10
<i>C. indicum</i>	2x = 18, 4x = 36	Yellow	9–11
<i>C. foliaceum</i>		Yellow	9–11
<i>C. lavandulifolium</i>	2x = 18	Yellow	9–11
<i>C. nankingense</i>	2x = 18	Yellow	10–11
<i>C. potentilloides</i>	2x = 18	Yellow	9–10
<i>B. gobicum</i>			8–9
<i>B. mongolicum</i>		Yellow	9
<i>B. pulvinatum</i>	2x = 18	Yellow	7–9
<i>A. achilleoides</i>	2x = 18		8
<i>A. fastigiata</i>	2x = 18		8–10
<i>A. fruticulosa</i>	4x = 36		7–9
<i>A. khartensis</i>	6x = 54	7–9	
<i>A. pallasiana</i>	2x = 18		8–9
<i>O. longilobus</i>		White	9–10
<i>O. taihangensis</i>	2x = 18	White	9–10
<i>E. intricatum</i>	2x = 18		9–10
<i>P. salicifolium</i>	2x = 18		8–9

Data source from the references: Dowrick 1952, 1953; Ling and Shih 1983; Fukai et al. 1998; Nakata et al. 1992; Zhou 1992; Kondo et al. 2003; Li et al. 2008

late flowering period. The details of the flower colors observed in the nature or nursery, which is the same as that described in Flora of China (Ling and Shih 1983), can be found in Table 1.

#### Ploidy variation

There is a wide range of ploidy variation among native Chinese *Chrysanthemum* germplasm including diploids, tetraploids, hexaploids, octoploids, and even pentaploids (Dowrick 1952, 1953; Fukai et al. 1998; Nakata et al. 1992; Zhou 1992; Kondo et al. 2003). The basic chromosome number is  $x = 9$ . To our best

knowledge, enneaploid *A. pacifica* recently found distributed in Taiwan is the highest ploidy level of germplasm of chrysanthemum in China (Suzuki et al. 2001). The chromosome numbers of *Chrysanthemum* and some related species collected in our nursery and studied so far could be found in the Table 1.

#### Habitat diversity

The habitat of germplasm of chrysanthemum native to China can be divided into the following zones: plain and sub-montane, lower montane, upper sub-alpine, high-alpine zone, plateau, grassland, desert



**Fig. 1** The pictures of the germplasm resources of *Chrysanthemum* in China

and Gobi (Table 2). *Chrysanthemum* species are largely distributed in the temperate plain and montane zones of central and eastern China. Several species mainly distributed in the alpine zones which include *C. oreastrum* (Hance) Y. Ling, *C. hypargyrum* (Diels) Y. Ling et C. Shih, *C. argyrophyllum* (Y. Ling) Y. Ling et C. Shih (Table 2). *C. zawadskii* (Herbert) Tzvelev is extensively and intermittently distributed in upper sub-alpine zones and grasslands in Eurasia from China, Japan, Korea, Mongolia, Siberia and Russia extending to Central Europe (the Carpathian Mountain Range). Almost all *Ajania* species dominate the cold deserts in northwestern China and steppe-like communities and Qinghai-Tibet Plateau and upper sub-alpine zone, high-alpine zone. All the three *Brachanthemum* species and *Elachanthemum* are distributed in the Gobi and Desert zones. *Phaeostigma* species are distributed in the alpine zones. The two endemic species of *Opisthopappus* are mainly growing on the cliff of south of Taihang Mountain (Table 2).

### Ecological suitabilities

Most *Brachanthemum* and some *Ajania* species are subshrubs, which may be the result of the harsh geographical environment of the Gobi and desert steppes. These species may be readily adaptable to container gardening due to their potential heat/drought tolerance (data not shown). They would not be adaptable for use as ground covers in areas with high rainfall (e.g., Beijing) because they are much taller and may lodge even to die when growing in fertile or wet soil conditions. Alpine plants, e.g. *C. oreastrum*, *C. hypargyrum*, and *A. khartensis* are highly adapted to growth in particularly harsh conditions, since they have evolved special characteristics in response to a particular combination of cool climate and strong winds and frequent fogs. Likewise they would not survive in high temperatures or low humidity conditions at lower elevations, especially in dry summers. Most genetic resources collected from harsh conditions resulted in poor performance at the low altitude of Beijing (data not shown). However, *A. achilleoides* and *A. fruticulosa* grow vigorously in the nursery next to our campus. Thus, these species may be readily adaptable to the cultural environments in Beijing. *C. hypargyrum* and

*C. oreastum* did not flower in the greenhouse and may require a cold treatment (vernalization) to flower. This trait is undesirable in commercial greenhouse and garden chrysanthemums (Anderson 2006). *P. salicifolium* (Mattf.) Muld. has not been flowering since being introduced to Beijing three years ago. *E. intricatum* (Franchet) Y. Ling et Y. R. Ling seems to become biennial in the nursery instead of annual in natural habit. *O. taihangensis* (Ling) Shih and *O. longilobus* Shih grow vigorously especially the former in the nursery.

### Propagation

Almost all the genetic resources are easy to vegetatively propagate by stem cutting except for the subshrubs from arid zones (which are seed-propagated). All of them are very easy to propagate by seed. We had multiplied *C. hypargyrum* (Yin and Zhao 2006) and *A. pallasiana* in tissue culture since they are so small being collected.

### Future directions

Among 33 species in the genera *sensu stricto* of *Ajania*, *Anthemis*, *Chrysanthemum*, *Crossostephium*, *Chrysanthemum*, *Leucanthemella*, *Nipponanthemum*, *Rhodanthemum*, and *Tanacetum* in *Chrysanthemum sensu lato*, 133 cross combinations have successfully produced F1 hybrid plants (Kondo et al. 2003). The hybrids from parents with very long distant relationship could not be further used in chrysanthemum breeding programs because of sterility. Hybridizing among the closest genera step by step might overcome the obstacles. We had produced successfully reciprocal intergeneric hybrids between *O. tianhangensis* and *C. lavandilifolium* after the intergeneric hybrids obtained between *A. pacifica* and three species of *Chrysanthemum* with different ploidy. Now we are trying to get the intergeneric or multi-generic hybrids among *Chrysanthemum*, *Ajania*, *Opisthopappus*, *Phaeostigma*, *Elachanthemum*, and *Brachanthemum*. Such focused efforts in this area will assure that future generations of chrysanthemum breeders will have access to much more intergeneric or multi-generic hybrids to be used in the creation of new flower colors, forms, and plant habits in facing of global warming.

**Table 2** Habitat and distribution of the genetic resources of chrysanthemums collected in China

Species	Habitat	Distribution <sup>a</sup>
<i>C. hypargyreum</i>	Meadows on mountain slopes; 1,400–3,900 m	<b>Shaanxi*</b> , Sichuan
<i>C. oreastrum</i>	Meadows; 1,800–3,000 m	<b>Hebei*</b> , <b>Jilin*</b> , Shanxi
<i>C. zawadskii</i>	Mountain slopes, streamsides, forest understories, grasslands, open places in forests; 800–1,800 m	<b>Anhui*</b> , Gansu, Hebei, Hubei, Heilongjiang, Jilin, Liaoning, Inner Mongolia, Ningxia, Shaanxi, Shandong, Shanxi, Sichuan, Zhejiang, [Mongolia, Russia]
<i>C. chanetii</i>	Grasslands, forest edges on mountain slopes, floodlands, by ditches; 300–2,700 m	<b>Hebei*</b> , Heilongjiang, Jilin, Liaoning, <b>Inner Mongolia*</b> , Ningxia, Shaanxi, Shandong, Shanxi, [Korea, Mongolia, Russia]
<i>C. naktongense</i>	Grasslands; 1,400–1,700 m	Gansu, <b>Hebei*</b> , Heilongjiang, Jilin, Liaoning, Inner Mongol, Shandong, Shanxi, [Korea, Mongolia, Russia]
<i>C. maximowiczii</i>	Mountain slopes, nearby lakes, sand dunes; 1,200–1,300 m	<b>Inner Mongolia*</b> , [Korea, Russia]
<i>C. mongolicum</i>	Rocky mountain slopes; 1,500–2,500 m	<b>Inner Mongolia*</b> [Mongolia, Russia]
<i>C. argyrophyllum</i>	On rocks of mountain slopes; 1,400–2,100 m	<b>Henan*</b> , Shaanxi
<i>C. rhombifolium</i>	Mountain slopes	<b>Chongqing*</b> (Wushan Xian)
<i>C. vestitum</i>	Low mountain slopes, hills; 300–1,500 m	<b>Anhui*</b> , <b>Henan*</b> , <b>Hubei*</b> , Shaanxi
<i>C. dichrum</i>	Mountain slopes	<b>Hebei*</b> (Neiqiu Xian)
<i>C. foliaceum</i>	Mountain slopes	<b>Shandong*</b> (Jinan City)
<i>C. glabrusculum</i>	Mountain slopes; 900–2,600 m	Shaanxi, <b>Sichuan*</b> , Yunnan
<i>C. indicum</i>	Grasslands on mountain slopes, thickets, wet places by rivers, fields, roadsides saline places by seashores, under shrubs; 100–2,900 m	Nearly throughout China—provinces: <b>Anhui*</b> , Fujian, Guangdong, Guizhou, Hebei, <b>Henan*</b> , <b>Hubei*</b> , Hunan, <b>Jiangsu*</b> , Jiangxi, Liaoning, Shaanxi, Shandong, Shanxi, <b>Sichuan*</b> , Taiwan, Yunnan, Zhejiang [India, Japan, Korea, Russia, Uzbekistan]
<i>C. lavandulifolium</i>	Mountain slopes, rocks, river valleys, river banks, wastelands, hilly lands	Gansu, Guizhou, <b>Hebei*</b> , <b>Henan*</b> , <b>Hubei*</b> , <b>Sichuan*</b> , Jiangsu, Jiangxi, Jilin, Liaoning, Inner Mongolia, Qinghai, Shaanxi, Shandong, Shanxi, Taiwan, Xinjiang, Yunnan, Zhejiang [India, Japan, Korea, Mongolia]
<i>C. nankingense</i>	Hilly lands, roadside, forest border	<b>Jiangsu*</b> , Anhui, Henan, Shaanxi, Zhejiang
<i>C. potentilloides</i>	Foothills of low mountains; 1,000–1,500 m	<b>Shanxi*</b> , Shaanxi
<i>Brachanthemum gobicum</i>	Gobi Desert	<b>Inner Mongolia*</b>
<i>B. mongolicum</i>	Gobi Desert	<b>Xinjiang*</b> [Mongolia]
<i>B. pulvinatum</i>	Mountain slopes, Gobi desert; 1,200–3,200 m	Gansu, <b>Inner Mongolia*</b> , Ningxia, Qinghai, Xinjiang.
<i>Ajania achilleoides</i>	Desert steppes, steppes	<b>Ningxia*</b> , <b>Inner Mongolia*</b> [Mongolia]
<i>A. khartensis</i>	Mountain slopes; 2,500–5,300 m	Gansu, Inner Mongolia, Ningxia, Qinghai, <b>Sichuan*</b> , Xizang, Yunnan [N India]
<i>A. fastigiata</i>	Steppes, semideserts, forest understories; 900–2,300 m	<b>Xinjiang*</b> [Afghanistan, Kazakstan]
<i>A. fruticulosa</i>	Deserts, desert steppes; 550–4,400 m	Gansu, <b>Inner Mongolia*</b> , Qinghai, Shaanxi, Xinjiang* Xizang [Kazakstan, Mongolia, Russia, Turkmenistan]
<i>A. pallasiana</i>	Thickets, mountain slopes; 200–2,900 m	Gansu, Heilongjiang, Jilin, Liaoning, <b>Shaanxi*</b> [Korea, Mongolia, Russia]
<i>P. salicifolium</i>	Mountain slopes, rocks, river valleys	<b>Ningxia**</b> , Gansu, Heilongjiang, Shaanxi, Hubei, Shichuan, Qinghai
<i>E. intricatum</i>	Deserts, desert steppes	<b>Ningxia*</b> , Inner Mongolia, Gansu, Qinghai, Xinjiang



**Table 2** continued

Species	Habitat	Distribution <sup>a</sup>
<i>O. longilobus</i>	Cliffs, mountain slopes	<b>Hebei*</b> , <b>Henan*</b> , <b>Shanxi*</b>
<i>O. taihangensis</i>	Cliffs, mountain slopes	<b>Henan*</b> , <b>Shanxi*</b>

<sup>a</sup> The locations where the germplasm resources were collected are in boldface and marked with an asterisk. The species introduced by colleagues with double asterisks

**Acknowledgements** This research was mainly supported by NSF of China (30271103), NSF of Beijing (6022014) and the main Project of Beijing Municipal Bureau of Landscape and Forestry (YIHH2008002) to HE. Zhao, Postgraduation Fund of BJFU to JL. Yin, and partially supported by NSF of China to GY. Rao, The Project of Science and Technology of Beijing (D0606003040191) to CL. Huang, Tenth Five Years Plan of National Program for Key Science and Technology Projects of China (2004BA525B1) to Q. X. Zhang.

## References

- Anderson N (2006) *Chrysanthemum*, *Chrysanthemum* × *grandiflora* Tzvelv. In: Anderson, N. (ed.) Flower breeding and genetics issues, challenges and opportunities for the 21<sup>st</sup> century. Springer, pp 389–437
- Anderson N, Gesick E (2003) Container production of prostrate garden chrysanthemums. *HortScience* 38(7):1344–1348
- Bremer K, Humphries CJ (1993) Generic monograph of the Asteraceae-Anthemideae. *Bull Nat Hist Mus Lond (Bot)* 23:71–177
- Chen JY, Wang SQ, Wang XC, Wang PW (1995) Thirty years' studies on breeding ground-cover chrysanthemum new cultivars. *Acta Hort* 404:30–36
- Dai S (1994) The comprehensive studies on the origin of modern chrysanthemums. Beijing Forestry University Doctoral Thesis
- De Jong J, Rademaker W (1989) Interspecific hybrids between two chrysanthemum species. *HortScience* 24:370–372
- Douzono M, Ikeda H (1998) All year round productivity of F1 and BC1 progenies between *Chrysanthemum grandiflorum* and *D. shiwogiku*. *Acta Hort* 454:303–310
- Dowrick GJ (1952) The chromosome of *Chrysanthemum* (I). *Heredity* 6:365–375
- Dowrick GJ (1953) The chromosomes of chrysanthemum (II). Garden varieties. *Heredity* 7(3):59–72
- Francisco-Ortega J, Santos-Guerra A, Hines A, Jansen RK (1997) Molecular evidence for a Mediterranean origin of the Macaronesian endemic genus *Argyranthemum* (Asteraceae). *Am J Bot* 84:1595–1613
- Fukai S (2003) *Dendranthema* species as *Chrysanthemum* genetic resources. *Acta Hort* 620:223–230
- Fukai S, Zhang W, Goi M (1998) Some *Dendranthema* species native to Japan. *Acta Hort* 454:85–90
- Fukai S, Nagira T, Goi M (2000) Cross compatibility between *Chrysanthemum* (*Chrysanthemum grandiflorum*) and *Chrysanthemum* species native to Japan. *Acta Hort* 508:337–340
- Kondo K, Abd El-Twab MH, Tanaka R (1999) Fluorescence in situ hybridization identifies reciprocal translocation of somatic chromosomes and origin of extra chromosome by an artificial, intergeneric hybrid between *Chrysanthemum japonica* × *Tanacetum vulgare*. *Chromosome Sci* 3:15–19
- Kondo K, Abd El-Twab MH, Idesawa R, Kimura S, Tanaka R (2003) Genome phylogenetics in *Chrysanthemum sensu lato*. In: Sharma AK, Sharma A (eds) Plant genome biodiversity and evolution, vol 1, Part A. Science Publishers, Enfield, NH, pp 117–200
- Li J, Chen SM, Chen FD, Fang WM (2008) Karyotype and meiotic analyses of six species in the subtribe Chrysantheminae. *Euphytica* 164:293–301
- Ling Y, Shih C (1983) Anthemideae, Flora Republicae Popularis Sinicae 76(1). Science Press, Beijing
- Nakata M, Hong D, Qiu J, Uchiyama H, Tanaka R, Chen X (1992) Cytogenetic studies on wild *Chrysanthemum sensu lato* in China. II. A natural hybrid between *Chrysanthemum indicum* (2n = 36) *D. vestitum* (2n = 54) from Hubei Province. *J Jpn Bot* 67:92–100
- Oberprieler C, Vogt R, Watson LE (2007) Anthemideae in Kubitzki. In: Kadereit JW, Jeffrey C (eds) The families and genera of vascular plants, vol 8, Asterales. Springer, New York, pp 342–374
- Ohashi H, Yonekura K (2004) New combinations in *Chrysanthemum* (Compositae-Anthemideae) of Asia with a list of Japanese species. *J Jpn Bot* 79:186–195
- Ohishi K, Hasegawa T, Itakura N, Kawai A (1996) Morphological characteristics and fertility of F1 hybrid of *Dendranthema grandiflora* and *Nipponanthemum nipponicum*. *J Japan Hort Soc* 65(Suppl.2):510–511
- Shibata M, Kawata J, Amano M, Kameno T, Yamagishi M, Toyoda T, Yamaguchi T, Okimura M, Uda M (1988) Breeding process and characteristics of Moonlight an interspecific hybrid between *Chrysanthemum morifolium* and *C. pacificum*. *Bull Nat Res Inst Veg Ornament Plant & Tea Ser A* 2:257–277
- Suzuki R, Kondo K, Peng C (2001) Chromosome studies in chrysanthemum flora of Taiwan. 2. *Ajania pacifica* (Nakai) Bremer et Humphries dwarf form, *Crossostephium chinense* (L.) M et Shih, akini, *Chrysanthemum arisanense* (Hayata) Ling *D. indica* (L.) Des Moul. and *D. lavandulifolia* (Fisch. ex Trautv.) Ling et Shih var. *tomentellum* (Hand.-Mazz.) Ling et Shih. *Chromosome Sci* 5:57–62
- Watson LE, Evans TM, Boluarte T (2000) Molecular phylogeny of tribe Anthemideae (Asteraceae), based on chloroplast gene *ndhF*. *Mol Phylog Evol* 15:59–69

- Yang WB, Glover J, Rao GY, Yang J (2006) Molecular evidence for multiple polyploidization and lineage recombination in the *Chrysanthemum indicum* polyploid complex (Asteraceae). *New Phytol* 171(4):875–886
- Yin JL, Zhao HE (2006) Tissue culture and rapid propagation of *Chrysanthemum hypargyrum* (Diels) Ling et Shih. *Plant Physiol Commun* 42(5):907
- Zhao HE (2000) The founding of the gene pool of *Chrysanthemum* and studies on the origin of garden chrysanthemum and the breeding of versatile ground cover chrysanthemum. Beijing Forestry University Doctoral Thesis
- Zhao HE, Wang XQ, Chen JY, Hong DY (2003) The origin of garden chrysanthemum and molecular phylogeny of chrysanthemum species based on nrDNA ITS, and intergenic spacers between *trnT-trnL*. *Plant Mol Breed* 1(5/6):597–604
- Zhao HB, Chen FD, Guo WM, Chen SM, Wu GS, Fang WM, Ren GB (2007) Phylogenetic analysis of tribe Anthemideae (Asteraceae) from east Asia based on ITS and cpDNA *trnL/trnF* IGS sequence. Abstracts of International workshop on Chrysanthemum 2007 of China, pp 30–32
- Zhou S (1992) Cytological and morphological studies on *Chrysanthemum* species. Peking University Master's Thesis