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Chromosome variation in the genus *Pinellia* (Araceae) in China and Japan

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The chromosome numbers of 23 populations belonging to seven species of *Pinellia* Tenore were counted. The basic chromosome number of all the species studied was $x = 13$, and the previously reported basic numbers $x = 9$ and $x = 14$ in *P. ternata* and *P. cordata* were not confirmed. Chromosome numbers of $2n = 26$ in *P. polyphylla* and $2n = 78$ in *P. integrifolia* are reported for the first time. Heptaploid ($7x$) and nonuploid ($9x$) are new ploidy levels reported for *P. ternata*, and hexaploid for *P. cordata*. Taxonomic, phylogenetic and phytogeographical inferences are made for the genus. Particular attention was given to *P. ternata*, the most widely distributed species in the genus, and considerable variation of chromosome number was found in its different populations. Based on chromosome studies of 11 populations of *P. ternata*, together with 12 populations reported in previous studies, the lower reaches of the Yangze River are identified as its centre of origin. From there it dispersed, with generation of hexaploid, heptaploid, octoploid and nonuploid forms.

ADDITIONAL KEYWORDS: cytotaxonomy – evolution – polyploidy.

INTRODUCTION

Pinellia Tenore is a small eastern Asian genus of the Araceae (Mayo, Bogner & Boyce, 1997; Fig. 1). As *P. yaoluopingensis* X. H. Guo & X. L. Liu has been combined with *P. ternata* (Thunb.) Breit. (Yi, 2002), it now includes only seven perennial herbaceous species. *Pinellia ternata* is disjunctively distributed from China to Korea and Japan, and *P. tripartita* (Blume) Schott is disjunctively distributed from Hong Kong to Japan (Li, 1979, 1996); there are five other Chinese endemic species. *Pinellia ternata* is widespread over the full distribution area of the genus. *Pinellia ternata* and *P. tripartita* are naturalized in Europe, North America and Australia. The centre of distribution is in central and eastern China (Yi, 2002). All *Pinellia* species are seasonally dormant herbs growing in woodlands and forests, on rocks with dripping water or among crops as weeds (e.g. *P. ternata*). They are important traditional Chinese medicinal plants and were recorded in Chinese herb classics more than 2000 years ago (Li, 1976). They have been used for the treatment of viper bites, lumbago, allergic reaction, and externally to treat traumatic injury, abscesses, neck lymphosarcoma, breast mastitis and uterine cancer (Li, 1976; Luo & Zhou, 1979).

Pinellia is characterized by a number of morphological characters, including perennial herbaceous habit, petioles sometimes with bulbils, persistent spathes constricting between tubes and blades, monoecism, long smooth sterile appendix, with a female zone adnate to spathes, orthotropous ovaries, and the oblong–ovoid berry-like green fruits. As a small genus with only seven species, *Pinellia* displays a great diversity in morphology and habitat: the petiole may bear bulbils (*P. ternata*, *P. cordata*) or not (other species); the leaf blades are simple, cordate, ovate or oblong (*P. integrifolia*, *P. cordata*, *P. peltata*, *P. polyphylla*); deeply tripartate (*P. tripartita*); trifoliolate, in 3–5 leaflets (*P. ternata*); pedate (*P. pedatisecta*). Morphological diversity occurs among the simple-leaved species, e.g. *P. peltata* has peltate leaves whereas *P. polyphylla* and *P. cordata* have

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deeply cordate leaf blade bases and *P. integrifolia* has obtuse or shallowly cordate leaf blade bases. Spathes of *P. pedatisecta* are lanceolate in general, without constriction between tubes and blades and no transverse septum, which makes it distinct from all of other species of the genus. *P. cordata* and *P. integrifolia* are distributed in moist locations, sometimes growing on rocks with dripping water, whereas other species are heliophilic and semi-heliophilic.

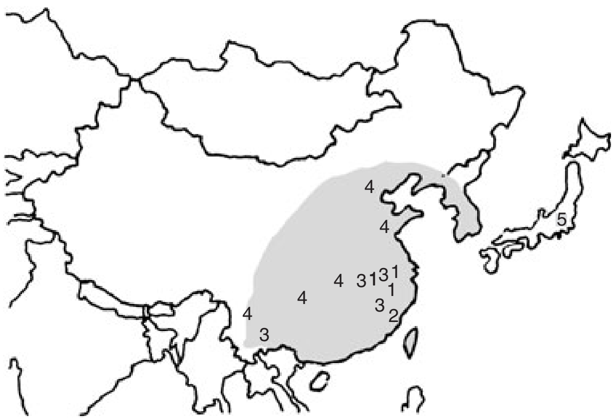


Figure 1. Distribution of *Pinellia* (grey shading). Numbers 1–5 represent different ploidy levels of *P. ternata* and their localities. 1, $2n = 2x = 26$; 2, $2n = 6x = 78$; 3, $2n = 7x = 91$; 4, $2n = 8x = 104$; 5, $2n = 9x = 117$.

Chromosome studies on *Pinellia* began in the early 1940s (Kurakubo, 1940; Ito, 1942; Malvesin-Fabre, 1945; Huttoleston, 1955; Jones, 1957; Marchant, 1972; Li & Xu, 1986; Guo & Zhuang, 1988; Gu & Xu, 1991; Li, 1995, 1999; Table 1). According to the literature, the genus has three basic chromosome numbers, $x = 9$, 13 or 14. *Pinellia ternata* has been reported to have two basic chromosome numbers, $x = 9$ and 14 (Huttoleston, 1955; Gu & Xu, 1991; Li, 1995; Li, Gu & Liu, 1997) and *P. cordata* has two basic numbers, $x = 9$ and 13 (Li, 1995; Li *et al.*, 1997). In addition to the different basic numbers reported for *P. ternata*, several ploidy levels have been found previously in this species and some populations were reported to be aneuploid (Ito, 1942; Malvesin-Fabre, 1945; Marchant, 1972). Therefore, further chromosome studies of the genus are necessary to resolve these problems.

In this study, all of the seven species of *Pinellia* are surveyed, based on 23 representatives, including 11

Table 1. Cytological data of *Pinellia* available in the literature

Species	Author	2*n*	*x*	Localities
P. cordata N. E. Brown	Li (1995)	26	13	China, Jiangxi, Lushan
	Li *et al*. (1997)	72	9	China, Anhui, Tianmushan
P. pedatisecta Schott	Jones (1957)	26	13	?
	Marchant (1972)	26	13	Strasbourg Bot. Gard. (Cult.)
	Marchant (1972)	26	13	(Cult.)
	Li & Xu (1986)	26	13	China, Shanghai (Cult.)
	Guo & Zhuang (1988)	26	13	?
	Li (1995)	26	13	China, Hubei (Cult.)
	Li *et al.* (1997)			China, Jiangsu, Nanjing
P. peltata P'ei	Li *et al.* (1997)	78	13	China, Zhejiang, Yandangshan
P. ternata Ten. ex Breitenb.	Ito (1942)	116	?	?
	Malvesin-Fabre (1945)	28	14	?
	Malvesin-Fabre (1945)	128	?	?
	Huttoleston (1955)	28	14	?
	Marchant (1972)	115	?	Anley
	Gu & Xu (1991)	72	9	China, Chongqing
	Li (1995)	28	14	China, Hubei, Shennujia
	Li *et al.* (1997)	54	9	China, Anhui, Shitai
	Li *et al.* (1997)	72	9	China, Anhui, Yaoluoping
P. tripartita (Blume) Schott	Kurakubo (1940)	26	13	Japan, Tokyo
	Ito (1942)	52	13	Japan
	Jones (1957)	52	13	Japan
	Marchant (1972)	52	13	Uppsala Bot. Gard. (Cult.)
P. yaoluopingensis Guo & Liu	Gu & Xu (1991)	26	13	China, Anhui, Yuexi
	Li *et al.* (1997)	26	13	China, Anhui, Jingde
	Li *et al.* (1997)	26	13	China, Jiangsu, Nanjing

populations of *P. ternata*, five of *P. pedatisecta*, two of *P. cordata* and one of each of the other species. This is the first comprehensive cytogenetic study of the genus, including *P. integrifolia* and *P. polyphylla*, for which there are no known previous reports of chromosome number. The objective was to study as many populations as possible, in particular of interesting cases such as *P. ternata*. With regard to *P. polyphylla*, *P. tripartita*, *P. peltata* and *P. integrifolia*, only one population of each has been investigated because of their limited areas of distribution.

MATERIAL AND METHODS

Accessions are listed in Table 2 with collection information. Voucher specimens are deposited in the herbarium of the Kunming Institute of Botany, the Chinese Academy of Sciences, Kunming, Yunnan, People's Republic of China (KUN).

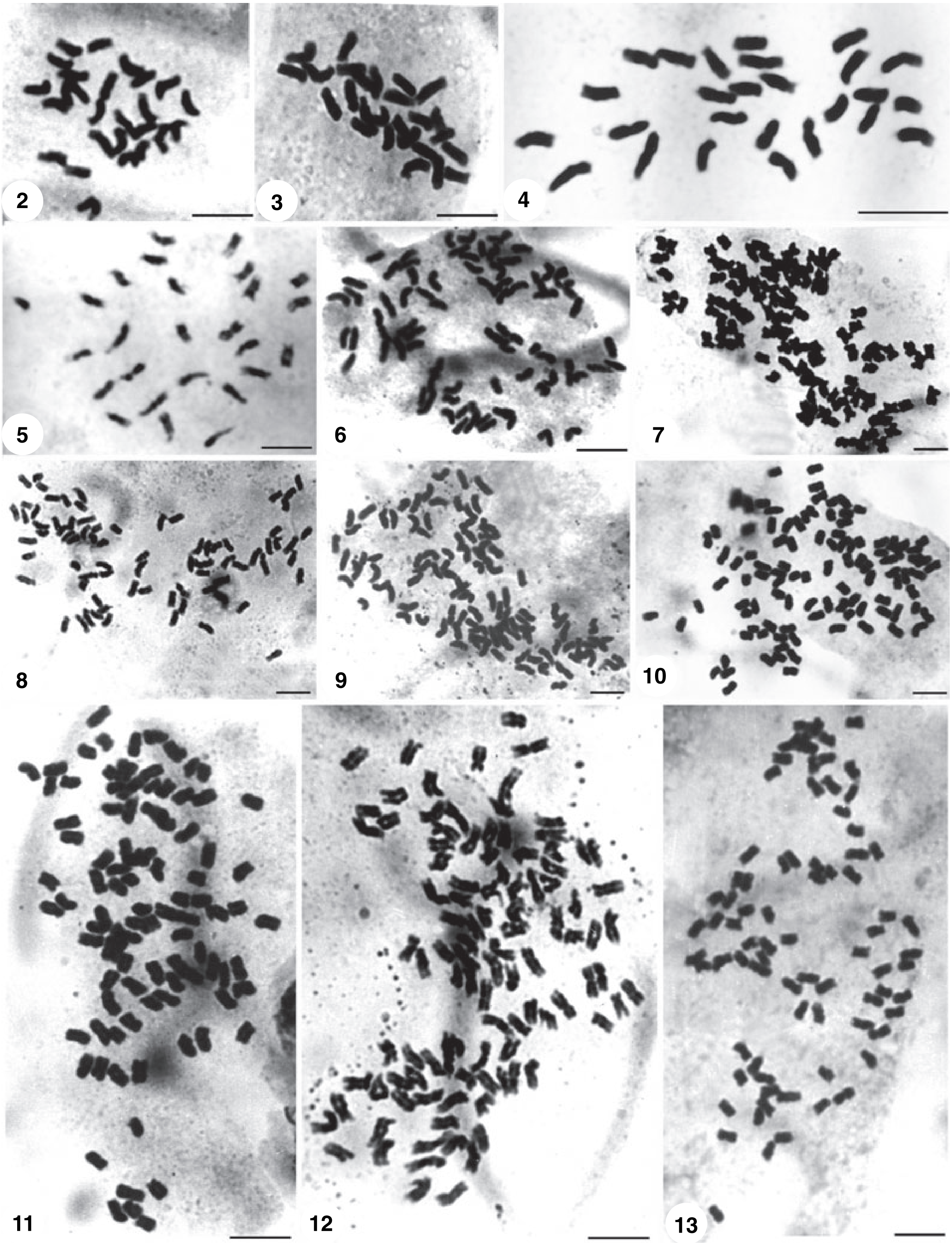
For observation of somatic chromosomes, root tips were pretreated in 0.1% colchicine at room temperature for 2–3 h before being fixed in Carnoy's solution (glacial acetic acid/95% ethanol 1 : 3) at 4 °C for 30 min. Then the fixed material was macerated in 1 N HCl at 60 °C for 5 min and stained and crushed in 1% aceto-orcein before observation. For each population at least five chromosome counts were made.

RESULTS

The chromosome numbers obtained are shown in Table 2 and Figures 2–17. All populations were found to have the basic chromosome number $x = 13$. Five populations of *P. pedatisecta* were studied, all diploids with $2n = 26$ (Fig. 5). *P. peltata* occupies a very small area of Fujian and Zhejiang provinces of China. The chromosome number was $2n = 78$, a hexaploid, which agrees with studies by Li *et al.* (1997) on material from the same locality (Fig. 8). *Pinellia polyphylla* is an endemic species of Sichuan Province. Its chromosome number is reported here for the first time as $2n = 26$, a diploid (Fig. 4). *Pinellia integrifolia* is endemic to the Hubei and Sichuang provinces with very restricted distribution. The chromosome number is reported here for the first time as $2n = 78$, a hexaploid (Fig. 11). *Pinellia cordata* is widely distributed in Anhui, Zhejiang, Jiangxi, Fujian, Hubei, Hunan, Guangdong, Guangxi and Guizhou provinces, but populations were sampled from only two locations. One population proved to be diploid with $2n = 26$ (Fig. 2) and the other hexaploid, $2n = 78$. The diploid number $2n = 26$ found by Li (1995) is confirmed by our results, but we do not agree with Li *et al.* (1997), who found $2n = 72$, with $x = 9$. *Pinellia tripartita* is disjunctively distributed from Hong Kong to Japan. However, we were able to sample material only from Japan. We obtained

Table 2. Chromosome numbers of all species of *Pinellia* ($x = 13$), with localities and vouchers

Species	$2n$	Ploidy	Localities	Voucher
P. cordata N. E. Brown	26	$2x$	Japan, Tokyo	Yi 086
	78	$6x$	China, Anhui, Huangshan	Yi 085
P. integrifolia N. E. Brown	78	$6x$	China, Sichuan, Xuyong	Yi 027
P. pedatisecta Schott	26	$2x$	China, Anhui, Yuexi	Yi 018
	26	$2x$	China, Beijing	YI 082
	26	$2x$	China, Hubei, Wuhan	Yi 022
	26	$2x$	Chian, Shandong, Mengyin	Yi 015
	26	$2x$	China, Yunnan, Kuming	Yi 083
P. peltata P'ei	78	$6x$	China, Zhejiang, Yandangshan	Yi 012
P. polyphylla S. L. Hu	26	$2x$	China, Sichuan, Ganluo	Yi 030
P. ternata Ten. ex Breitenb.	78	$6x$	China, Fujian, Jinjishan	Yi 006
	91	$7x$	China, Anhui, Yuexi	Yi 032
	91	$7x$	China, Hubei, Wuhan	Yi 020
	91	$7x$	China, Yunnan, Kunming	Yi 003
	104	$8x$	China, Beijing	Yi 054
	104	$8x$	China, Chongqing	Yi 025
	104	$8x$	China, Fujian, Wuyishan	Yi 010
	104	$8x$	China, Hubei, Yichang	Yi 019
	104	$8x$	China, Shandong, Mengyin	Yi 014
	104	$8x$	China, Yunnan, Lijiang	Yi 086
	117	$9x$	Japan, Tokyo	Yi 084
P. tripartita (Blume) Schott	26	$2x$	Japan, Tokyo	Yi 048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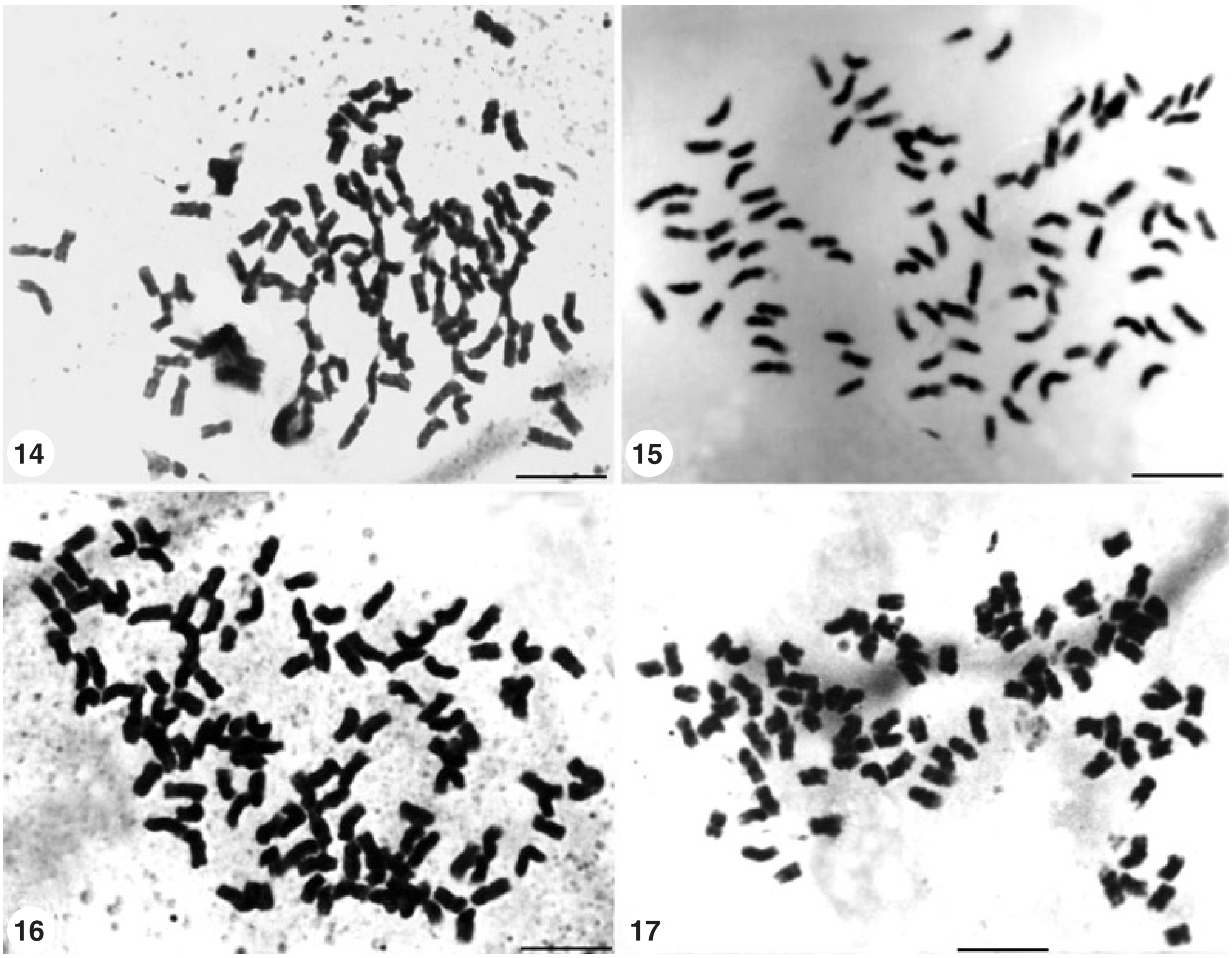
Figures 2–13. Metaphase chromosomes in species of *Pinellia*. Scale bars = 10 µm. Fig. 2. *P. cordata*, $2n = 26$ (Japan, Tokyo). Fig. 3. *P. tripartita*, $2n = 26$ (Japan, Tokyo). Fig. 4. *P. polyphylla*, $2n = 26$ (China, Sichuan, Ganluo). Fig. 5. *P. pedatisecta* $2n = 26$ (China, Yunnan, Kunming). Fig. 6. *P. ternata*, $2n = 78$ (China, Fujian, Fuzhou). Fig. 7. *P. ternata*, $2n = 104$ (China, Yunnan, Lijiang). Fig. 8. *P. peltata*, $2n = 78$ (China, Zhejiang, Yandangshan). Fig. 9. *P. ternata*, $2n = 104$ (China, Fujian, Wuyishan). Fig. 10. *P. ternata*, $2n = 104$ (China, Hubei, Yichang). Fig. 11. *P. integrifolia*, $2n = 78$ (China, Sichuan, Xuyong). Fig. 12. *P. ternata*, $2n = 104$ (China, Shandong, Mengyin). Fig. 13. *P. ternata*, $2n = 91$ (China, Hubei, Wuhan).



Figures 14–17. Metaphase chromosomes in *Pinellia ternata*. Scale bars = 10 µm. Fig. 14. $2n = 104$ (China, Chongqing). Fig. 15. $2n = 91$ (China, Yunnan, Kunming). Fig. 16. $2n = 117$ (Japan, Tokyo). Fig. 17. $2n = 91$ (China, Anhui, Yuexi).

$2n = 26$, a diploid (Fig. 3). All the cytological studies of *P. tripartita*, including ours, have used material from Japan and diploid and tetraploid cytotypes are known. This shows that the species has some degree of divergence in Japan. Eleven representative populations of *P. ternata* were collected over its distributional area. Hexaploid, heptaploid, octoploid and nonuploid were obtained, the results supporting a basic chromosome number of $x = 13$ (Figs 6, 7, 9, 10, 12–17).

DISCUSSION

The basal position of *P. pedatisecta* inferred from chromosomal evidence

All polyploids must ultimately come from diploids and only a few exceptions such as *Saccharum*, *Poa* and *Rubus* have been proved to reduce their ploidy level by failure of fertilization (Darlington, 1956; Raven, 1975; Stace, 2000). All of 12 studied populations of *P. pedatisecta* were diploid ($2n = 26$), but most other species of this genus have polyploid populations, so we suspect that this species might represent the basal lineage of the genus. This is contrary to the results of Li (1999), who considered *P. pedatisecta* to be the most highly derived species of the genus, but is congruent with results from floral organogenesis and molecular phylogeny (T. Yi, unpubl. data).

The distribution pattern of *P. ternata* inferred from chromosome numbers

Pinellia ternata occupies the widest distributional area of any species in the genus and exhibits the most highly divergent morphological characters. With data from the literature taken into consideration, chromosome numbers of 23 populations of this species have been counted and different ploidy levels have been found. Polyploids have been shown in some taxa to have a special faculty for breaking across ecological or geographical barriers are closed to their diploid parents and for colonizing new habitats. A gradual increase of polyploidy occurs as these plants move in different directions from their centre of origin (Stern, 1949; Janaki Ammal, 1950, 1954; Darlington, 1956). Using cytological information, we can easily locate the origin centre and its distribution pattern (Fig. 1, only populations with the basic chromosome number of $x = 13$ are shown on the map). Diploids were found only in Jiangxi and Anhui provinces, perhaps including Hubei Province, where Li (1995) found a $2n = 28$ population with the base number of $x = 14$. The lower reaches of the Yangtze River are therefore suggested to be the original centre of the species. From there, it has spread: southwards, generating the hexaploid and heptaploid in Fujiang Province; north-eastwards, where octoploids are found in Shandong Province and Beijing, and it reaches its highest ploidy levels in Japan; north-westwards, with heptaploids found in Wuhan and Yi Chang of Hubei Province and octoploids in Chongqing; westwards, with heptaploids in Kunming and octoploids in Lijiang of Yunnan Province. The diploid populations of most species of *Pinellia* are distributed mainly in central and eastern China (Tables 1, 2), which suggests these areas may be the original centre of the genus.

Wide polyploidy level differences found in *P. ternata* make it an ideal model for the investigation of the mode of polyploidization and speciation. Molecular markers have been applied to identify the nature of polyploid speciation (Grant, 1981; Sang, Crawford & Stuessy, 1997; Soltis & Soltis, 2000; Wendel, 2000). Similar work is required to clarify the nature of polyploidization in *P. ternata*.

The basic chromosome number of *Pinellia*

Chromosome studies on 11 populations of *P. ternata* have revealed all to have basic chromosome number $x = 13$, although it was previously reported to have $2n = 28$ ($x = 14$) by Huttoleston (1955) and Li (1995), $2n = 54$ ($x = 9$) by Li *et al*. (1997), $2n = 72$ ($x = 9$) by Gu & Xu (1991) and Li *et al*. (1997) and $2n = 116$, 128, 115 by Ito (1942), Malvesin-Fabre (1945) and Marchant (1972), respectively, which do not fit any of the above base numbers. The base numbers $x = 9$ and 13 were reported for *P. cordata* (Li, 1995; Li *et al*., 1997). Different base numbers in single species have been found in a few cases (Hollings & Stace, 1974; Khan & Stace, 1999; James, Wurzell & Stace, 2000). If identification was correct and chromosome counting techniques were accurate in these previous reports, it is clear that *Pinellia* is a genus with different polyplotypes within some of its species. Our results found that all species of *Pinellia* have the base number $x = 13$, which is at variance with many of the reports given above. Cytological studies of more populations of *P. ternata* and *P. cordata* are required to verify our results.

Polyploidization in *Pinellia*

Polyploidy is an important cytogenetic process affecting the evolution of higher plants (Stebbins, 1971; Grant, 1981; Masterson, 1994). Somatic and gametic doubling have been suggested to be two major routes of polyploid formation (Ramsey & Schemske, 1998). Gametic non-reduction is also suggested as the predominant mechanism of polyploid formation in angiosperms through either one-step or triploid-bridge stages (Briggs & Walters, 1969; Harlan & de Wet, 1975; Bretagnole & Thompson, 1995). However, somatic doubling in meristem tissue has been observed in some plants (D'Amato, 1952, 1964; Lewis, 1980). All the species of *Pinellia* except *P. pedatisecta* and *P. polyphylla* were found to have polyploid populations, often with high ploidy levels, with some populations of *P. ternata* being aneuploid (Tables 1, 2). Polyploidy has thus played an important role in evolution and speciation of *Pinellia*. The limited information on polyploid evolution in the genus deserves further research. A high frequency of polyploidy occurs in perennial herbs with vegetative reproduction by rhizomes or stolons (Stebbins, 1971). All the species of *Pinellia* can propagate by tubers or rhizomes, and some by bulbils, which might provide an explanation for the diverse polyploidy levels found in this genus, as well as the aneuploids occurring in some populations of *P. ternata*.

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