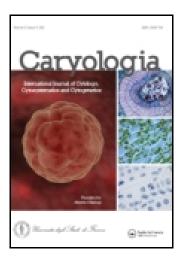
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Chromosome numbers and polyploidy in Leontopodium (Asteraceae: Gnaphalieae) from the Qinghai-Tibet Plateau of S.W. China

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Chromosome numbers and polyploidy in *Leontopodium* (Asteraceae: Gnaphalieae) from the Qinghai-Tibet Plateau of S.W. China

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Leontopodium R. Br. ex Cass. is the second largest genus within the Asian Gnaphalieae (Asteraceae) and is most diversified on the Qinghai-Tibet Plateau and its adjacent areas of SW China. The chromosome numbers and karyomorphology of five species from this region were investigated for the first time: Leontopodium sinense (2n=28=22m+6sm), L. muscoides (2n=24=22m+2sm), L. souliei (2n=52=32m+20sm), L. pusillum (2n=72=52m+20sm), and L. nanum (2n=48=24m+24sm). The results suggest that the basic chromosome number of Leontopodium is x=14, followed with dysploidy numbers (e.g. x=12, 13). Polyploidization has also played an important role in the evolution of Leontopodium in this region.

Keywords: chromosome number; Gnaphalieae; Leontopodium; polyploidy; Qinghai-Tibet Plateau

Introduction

The tribe Gnaphalieae (paper daisies) of the family Asteraceae (or Compositae) contains c.185 genera and 1240 species distributed on most continents (Anderberg 1991; Bayer et al. 2007). They are most diverse in South Africa and Australia, with only two genera well diversified in Asia (Anaphalis DC. and Leontopodium R. Br. Ex Cass). Anaphalis is the largest genus within the Asian Gnaphalieae and Leontopodium is the second largest, comprising 30-41 species (Blöch et al. 2010; Safer et al. 2011). The main distribution of the genus is central and eastern Asia, including Russia, Japan, South Korea, Mongolia, China and the Himalayas to the borders of Afghanistan and Pakistan, with two species extending to Europe. Results based on AFLP (Amplified Fragment Length Polymorphism) suggest that the south-west of China is the centre of diversity and perhaps also the origin area of the genus (Safer et al. 2011). Molecular data also indicate that the monophyly Leontopodium (including Sinoleontopodium) is a characteristic Sino-Himalayan element that appears to have found its way into the mountains of Europe in geologically recent times (Anderberg 1991; Blöch et al. 2010).

Polyploidy is common in plants of cold climates with harsh and stressful environments (Löve and Löve 1949, 1967; Grant 1981). The Qinghai-Tibet Plateau has extreme elevation ranges compressed over short distances, largely because of the collision of India with Eurasia (Zhang et al. 1984; Dewey et al. 1988; Wen

1999). This alpine region has been designated a Himalayan biodiversity hotspot because of its high species richness and endemism (Myers et al. 2000). A high rate of polyploidy could be expected in this region because of the unusually high species diversity and endemism, the widespread alpine environment, and the importance of polyploidy in plant evolution. However, Nie et al. (2005) indicated that polyploidy may have played only a minor role in the evolutionary diversification in the region. More data need to be accumulated for a better understanding of chromosomal evolution of plants from this interesting region.

The chromosome number and karyology of six species in *Leontopodium* has been reported, mainly from the western Himalayan region, with the reported chromosome numbers of n = 12, 14 or 2n = 26, 48, 49, 52 and 73 (Siljak 1977; Krogulevich 1978; Murin and Paclova 1979; Zhukova 1980; Nishikawa 1985; Vir Jee and Kachroo 1985; Khatoon and Ali 1988). However, no cytological reports have been performed on *Leontopodium* from the Sino-Himalayas, especially the Qianghai-Tibet Plateau. The present study aims at broadening our karyological knowledge of *Leontopodium* species of the Qinghai-Tibet Plateau and investigating whether polyploidy plays an important role in this genus.

Materials and methods

Seeds were collected representing five species of *Leonto-podium* (Table 1). Voucher specimens are deposited in

Table 1. Locality, geographical position, altitude and voucher number of the investigated species of Leontopodium.

Taxon	Locality	Position	Altitude (m)	Voucher
Leontopodium sinense Hemsl.	Zuogong, Tibet	29°55′ N, 97°26′ E	4350	Sunh-07zx-0652
Leontopodium muscoides (Hook. f. et Thoms.) HandMazz.	Mangkang, Tibet	29°54′ N, 98°36′ E	4000	Sunh-07zx-1732
Leontopodium souliei Beauv.	Zuogong, Tibet	29°31′ N, 97°56′ E	3710	Sunh-07zx-2098
Leontopodium pusillum HandMazz.	Naqu, Tibet	30°46′ N, 90°57′ E	4715	Yangyp-Q-0152
Leontopodium nanum (Hook. f. et Thoms.) HandMazz.	Dangxiong, Tibet	30°49′ N, 91°08′ E	4653	Yangyp-Q-1000

the Herbarium of Kunming Institute of Botany (KUN). All cytological observations were made from root tips. Seeds were stored at 4°C, soaked overnight in distilled water at room temperature, and germinated on wet filter paper in Petri dishes. Fresh root tips c.1 cm long were cut, pretreated in 0.003 M 8-hydroxyquinoline solution at 22–23°C in the dark for 6–8 h, then fixed with Carnoy's fluid (1:3 glacial acetic acid/absolute alcohol) at approximately 4°C for 2–5 h. They were then placed in 70% ethanol for 10 min and rinsed in distilled water twice for c.20 min. Prior to staining, the root tips were hydrolysed in 1:1 1N HCl:45% acetic acid at 60°C for 30 s, stained with 1% aceto-orcein overnight, and squashed for cytological observation. Permanent slides were made using the standard liquid nitrogen method.

Observations were made of somatic mitotic interphase, prophase and metaphase. Karyomorphological classification of the mitotic interphase nuclei and prophase chromosomes follows Tanaka (1971, 1977, 1987), the designation of the centromeric position as median region (m) or submedian region (sm) follows Levan et al. (1964) and the karyotype asymmetry is classified according to Stebbins (1971).

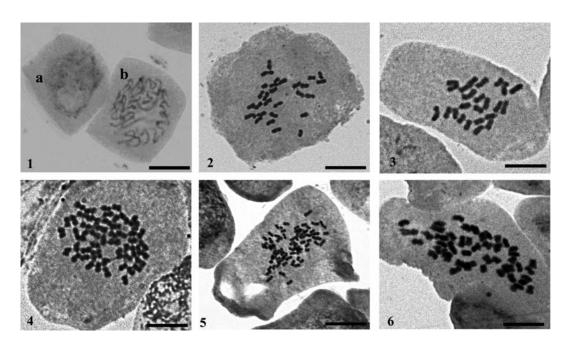
Results

The interphase nuclei of *Leontopodium* can be categorized based on their shapes and the distribution patterns of chromatin. The chromatin has an almost homogeneous distribution throughout the nucleus, forming a fibrous network of the chromonemata (Figure 1a). According to the system of Tanaka (1971, 1977), it can be categorized as a diffuse type.

The chromosomes at mitotic prophase stain darkly and homogeneously, showing several small elastic constrictions (Figure 1b). There were no conspicuously heterochromatic or euchromatic segments in five species. Using the system of Tanaka (1971, 1977, 1987), the prophase chromosomes of *Leontopodium* are classified as an interstitial type. Brief descriptions of the karyotypic features of each species are given below.

Leontopodium sinense Hemsl.

The species is endemic to China. Its chromosome number is 2n=28. It consists of 22 median (m), and six submedian (sm) chromosomes. The ratio of the longest to the shortest chromosomes is 2.21 and the karyotype symmetry is 2B (Tables 2 and 3; Figures 2 and 7A).



Figures 1–6. Mitotic nuclei and metaphase chromosomes of *Leontopodium*. (1a) Mitotic interphase nuclei; (1b) mitotic prophase; (2) L. sinense, 2n = 28; (3) L. muscoides, 2n = 24; (4) L. souliei, 2n = 52; (5) L. pusillum, 2n = 72; (6) L. nanum, 2n = 48. Scale bar = 5 μ m.

Dangxiong, Tibet

Present study

-					
Taxon	Number	Karyotype formula (2n)	KA	Locality	Data source
L. alpinum	48/2 <i>n</i>	_	_		Siljak (1977)
•	52/2n	_			Murin and Paclova (1979)
L. hayachinense	73/2n	_	_	Hokkaido, Japan	Nishikawa (1985)
L. jacotianum	12,14/n	_		Pakistan	Khatoon and Ali (1988)
L. kurilense	48/2n	_	_	Chukotka, Russia	Zhukova (1980)
L. leontopodium	26/2n	_		Kashmir Himalaya	Vir Jee and Kachroo (1985)
L. ochroleucum	49/2n	_	_	Eastern Sayan Mt.	Krogulevich (1978)
L. sinense	28/2n	22m + 6sm	2B	Zuogong, Tibet	Present study
L. muscoides	24/2n	22m + 2sm	1A	Mangkang, Tibet	Present study
L. souliei	52/2n	32m + 20sm	1A	Zuogong, Tibet	Present study
L. pusillum	72/2n	52m + 20sm	2B	Nagu, Tibet	Present study

24m + 24sm

2B

Table 2. Somatic chromosome number (2n), karyotype formula (2n), karyotype asymmetry (KA), locality, and data source of *Leontopodium* examined in this and previous reports.

Leontopodium muscoides Handel-Mazzetti.

48/2n

The species is endemic to the Qinghai-Tibet Plateau with chromosome number firstly reported as 2n = 24. The ratio of the longest to the shortest chromosomes is 1.79 and the karyotype symmetry is type 1A. It consists of 22 m and two sm chromosomes (Tables 2 and 3; Figures 3 and 7B).

Leontopodium souliei Beauverd.

L. nanum

The species is endemic to the Qinghai-Tibet Plateau with chromosome number firstly reported as 2n = 52. The ratio of the longest to the shortest chromosomes is 1.75 and the karyotype symmetry is type 1A. It consists of 32 m and 20 sm chromosomes (Tables 2 and 3; Figures 4 and 7C).

Leontopodium pusillum Hand.-Mazz.

This is the first time that 2n = 72 has been reported for this species, which is mainly distributed in the Qinghai-Tibet Plateau, extending to the north of Sikkim. The ratio of the longest to the shortest chromosomes is 2.35 and the karyotype symmetry is type 2B. It consists of 52 m and 20 sm chromosomes (Tables 2 and 3); Figures 5 and 7D).

Leontopodium nanum (Hook. f. et Thoms.) Hand.-Mazz.

This species is restricted into the Qinghai-Tibet Plateau with a chromosome number of 2n=48. The ratio of the longest to the shortest chromosomes is 2.00 and the karyotype symmetry is type 2B. It consists of 24 m and 24 sm chromosomes (Tables 2 and 3; Figures 6 and 7E).

Discussion

Most genera of the Gnaphalieae have chromosome numbers that are multiples of 7 (Merxmüller et al. 1977; Anderberg 1994; Watanabe et al. 1999). However, n=14 or 2n=28 is the most frequent number in the tribe and Watanabe et al. (1999) suggested x=14 as the possible base number of the tribe. In *Leontopodium*, the chromosome number were reported as n=12, 14 or 2n=26, 48,

49, 52, 73 (Siljak 1977; Krogulevich 1978; Murin and Paclova 1979; Zhukova 1980; Krasnikova et al. 1984; Nishikawa 1985; Vir Jee and Kachroo 1985; Khatoon and Ali 1988), and our results are 2n=24, 28, 48, 52 and 72. Three species have the basic chromosome number x=12, with L. muscoides being diploid, L. nanum tetraploid, and L. pusillum hexaploid. Different chromosome basic numbers are also observed in another two species, L. sinense (2n=2x=28) and L. souliei (2n=4x=52), with x=14 and 13. The molecular data support Leontopodium, Filago, Antennaria and Gamochaeta forming the "FLAG clade" with a base chromosome number of x=14, which have an allopolyploid origin (Galbany-Casals et al. 2010; Smissen et al. 2011). The other number, x = 12 and 13 probably are the results of secondary reduction. This is consistent with previous suggestions of secondary chromosome number reduction in Gnaphalieae (Watanabe et al. 1999) particularly Podolepis Labill. (Konishi et al. 2000), in which n=12, 11,10, 9, 8, 7 and 3 were reported.

Interspecific polyploidy in the Gnaphalieae has played an important role in the evolution of many genera (Watanabe et al. 1999). In *Leontopodium*, polyploidy has been reported in four species (Siljak 1977; Krogulevich 1978; Murin and Paclova 1979; Zhukova 1980; Nishikawa 1985). Three out of the five counts are observed to be tetraploidy (*L. souliei*, *L. nanum*) or hexaploidy (*L. pusillum*) in this report (Table 2). It seems that polyploidy has probably played a relatively important role in the chromosome evolution of *Leontopodium*.

Dysploidy is observed in *Leontopodium*, and was supposed to take place in *Leontopodium* during its adaptation to different habitats. Dysploidy is common in many genera of Asteraceae, e.g. *Centaureinae*, *Artemisia* and *Cousinia* (Garcia-Jacas et al. 1996; Vallès et al. 2001; Vallès and Kapustina 2001; Zhao et al. 2009; Susanna et al. 2003; Ghaffari et al. 2006; Djavadi and Attar 2010).

Karyomorphology and karyotype are also reported for the first time for *Leontopodium*. All species show similar karyotypic asymmetry of 1A and 2B (Table 2). Karyotype asymmetry is one of the important standards

Table 3. Karyomorphological parameters of studied Leontopodium species. Chromosome pairs are assigned Arabic numerals.

Londopodifium striteous 2.00 (1959) Incomposedifium striteous 1.50 (1959) (1950) <th>Pair no. RL</th> <th>AR</th> <th>CI</th> <th>Type</th> <th>Pair no.</th> <th>RL</th> <th>AR</th> <th>CI</th> <th>Type</th>	Pair no. RL	AR	CI	Type	Pair no.	RL	AR	CI	Type
526 155 0.39 nm 1 2.56 182 0.36 371 125 0.44 m 1 2.54 182 0.36 371 125 0.44 m 4 2.34 167 0.44 371 125 0.44 m 4 2.24 155 0.44 371 125 0.44 m 4 2.24 155 0.45 371 125 0.44 m 6 2.08 133 0.45 370 126 0.40 m 10 2.05 133 0.45 330 150 0.44 m 10 2.05 133 0.45 330 150 0.44 m 10 2.05 133 0.45 330 150 0.44 m 11 1 1.05 1.04 330 150 0.44 m 12 1.05 1.33 0.45					Leontopodium so				
592 2.17 0.32 8m 2.34 1.67 0.38 571 1.25 0.44 m 4 2.24 1.67 0.38 571 1.25 0.44 m 6 2.05 1.35 0.43 571 1.20 0.44 m 6 2.05 1.33 0.43 571 1.20 0.44 m 7 2.05 1.33 0.43 577 1.27 0.44 m 7 2.05 1.33 0.43 5.70 1.20 0.44 m 7 2.03 1.35 0.43 5.30 1.50 0.44 m 1 2.03 1.48 0.43 5.30 1.50 0.44 m 1 1 1.42 0.43 5.30 1.50 0.44 m 1 1 1.42 0.43 0.43 5.30 1.50 0.44 m 1 1 1.42		1.55	0.39	ш		2.56	1.82	0.36	sm
3.7. 1.25 0.44 m 4 2.34 1.29 0.044 3.7. 1.28 0.44 m 4 2.24 1.29 0.043 3.7. 1.28 0.44 m 4 2.24 1.29 0.043 3.7. 1.20 0.35 sm 6 2.08 1.35 0.43 3.7. 1.20 0.44 m 8 2.05 1.33 0.43 3.30 1.20 0.44 m 10 2.03 1.35 0.43 3.30 1.20 0.44 m 1.4 1.77		2.17	0.32	sm	2	2.34	1.67	0.38	m
3.71 1.23 0.44 n 4 2.24 1.55 0.039 3.71 1.81 0.64 n 5 2.08 1.35 0.045 3.71 1.20 0.43 ssn 6 2.08 1.35 0.43 3.71 1.27 0.44 m 7 2.05 1.35 0.43 3.40 1.46 0.40 m 9 1.99 1.29 0.43 3.30 1.57 0.43 m 11 2.05 1.35 0.43 2.89 1.20 0.44 m 11 2.05 1.37 0.43 3.30 1.57 0.44 m 1.2 1.99 1.23 0.43 4.73 1.14 0.44 m 1.2 1.99 1.21 0.44 4.1 1.1 0.44 m 1.2 1.99 1.23 0.43 4.1 1.1 0.44 m 1.2 1.8 <t< td=""><td></td><td>1.25</td><td>0.44</td><td>ш</td><td>3</td><td>2.34</td><td>1.29</td><td>0.44</td><td>ш</td></t<>		1.25	0.44	ш	3	2.34	1.29	0.44	ш
3.71 1.81 0.36 sm 5 2.08 1.36 0.42 3.71 1.20 0.43 sm 5 2.08 1.35 0.43 3.71 1.25 0.44 sm 6 2.05 1.33 0.43 3.37 1.26 0.40 sm 10 2.05 1.33 0.43 3.39 1.26 0.40 sm 10 2.03 1.38 0.43 2.89 1.26 0.44 sm 11 1.27 1.49 0.44 2.89 1.26 0.44 sm 11 1.77 1.49 0.44 2.89 1.26 0.44 sm 11 1.77 1.49 0.44 3.40 1.45 0.44 sm 1.7 1.7 1.40 0.44 4.43 1.15 0.44 sm 1.7 1.7 1.40 0.44 4.43 1.15 0.44 sm 1.7 1.7		1.25	0.44	ш	4	2.24	1.55	0.39	m
3.71 2.00 0.33 ssm 6 2.05 1.33 0.43 3.77 1.25 0.44 m 7 2.05 1.33 0.43 3.30 1.67 0.44 m 9 2.05 1.33 0.43 3.30 1.67 0.40 m 11 2.05 1.33 0.44 2.89 1.60 0.44 m 11 2.05 1.33 0.44 stropodium muscoide 1.25 0.44 m 11 2.05 1.33 0.44 stropodium muscoide 1.25 0.44 m 12 1.75 1.45 0.44 stropodium muscoide 1.25 0.44 m 1.6 1.75 1.44 0.44 stropodium muscoide 1.25 0.44 m 1.6 1.75 1.44 0.44 stropodium muscoide 1.25 0.44 m 1.6 1.75 1.44 0.44 1.75 1.44 0.44 <th< td=""><td></td><td>1.81</td><td>0.36</td><td>sm</td><td>5</td><td>2.08</td><td>1.36</td><td>0.42</td><td>ш</td></th<>		1.81	0.36	sm	5	2.08	1.36	0.42	ш
3.71 1.25 0.44 m 8 2.05 1.33 0.43 3.40 1.26 0.40 m 9 2.05 1.33 0.43 3.40 1.46 0.40 m 10 2.05 1.33 0.44 3.30 1.50 0.46 m 11 2.05 1.33 0.44 5.30 1.20 0.46 m 11 1.75 1.99 1.77 0.44 6.20 1.20 0.44 m 12 1.79 1.99 0.43 8.30 1.20 0.44 m 11 1.77 1.40 0.44 8.31 1.25 0.44 m 1.7 1.7 1.42 0.44 8.31 1.32 0.44 m 1.7 1.7 1.4 0.44 8.31 1.32 0.44 m 1.6 1.7 1.4 0.44 8.31 1.32 0.44 m 1.8 <td< td=""><td></td><td>2.00</td><td>0.33</td><td>sm</td><td>9</td><td>2.05</td><td>1.33</td><td>0.43</td><td>ш</td></td<>		2.00	0.33	sm	9	2.05	1.33	0.43	ш
3.57 1.27 0.644 m 8 2.05 1.33 0.43 3.30 1.56 0.640 m 10 2.08 1.78 0.40 3.30 1.50 0.640 m 11 2.08 1.78 0.40 2.38 1.26 0.64 m 11 1.78 1.91 0.44 5.38 1.30 0.44 m 11 1.76 1.81 0.44 475 1.15 0.46 m 17 1.76 1.40 0.44 475 1.15 0.44 m 17 1.76 1.40 0.44 443 1.14 0.46 m 17 1.76 1.40 0.44 443 1.14 0.44 m 17 1.76 1.40 0.44 443 1.14 0.44 m 18 1.76 1.40 0.44 443 1.14 0.44 m 18 1.76		1.25	0.44	m	7	2.05	1.33	0.43	ш
3.40 1.46 0.40 m 9 1.72 0.37 3.30 1.57 0.46 m 10 2.05 1.48 0.49 3.30 1.57 0.46 m 11 2.05 1.38 0.44 2.89 1.26 0.44 m 13 1.97 1.91 0.34 5.91 1.25 0.44 m 13 1.86 1.87 0.49 5.75 1.15 0.46 m 16 1.86 1.87 0.44 4.11 1.14 0.46 m 16 1.89 1.54 0.49 5.75 1.15 0.46 m 16 1.89 1.54 0.39 5.75 1.15 0.46 m 1.6 1.89 1.54 0.39 4.11 1.14 0.46 m 1.6 1.89 1.54 0.39 3.89 1.60 0.49 m 2.2 1.76 1.89		1.27	0.44	m	∞	2.05	1.33	0.43	m
3.30 1.50 0.40 m 110 2.03 1.48 0.40 1.33 1.20 0.44 m 11 2.03 1.33 0.44 2.89 1.20 0.44 m 11 1.78 1.91 0.34 2.89 1.20 0.44 m 1.9 1.57 1.51 0.44 4.75 1.15 0.44 m 1.6 1.86 1.40 0.44 4.75 1.15 0.44 m 1.9 1.27 0.44 0.44 4.75 1.15 0.44 m 1.9 1.27 0.44 0.44 4.75 1.15 0.44 m 2.0 1.76 1.40 0.44 4.11 1.14 0.44 m 2.0 1.77 1.40 0.44 4.43 1.14 0.46 m 2.0 1.76 1.8 0.44 4.43 1.14 0.46 m 2.0 1.76		1.46	0.40	m	6	1.99	1.72	0.37	sm
3.30 1.67 0.38 m 11 2.05 1.33 0.43 5.30 1.26 0.44 m 12 1.78 1.91 0.44 5.31 1.26 0.44 m 13 1.77 1.42 0.44 5.91 1.26 0.44 m 14 1.77 1.42 0.44 5.91 1.33 0.44 m 16 1.86 1.24 0.44 4.73 1.14 0.40 m 16 1.86 1.24 0.44 4.13 1.14 0.46 m 20 1.76 1.40 0.42 4.13 1.14 0.46 m 20 1.76 1.40 0.42 3.99 1.08 0.48 m 20 1.77 1.60 0.43 3.89 1.60 0.48 m 22 1.76 1.80 0.35 3.89 1.50 0.44 m 22 1.62		1.50	0.40	m	10	2.03	1.48	0.40	ш
2.89 1.20 0.44 m 12 1.87 1.51 0.34 2.89 1.26 0.44 m 14 1.75 1.51 0.94 4.7 1.30 0.44 m 14 1.77 1.42 0.44 5.34 1.30 0.44 m 16 1.86 1.40 0.44 4.7 1.15 0.46 m 17 1.76 1.40 0.42 4.43 1.14 0.46 m 18 1.76 1.40 0.42 4.43 1.14 0.46 m 20 1.77 1.09 0.42 4.43 1.16 0.46 m 21 1.76 1.40 0.43 3.89 1.36 0.44 m 22 1.77 1.09 0.44 4.11 1.14 0.46 m 22 1.25 1.60 0.48 3.89 1.20 0.44 m 22 1.25 <t< td=""><td></td><td>1.67</td><td>0.38</td><td>ш</td><td>11</td><td>2.05</td><td>1.33</td><td>0.43</td><td>ш</td></t<>		1.67	0.38	ш	11	2.05	1.33	0.43	ш
2.89 1.26 0.44 m 13 1.05 1.51 0.49 contapodium muscoides 1.3 0.44 m 14 1.75 1.42 0.44 4.75 1.15 0.46 m 14 1.76 1.42 0.44 4.75 1.15 0.40 m 17 1.76 1.40 0.44 4.75 1.15 0.40 m 17 1.76 1.40 0.44 4.11 1.14 0.46 m 18 1.76 1.40 0.44 4.11 1.14 0.46 m 20 1.77 1.40 0.44 4.11 1.14 0.42 m 22 1.76 1.86 0.35 3.89 1.60 0.43 m 22 1.76 1.86 0.48 3.80 1.50 0.42 m 22 1.65 1.86 0.35 3.80 1.50 0.44 m 24 1.		1.20	0.46	m	12	1.78	1.91	0.34	sm
4 1.30 0.44 m 14 1.77 1.42 0.41 contopodium muscoides 1.30 0.44 m 14 1.77 1.42 0.44 4.75 1.15 0.46 m 16 1.86 1.54 0.44 4.75 1.15 0.44 m 18 1.76 1.40 0.44 4.13 1.15 0.44 m 18 1.76 1.40 0.42 4.11 1.14 0.44 m 18 1.76 1.40 0.44 4.11 1.14 0.44 m 20 1.77 1.09 0.44 3.99 1.16 0.44 m 20 1.77 1.09 0.44 3.84 1.60 0.43 m 22 1.77 1.80 0.38 3.89 1.14 0.44 m 22 1.82 0.38 3.89 1.14 0.44 m 22 1.82 1.80		1.26	0.44	m	13	1.95	1.51	0.39	ш
contapodium muscoides 15 1.99 1.27 0.44 contapodium muscoides 4.75 1.15 0.46 m 16 1.86 1.27 0.44 4.75 1.15 0.46 m 17 1.76 1.40 0.42 4.75 1.15 0.46 m 17 1.76 1.40 0.42 4.11 1.14 0.46 m 20 1.77 1.09 0.42 4.11 1.14 0.46 m 20 1.77 1.09 0.42 3.89 1.36 0.48 m 20 1.77 1.09 0.42 3.89 1.36 0.48 m 21 1.77 1.80 0.45 3.89 1.36 0.49 m 22 1.77 1.80 0.45 3.89 1.50 0.40 m 22 1.62 1.80 0.45 3.40 1.50 0.44 m Lecompodium mumm 1.44		1.30	0.44	m	14	1.77	1.42	0.41	m
4.51 1.93 0.34 sm 16 1.86 1.54 0.39 5.75 1.15 0.46 m 17 1.76 1.40 0.42 4.43 1.25 0.44 m 19 1.76 1.40 0.42 4.43 1.25 0.44 m 21 1.76 1.40 0.42 4.41 1.14 0.46 m 21 1.76 1.82 0.35 3.89 1.50 0.42 m 22 1.65 1.82 0.35 3.89 1.50 0.49 m 22 1.65 1.82 0.35 3.89 1.50 0.40 m 22 1.65 1.82 0.35 3.89 1.50 0.40 m 22 1.65 1.82 0.35 3.89 1.50 0.40 m 2.2 1.65 1.82 0.35 3.80 1.20 0.47 m 2.6 1.52	Leontopodium muscoides				15	1.99	1.27	0.44	m
4.75 1.15 0.46 m 17 1.76 14.0 0.42 4.75 1.14 0.40 m 18 1.76 14.0 0.42 4.43 1.25 0.44 m 19 1.96 1.97 0.43 3.49 1.36 0.42 m 21 1.76 1.89 0.48 3.89 1.36 0.48 m 22 1.67 1.86 0.45 3.89 1.36 0.49 m 22 1.67 1.86 0.45 3.89 1.36 0.49 m 22 1.67 1.86 0.45 3.89 1.14 0.47 m 24 1.82 0.45 0.45 3.89 1.14 0.47 m 2.22 1.67 0.48 0.45 3.50 1.14 0.44 m 2.64 0.45 m 0.45 0.49 0.45 1.86 2.64 0.27 sm	1 5.91	1.93	0.34	sm	16	1.86	1.54	0.39	m
5.75 1.47 0.40 m 18 1.76 140 0.44 4.43 1.25 0.44 m 20 1.76 1.86 0.44 4.11 1.14 0.46 m 20 1.76 1.86 0.35 3.89 1.36 0.48 m 22 1.65 1.86 0.35 3.89 1.36 0.49 m 23 1.65 1.86 0.35 3.89 1.50 0.49 m 23 1.65 1.86 0.35 3.89 1.50 0.49 m 23 1.65 1.86 0.35 3.84 1.60 0.34 m 22 1.65 1.86 0.35 3.50 1.14 0.47 m 1.60 0.38 1.36 0.40 0.38 2.12 1.60 0.44 m 1.60 0.45 1.8 0.45 0.45 0.45 0.45 0.45 0.45 0.45 <td></td> <td>1.15</td> <td>0.46</td> <td>ш</td> <td>17</td> <td>1.76</td> <td>1.40</td> <td>0.42</td> <td>ш</td>		1.15	0.46	ш	17	1.76	1.40	0.42	ш
443 125 0.44 m 19 199 127 0.44 431 1.14 0.46 m 20 1.77 1.09 0.48 3.89 1.36 0.42 m 22 1.65 1.82 0.35 3.89 1.50 0.42 m 22 1.65 1.82 0.35 3.89 1.50 0.40 m 22 1.65 1.82 0.35 3.50 1.14 0.47 m Leontopodium namm 1.46 1.50 0.40 2.00 2.44 m Leontopodium namm 1.46 0.45 m 1.53 0.45 2.00 2.64 0.24 m		1.47	0.40	m	18	1.76	1.40	0.42	m
4.11 1.14 0.46 m 20 1.77 1.09 0.48 3.99 1.36 0.48 m 22 1.76 1.86 0.35 3.89 1.36 0.48 m 22 1.62 1.82 0.35 3.89 1.50 0.40 m 22 1.62 1.22 0.45 3.50 1.14 0.47 m 25 1.52 1.60 0.38 21 1.20 0.46 m 26 1.52 1.60 0.38 21 1.20 0.46 m 26 1.52 1.60 0.38 21 1.20 0.46 m Lontopodium namm 1.46 1.50 0.40 21 1.40 0.42 m Lontopodium namm 1.14 1.50 0.40 21 2.41 1.81 1.73 0.27 1.81 0.32 21 2.41 1.81 1.81 0.33 1.81		1.25	0.44	ш	19	1.99	1.27	0.44	m
3.99 1.08 0.48 m 21 1.76 1.86 0.35 3.89 1.36 0.42 m 22 1.65 1.82 0.35 3.89 1.50 0.42 m 22 1.65 1.22 0.45 3.50 1.14 0.47 m 24 1.52 1.60 0.38 1 3.35 1.27 0.44 m 26 1.46 1.50 0.40 2 3.35 1.27 0.44 m Leontopodium namum 1.46 1.50 0.40 2.12 0.44 m Leontopodium namum 1.46 1.50 0.40 1.72 0.44 m Leontopodium namum 1.46 1.50 0.40 2.12 0.44 m Leontopodium namum 1.46 1.50 0.40 3.45 1.74 0.42 m Leontopodium namum 1.46 0.35 1.86 2.50 2.64 0.27 sm <td></td> <td>1.14</td> <td>0.46</td> <td>m</td> <td>20</td> <td>1.77</td> <td>1.09</td> <td>0.48</td> <td>m</td>		1.14	0.46	m	20	1.77	1.09	0.48	m
3.89 1.36 0.42 m 22 1.65 1.82 0.45 3.84 1.60 0.38 m 23 1.62 1.22 0.45 3.69 1.50 0.40 m 24 1.52 1.60 0.38 3.50 1.14 0.47 m 25 1.52 1.60 0.38 1.20 0.46 m 2.6 1.50 1.60 0.38 2.12 1.20 0.44 m 2.64 1.52 1.60 0.36 2.12 1.40 0.42 m 2.63 2.10 0.36 1.73 0.36 1.96 2.54 0.27 sm 4 2.41 1.83 0.35 1.93 1.77 2.10 0.23 sm 6 2.27 1.67 0.38 1.50 1.43 0.43 m 10 2.27 1.67 0.38 1.41 1.43 0.44 m 11		1.08	0.48	m	21	1.76	1.86	0.35	sm
3.84 1.60 0.38 m 23 1.62 1.22 0.45 3.69 1.50 0.40 m 24 1.52 1.60 0.38 3.69 1.50 0.40 m 25 1.52 1.60 0.38 1.20 0.46 m 26 1.52 1.60 0.40 2.33 1.27 0.44 m Leontopodium nanum 1.60 0.40 2.10 0.44 m Leontopodium nanum 1.75 0.40 0.40 1.86 2.64 0.27 sm 2.63 2.10 0.45 1.86 2.50 0.29 sm 4 2.41 1.83 0.35 1.77 1.86 0.35 sm 6 2.27 1.67 0.38 1.77 1.86 0.35 sm 8 2.27 1.67 0.38 1.63 1.47 0.49 m 10 2.27 1.67 0.38 <tr< td=""><td></td><td>1.36</td><td>0.42</td><td>ш</td><td>22</td><td>1.65</td><td>1.82</td><td>0.35</td><td>sm</td></tr<>		1.36	0.42	ш	22	1.65	1.82	0.35	sm
3.69 1.50 0.40 m 24 1.52 1.60 0.38 3.50 1.14 0.47 m 26 1.52 1.60 0.38 3.35 1.20 0.46 m Leontopodium nanum 1.60 0.38 2012 1.20 0.44 m Leontopodium nanum 1.75 0.40 0.40 2012 1.40 0.42 m Leontopodium nanum 1.75 0.40 0.38 2012 2.12 0.44 m Leontopodium nanum 1.75 0.40 0.38 1.86 2.64 0.27 m 2.63 2.10 0.36 0.35 1.86 2.54 0.29 sm 4 2.41 1.83 0.35 1.77 1.86 0.37 sm 6 2.27 1.67 0.38 1.63 1.47 0.49 m 1.67 0.38 1.84 0.43 1.50 1.41 1.58 1.33		1.60	0.38	m	23	1.62	1.22	0.45	m
3.50 1.14 0.47 m 25 1.52 1.60 0.38 3.35 1.20 0.46 m Leontopodium nanum 1.46 1.50 0.40 2.12 0.46 m Leontopodium nanum 1.17 0.40 0.40 2.12 1.40 0.42 m 2 2.63 2.10 0.32 1.86 2.64 0.27 sm 2 2.63 1.23 0.45 1.86 2.54 0.27 sm 4 2.41 1.83 0.35 1.77 1.86 0.23 sm 6 2.27 1.67 0.38 1.77 1.86 0.33 sm 6 2.27 1.67 0.38 1.63 1.47 0.43 m 9 2.27 1.67 0.38 1.57 1.28 0.44 m 11 1.98 1.33 0.43 1.41 1.41 1.67 0.38 m 14		1.50	0.40	m	24	1.52	1.60	0.38	m
3.35 1.20 0.46 m 26 1.46 1.50 0.40 2 3.35 1.27 0.44 m Leontopodium nanum 1 1.50 0.40 2.12 1.40 0.42 m 2.63 2.10 0.35 1.96 2.64 0.27 sm 2.52 1.23 0.45 1.86 2.50 0.29 sm 4 2.41 1.83 0.45 1.77 1.86 0.27 sm 4 2.41 1.83 0.35 1.77 1.86 0.35 sm 6 2.41 1.83 0.35 1.77 1.78 0.35 sm 6 2.41 1.83 0.35 1.77 1.77 2.10 0.33 sm 7 2.27 1.67 0.38 1.63 1.47 0.40 m 10 2.27 1.67 0.38 1.57 1.28 0.44 m 1.29 1		1.14	0.47	m	25	1.52	1.60	0.38	m
3.35 1.27 0.44 m Leontopodium nanum 2.12 1.40 0.42 m 2 2.63 2.10 0.35 2.12 1.40 0.42 m 2 2.63 2.10 0.35 1.96 2.64 0.27 sm 3 2.52 1.23 0.45 1.86 2.50 0.29 sm 4 2.41 1.83 0.35 1.93 1.73 0.37 sm 6 2.21 1.83 0.35 1.77 2.10 0.35 sm 6 2.27 1.67 0.38 1.77 2.10 0.33 sm 7 2.27 1.67 0.38 1.63 1.47 0.40 m 9 2.27 1.67 0.38 1.50 1.43 0.44 m 10 2.27 1.67 0.38 1.41 1.67 0.38 m 12 1.98 1.33 0.43 <tr< td=""><td></td><td>1.20</td><td>0.46</td><td>m</td><td>26</td><td>_</td><td>1.50</td><td>0.40</td><td>m</td></tr<>		1.20	0.46	m	26	_	1.50	0.40	m
contopodium pusillum 1.40 0.42 m 1 3.11 1.75 0.36 2.12 1.40 0.42 m 2 2.63 2.10 0.32 1.96 2.64 0.27 sm 3 2.52 1.23 0.45 1.86 2.50 0.29 sm 4 2.41 1.83 0.35 1.77 1.86 0.35 sm 6 2.27 1.67 0.38 1.77 2.10 0.33 sm 7 2.27 1.67 0.38 1.63 1.47 0.40 m 9 2.27 1.67 0.38 1.50 1.43 0.41 m 10 2.27 1.67 0.38 1.51 1.43 0.44 m 11 1.98 1.80 0.36 1.52 1.41 1.67 0.38 m 12 1.98 1.33 0.43 1.41 1.67 0.38 m 14<	12 3.35	1.27	0.44	ш	Leontopodium na				
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1.96 2.64 0.27 sm 3 2.52 1.23 0.45 1.86 2.50 0.29 sm 4 2.41 1.83 0.35 1.93 1.77 1.86 0.35 sm 6 2.27 1.67 0.38 1.77 2.10 0.33 sm 7 2.27 1.67 0.38 1.63 1.47 0.40 m 9 2.27 1.67 0.38 1.50 1.43 0.41 m 10 2.27 1.67 0.38 1.51 1.28 0.44 m 11 1.98 1.33 0.43 1.41 1.67 0.38 m 12 1.98 1.33 0.43 1.41 1.67 0.38 m 14 1.98 1.33 0.43 1.41 1.67 0.38 m 14 1.98 1.33 0.43 1.41 1.29 0.44 m 15 1.98 1.33 0.43		1.40	0.42	ш	2	2.63	2.10	0.32	sm
1.86 2.50 0.29 sm 4 2.41 1.83 0.35 1.93 1.73 0.37 sm 5 2.41 1.83 0.35 1.77 1.86 0.35 sm 6 2.27 1.67 0.38 1.77 2.10 0.33 sm 7 2.27 1.67 0.38 1.63 1.31 0.43 m 9 2.27 1.67 0.38 1.50 1.43 0.44 m 11 1.98 1.33 0.43 1.41 1.67 0.38 m 12 1.98 1.33 0.43 1.41 1.67 0.38 m 14 1.98 1.33 0.43 1.41 1.67 0.38 m 14 1.98 1.33 0.43 1.41 1.67 0.38 m 14 1.98 1.33 0.43 1.41 1.59 0.44 m 15 1.98 1.33 0.43		2.64	0.27	sm	3	2.52	1.23	0.45	m
1.93 1.73 0.37 sm 5 2.41 1.83 0.35 1.77 1.86 0.35 sm 6 2.27 1.67 0.38 1.77 2.10 0.33 sm 7 2.27 1.67 0.38 1.63 1.31 0.43 m 8 2.27 1.67 0.38 1.63 1.47 0.40 m 9 2.27 1.67 0.38 1.50 1.43 0.44 m 11 1.98 1.80 0.43 1.41 1.61 0.38 m 12 1.98 1.33 0.43 1.41 1.67 0.38 m 1.4 1.98 1.33 0.43 1.41 1.29 0.44 m 12 1.98 1.33 0.43 1.41 1.67 0.38 m 1.4 1.98 1.33 0.43 1.41 1.29 0.44 m 1.5 1.98		2.50	0.29	sm	4	2.41	1.83	0.35	sm
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1.77 2.10 0.33 sm 7 2.27 1.67 0.38 1.63 1.31 0.43 m 8 2.27 1.67 0.38 1.63 1.47 0.40 m 9 2.27 1.67 0.38 1.50 1.43 0.41 m 10 2.27 2.20 0.31 1 1.57 1.28 0.44 m 11 1.98 1.80 0.36 1 1.43 1.61 0.38 m 1.3 0.43 2 1.41 1.67 0.38 m 1.4 1.98 1.33 0.43 3 1.41 1.29 0.44 m 15 1.98 1.33 0.43		1.86	0.35	sm	9	2.27	1.67	0.38	ш
1.63 1.31 0.43 m 8 2.27 1.67 0.38 1.63 1.47 0.40 m 9 2.27 1.67 0.38 1.50 1.43 0.41 m 10 2.27 2.20 0.31 1 1.57 1.28 0.44 m 11 1.98 1.80 0.36 1 1.43 1.61 0.38 m 12 1.98 1.33 0.43 2 1.41 1.67 0.38 m 14 1.98 1.33 0.43 3 1.41 1.29 0.44 m 15 1.98 1.33 0.43		2.10	0.33	sm	7	2.27	1.67	0.38	m
1.63 1.47 0.40 m 9 2.27 1.67 0.38 1.50 1.43 0.41 m 10 2.27 2.20 0.31 1 1.57 1.28 0.44 m 11 1.98 1.80 0.36 1 1.43 1.61 0.38 m 12 1.98 1.33 0.43 2 1.41 1.67 0.38 m 14 1.98 1.33 0.43 3 1.41 1.29 0.44 m 15 1.98 1.33 0.43		1.31	0.43	m	8	2.27	1.67	0.38	m
1.50 1.43 0.41 m 10 2.27 2.20 0.31 1.57 1.28 0.44 m 11 1.98 1.80 0.36 1 1.43 1.61 0.38 m 12 1.98 1.33 0.43 2 1.41 1.67 0.38 m 14 1.98 1.33 0.43 3 1.41 1.29 0.44 m 15 1.98 1.33 0.43		1.47	0.40	m	6	2.27	1.67	0.38	m
1.57 1.28 0.44 m 11 1.98 1.80 0.36 1.43 1.61 0.38 m 12 1.98 1.33 0.43 1.41 1.67 0.38 m 14 1.98 1.33 0.43 1.41 1.67 0.38 m 14 1.98 1.33 0.43 1.41 1.29 0.44 m 15 1.98 1.33 0.43		1.43	0.41	ш	10	2.27	2.20	0.31	sm
1.43 1.61 0.38 m 12 1.98 1.33 0.43 1.41 1.67 0.38 m 14 1.98 1.33 0.43 1.41 1.67 0.38 m 14 1.98 1.33 0.43 1.41 1.29 0.44 m 15 1.98 1.33 0.43	_	1.28	0.44	ш	11	1.98	1.80	0.36	sm
1.41 1.67 0.38 m 1.3 1.98 1.33 0.43 1.41 1.67 0.38 m 1.4 1.98 1.33 0.43 1.41 1.29 0.44 m 1.5 1.98 1.33 0.43		1.61	0.38	ш	12	1.98	1.33	0.43	m
1.41 1.67 0.38 m 1.4 1.98 1.33 0.43 1.41 1.29 0.44 m 1.5 1.98 1.33 0.43		1.67	0.38	m	13	1.98	1.33	0.43	m
1.41 1.29 0.44 m 1.5 1.98 1.33 0.43		1.67	0.38	m	14	1.98	1.33	0.43	m
Commission		1.29	0.44	m	15	1.98	1.33	0.43	m
									(Continued)

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Table 3. (Continued).

Pair no.	RL	AR	CI	Type	Pair no.	RL	AR	CI	Type
15	1.41	2.64	0.28	sm	16	1.98	1.50	0.40	ш
16	1.41	1.67	0.38	m	17	1.76	1.82	0.35	sm
17	1.37	1.21	0.45	m	18	1.76	1.82	0.35	sm
18	1.25	1.35	0.43	m	19	1.84	1.60	0.38	ш
19	1.29	1.43	0.41	m	20	1.70	2.00	0.33	sm
20	1.36	1.57	0.39	m	21	1.70	2.00	0.33	sm
21	1.29	1.43	0.41	m	22	1.70	2.00	0.33	sm
22	1.25	1.35	0.43	m	23	1.70	1.40	0.42	Ш
23	1.24	1.33	0.43	m	24	1.56	1.75	0.36	sm
24	1.24	1.33	0.43	m					
25	1.24	1.33	0.43	m					
26	1.18	1.23	0.45	m					
27	1.11	2.15	0.32	sm					
28	1.28	1.42	0.42	m					
29	1.15	1.17	0.46	m					
30	1.24	1.80	0.36	sm					
31	1.13	1.56	0.39	m					
32	1.15	1.17	0.46	m					
33	1.06	1.40	0.42	m					
34	1.06	2.00	0.33	sm					
35	0.97	1.75	0.36	sm					
36	0.90	1.43	0.41	m					

RL, relative length; AR, arm ratio L/S (length of long arm/length of short arm); CI, centrometic index 100S/TL (100 × length of short arm/total chromosome length); M, median point; m, median region; sm, submedian region; st, acrocentric region.

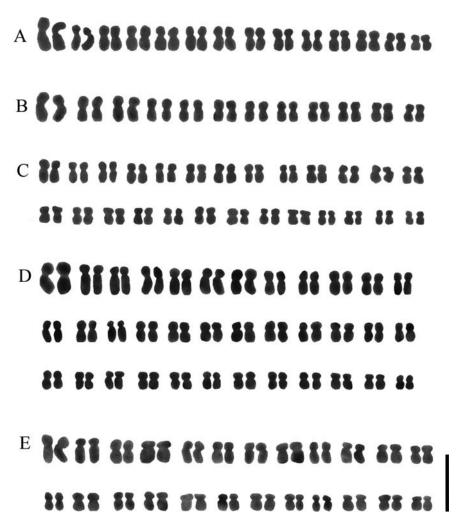


Figure 7. Karyotypes of Leontopodium. (A) L. sinense, 2n=28; (B) L. muscoides, 2n=24; (C) L. souliei, 2n=52; (D) L. pusillum, 2n=72; (E) L. nanum, 2n=48. Scale bar=5 μ m.

for evaluating evolutionary relationship (Stebbins 1971; Li and Chen 1985). There is a general assumption that, within the angiosperms, asymmetrical karyotypes are derived from symmetrical ones (Stebbins 1971; Stace 1989). However, the change in ploidy levels and karyotype asymmetry in Leontopodium is not necessarily coincident. It suggests not only that polyploidy and dysploidy play important roles during the karyotype evolution and the speciation, but also that ecological selection should be an alternative important factor for karyotype asymmetry. There is a great diversity of karyotypes in Gnaphalieae genera (Watanabe et al. 1999). In our study, however, karyotypes of all Leontopodium species seem to be unimodal with no obvious gaps among all their chromosome length (Figure 7, Table 3). More cytological studies on this genus as well as from the tribe are needed to better understand their chromosomal evolution.

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