Cytological studies on the Sino-Himalayan endemic *Solms-laubachia* (Brassicaceae) and two related genera

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The karyotypes of six species of *Solms-laubachia* and one each of *Parrya* and *Desideria* (Brassicaceae) from the Himalayan-Hengduan Mountains (Tibet, Sichuan and Yunnan provinces) were investigated. Chromosome counts of *S. xerophyta*, *S. lanata*, *S. platycarpa* and *D. baiogoinensis* are reported for the first time and found to be diploid with $2n = 14$. Diploid counts were also made of *S. retropilosa*, a species previously known to be a tetraploid. The karyotype formulae of *D. baiogoinensis*, *S. eurycarpa*, *S. pulcherrima*, *S. retropilosa*, *S. xerophyta* and *S. platycarpa* are $2n = 14 = 6 \, \text{m} + 6 \text{sm} + 2 \text{st}$, whereas those of *S. lanata* and *P. nudicaulis* are $2n = 14 = 6 \, \text{m} + 2 \text{sm} + 6 \text{st}$ and $2n = 14 = 8 \, \text{m} + 4 \text{sm} + 2 \text{st}$, respectively. Karyotypes and counts of *S. eurycarpa* and *S. pulcherrima* are in agreement with prior studies. The relationships within *Solms-laubachia* and among the three genera are discussed. Speciation within *Solms-laubachia* may have been the result of primarily intrachromosomal variation at the diploid level, and the genus probably evolved within the Himalayan-Hengduan Mountains instead of migrating from other regions. © 2004 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2004, **145**, 77–86.

ADDITIONAL KEYWORDS: *Desideria* – Himalayan-Hengduan Mountains – karyotypes – *Parrya* – speciation.

INTRODUCTION

The Himalayan-Hengduan Mountains are among the most diverse in the world in topography, habitat and species composition, especially endemic plants, and have been the focus of studies dealing with relationships between florigenesis and plate tectonics, the origin of the North temperate floras and evolution of seed plants in general (Wu, 1988; Axelrod, Al-Shehbaz & Raven, 1998). These mountains are considered to be one of the worlds 'hot spots' of biodiversity (Myers, 1988; Boufford & Van Dijk, 1999; Myers *et al.*, 2000). Their floras comprise the main phytogeographical components: Laurasian, Gondwanan and Tethyan (Wu, 1988). Detailed phylogenetic studies of some of the endemic genera will, it is hoped, enable us understand the florigenesis of this region and the relationship between it and other parts of the world.

We selected the genus *Solms-laubachia* Muschler (Brassicaceae) with that goal in mind.

The species of *Solms-laubachia* are restricted to south-western China, although the range of *S. platycarpa* (J.D. Hooker & Thomson) Botschantzev extends into Bhutan and Sikkim (Fig. 1). They grow on scree slopes and in rocky crevices at altitudes of 3400–5700 m (Lan & Cheo, 1981; Wu, 1984; Lan, 1987; Wang, 1993; Yin, Boufford & Zhang, 1993; Al-Shehbaz & Yang, 2001). Their habitats are characterized by abundant ultraviolet irradiation, wide diurnal range of air temperature, strong winds and limited water supply. The plants are cushion-forming perennials with well-developed caudices covered with petiolar remains from previous years.

Solms-laubachia was placed by Schulz (1936) in the tribe Matthioleae, nearest to *Parrya* R.Brown. His treatment was followed by several Chinese taxonomists (e.g. An, 1995; Kuan, 1985; Lan, 1987; Li, 1995; Huang, 1997; Tan *et al.*, 1999). However, Schulz's tribal classification of the Brassicaceae was considered to be highly artificial (Hedge, 1976; Al-Shehbaz, 1984).

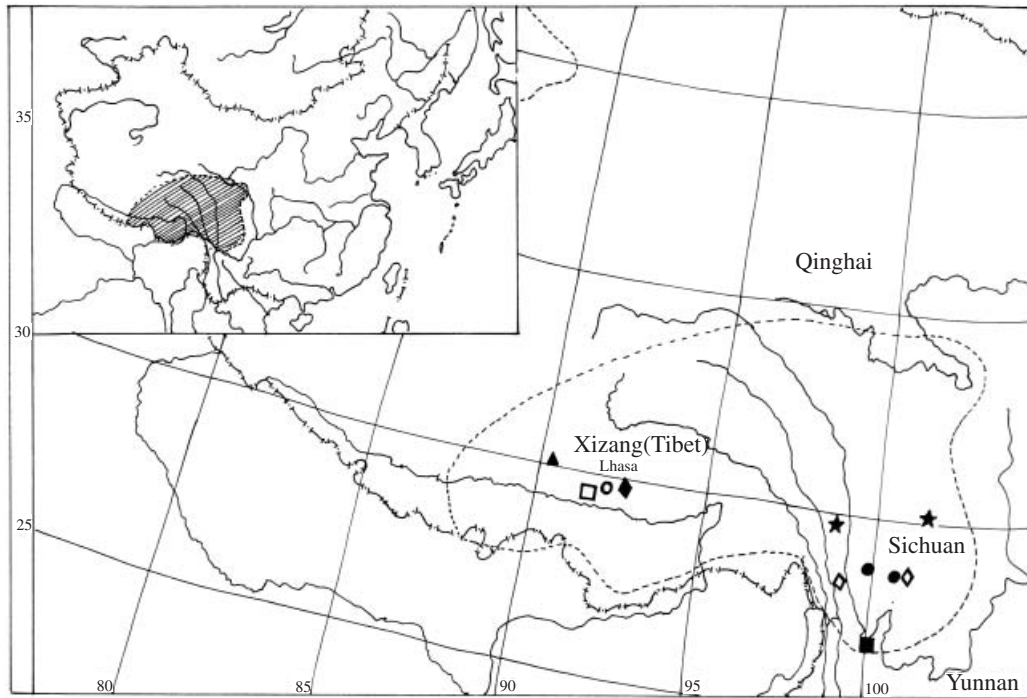*Corresponding author. E-mail: hsun@mail.kib.ac.cn

Figure 1. Approximate distribution range of the genus *Solms-laubachia* and the localities from which seed material of *Solms-laubachia*, *Parrya*, and *Desideria* was collected. (★) *S. retropilosa;* (●) *S. xerophyta;* (□) *S. lanata;* (■) *S. pulcherrima;* (◇) *S. eurycarpa;* (▲) *S. platycarpa;* (○) *P. nudicaulis;* (◆) *D. baiogoinensis.*

Janchen (1942) united the Matthioleae with the Hesperideae, a position followed by Al-Shehbaz (1984), who subsequently adopted the earlier tribal name Anchonieae and suggested the exclusion of *Solms-laubachia* and some other genera from the combined tribe (Al-Shehbaz, 1988). Thereafter, the systematic position and phylogenetic relationships of *Solms-laubachia* remained unresolved.

Cytological data are of great importance in the study of plant evolution and diversification (Stebbins, 1950, 1971; Hong, 1990; Stace, 2000). Despite difficulties in obtaining material of *Solms-laubachia,* repeated attempts were made to collect seeds of all species and of some members of related genera to achieve a better understanding of evolutionary relationships within the genus. The present paper is a continuation of a previous one dealing with the karyomorphology of five species (Yue *et al*., 2003), which suggested a basic chromosome number of $x = 7$ for the genus. Ten additional populations of six species and one each of the related genera *Parrya* and *Desideria* Pampanini are included in this study. With the exception of *S. gamosepala* Al-Shehbaz & G. Yang, all species of *Solms-laubachia* have been studied cytologically. As shown below, however, this taxon is conspecific with *S. eurycarpa* (Maximowicz) Botschantzev. Therefore, it is now possible to discuss the chromosomal relationships of all species of the genus.

MATERIAL AND METHODS

Seeds of all species studied were collected in the Himalayan-Hengduan Mountains (Fig. 1). Detailed collection data are shown in Table 1, and voucher specimens and permanent slides are deposited in the herbarium of the Kunming Institute of Botany (KUN).

All cytological observations were made from root tips. Seeds were stored for 10 days at 4°C in the refrigerator. They were soaked overnight in distilled water at room temperature and were allowed to germinate on wet filter paper in Petri dishes. Fresh root tips about 1.5 cm long were cut, pretreated in 0.002 M 8-hydroxyquinoline at 23°C for 3–3.2 h, then fixed with Carnoy (1 : 3 glacial acetic acid/absolute alcohol) at 4°C for 30 min. They were then rinsed in distilled water several times and placed in 70% ethanol for 10 min. Prior to staining, the root tips were hydrolysed in 1 : 1 1 N HCl :45% acetic acid at 60°C for 30 s and squashed and stained in 1% aceto-orcein. Permanent slides were made using the standard liquid nitrogen method.

Observations were made on nuclei at the somatic mitotic interphase and metaphase, and measure-

Table 1. Locality, geographical position, altitude and voucher number of the investigated species of *Solms-laubachia*, *Desideria* and *Parrya*. All collections were made from the Himalayan-Hengduan Mountains in Yunnan (Y), Sichuan (S), and Tibet (T) provinces, China

Taxon	Locality	Position	Altitude	Voucher (KUN)
S. platycarpa	Nychentan La, Dangxion (T)	30°19′N, 90°38′E	5180 m	*J. P. Yue* 0238
S. lanata	Resela, Lhasa (T)	29°44′N, 91°10′E	4800 m	*J. P. Yue* 0234
	Semula, Lhasa (T)	29°45′N, 91°12′E	5100 m	*J. P. Yue* 0237
S. eurycarpa	Yelashan, Basho (T)	30°10′N, 97°19′E	4710 m	*J. P. Yue* 0247
	Yading, Daocheng (S)	28°23′N, 100°23′E	4510 m	*J. P. Yue* 0249
S. retropilosa	Dongdashan, Zuogong (T)	29°42′N, 98°00′E	5090 m	*J. P. Yue* 0246
	Zheduoshan, Kangding (S)	30°04′N, 101°48′E	4060 m	*J. P. Yue* 0248
S. xerophyta	Yading, Daocheng (S)	28°23′N, 100°23′E	4530 m	*J. P. Yue* 0250
	Daxueshan, Zhongdian (S)	28°34′N, 99°48′E	4340 m	*J. P. Yue* 0251
S. pulcherrima	Gangheba, Lijiang (Y)	27°04′N, 100°11′E	3670 m	*J. P. Yue* 0245
D. baiogoinensis	Milashan, Mozhugongka (T)	29°49′N, 92°20′E	5090 m	*J. P. Yue* 0246
P. nudicaulis	Semula, Lhasa (T)	29°44′N, 91°11′E	4900 m	*J. P. Yue* 0244

ments of chromosome arms were taken from at least ten well-spread metaphases of five or more different root tips from each species. The karyomorphological classification of the interphase and mitotic prophase chromosomes follows Tanaka (1971, 1977); the designation of the centromeric position as median (m), submedian (sm), and subterminal (st) is that of Levan, Fredga & Sandberg (1964); the karyotype symmetry follows Stebbins (1971) and the index of karyotype asymmetry follows Arano (1963).

RESULTS

Species of *Solms-laubachia* are similar to those of *Desideria* and *Parrya* in chromosome morphology. The interphase nucleus is generally recognized as the simple chromosome type (Figs 2, 4). They are also similar in the morphology of mitotic prophase chromosomes, recognized as the interstitial type (Figs 3, 5). For features of the interphase nucleus and mitotic prophase of *Solms-laubachia*, see Yue *et al*. (2003). The metaphase chromosomes of each species are shown in Figures 6–18; detailed parameters are listed in Table 2 and karyotype comparisons in Table 3.

DESIDERIA BAIOGOINENSIS (K. C. KUAN & Z. X. AN) AL-SHEHBAZ

The chromosome count for this Tibetan (Xizang) endemic is reported here for the first time. This species has the karyotype formula $2n = 14 = 6$ m $+ 6$sm $+ 2$st. Pairs 1, 4 and 7 have median centromeres (m-type). Pair 2 is st-type, and the other chromosomes are sm-type. The ratio of the longest to the shortest chromosomes is $1.6 : 1$, and the karyotype symmetry (Stebbins, 1971) is 3A (Figs 6, 18A).

PARRYA NUDICAULIS (LINNAEUS) REGEL.

The species is widely distributed in Asia and North America, its formula $2n = 14 = 8$ m $+ 4$sm $+ 2$st. Pairs 1, 2, 5 and 7 are m-type chromosomes, pairs 4 and 6 are sm-type and pair 3 is st-type. There are satellites on the short arms of the fourth pair. The chromosome number agrees with the counts made by Hedberg (1967) and Knaben (1968). Diploid and tetraploid populations in this species were reported by Zhukova & Petrovsky (1971, 1976), Yurtsev & Zhukova (1972) and Petrovsky & Zhukova (1983). The ratio of the longest to the shortest chromosomes is $2.3 : 1$, and the karyotype symmetry is 2B (Figs 9, 18D).

SOLMS-LAUBACHIA PULCHERRIMA MUSCHLER

Both this species and *Desideria baiogoinensis* have the same karyotype formula ($2n = 14 = 6$ m $+ 6$sm $+ 2$st), which agrees with our previous study of a different population (Yue *et al*., 2003). The ratio of the longest to the shortest chromosomes is $1.7 : 1$, and the karyotype symmetry is 3A (Figs 15, 18J).

SOLMS-LAUBACHIA XEROPHYTA (W.W. SMITH) COMBER.

Plants of both populations in Daxueshan and Yading have the formula $2n = 14 = 6$ m $+ 6$sm $+ 2$st, but Daxueshan differs significantly in the length of pairs 1, 3 and 4. The two populations are about 300 km apart. The population in Yading grows primarily in an alpine meadow and its individuals are generally weaker than those of Daxueshan; the latter grow mainly on scree slopes and in rock crevices. Since all species of the genus grow on scree slopes, it is believed that the
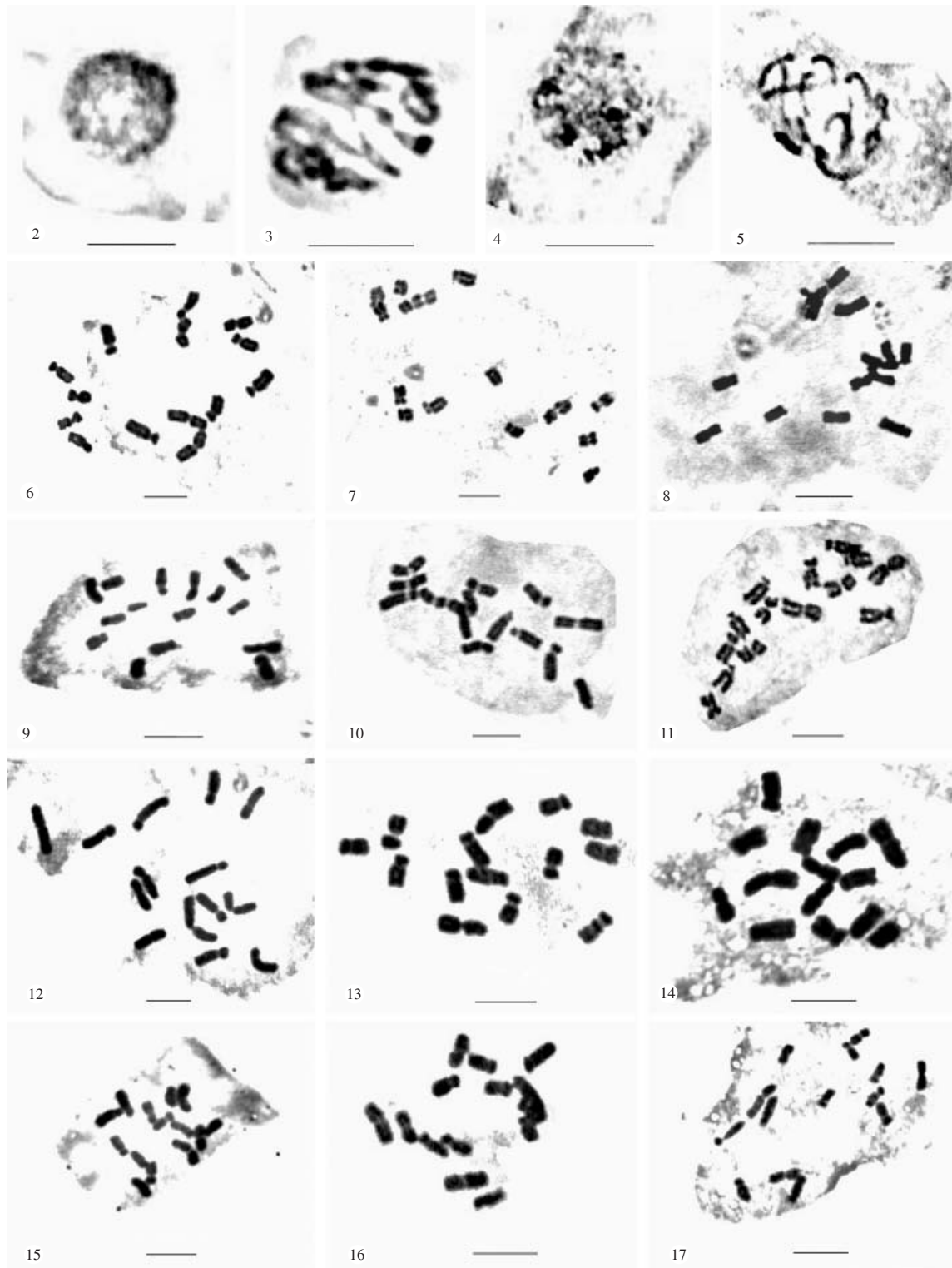
Figures 2–17. Mitotic nuclei and metaphase chromosomes of species of *Solms-laubachia*, *Desideria* and *Parrya*. Figs 2, 3, 6. *D. baiogoinensis*. Figs 4, 5 9. *P. nudicaulis*. Fig. 7. *S. eurycarpa* (Yelashan). Fig. 8. *S. eurycarpa* (Yading). Fig. 10. *S. lanata* (Resela). Fig. 11. *S. lanata* (Semula). Fig. 12. *S. platycarpa* (Nychentan La). Fig. 13. *S. retropilosa* (Dongdashan). Fig. 14. *S. retropilosa* (Zheduoshan). Fig. 15. *S. pulcherrima* (Gangheba). Fig. 16. *S. xerophyta* (Yading). Fig. 17. *S. xerophyta* (Daxueshan). Figs 2, 4 = interphase. Figs 3, 5 = prophase. Figs 6–17 = metaphase. Scale bars = 5 μm.

Figure 18. Karyotypes of species of *Solms-laubachia*, *Desideria*, and *Parrya*. A, *D. baiogoinensis*. B, *S. eurycarpa* (Yelashan). C, *S. eurycarpa* (Yading). D, *P. nudicaulis*. E, *S. lanata* (Resela). F, *S. lanata* (Semula). G, *S. platycarpa* (Nychentan La). H, *S. retropilosa* (Dongdashan). I, *S. retropilosa* (Zheduoshan). J, *S. pulcherrima* (Gangheba). K, *S. xerophyta* (Yading). L, *S. xerophyta* (Daxueshan). Scale bar = 5 μm.

adaptation to grow in alpine meadows is more recent. The karyotype symmetry of both populations is 3A (Figs 16, 17, 18K, L).

SOLMS-LAUBACHIA EURYCARPA (MAXIMOWICZ) BOTSCHANTZEV

Plants in Yading have the same formula as those in Yelashan ($2n = 14 = 6$ m + 6sm + 2st), confirming the previous results obtained from plants of the Baimashan population (Yue *et al.*, 2003). The only difference is that the Baimashan plants have B-chromosomes that were not observed in those of Yading and Yelashan. S. *eurycarpa* is distributed more widely than any other species of the genus and grows in Yunnan, Xizang, Qinghai, Gansu, and Sichuan provinces (Zhou *et al.*, 2001). It has the broadest leaves (1–2.3 cm wide); the Yading plants have leaves which are even wider than those of other populations (a maximum of 7 cm). Lan & Cheo (1981) and Lan (1987) recognized plants of this population as S. *latifolia* (O. E. Schulz) Y. C. Lan & T. Y. Cheo, but leaf width varies greatly in the species and S. *latifolia* cannot be separated from S. *eurycarpa* on morphological grounds (Al-Shehbaz & Yang, 2001).

Solms-laubachia gamosepala was described from Baimashan, and the features that distinguish it from other species of the genus are the small flowers and gamosepalous calyx (Al-Shehbaz & Yang, 2001). According to the specimens collected by the authors, S. *eurycarpa* and S. *gamosepala* are sympatric, and the latter is known only from the type locality. As a result of intensive field studies by two of us (Yue & Al-Shehbaz) in June 2002 in the type locality of S. *gamosepala*, it is concluded that this species was based on flowering material of S. *eurycarpa*, a species for which no description of the flowers was known previously. With the study of additional populations of S. *eurycarpa,* no other differences were found between it and S. *gamosepala*. S. *eurycarpa* is easily distinguished from other species of the genus by its wider leaves, usually purplish petioles, smaller flowers, and small tufts of hairs at the leaf and sepal apices. The karyotype of the species is shown in Figures 7, 8, 18B, C.

SOLMS-LAUBACHIA RETROPILOSA BOTSCHANTZEV

Plants of the Zheduoshan and Dongdashan populations have the same formula, $2n = 14 = 6$ m + 6sm + 2st (Figs 13, 14, 18H, I). In contrast, plants in Xiancheng were reported by Yue *et al.* (2003) to be tetraploids with $2n = 28 = 12$ m + 12sm + 4st, a direct doubling of the above formula, indicating intraspecific polyploidy. The Dongdashan population was recognized by Lan & Cheo (1981) and Lan (1987) as S. *floribunda* Y.C. Lan et T.Y. Cheo, but the examination of the types of both species clearly shows that they are conspecific (Al-Shehbaz & Yang, 2001).

SOLMS-LAUBACHIA LANATA BOTSCHANTZEV

The cytology of this species has been studied here for the first time. Plants of two populations have the formula $2n = 14 = 6$ m + 2sm + 6st (Figs 10, 11, 18E, F). Pairs 1, 3, and 7 are m-type chromosomes, pair 6 is sm-type, and pairs 2, 4 and 5 are st-type. The karyotype is somewhat more asymmetrical than those of other species. Both S. *lanata* and S. *retropilosa* have lanate (woolly) leaves and fruits, and the main difference between them is that the former is antrorsely instead of retrorsely lanate. S. *lanata* is confined to Xizang and occupies the northernmost portion of this province, though S. *eurycarpa* extends much farther to the north in Qinghai and Gansu provinces (Wu, 1991).

SOLMS-LAUBACHIA PLATYCARPA (J. D. HOOKER & THOMSON) BOTSCHANTZEV

This is the only species of the genus with flowers in distinct racemes; all the others have solitary flowers borne on long pedicels originating from the basal rosette. Its cytology is reported here for the first time. S. *platycarpa* resembles the other species of the genus in its karyotype morphology and has the formula $2n = 14 = 6$ m + 6sm + 2st. The ratio of the longest to the shortest chromosomes is 1.7 : 1, and the karyotype symmetry is 3A (Figs 12, 18G).

DISCUSSION

Compared with our previous data (Yue *et al.*, 2003), the karyotypes of all species of *Solms-laubachia* are quite similar. Except for S. *lanata* ($2n = 14 = 6$ m + 2sm + 6st), the other seven species have same formula, $2n = 14 = 6$ m + 6sm + 2st. Chromosome pairs 1, 4 and 7 are m-type, pairs 3, 5 and 6 are sm-type and pair 2 is st-type. The species have similar karyotype symmetry (Tables 2, 3). The slight differences in the ratio of longest to shortest chromosomes and centromeric index might be the result of unavoidable measurement errors. The similarities of the karyotypes accord with their common morphological characters that distinguish the genus from related genera (Yue *et al.*, 2003) and suggest that *Solms-laubachia* is a natural genus based on both morphological and cytological grounds. There also appears to be some divergence in the karyotype of some species. For example, the occurrence of the tetraploid population in

Table 2. Karyomorphological parameters of species of *Solms-laubachia, Desideria,* and *Parrya* (all 2*n* = 14). *Abbreviations*: RL, relative length; AR, arm ratio (L/S); CI, centromeric index (100S/TL); m, median region; sm, submedian region; st, subterminal region. Chromosome pairs are assigned Roman numerals

Pair no.	RL	AR	CI	Type	Pair no.	RL	AR	CI	Type
D. baiogoinensis (Milashan)					*P. nudicaulis* (Semula)				
I	9.0	1.2	45.3	m	I	10.7	1.3	44.4	m
II	8.8	3.4	22.6	st	II	8.0	1.1	48.1	m
III	7.2	2.2	31.5	sm	III	7.8	3.4	22.8	st
IV	7.1	1.1	48.0	m	IV	6.2	2.0	33.3	sm*
V	6.3	2.5	28.7	sm	V	6.1	1.3	43.5	m
VI	6.0	2.2	31.7	sm	VI	6.0	2.0	33.2	sm
VII	5.7	1.2	46.4	m	VII	5.3	1.4	41.0	m
S. retropilosa (Dongdashan)					*S. retropilosa* (Zheduoshan)				
I	9.1	1.0	48.8	m	I	9.6	1.2	46.2	m
II	8.6	3.5	22.0	st	II	8.7	3.6	21.6	st
III	6.8	2.5	28.6	sm	III	6.7	2.9	25.7	sm
IV	6.7	1.6	38.7	m	IV	6.6	1.1	47.1	m
V	6.5	2.5	28.3	sm	V	6.5	2.8	26.6	sm
VI	6.3	2.2	31.0	sm	VI	6.2	2.3	30.6	sm
VII	6.0	1.6	38.2	m	VII	5.7	1.4	41.1	m
S. xerophyta (Daxueshan)					*S. xerophyta* (Yading)				
I	9.6	1.4	40.9	m	I	8.8	1.2	46.4	m
II	8.9	3.1	24.5	st	II	8.6	3.4	22.6	st
III	7.3	2.7	26.9	sm	III	7.2	2.6	27.5	sm
IV	6.9	1.3	44.4	m	IV	6.9	1.2	45.9	m
V	6.1	2.1	32.1	sm	V	6.6	2.1	32.0	sm
VI	5.7	2.3	30.8	sm	VI	6.2	2.3	30.3	sm
VII	5.6	1.6	39.2	m	VII	5.7	1.4	42.5	m
S. eurycarpa (Yalashan)					*S. eurycarpa* (Yading)				
I	9.8	1.1	46.6	m	I	9.6	1.5	40.5	m
II	7.7	3.8	21.1	st	II	8.0	4.2	19.4	st
III	7.6	1.8	35.6	sm	III	7.6	2.7	27.1	sm
IV	7.4	1.2	45.5	m	IV	7.1	1.3	43.6	m
V	6.0	2.1	32.6	sm	V	6.5	2.3	30.0	sm
VI	5.9	2.2	31.4	sm	VI	5.8	2.0	33.3	sm
VII	5.6	1.5	39.4	m	VII	5.4	1.3	42.9	m
S. lanata (Resela)					*S. lanata* (Semula)				
I	9.4	1.2	45.5	m	I	9.3	1.3	43.4	m
II	7.7	3.2	23.6	st	II	8.3	3.4	23.0	st
III	7.7	1.1	47.6	m	III	6.8	1.2	45.9	m
IV	7.3	4.5	18.3	st	IV	6.7	3.6	21.7	st
V	6.4	3.4	22.6	st	V	6.5	3.8	20.7	st
VI	6.2	2.0	33.3	sm	VI	6.4	2.2	31.6	sm
VII	5.3	1.6	38.6	m	VII	6.1	1.2	45.5	m
S. platycarpa (Nychentan La)					*S. pulcherrima* (Ganheba)				
I	9.5	1.2	44.8	m	I	8.4	1.5	39.7	m
II	8.4	3.8	21.0	st	II	8.4	3.3	23.2	st
III	7.0	2.8	26.5	sm	III	7.6	2.6	27.9	sm
IV	6.8	1.2	45.5	m	IV	7.0	1.1	47.2	m
V	6.5	2.3	30.2	sm	V	6.6	2.1	32.3	sm
VI	5.9	2.5	28.8	sm	VI	6.0	2.8	26.5	sm
VII	5.9	1.5	40.2	m	VII	6.0	1.5	40.4	m

*Chromosome with satellite

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Table 3. Karyotype comparisons of species of *Solms-laubachia*, *Desideria* and *Parrya*. *Abbreviations*: RLR, relative length ratio (longest/shortest); P, proportion of chromosomes with arm ratio over 2 : 1; KS, karyotype symmetry; IKA, index of karyotype asymmetry; m, median region; sm, submedian region; st, subterminal region; Chromosome pairs are assigned Roman numerals

Taxon	Karyotypic formula	RLR	P	KS	IKA
D. baiogoinensis (Milashan)	$2n = 14 = 6$ m (I, IV, VII) + 6sm (III, V, VI) + 2st (II)	1.6	0.50	3A	63.9
P. nudicaulis (Semula)	$2n = 14 = 8$ m (I, II, V, VII) + 4sm (IV*, VI) + 2st (III)	2.3	0.43	2B	61.5
S. retropilosa (Dongdashan)	$2n = 14 = 6$ m (I, IV, VII) + 6sm (III, V, VI) + 2st (II)	1.6	0.57	3A	66.1
S. retropilosa (Zheduoshan)	$2n = 14 = 6$ m (I, IV, VII) + 6sm (III, V, VI) + 2st (II)	1.7	0.57	3A	65.8
S. xerophyta (Daxueshan)	$2n = 14 = 6$ m (I, IV, VII) + 6sm (III, V, VI) + 2st (II)	1.9	0.57	3A	66.1
S. xerophyta (Yading)	$2n = 14 = 6$ m (I, IV, VII) + 6sm (III, V, VI) + 2st (II)	1.6	0.50	3A	64.8
S. eurycarpa (Yalashan)	$2n = 14 = 6$ m (I, IV, VII) + 6sm (III, V, VI) + 2st (II)	1.9	0.43	2A	63.0
S. eurycarpa (Yading)	$2n = 14 = 6$ m (I, IV, VII) + 6sm (III, V, VI) + 2st (II)	1.8	0.50	3A	66.4
S. lanata (Resela)	$2n = 14 = 6$ m (I, III, VII) + 2sm (VI) + 6st (II, IV, V)	1.9	0.50	3A	66.7
S. lanata (Semula)	$2n = 14 = 6$ m (I, III, VII) + 2sm (VI) + 6st (II, IV, V)	1.6	0.50	3A	66.7
S. platycarpa (Nychentan La)	$2n = 14 = 6$ m (I, IV, VII) + 6sm (III, V, VI) + 2st (II)	1.7	0.57	3A	66.0
S. pulcherrima (Ganheba)	$2n = 14 = 6$ m (I, IV, VII) + 6sm (III, V, VI) + 2st (II)	1.7	0.57	3A	66.3

*chromosome with satellite.

S. retropilosa, the more asymmetrical karyotype of *S. lanata* and the difference in the length of the members of some pairs in *S. xerophyta* from Daxueshan. However, we did not find any distinct correlation between these karyotypic differences and morphological ones. Therefore, the cytological data do not seem to be significant in the study of phylogenetic relationships within *Solms-laubachia*. It is suggested that the morphological divergence among species was not the result of major chromosomal variation.

As indicated above, the systematic position of *Solms-laubachia* is still unresolved. Schulz (1936) and subsequent workers believed that the genus is closely related to *Parrya*. On the basis of differences in fruit morphology and the mechanism of detachment of fruits from fruiting pedicels, Al-Shehbaz (2001) and Al-Shehbaz & Yang (2001) suggested a closer relationship of *Solms-laubachia* to *Desideria* and *Leiospora* (C.A. Meyer) Dvorák. Our study of *D. baiogoinensis* shows a karyotype formula similar to that of *Solms-laubachia*. In contrast, the karyotype formula of *Parrya nudicaulis* ($2n = 14 = 8$ m + 4sm + 2st) reveals that it has more m-type chromosomes. Furthermore, the ratio of longest to shortest chromosomes in *P. nudicaulis* is more than 2 : 1 and, according to Stebbins (1971), its karyotype belongs to 2B type, which is more asymmetrical than that of *Solms-laubachia*. Another difference is that the fourth pair of chromosomes of this species has satellites on the short arms, whereas *Solms-laubachia* lacks them. Therefore, as predicted on the basis of morphology by Al-Shehbaz (2001) and Al-Shehbaz & Yang (2001), the study of karyotypes indicates that *Solms-laubachia* has a closer relationship to *Desideria* than to *Parrya*. Further karyotypic studies on additional

species of the latter two genera are needed to test the robustness of this observation.

Christolea Cambessèdes, a Himalayan and Central Asian genus containing two species (Al-Shehbaz, 2001), somewhat resembles *Solms-laubachia* morphologically, although it differs significantly in the persistent attachment of its fruits to the fruiting pedicels, the venation of valves, the position of the valve margin in relation to the replum, and in the branched leafy stems. However, *C. crassifolia* resembles *Solms-laubachia* in having the formula $2n = 14 = 6$ m + 6sm + 2st (Gu *et al*., 1993).

Although similarities in the karyotype provide some help in assessing generic relationships, data from other disciplines, especially molecular systematics, are needed to establish firmly the phylogenies within and among genera. The Brassicaceae are well known for the artificial delimitation of tribes and genera, and most infra-familial subdivisions of the family need reevaluation. With the rapidly accumulating molecular data on the major genera of the family, perhaps a more realistic classification can be achieved by grouping the closely related genera and working towards establishing more natural tribes (Al-Shehbaz, 1984).

Polyploidy has been considered to play an important role in plant speciation, especially in the harsh conditions of alpine regions (Hanelt, 1966; Löve & Löve, 1967, 1975), although it appears to be rather uncommon in genera such as the Himalayan alpine *Saxifraga* L. (Wakabayashi & Ohba, 1988), *Potentilla* L. (Ikeda, 1989) and the Hengduan Mountains endemic *Tibetia* (Ali) Tsui (Nie, Gu & Sun, 2002). On the basis of cytological data from 506 taxa from the Himalayan-Hengduan Mountains (Nie, 2002) and 59 from the

Qinghai-Tibet Plateau (Wu, Yang & Fei, 1995), Nie (2002) concluded that polyploidy is far less common in the alpine flora of China and neighbouring areas. Of the 15 populations of *Solms-laubachia* included in this and the previous study (Yue *et al.*, 2003), only one (*S. retropilosa*) is tetraploid. Therefore, the genus fits the picture presented by Nie (2002); we conclude that polyploidy did not play an important role in the evolution within it. Other factors (e.g. asymmetry of the karyotype, differences in chromosome length) discussed above probably played more important roles.

According to Wu (1987), all endemic genera of the Qinghai-Tibet Plateau probably originated *in situ* or in adjacent areas following its uplift. Wus hypothesis might be applicable to *Solms-laubachia*, though there are several exceptions, among which is the Asteraceae genus *Nannoglottis* (Liu *et al.* 2002). The karyotypic similarities among species of *Solms-laubachia* indicate that they are all diploid and perhaps have a common origin. Based on morphological and cytological data, the genera related most closely to *Solms-laubachia* are *Christolea, Desideria*, *Leiospora,* and *Parrya*. With the exception of *Parrya*, all are restricted to the Himalayan-Hengduan Mountains and central Asia. *Parrya* is most highly diversified in central Asia and only two species have spread into arctic and subarctic Asia and northern North America. Critical studies of some genera (e.g. *Piptanthus* Sweet and *Lamiophlomis* Kudo) have shown that many Sino-Himalayan elements and alpine plants of the Himalayan-Hengduan Mountains originated from the semiarid or arid flora of the Mediterranean during the Cenozoic (Sun, 2002). The gradual differentiation of the present-day flora most probably resulted after the Neogene, especially as a result of the uplift of the Mountains. It would be interesting to test whether or not *Solms-laubachia* follows this general pattern, though it mostly probably evolved within the Himalayan-Hengduan Mountains instead of migrating from other regions.

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