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Chromosomal evolution in Balsaminaceae, with cytological observations on 45 species from Southeast Asia

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Abstract - Balsaminaceae consists of two genera, *Hydrocera* with only one species *H. triflora* and *Impatiens* with over 900 species. The chromosome number of *H. triflora* was consistently reported as 2*n*=16 or *n*=8. The somatic chromosome numbers vary greatly from 2*n*=6 to 2*n*=66 in *Impatiens*. In order to provide more complete information to understand the chromosomal evolution and cytogeography of Balsaminaceae, we counted chromosome numbers for 45 species of *Impatiens* from southwest China and the adjacent areas. Chromosome numbers were confirmed for 11 species, and numbers different from previous reports were found for two species. 32 species were examined for the first time, and the numbers 2*n*=12, 14, 16, 18, 20, 40, 54 (or the relevant gametic numbers) were found. The number *n*=27 found in *I. pseudokingii* is new for the family. The number 2*n*=18, mostly involving a bimodal karyotype with one pair of chromosomes conspicuously longer than others, is predominant among the species studied. Considering all the available chromosomal data, x=7, 8, 9, 10 are the most frequent basic numbers of the family. Previous authors have suggested x=7 or x=8 to be ancestral. Based on the present data, we suppose that x=8, x=9, or x=10 are all possible candidates of the ancestral basic numbers in *Impatiens*. Geographic distributions of the most frequent basic numbers show interesting patterns: x=7 and 8 occur in Africa, x=7, 8, 10 in Southern India and Sri Lanka, x=7, 9, 10 in the Himalayas, x=7, 8, 9, 10 in Southeast Asia, and x=10 in northern Asia, Europe and North America.

Key words: Balsaminaceae; *Hydrocera*; *Impatiens*; chromosome numbers; cytogeography.

INTRODUCTION

Balsaminaceae is a diversified family with two genera: *Hydrocera* and *Impatiens*. Other generic names such as: *Petalonema, Semeiocardium* and *Impatientella* are confirmed to be synonyms of *Impatiens* (GREY-WILSON 1980a; RAO *et al*. 1986). *Hydrocera*, has only one species, *H. triflora* (L.) Wight et Arn., a semi-aquatic herb native to the Indo-Malesian countries. It can be readily distinguished from *Impatiens* by its five free petals and indehiscent berry. *Impatiens* is a large genus with annual or perennial species distributed primarily in the highlands and mountains of the Old-World tropical and subtropical regions. GREY-WILSON (1980a) estimated conservatively the total number of species to be around 850, but it perhaps has more, as many new species are still being described from different regions such as southwestern China and Madagascar (e. g. AKIYAMA *et al*. 1995, 1996b; FISCHER and

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Table 1 – The chromosome numbers observed, and the origins of materials and voucher specimens. The chromosome numbers reported for the first time are marked with "*", the number different from previous reports is marked with "!", and the numbers confirmed some of the previous reports but different from other reports are marked with "◊".

Taxon	Coll. No.	Origin and altitude	Chromosome Number
I. acehensis C. Grey-Wilson	AF1	Gunung Sinabung, Indonisia	2*n* = 14*
I. aquatilis Hook. f.	cn2k1-75	Kunming, Yunnan, China, 2100m	*n* = 9*
I. apsotis Hook. f.	cn2k2-159	Kangding, Sichuan, China, 2915m	*n* = 9*
I. arguta Hook. f. et Thomas.	cn2k-52	Gongshan, Yunnan, China, 2600 m	*n* = 10◊
I. aureliana Hook. f.	cn2k1-63	Longchuan, Yunnan, China, 1700m	*n* = 6
I. bahanensis Hand.-Mazz.	cn2k-30	Gongshan jidu, Yunnan, China, 2550m	*n* = 9*
I. bicornuta Wall.	cn2k-55	Gongshan, Yunnan, China, 2600m	2*n* = 18◊
I. chimiliensis Comber	cn2k-51	Gongshan, Yunnan, China, 3500m	2*n* = 18*
I. chinensis L.	cn2k1-49	Tengchuan, Yunnan, China, 1630m	*n* = 8
I. chungtienensis Y. L. Chen	cn2k2-179	Zhongdian, Yunnan, China, 2700m	*n* = 9*
I. crassicaudex Hook. f.	cn2k2-104	Batang, Sichuan, China, 3800m	*n* = 9*
I. cyathiflora Hook. f.	cn2k1-74	Kunming, Yunnan, China, 2100m	2*n* = 18*
I. delavayi Franch.	cn2k-76	Dali, Yunnan, China, 2650m	2*n* = 20*
	cn2k2-14	Zhongdian, Yunnan, China, 3160m	*n* = 10*
I. desmantha Hook. f.	cn2k2-30	Zhongdian, Yunnan, China, 3410m	*n* = 9*
I. dolichoceras Pritz. ex Diels	cn2k1-80	Nanning, Guangxi, China, 1519m	2*n* = 18*
I. drepanophora Hook. f.	cn2k1-39	Longling, Yunnan, China, 1580m	*n* = 9!
	cn2k-16	Fugong, Yunnan, China, 1335m	*n* = 9!
	cn2k-20	Gongshan, Yunnan, China, 1433m	*n* = 9!
I. eubotrya Miq.	AF2	Gunung Merapi, Indonisia, 2502m	2*n* = 18!
I. fenghwaiana Y. L. Chen	cn2k1-78	Nanning, Guangxi, China, 1519m	2*n* = 18*
I. gongshanensis Y. L. Chen	cn2k-26	Gongshan, Yunnan, China, 2040m	*n* = 10*
I. holocentra Hand.-Mazz.	cn2k-54	Gongshan, Yunnan, China, 2700m	*n* = 9*
I. imbecilla Hook. f.	Hao 426	Omei Mt., Sichuan, China	2*n* = 20*
I. infirma Hook. f.	cn2k2-60	Xiangcheng, Sichuan, China, 2950m	*n* = 9*
I. lecomtei Hook. f.	cn2k2-202	Lijiang, Yunnan, China, 2900m	2*n* = 18*
I. mengtszeana Hook. f	cn2k1-60	Longchuan. Yunnan, China, 1450m	*n* = 8, 9
	cn2k2-214	Jiangcheng, Yunnan, China, 1100m	*n* = 8
I. microcentra Hand.-Mazz.	cn2k-50	Gongshan, Yunnan, China, 2800m	*n* = 9*
I. napoensis Y. L. Chen	cn2k1-61	Longchuan, Yunnan, China, 1450m	*n* = 8*
I. oxyanthera Hook. f.	00-s008	Omei Mt., Sichuan, China	*n* = 7*
I. poculifer Hook. f.	cn2k2-209	Weixi, Yunnan, China, 3000m	2*n* = 20*
I. principis Hook. f.	01-yjp006	Lushui, Yunnan, China	*n* = 9*
I. pseudokingii Hand.-Mazz.	cn2k-29	Gongshan, Yunnan, China, 2550m	*n* = 27*
I. radiata Hook. f.	cn2k1-43	Tengchun, Yunnan, China, 2097m	2*n* = 18◊
I. rectangula Hand.-Mazz.	cn2k-19	Gongshan, Yunnan, China, 1433m	*n* = 9*
	cn2k-28	Gongshan, Yunnan, China, 2050m	*n* = 9*
	cn2k1-17	Gongshan, Yunnan, China, 1580m	2*n* = 18*
I. rostellata Franch.	cn2k2-167	Shimian, Sichuan, China, 2245m	*n* = 10*
I. rubrostriata Hook. f.	cn2k1-44	Tengchun, Yunnan, China, 2097m	2*n* = 20◊
I. scutisepala Hook. f.	cn2k-56	Gongshan, Yunnan, China, 2500m	*n* = 9*
I. siculifer Hook. f.	cn2k2-215	Jiangcheng, Yunnan, China, 1200m	*n* = 9
I. stenantha Hook. f.	01-yjp008	Lushui, Yunnan, China	*n* = 9
I. taronensis Hand.-Mazz.	cn2k-57	Gongshan, Yunnan, China, 2600m	2*n* = 18*
I. tenuibracteata Y. L. Chen	01-yjp003	Lushui, Yunnan, China	*n* = 9*
I. tortisepala Hook. f.	cn2k2-166	Shimian, Sichuan, China, 2245m	*n* = 10*
I. trichocepala Y. L. Chen	cn2k1-68	Longling, Yunnan, China, 1260m	*n* = 7*
I. uliginosa Franch.	99-174	Binchuan, Yunnan, China, 2200m	*n* = 9
	cn2k2-173	Huaping, Yunnan, China, 2150m	*n* = 9
I. uniflora Hayata	AF3	Taiwan, China, 2565m	*n* = 20*
I. xanthina Comber	cn2k1-35	Gongshan, Yunnan, China, 2070m	*n* = 7*
I. yingjiangensis S. Akiyama et H. Ohba	cn2k1-55	Yingjiang, Yunnan, China, 1435m	*n* = 8

RAHELIVOLOLONA 2002). Five conspicuous diversification centres in the paleotropical regions can be recognized: tropical Africa ca. 109 spp. (GREY-WILSON 1980a); Madagascar ca. 120 spp. (FISCHER and RAHELIVOLOLONA 2002); southern India and Sri Lanka ca. 150 spp., the eastern Himalayas ca. 120 spp., and Southeast Asia area in its broad sense (including Burma, Thailand, southwest China, Indochina peninsula, and the Malesia archipelagos) ca. 250 spp. High proportion of endemic species are found in these centres. For example, as many as 91% of the southern Indian species are endemic (CHATTERJEE 1940; RAO *et al.* 1986). On the contrary to the paleotropical areas, only a few species of *Impatiens* are represented in the temperate areas in northern Asia, Europe and North America. There is notably no native species in South America and Australia.

Chromosomal variation contributes to the processes of species evolution (HONG 1990; STEBBINS 1971). Knowledge of chromosomal evolution in Balsaminaceae stands as an important aspect in understanding the extraordinary diversity, endemism, and biogeography of the family. About 157 species of *Impatiens* from most of the distribution areas have been karyologically studied (Table 2) prior to our present study. Some important observations include SMITH (1934), KHOSHOO (1955a, b, 1956, 1957, 1966), JONES and SMITH (1966), BHASKAR (1976, 1980), LARSEN (1981), ZINOV'EVA-STAHEVITCH and GRANT (1984,1985), RAO *et al.* (1986), GOVINDARAJAN and SUBRAMANIAN (1986), AKIYAMA *et al.* (1992, 1993, 1996a), SUGAWARA *et al.* (1994, 1997), etc. The following somatic chromosome numbers have been reported: $2n$ = 6, 8, 10, 12, 14, 15, 16, 17, 18, 19, 20, 24, 26, 28,30, 32, 34, 36, 40, 44, 48, 50, 56, 66. The lowest chromosome number $2n$ = 6 was found in *I. latifolia* and *I. leschenaultii* from southern India (GOVINDARAJAN and SUBRAMANIAN 1986), and the highest number $2n$ = 66 was found in *I. mooreana* from New Guinea (JONE and SMITH 1966). The most frequent chromosome numbers encountered so far are $2n$ = 16 (55 taxa), $2n$ = 18 (49 taxa), $2n$ = 20 (45 taxa), $2n$ = 14 (42 taxa), $2n$ = 12 (18 taxa) and $2n$ = 32 (10 taxa). The other numbers are represented by less than 5 taxa. As to the evolution of the basic chromosome numbers, KHOSHOO (1957) proposed that 7 and/or 10 were the ancestral basic numbers of *Impatiens*. JONES and SMITH (1966) and AKIYAMA *et al.* (1992) suggested x = 7 to be the ancestral type from which the other numbers were derived by mainly ascending dysploidy, whereas RAO *et al.* (1986) suggested that x = 8 might be the original basic number from which the other numbers, lower or higher, were derived by both descending and ascending dysploidy.

So far, the available karyological studies on *Impatiens* were mostly carried out on Indian and African species. Although the mainland Southeast Asia and the adjacent Sino-Himalayan area represent the biggest diversification centre of the family, only a few studies were done on the species growing in these regions. For example, about 220 *Impatiens* species are so far recognized from China (CHEN 2001), highly concentrated in the southwestern part (ca. 90 spp. in Yunnan Province), but chromosome numbers have been counted for 21 species only (SUGAWARA *et al.* 1994, 1997). The chromosome data for the majority of species are still not available. In the present paper, we present the results of our recent observations on chromosome numbers of Chinese and other Asian species, in order to provide complementary karyological information for this family. By incorporating our present results into a thorough survey of previous studies, a review of the chromosome numbers and the possible evolutionary relationships among different basic numbers are also presented.

MATERIALS AND METHODS

Most of the species observed were collected from southwest China. The species examined, their origin and voucher specimen are listed in Table 1, together with the corresponding chromosome numbers. Voucher specimens were deposited in the herbarium of the University of Neuchâtel, Switzerland (NEU).

Chromosome number determinations were made from flower buds fixed in Carnoy fluid (99% ethanol - glacial acetic acid, 3:1 v/v). After washing thoroughly with 70% ethanol, the flower buds were stained in alcohol-HCL-carmine (SNOW 1963) for about 48 hrs at 60°C. Then the stained flower buds were heated in 45% acetic acid in a ceramic cup for 2-3 minutes. The anthers or young ovaries were then squashed in the standard way and observed using a light microscope. Chromosome numbers were counted from the meiosis of pollen mother cells, or from mitosis in pollen or ovary somatic cells. Drawings were made with a camera lucida apparatus using temporary slides.

RESULTS

52 samples representing 45 species of *Impatiens* collected from southwest China, Taiwan and Sumatra were examined for their chromosome numbers. The results are shown in Table 1. The gametic numbers n = 6, 7, 8, 9, 10, 20, 27 or the corresponding somatic numbers were found (Fig. 1 A through I). The number n = 27, new for the Balsaminaceae, was found in *I. pseudokingii* (Fig. 1G). The number n = 9 (or $2n$ = 18) appeared most frequently in 26 species observed, followed by the number n = 10 (or $2n$ = 20) which was counted in 8 species. The numbers n = 7 (or $2n$ = 14) and n = 8 (or $2n$ = 16) were found in 4 species respectively, and both n = 6 and n = 27 were found only in one species respectively. The chromosome numbers for 32 species are reported here for the first time (see the species marked with an asterisk in Table 1). For seven species, *I. aureliana* n = 6 (Fig 1A), *I. chinensis* n = 8, *I. mengtszeana* n = 8 and 9 (Fig.1H-I), *I. siculifer* n = 9, *I. stenantha* n = 9, *I. uliginosa* n = 9, and *I. yingjianensis* n= 8, our results confirmed all previous reports for them (SUGAWARA *et al.* 1994, 1997; AKIYAMA *et al.* 1996a; RAO *et al.* 1986; LARSEN 1981; STAHEVITCH 1995). For four species our results confirmed some previous

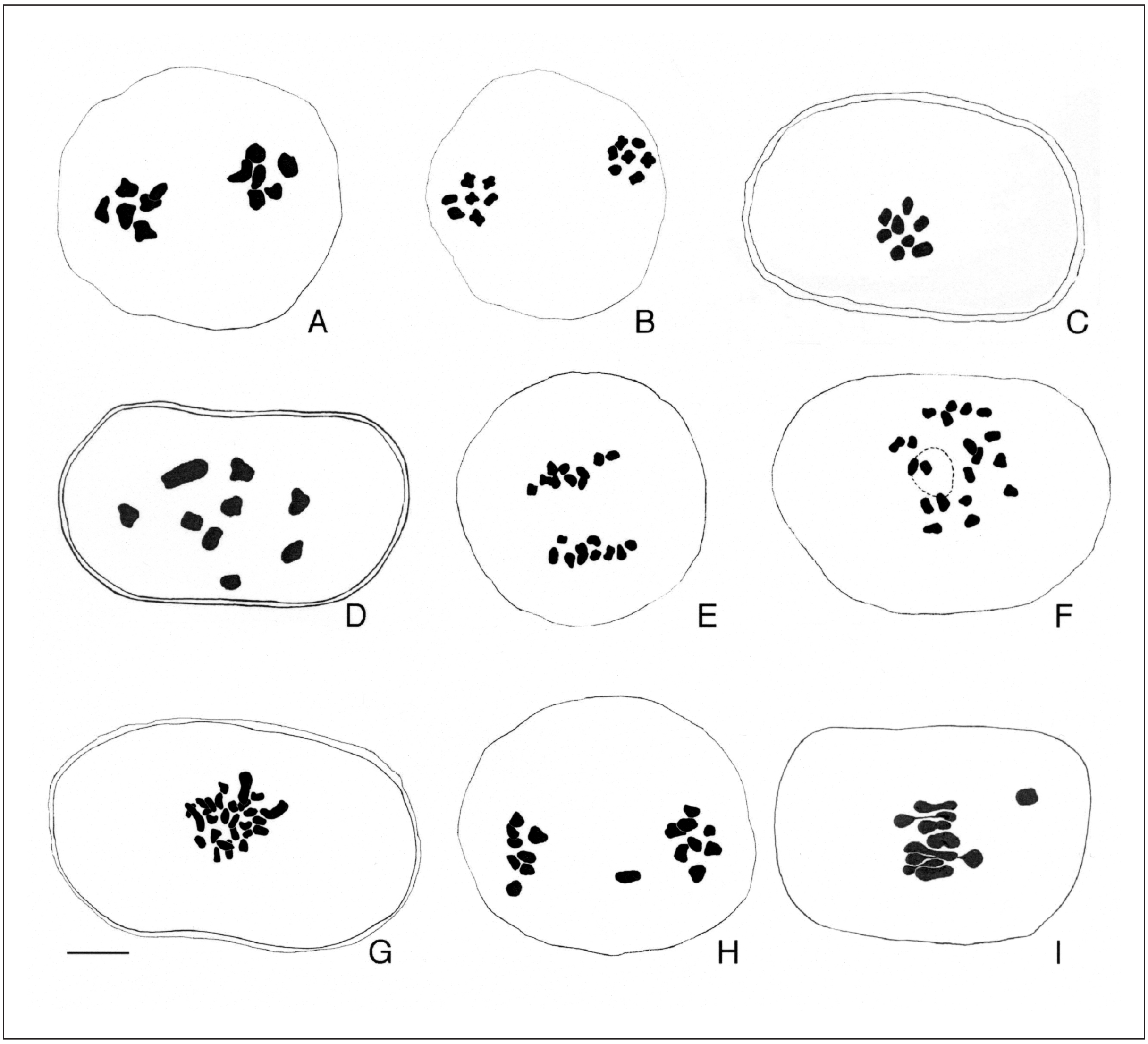

Fig. 1 – Drawings of chromosomes of selected species. A: meiosis of *I. aureliana* (n = 6); B: meiosis of *I. trichosepala* (n = 7); C: pollen mitosis of *I. nopoensis* (n = 8); D: pollen mitosis of *I. radiata* (n = 9); E: meiosis of *I. arguta* (n = 10); F: meiosis of *I. uniflora* (n = 20); G: pollen mitosis of *I. pseudokingii* (n = 27); H and I: meiosis of *I. mengtseana* showing one unpaired chromosome and the unbalanced segregation ($2n$ = 16 + 1). Bar 5 µm.

reports but were different from some other reports: *I. arguta* (present result n = 10, previous reports n = 6, 9, or 10) (Fig. 1E), *I. bicornuta* (present $2n$ = 18, previous n = 8 or $2n$ = 18), *I. radiata* (present $2n$ = 18, previous n = 10 or $2n$ = 18) (Fig. 1D), and *I. rubrostriata* (present $2n$ = 20, previous $2n$ = 20 or 40). A different number, $2n$ = 18, was found for *I. eubotrya* from Sumatra which was previously reported as $2n$ = 28, and a different number n = 9 was found for *I. drepanophora* which was previously reported as n = 10. The number n = 27, new for the family, was found in *I. pseudokingii*, with three chromosomes conspicuously longer than others in the pollen mitoses suggesting the species as a hexaploid. Intraspecific variation was found in *I. mengtszeana* only, where unbalanced gametes with the numbers of n = 8 and n = 9 were observed from the mitosis of pollen cells in one population (Fig. 1H-I), whereas only n = 8 was observed in another population.

Most of our observations were made on meiosis of pollen mother cells. Therefore, we do not obtain much of karyomorphological data. Nevertheless, noticeably almost all the species we observed with n = 9 or $2n$ = 18 showed a bimodal karyotype structure: one pair of chromosomes (or one in gamete) is distinctly longer than other chromosomes, for examples, *I. drepanophora* (Fig. 2D), *I. holocentra* (Fig. 2B), *I. radiata* (Fig. 1D), *I. rectangula* (Fig. 2C), etc. In the possible hexaploid *I. pseudokingii* (n = 27), three distinctively longer chromosomes were found in its gamete (Fig. 1G). Such bimodal karyotype structure seems to be specific to the species with basic number x = 9. All the species we observed with basic number x = 9 show such karyotype, except only *I. apsotis*, which has 9 chromosomes with similar size in its gametes. All the species we observed with other chromosome numbers do not show such bimodal structure, where all the chromosomes are more or less the same size, for example, *I. delavayi* (Fig. 2A).

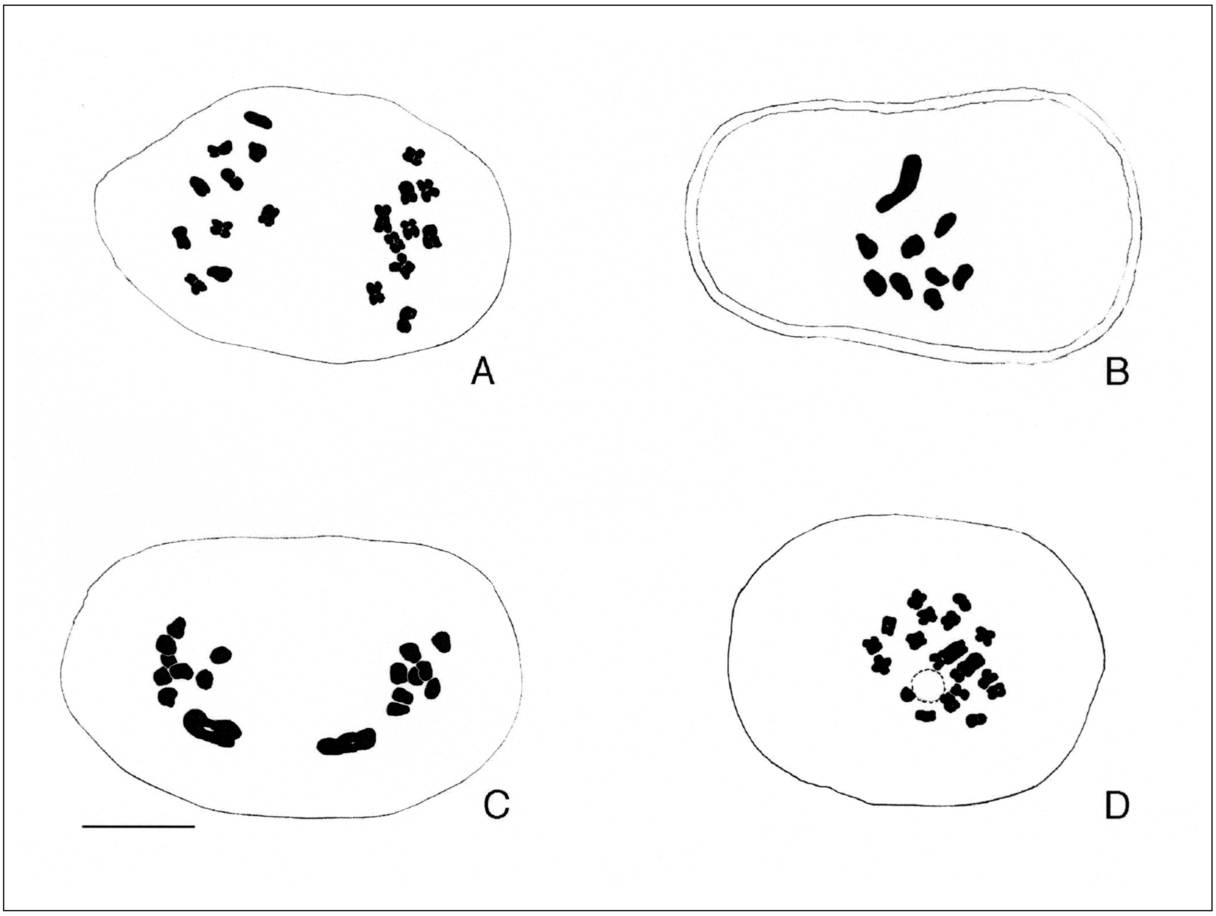

Fig. 2 – Comparison of non-bimodal and bimodal karyotypes. A: regular non-bimodal karyotype of *I. delavayi* (n = 10); B: bimodal karyotype of *I. holocentra* (pollen mitosis, n = 9); C: bimodal karyotype of *I. rectangula* (meiosis, n = 9); D: bimodal karyotype of *I. drepanophora* (mitosis, $2n$ = 18). Bar 5 µm.

DISCUSSIONS

Variation and evolution of chromosome numbers in Impatiens

Our present study contributed new documentation of chromosome numbers for 32 species from one of the most important, yet poorly studied, diversification centres of *Impatiens*. While our observations confirmed previous reports for seven species, some differences from previous reports were also revealed. We observed n = 9 with one long chromosome in *I. eubotrya*, but it was reported as $2n$ = 28 (OKADA *et al.* 1989). The number n = 10 was reported for *I. drepanophora* from India (SARKAR *et al.* 1975), but all our samples collected from three localities in southwest China had the same number of n = 9 or $2n$ = 18 (Fig. 2D). We observed n = 10 in *I. arguta* (Fig. 1E), which is the same as the report of SUGAWARA *et al.* (1997), but different from the results of AKIYAMA *et al.* (1996a) and SHIMIZU (1984) of n = 9 and $2n$ = 18, and also different from the report of CHATTERJEE and SHARMA (1970) of n = 6. For *I. bicornuta* we observed $2n$ = 18 for the samples collected from southwest China, the same as the results of AKIYAMA *et al.* (1992) and WAKABAYASHI (1992), but different from the report of MALLA *et al.* (1978) with n = 8 for samples collected from Nepal. For *I. radiata*, we observed n = 9 or $2n$ = 18 (Fig. 2C) from southwest China, the same as the results of AKIYAMA *et al.* (1992, 1996a) and SUGAWARA *et al.* (1997), but SARKAR *et al.* (1975) reported n = 10 from India. In *I. mengtszeana* $2n$ = 16 (LARSEN 1981; AKIYAMA *et al.* 1996a; SUGAWARA *et al.* 1997) or both $2n$ = 16 and $2n$ = 17 (SUGAWARA *et al.* 1994) were found. In our observation, only n = 8 was found in one population, but unbalanced separation of gametes with n = 8 and 9 were observed in the pollen mitosis from another population (Fig 1H-I). These different numbers found for a species could be due to true intraspecific variation (as in *I. mengtszeana*), but it might be also the results of misidentifications of different authors, since the determination of species is a well-known difficulty in *Impatiens*.

Combining our present results with all previous reports, chromosome numbers are available for 189 (out of over 900) species of *Impatiens* (Table 2). The distribution of the documented

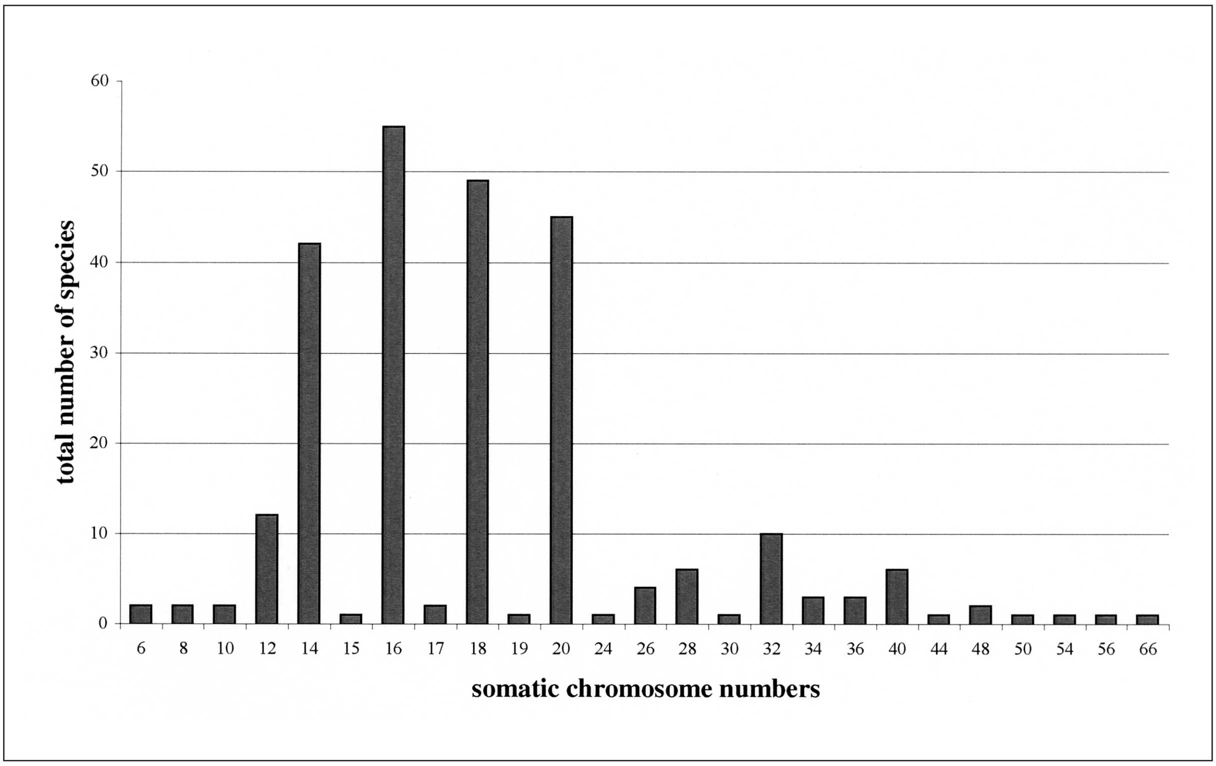

Fig. 3 – Frequency of species with different chromosome numbers based on the available chromosome data including our present results. Species with more than one chromosome numbers were counted repeatedly. The unusual numbers $2n$ = 15, 17, and 19 are intraspecific variations occasionally observed.

chromosome numbers is presented in Fig 3. As can be seen from the figure, *Impatiens* shows a wide range of chromosome number variation of 2*n* = 6, 8, 10, 12, 14, 15, 16, 17, 18, 19, 20, 24, 26, 28, 30, 32, 34, 36, 40, 44, 48, 50, 54, and 66. However, the most frequent numbers are 2*n* = 14, 16, 18, and 20, that take the major part (78%) of the species observed. The unusual numbers 2*n* = 15, 17, and 19, which were observed occasionally, represent the intraspecific aneuploid variations as observed in *I. mengtszeana* (present study; SUGAWARA *et al.* 1994). They may also result from hybridisation of parents with different basic numbers. It is not known yet whether these numbers are stable in natural populations.

Except for these few aneuploid cases, *Impatiens* shows a typical dysploid variation. Most of the species can be considered as diploids with the basic numbers of x = 3, 4, 5, 6, 7, 8, 9, 10, 12, 13, etc., and some higher numbers such as 2*n* = 32,

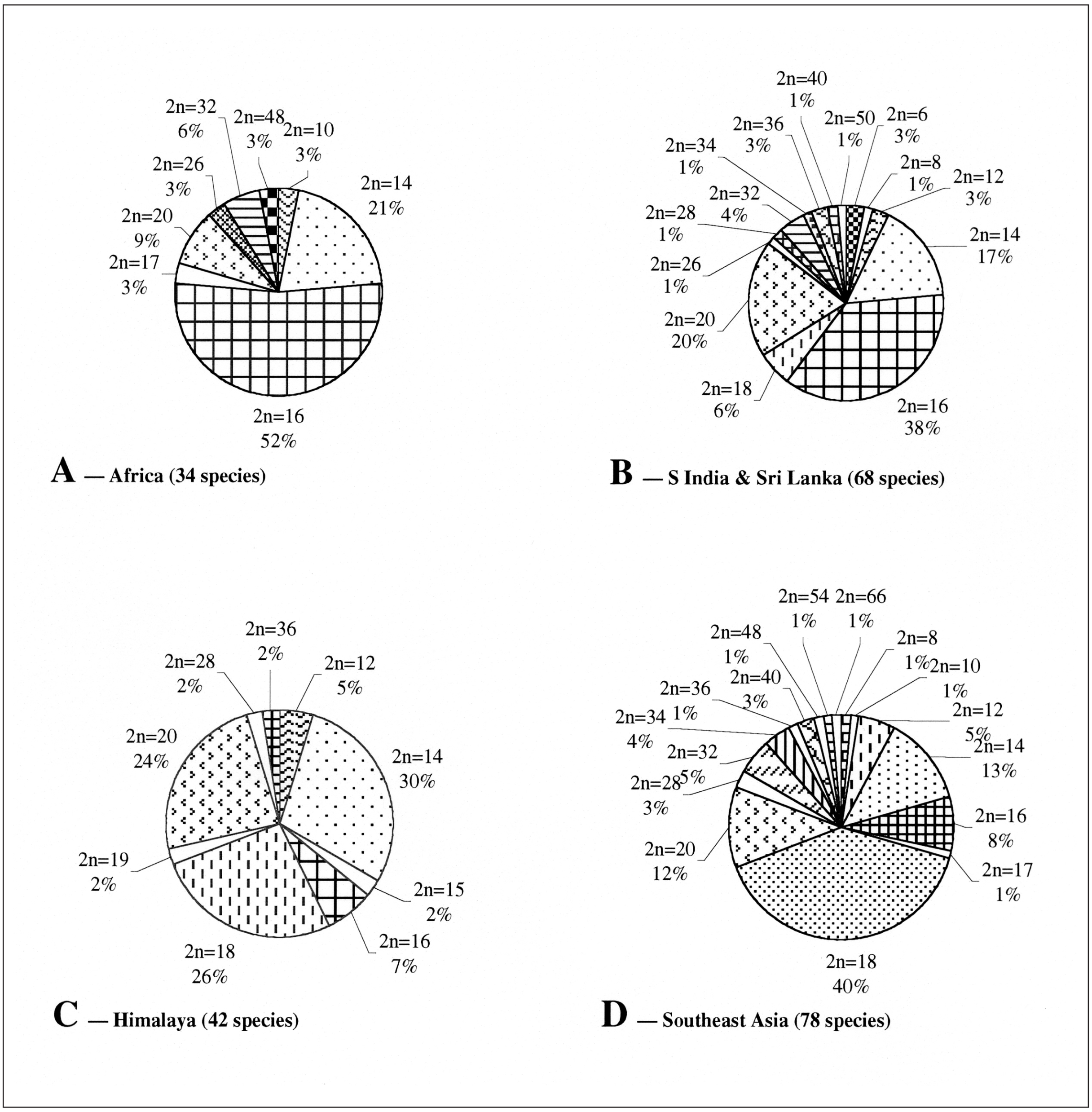

Fig. 4 – Partition of species numbers with different somatic chromosome numbers observed from the hotspots of species diversity of *Impatiens*. Total species number counted for each area is indicated on the figure. Species with more than one chromosome numbers were counted repeatedly. A: Africa; B: southern India and Sri Lanka; C: the Himalayas; D: Southeast Asia in broad sense including southwest China.

36, 40 etc. can be considered as polyploid of these lower basic numbers. Higher numbers such as 2*n* = 34, 44, 54, and 66 can be explained either as diploid with higher secondary basic numbers, or dysploid at polyploid levels. Different hypotheses have been proposed regarding the evolution of the basic numbers through dysploidy in conjunction with polyploidy in *Impatiens*. JONES and SMITH (1966) and AKIYAMA *et al*. (1992) suggested x = 7 to be the ancestral type, from which the other numbers were derived mainly by ascending dysploidy, whereas RAO *et al*. (1986) suggested evolution of x = 7, 9 and 10 from the basic number x = 8 through both descending and ascending dysplody. Considering the chromosome number of *Hydrocera triflora* (consistently reported as 2*n* = 16), the sister group of *Impatiens*, the suggestion of RAO *et al*. (1986) sounds reasonable. However, the possibility of the basic numbers x = 9 and 10 being ancestral in *Impatiens* cannot be ruled out yet. Chromosome numbers alone may not be able to offer a solid solution to the evolution of the basic numbers, particularly concerning the polarity of the dysploidy. Phylogenetic studies may hopefully bring an insight on these questions. Yet, the mechanism of the dysploidy is not well understood. Meiosis involving irregular segregation, unequal translocation, centric fusion and centric fission are all possible causes of dysploid variations (STEBBINS 1971).

Polyploidy holds certain importance in the chromosomal evolution in *Impatiens*. In particular, it may play an important role in the natural hybridisations reported in this genus (GREY-WILSON 1980b; MERLIN and GRANT 1985). Some polyploid numbers such as 2*n* = 32, 36, and 40 can be simply considered as originated via autoploidization of diploid species with basic numbers x = 8, 9, 10, as in e. g. the African species *I. schlechteri* and *I. niamniamensis* 2*n* = 32 (JONES and SMITH 1966), *I. linearisepala* 2*n* = 36 (SUGAWARA *et al.* 1997), and *I. rubrostriata* 2*n* = 20 and 40 (present result and SUGAWARA *et al*. 1994, 1997) from southwest China. The high numbers as shown by *I. coelotropis* 2*n* = 34 (ZINOV'EVA-STAHEVICH and GRANT 1982, 1984) from southern India, *I. mirabilis n* = 17 (JONES and SMITH 1966) from Malaysia, *I. mooreana* 2*n* = 66 (JONES and SMITH 1966), and *I. pseudokingii n* = 27 (present results) could have resulted from hybridization, and therefore, can be considered as secondary dibasic polyploids. For example, one may

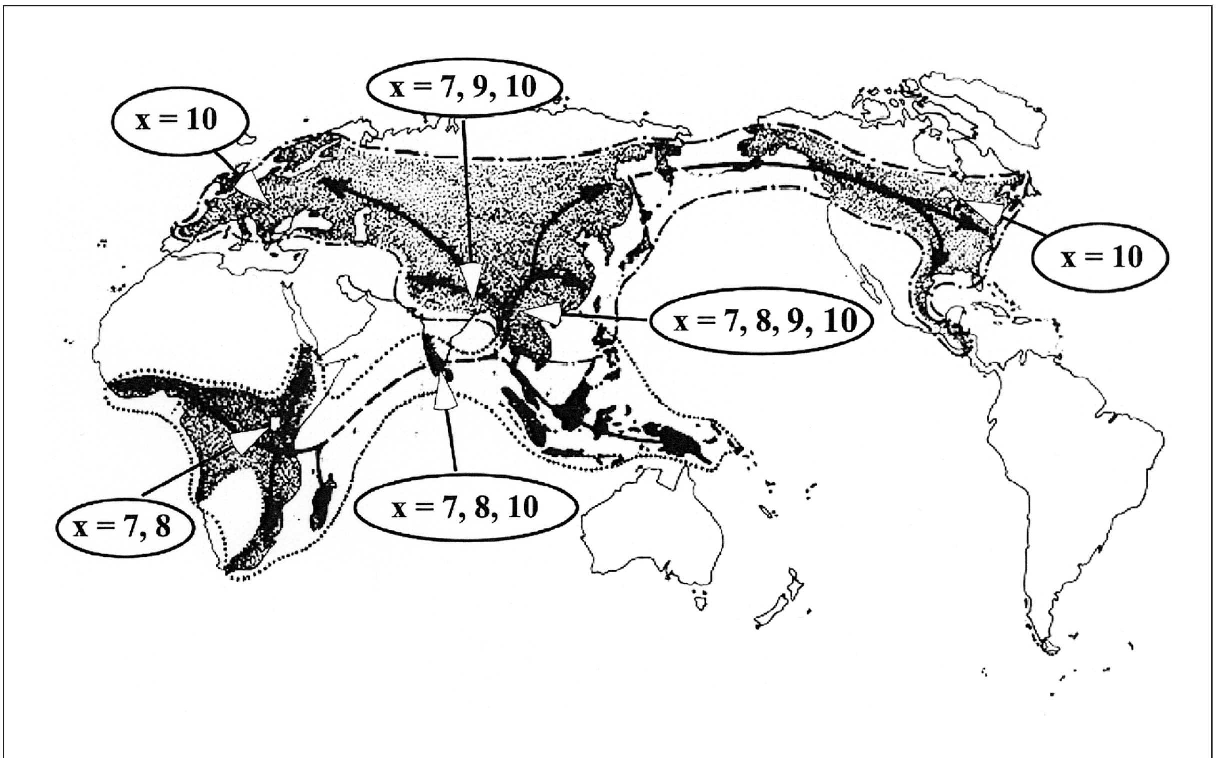

Fig. 5 – Distribution of the most frequent basic chromosome numbers and the migration routes proposed by GREY-WILSON (1980a).

consider $2n = 34$ ($n = 17$) as a result of hybridisation of parent species of $n = 7$ and $n = 10$, or $n = 8$ and $n = 9$ respectively. Dysploid variation at polyploid level can also result in such high secondary basic numbers, e. g. descending dysploidy from $2n = 4x = 36$ can bring about the same number $2n = 34$. Further phylogenetic studies may supply independent and more robust test of these hypotheses.

Karyotype structure

Most *Impatiens* species have symmetrical karyotypes, i. e. all the chromosomes of a species are similar to each other in size and are mostly metacentric or submetacentric (LEVAN *et al.* 1964). Noticeably, *Impatiens* species with $2n = 18$ (or $n = 9$) from the Sino-Himalayan area, Indochina and Southeast Asia show special bimodal karyotypes: one pair (one in gamete) of chromosomes is distinctly longer than other chromosomes. SMITH (1934) first noticed this phenomenon in *I. glandulifera* (*I. roylei*) from the Himalayas. AKIYAMA *et al*. (1992) found that such bimodal karyotypes are characteristic of the species with $n = 9$, predominantly in central and eastern Nepal. In our present observations, almost all the species with $n = 9$ or $2n = 18$ showed such bimodal karyotypes (Fig. 2B-D), with exception of only one species, *I. apsotis*, which has 9 chromosomes of similar size in its gametes. We did not observe species with any other number showing the bimodal karyotype. However, SUGAWARA *et al*. (1994) reported such bimodal karyotypes for species with $2n = 12, 20$ from China.

Asymmetrical bimodal karyotypes can result from symmetrical karyotypes via unequal translocations (STEBBINS 1971). KHOSHOO (1957) suggested that the bimodal karyotype with $x = 9$ was derived from a symmetrical karyotype with $x = 10$ by translocation of the essential material of one chromosome onto one of the arms of another chromosome followed by the loss of one centromere. At present, there is no clear evidence to indicate the origin of the bimodal karyotype in species of *Impatiens* with $x = 9$. If we accept the assumption of $x = 8$ as the ancestral basic number for *Impatiens* as suggested by RAO *et al.* (1986), an alternative hypothesis has to be proposed to explain the origin of the bimodal karyotypes related to the basic number $x = 9$. Such an alternative hypothesis to explain the origin of the bimodal karyotypes via ascending dysploidy is not available yet.

Cytogeography of Impatiens

Chromosome number variations in *Impatiens* show interesting geographical patterns, that strongly related to the centres of species diversity and endemism. Of the five hotspots of species diversity, karyological data are almost blank for Madagascar. We made a brief partition of the available chromosome data for the other diversification centres according to the origin of the samples. The results are shown in Fig. 4. Most African species have the chromosome number of $2n = 16$ (shown by 52% of species observed) or $2n = 14$ (21%), other numbers such as $2n = 10, 20, 32$ occurred less frequently, and the number $2n = 18$ has never been found (Fig. 4A). Southern India and Sri Lanka, particularly the Western Ghats host a lot of *Impatiens* species with high proportion of endemics. Most species from this region have the chromosome number of $2n = 16$ (38%), followed by $2n = 20$ (20%) and $2n = 14$ (17%) (Fig. 4B). The lowest chromosome number in *Impatiens*, $2n = 6$, occurred only in this region. JONES and SMITH (1966) believed that the Himalayas represent the centre of origin of *Impatiens* and that species diversified and radiated from an ancestral stock of $2n = 2x = 14$, but KHOSHOO (1966) suggested that the chromosome number $2n = 2x = 20$ was more typical of the Himalayan species. The available data today show three main basic numbers, $x = 7, 9, 10$, with similar frequencies for the Himalayan species: $2n = 14$ (30%), $2n = 18$ (26%), and $2n = 20$ (24%) (Fig. 4C). The region of the broad Southeast Asia including mainland Southeast Asia, southwest China, Indochina peninsula, and Malesia harbours species mostly with $2n = 18$ (40%), $2n = 14$ (13%), $2n = 20$ (12%), and $2n = 16$ (8%) (Fig. 4D). All native species in northern Asia, Europe and North America have the number of $2n = 2x = 20$ only.

Based on the pronounced similarity of species occurring in Africa, Madagascar, and Southern India, Grey-WILSON (1980a) believed that *Impatiens* originated in west Gondwana in the Paleogene and spread to Southeast Asia through the Indian subcontinent. He further suggested that the spreading drought during the Neogene caused the isolation of *Impatiens* species in Africa, Madagascar, southern India and Sri Lanka and Southeast Asia. Subsequently, from Southeast Asia and the adjacent Himalayan area, *Impatiens* further diversified into two lineages, one lineage radiating to the temperate Eurasian areas and North America, another radiating in the tropical and subtropical areas. Moreover, he pro-

Table 2 – Chromosome numbers documented for the family Balsaminaceae including present results.

Taxon	Chrom. No. *n*	Chrom. No. 2*n*	Origin	References
Hydrocera triflota Wight et Arn.		16	S India	GOVINDARAJAN and SUBRAMANIAN 1986
		16	S India	RAO *et al.* 1986
	8		S India	AYYANGAR *et al.* 1987
Impatiens acaulis Arn.	10		Karnataka, India	BHASKAR 1976
	10		Udipi, India	BHASKAR 1980
I. acaulis Arn. var. *granulata* Bhask.	9		S India	BHASKAR 1980
	8, 9		Agumbe, India	BHASKAR 1980
I. acehensis C. Grey-Wilson		14	Sumatra, Indonesia	present study
I. agumbeyana V. Bhaskar et B. A. Razi	8		Karnataka, India	BHASKAR 1976
	8		Agumbe, India	BHASKAR 1980
I. alboflava Miq.		14	W Sumatra	OKADA 1989
I. aliciae C. E. C. Fischer var. *bababudensis* Bhask.	8		Karnataka, India	BHASKAR 1976
I. amphorata Edgew.	7	14	Kashmir	KHOSHOO 1957
	7		W Himalaya	FEDOROV 1969
I. amplexicaulis Edgew.		20	Himalaya	FEDOROV 1969
I. aquatilis Hook. f.	9		Yunnan, China	present study
I. apsotis Hook. f.	9		Sichuan, China	present study
I. arguta Hook. f. et Thoms.	6		E Himalaya	CHATTERJEE and SHARMA 1970
	9		E Himalaya	SHIMIZU 1984
		18	Himalaya	AKIYAMA *et al.* 1996a
		20	Yunnan, China	SUGAWARA *et al.* 1997
	10		Yunnan, China	present study
*I. assurgens*Baker	5		Tanzania	GIL and CHINNAPPA 1977
I. aureliana Hook. f.		12	Yunnan, China	SUGAWARA *et al.* 1994
		12	Yunnan, China	AKIYAMA *et al.* 1996a
	6		Yunnan, China	present study
I. auricoma Baill.		16	Africa	ARISUMI 1987
I. bahanensis Hand.-Mazz.	9		Yunnan, China	present study
I. balfourii Hook. f.	7	14	Himalaya	FEDOROV 1969
	7		Cult. USA	CHINNAPPA and GILL 1974
		14	Cult. France	ZINOV'EVA-STAHEVITCH and GRANT 1982
		14	W Himalaya	ZINOV'EVA-STAHEVITCH and GRANT 1984
		14	Cult. Mediterrtanean region	CHESHMEDYIEV 1994
I. balsamina L.		14	?	FEDOROV 1969
	5, 6, 7		S India	RAO 1975
		14	Cult. Beijing, China	GAO and ZHANG 1984
		44	S India	GOVINDARAJAN 1985
		44	S India	GOVINDARAJAN and SUBRAMANIAN 1986
		14	Maharashtra, India	ZINOV'EVA-STAHEVITCH and GRANT 1982
	7	14	Maharashtra, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. balsamina L. var. *arcuata* Wall.		44	S India	GOVINDARAJAN and SUBRAMANIAN 1986
I. balsamina L. var. *azaleiflora*	7	14	Maharashtra, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
		14	S India	RAO *et al.* 1986
	7		S India	AYYANGAR *et al.*1987
I. balsamina L. var. *bicolor*		14+2b	?	RAGHUVANSHI and MAHAJAN 1985
I. balsamina L. var. *camelliaeflora*	7	14	Maharashtra, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
		14	S India	RAO *et al.* 1986
	7		S India	AYYANGAR *et al.*1987
I. balsamina L. var. *coccinea* (Wall.) Hook. f.	7	14	S India	ZINOV'EVA-STAHEVITCH and GRANT 1984
		14	S India	RAO *et al.* 1986
	7		S India	AYYANGAR *et al.*1987
I. balsamina L. var. *rosea* Hook. f.		14, 28	Maharashtra, India	ZINOV'EVA-STAHEVITCH and GRANT 1982
	7	14	S India	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. balsamina L. var. *vulgaris*		14	S India	RAO *et al.* 1986
	7		S India	AYYANGAR *et al.* 1987
I. barberi Hook. f.	8		Karnataka, India	BHASKAR 1976
	8		S India	BHASKAR 1980
I. begonifolia S. Akiyama et H. Ohba		16	Yunnan, China	SUGAWARA *et al.* 1994
		16	Himalaya	AKIYAMA *et al.* 1996a
I. bella Hook. f. et Thoms.		14	Himalaya	FEDOROV 1969
I. bicornuta Wall.	8		Nepal	MALLA *et al.* 1978
		18	Nepal	AKIYAMA *et al.* 1992
		18	?	WAKABAYASHI 1992
		18	Yunnan, China	present study

Taxon	Chrom. No.		Origin	References
	n	2*n*		
I. biflora Walt.		20	N America ?	SMITH 1934
	10		?	FEDOROV 1969
	10		N America	CHINNAPPA and GILL 1974
I. brachycentra Kar. et Kir.		14	Himalaya	FEDOROV 1969
	7		Kashmir, India	BHAT *et al.* 1975
I. burtonii Hook. f.	8	16	Congo	JONES and SMITH 1966
		16	Cameroon	GADELLA 1977
		14	Cameroon	GADELLA 1982
I. campanulata Wight	10	20	Paini Hills, India	JONES and SMITH 1966
	10	20	Travancore, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
	10		S India	ZINOV'EVA-STAHEVITCH and GRANT 1985
		20	S India	RAO *et al.* 1986
		18	India	ARISUMI 1987
I. capensis Meerb.		14	?	FEDOROV 1969
		20	Manitoba, Canada	LÖVE and LÖVE 1982
		20	Montreal, Canada	ZINOV'EVA-STAHEVITCH and GRANT 1982
	10		Ottawa, Canada	MULLIGAN 1984
		20	Québec, Canada	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. chiangdaoensis Shimizu		12	Thailand	LARSEN 1981
	6	12	Thailand	SHIMIZU 1979
I. chimiliensis Comber		18	Yunnan, China	present study
I. chinensis L.		16	S India	RAO *et al.* 1986
	8		Yunnan, China	present study
I. chungtienensis Y. L .Chen	9		Yunnan, China	present study
I. cinnabarina C. Grey-Wilson		16	Tanzania	ZINOV'EVA-STAHEVITCH and GRANT 1982
		16	Tanzania	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. clavicornu Turcz.	8		Doddabetta, India	BHASKAR 1980
		14	S India	GOVINDARAJAN and SUBRAMANIAN 1986
		14	S India	RAO *et al.* 1986
	7		S India	AYYANGAR *et al.* 1987
I. clavigeroides S. Akiyama, H. Ohba et S. K. Wu		34	Yunnan, China	SUGAWARA *et al.* 1997
I. coelotropis Fisch.		34	Kerala, India	ZINOV'EVA-STAHEVITCH and GRANT 1982
		34	Kerala, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
	17		Kerala, India	ZINOV'EVA-STAHEVITCH and GRANT 1985
I. congolensis G. M. Schulze et R. Wilczek				
var. longicarata G. M. Schulze et R. Wilczek	24	48	Congo	JONES and SMITH 1966
I. corchorifolia Franch.		18	Yunnan, China	SUGAWARA *et al.* 1997
I. cordata Wight	10		Tamil Nadu, India	BHASKAR 1976
		20	Kerala, India	ZINOV'EVA-STAHEVITCH and GRANT 1982
		20	Travancore, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
		20	S India	RAO *et al.* 1986
I. crassicaudex Hook. f.	9		Yunnan, China	present study
I. cuspidata Wight et Arn.		14	Tamil Nadu, India	ZINOV'EVA-STAHEVITCH and GRANT 1982
	7	14	Tamil Nadu, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
		14	Tamil Nadu, India	ZINOV'EVA-STTAHEVITCH and GRANT 1985
		14	S India	GOVINDARAJAN and SUBRAMANIAN 1986
		14	S India	RAO *et al.* 1986
I. cyathiflora Hook. f.		18	Yunnan, China	present study
I. cymbifera Hook. f.		18, 19	Nepal	AKIYAMA *et al.* 1992
I. dalzellii Hook. f. et Thoms.		16	Maharashtra, India	ZINOV'EVA-STAHEVITCH and GRANT 1982
		16	Maharashtra, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. delavayi Franch.	10	20	Yunnan, China	present study
I. dendricola C. E. C. Fischer	7		Karnataka, India	BHASKAR 1976
	7		Tadiandamol, India	BHASKAR 1980
I. desmantha Hook. f.	9		Yunnan, China	present study
I. diepenhorstii Miq.		28	W Sumatra	OKADA *et al.* 1989
I. digitata Warb	10		Tanzania	GILL and CHINNAPPA 1977
I. discolor DC.		20	Nepal	AKIYAMA *et al.* 1992
I. dolichoceras E. Pritz. ex Diels		18	Guangxi, China	present study
I. drepanophora Hook. f.	10		India	SARKAR *et al.* 1975
	9		Yunnan, China	present study
I. ecalcarata Blank.	10		N America	CHINNAPPA and GILL 1974
I. edgeworthii Hook. f.	6	12	Himalaya	FEDOROV 1969
	7		Kashmir	GOHIL *et al.* 1981
	7		Kashmir	JEE *et al.* 1989

Taxon	Chrom. No.		Origin	References
	n	2*n*		
I. elegans Bedd.		20	Travancore, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. eubotrya Miq.		28	Sumatra, Indonesia	OKADA *et al.* 1989
		18	Sumatra, Indonesia	present study
I. exlis Hook. f.		28	?	WAKABAYASHI 1992
		28	Nepal	AKIYAMA *et al.* 1992
		28	Himalaya	AKIYAMA *et al.* 1993
I. falcifera Hook. f.	8		Nepal	MALLA *et al.* 1975
		14	Nepal	AKIYAMA *et al.* 1992
		14	?	WAKABAYASHI, 1992
I. fenghwaiana Y. L. Chen		18	Guangxi, China	present study
I. firmula Baker		14	Madagascar ?	FEDOROV 1969
I. flaccida Arn.	7	14	Mauritius	JONES and SMITH 1966
		14	Sri. Lanka	ZINOV'EVA-STAHEVITCH and GRANT 1982
	7	14	Sri. Lanka	ZINOV'EVA-STAHEVITCH and GRANT 1984
	7	14	Sri Lanka	ZINOV'EVA-STAHEVITCH and GRANT 1985
		14	India	ARISUMI 1987
I. flanaganae Hemsl.		16	S Africa	ZINOV'EVA-STAHEVITCH and GRANT 1982
		16	S Africa	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. fruticosa Leschen. ex DC.		16	S India	RAO *et al.* 1986
I. furcillata Hemsl.ex Forb. et Hemsl.		20	?	FEDOROV 1969
I. gadutensis		14	W Sumatra	OKADA *et al.* 1989
I. gardneriana Wight ex Hook. f.		16	Kerala, India	ZINOV'EVA-STAHEVITCH and GRANT 1982
		16	Kerala, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. gongshanensis Y. L. Chen	10		Yunnan, China	present study
I. glandulifera Royle		18	Himalaya	SMITH 1934
		18, 20	Himalaya	FEDOROV 1969
	9, 10		Cult. Kew	JONES and SMITH 1966
	10		N America	CHINNAPPA and GILL 1974
		18	Czechoslovakia?	JAVURKOVA 1979
		18	Mediterranean region?	CHESHMEDYIEV 1994
		18	Austria	DOBES *et al.* 1997
I. gordonii Horne		16	Seychelles	ZINOV'EVA-STAHEVITCH and GRANT 1982
	8	16	Seychelles	ZINOV'EVA-STAHEVITCH and GRANT 1984
		16	Seychelles	ZINOV'EVA-STTAHEVITCH and GRANT 1985
	8		Seychelles	MERLIN and GRANT 1985
I. goughii Wight		16	S India	RAO 1973
	10		Kerala, India	BHASKAR 1976
		32	Tamil Nadu, India	ZINOV'EVA-STAHEVITCH and GRANT 1982
		32	Tamil Nadu, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. grandis Heyne	20		Tamil Nadu, India	BHASKAR 1976
		36	Coonoor, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
		40	Sri Lanka; S India	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. hamata Warb.	7		Tanzania	GILL and CHINNAPPA 1977
I. harlandii Dranfield		12	Borneo	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. hawkeri W. Bull ex Gard.		48	South Sea Islands	JONES and SMITH 1966
	24		NE New Guinea	ZINOV'EVA-STAHEVITCH and GRANT 1982
	24		NE New Guinea	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. hensloviana Arn.	8		Kerala, India	BHASKAR 1976
		16	S India	GOVINDARAJAN 1985
		16	S India	GOVINDARAJAN and SUBRAMANIAN 1986
I. herbicola Hook. f.	7		Karnataka, India	BHASKAR 1976
I. hochstetteri Warb.		16	Kenya	JONES and SMITH 1966
I. holocentra Hand.-Mazz.	9		Yunnan, China	present study
I. hookeriana Arn.		40	India	JONES and SMITH 1966
		18	Tamil Nadu, India	ZINOV'EVA-STAHEVITCH and GRANT 1982
		16	S India	RAO *et al.* 1986
		36	India	ARISUMI 1987
		50	Sri Lanka	STAHEVITCH 1995
I. hypophylla Makino		20	?	TAGAWA *et al.* 1997
I. hypophylla Makino *var. microhypophylla* Hara		20	?	TAGAWA *et al.* 1997
I. imbecilla Hook. f.		20	Sichuan, China	present study
I. infirma Hook. f.	9		Sichuan, China	present study
I. irvingii Hook. f. ex Oliv.		14	Cameroon	MORTON 1993
I. junghuhnii Miq.		14	W Sumatra	OKADA *et al.* 1989
I. kamtilongensis Toppin		14	Yunnan, China	SUGAWARA *et al.* 1997

Taxon	Chrom. No. *n*	*2n*	Origin	References
I. keilii Grig.	7		Tanzania	GILL and CHINNAPPA 1977
		16	Africa	ARISUMI 1987
I. kilimanjari Oliver	13		Tanzania	GILL and CHINNAPPA 1977
I. kleinii Wight et Arn.		16	Maharashtra, India	ZINOV'EVA-STAHEVITCH and GRANT 1982
		16	Maharashtra, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. latifolia L.	3		S India	RAO 1975
		6	S India	GOVINDARAJAN and SUBRAMANIAN 1986
		6	S India	RAO *et al.* 1986
	3		S India	AYYANGAR *et al.*1987
I. lawsoni Hook. f.	10		Karnataka, India	BHASKAR 1976
	10		Charmadi Ghat, India	BHASKAR 1980
I. lecomtei Hook. f.		18	Yunnan, China	present study
I. lenta Hook. f.	8		Kerala, India	BHASKAR 1976
I. leptopoda Arn.		8	Sri Lanka	STAHEVITCH 1995
I. leschenaultii Wall.		6	S India	BHASKAR and RAZI 1972-1973
	3		S India	RAO 1975
		6	Tamil Nadu, India	ZINOV'EVA-STAHEVITCH and GRANT 1982
	3	6	Tamil Nadu, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
	3		Tamil Nadu, India	ZINOV'EVA-STAHEVITCH and GRANT 1985
		6	S India	GOVINDARAJAN and SUBRAMANIAN 1986
		6	S India	RAO *et al.* 1986
	3		S India	AYYANGAR *et al.*1987
I. levingei Gamble ex Hook. f.		16	Tamil Nadu, India	ZINOV'EVA-STAHEVITCH and GRANT 1982
	8	16	Tamil Nadu, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
	8	16	Tamil Nadu, India	ZINOV'EVA-STAHEVITCH and GRANT 1985
I. linearifolia Warb.		32	New Guinea	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. linearisepala S. Akiyama, H. Ohba et S. K. Wu		36	Yunnan, China	SUGAWARA *et al.* 1997
I. longiloba Craib		18	Thailand	SHIMIZU *et al.* 1984
I. luchunensis S. Akiyama, H. Ohba et S. K. Wu				
I. maculata Wight		18	Yunnan, China	SUGAWARA *et al.* 1997
	10		Tamil Nadu, India	BHASKAR 1976
		20	Kerala, India	ZINOV'EVA-STAHEVITCH and GRANT 1982
		20	Travancore, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
		20	S India	GOVINDARAJAN and SUBRAMANIAN 1986
		20	S India	RAO *et al.* 1986
I. maguanensis S. Akiyama, H. Ohba et S. K. Wu		18	Yunnan, China	SUGAWARA *et al.* 1997
I. mathildae Chiov.		14	Himalaya ?	FEDOROV 1969
I. mengtzeana Hook. f.		16	Thailand	LARSEN 1981
		16, 17	Yunnan, China	SUGAWARA *et al.* 1994
		16	Himalaya	AKIYAMA *et al.* 1996a
		16	Yunnan, China	SUGAWARA *et al.* 1997
	8, 9		Yunnan, China	present study
I. meruensis Gilg		16	Kenya	OGIUMA and TOBE 1991
I. microcentra Hand.-Mazz.	9		Yunnan, China	present study
I. mirabilis Hook. f.	17		Malaysia	JONE and SMITH 1966
I. modesta Wight	8, 9, 16		Tamil Nadu, India	BHASKAR 1976
	8, 9, 16		Naduvattam, India	BHASKAR 1980
I. mooreana Schlechter		66	New Guinea	JONES and SMITH 1966
I. mysorensis Roth.	7		Karnataka, India	BHASKAR 1976
I. nalampoonii Shimizu		32	Thailand	SHIMIZU 1979
I. napoensis Y. L .Chen	9		Yunnan, China	present study
I. niamniamensis Gilg		32	Uganda	JONES and SMITH 1966
		32	Uganda	ZINOV'EVA-STAHEVITCH and GRANT 1982
	16	32	Tropical W Africa	ZINOV'EVA-STAHEVITCH and GRANT 1984
	16		Uganda	ZINOV'EVA-STAHEVITCH and GRANT 1985
		32	Africa	ARISUMI 1987
I. nolitangere L.		20, 40	?	FEDOROV 1969
	10		N America	CHINNAPPA and GILL 1974
		12	Russia	GVNINIANIDZE and AVAZNELI 1982
		20	Japan	NISHIKAWA 1990
		20	Mediterranean region?	CHESHMEDYIEV 1994
		20	Russian Far East	RUDYKA 1995
I. occultans Hook. f.		18	Nepal	AKIYAMA *et al.* 1992
I. omissa Hook. f.		28	S India	RAO *et al.* 1986
I. oncidioides Ridley ex Hook. f.		14	SE Asia	HELLMAYR *et al.* 1994

Taxon	Chrom. No.		Origin	References
	n	2*n*		
I. oppositifolia L.		16, 32	Mahabaleshwar, India	ZINOV'EVA-STAHEVITCH and GRANT 1982
		16	Mahabaleshwar, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. orchioides Bedd.		18	S India	GOVINDARAJAN 1985
		18	S India	GOVINDARAJAN and SUBRAMANIAN 1986
I. oxyanthera Hook. f.	7		Sichuan, China	present study
I. pallida Nutt.		20	N America	SMITH 1934
		20, 24?	?	FEDOROV 1969
	10		N America	CHINNAPPA and GILL 1974
		20, 30	Montréal, Canada	ZINOV'EVA-STAHEVITCH and GRANT 1982
	10	20	Montréal, Canada	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. pallidiflora Hook. f.	13		Kerala, India	BHASKAR 1976
		16	S India	RAO *et al.* 1986
I. parasitica Bedd.	9		?	BHASKAR 1975
	10		Kerala, India	BHASKAR 1976
		20	Kerala, India	ZINOV'EVA-STAHEVITCH and GRANT 1982
	7, 9, 10		Travancore, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
	7		Kerala, India	ZINOV'EVA-STAHEVITCH and GRANT 1985
I. parviflora DC.		20, 24, 26	?	FEDOROV 1969
	13		N America	CHINNAPPA and GILL 1974
	13		Montreal, Canada	ZINOV'EVA-STAHEVITCH and GRANT 1982
	13		NE Asia	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. parvifolia Bedd.	10		Kerala, India	BHASKAR 1976
I. phoenicea Bedd.	10		Tamil Nadu, India	BHASKAR 1976
		16	S India	GOVINDARAJAN 1985
		16	S India	GOVINDARAJAN and SUBRAMANIAN 1986
I. petersiana Gilg ex Grignan		16	Africa ?	FEDOROV 1969
I. plaghuhnii		16	W Sumatra	OKADA *et al.* 1989
I. platypetala x *aurantiaca* Steen		8	New Guinea	ARISUMI 1987
I. platypetala Lindl.		14	?	FEDOROV 1969
	7	14	Java, Indonesia	ZINOV'EVA-STAHEVITCH and GRANT 1984
	7		Java, Indonesia	ZINOV'EVA-STAHEVITCH and GRANT 1985
I. platypetala Lindl. ssp. *aurantiaca* x spp. Indet.		12	?	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. platypetala Lindl. ssp. *aurantiaca* (Teysm.ex Kds.) Steen.		14	Celebes, Indonesia	ZINOV'EVA-STAHEVITCH and GRANT 1984
	7		Celebes, Indonesia	ZINOV'EVA-STAHEVITCH and GRANT 1985
I. platypetala Lindl. ssp. *nematoceras* (Miq) Steen.	8	16	Indonesia	ZINOV'EVA-STAHEVITCH and GRANT 1982
	8		Indonesia	ZINOV'EVA-STAHEVITCH and GRANT 1985
		16	Indonesia	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. poculifer Hook. f.		20	Yunnan, China	present study
I. porphyrea Toppin		18	Yunnan, China	SUGAWARA *et al.* 1997
I. pradhani Hara		18	Nepal	AKIYAMA *et al.* 1992
I. principis Hook. f.	9		Yunnan, China	present study
I. pseudokingii Hand.-Mazz.	27		Yunnan, China	present study
I. pseudoviola Gilg		16	Kenya	JONES and SMITH 1966
	8	16	Kenya	ZINOV'EVA-STAHEVITCH and GRANT 1982
	8	16	Tropical E Africa	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. psittaciana Hook. f.		34	Thailand	SHIMIZU 1979
I. psychadelphoides Launert		32	Mozambique	JONES and SMITH 1966
I. puberula DC.	14		Nepal	MALLA *et al.* 1977A
		20	Nepal	AKIYAMA *et al.* 1992
		20	?	WAKABAYASHI 1992
I. pulcherrima Dalzell		12	Maharashtra, India	ZINOV'EVA-STAHEVITCH and GRANT 1982
	6	12	Maharashtra, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
	6		Maharashtra, India	ZINOV'EVA-STAHEVITCH and GRANT 1985
I. pusilla Heyne	8		Kerala, India	BHASKAR 1976
		16	S India	RAO *et al.* 1986
I. racemosa DC.	9		Himalaya	CHATTERJEE and SHARMA 1970
	10		Nepal	MALLA *et al.* 1977B
		18	Thailand	SHIMIZU *et al.* 1984
		18	Himalaya	AKIYAMA *et al.* 1992
		18	Yunnan, China	SUGAWARA *et al.* 1994
		18	Himalaya	AKIYAMA *et al.* 1996a
		18	Yunnan, China	SUGAWARA *et al.* 1997

Taxon	Chrom. No. *n*	*2n*	Origin	References
I. radiata Hook. f.	10		India	SARKAR *et al.* 1974
		18	Nepal	AKIYAMA *et al.* 1992
		18	Himalaya	AKIYAMA *et al.* 1996a
		18	Yunnan, China	SUGAWARA *et al.* 1997
		18	Yunnan, China	present study
I. rectangula Hand.-Mazz.	9	18	Yunnan, China	present study
I. repens Moon		14	Sri Lanka	JONES and SMITH 1966
		14	Sri Lanka	ZINOV'EVA-STAHEVITCH and GRANT 1982
	7	14	Sri Lanka	ZINOV'EVA-STAHEVITCH and GRANT 1984
	7		Sri Lanka	ZINOV'EVA-STAHEVITCH and GRANT 1985
		14	India	ARISUMI 1987
I. rostellata Franch.	10		Sichuan, China	present study
I. rubromaculata Warb.		16	Kenya	JONES and SMITH 1966
I. rubrostriata Hook. f.		20	Yunnan, China	SUGAWARA *et al.* 1994
		40	Yunnan, China	SUGAWARA *et al.* 1997
		20	Yunnan, China	present study
I. ruiliensis S. Akiyama et H. Ohba		18	Yunnan, China	SUGAWARA *et al.* 1994
		18	Yunnan, China	AKIYAMA *et al.* 1996a
		18	Yunnan, China	SUGAWARA *et al.* 1997
I. sarcantha Hook. f. ex Ridley	16		SE Asia	HELLMAYR *et al.* 1994
I. scabrida DC.		14	Himalaya ?	SMITH 1934
		14, 20	Himalaya	FEDOROV 1969
	6, 7		Cult. Kew, UK	JONES and SMITH 1966
	8		Himalaya	SHARMA and GHOSH 1976
		14	Himalaya	ZINOV'EVA-STAHEVITCH and GRANT 1982
	7	14	Himalaya	ZINOV'EVA-STAHEVITCH and GRANT 1984
		14	Nepal	AKIYAMA *et al.* 1992
		14	?	WAKABAYASHI 1992
I. scapiflora Heyne	6, 10		Karnataka, India	BHASKAR 1976
	8		Kerala, India	BHASKAR 1976
	6		Koyanad, India	BHASKAR 1980
	7, 8		Neilliambudi, India	BHASKAR 1980
	8		Devicolam, India	BHASKAR 1980
	10		Jodpala, India	BHASKAR 1980
I. scapiflora Heyne var. *pseudoacaulis* Bhaskar	10		Shevaroys, India	BHASKAR 1980
	10, 16, 20		Naduvattam, India	BHASKAR 1980
I. schlechteri Warb.		32	New Guinea	JONES and SMITH 1966
	16	32	New Guinea	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. scullyi Hook. f.		18	Nepal	AKIYAMA *et al.* 1992
		18	?	WAKABAYASHI 1992
I. scutisepala Hook. f.	9		Yunnan, China	present study
I. serrata Benth.		14	Himalaya	FEDOROV 1969
		14, 15	Nepal	AKIYAMA *et al.* 1992
		15	?	WAKABAYASHI 1992
I. siculifer Hook. f.		18	Yunnan, China	SUGAWARA *et al.* 1994
	9		Yunnan, China	present study
I. sodenii Engl. et Warb. ex Engl.		16	Kenya	ZINOV'EVA-STAHEVITCH and GRANT 1982
	8	16	Tropical E Africa	ZINOV'EVA-STAHEVITCH and GRANT 1984
	8		Kenya	ZINOV'EVA-STAHEVITCH and GRANT 1985
		16	S India	RAO *et al.* 1986
I. stenantha Hook. f.		18	Nepal	STAHEVITCH 1995
	9		Yunnan, China	present study
I. stocksii Hook. f. et Thoms.	7		Bababudangiri, India	BHASKAR 1980
I. sulcata Wall.		18	Nepal	AKIYAMA *et al.* 1992
	10	20	Himalaya	FEDOROV 1969
I. sunkoshiensis S. Akiyama, H. Ohba et M. Wakabayashi		18	Nepal	AKIYAMA *et al.* 1992
I. talangensis		c.60	W Sumatra	OKADA *et al.* 1989
I. talbotii Hook. f.	6		Karnataka, India	BHASKAR 1976
I. tangachee Bedd.	10		India ?	ZINOV'EVA-STAHEVITCH and GRANT 1985
I. taronensis Hand.-Mazz.		18	Yunnan, China	present study
I. tenella Heyne		16	S India	GOVINDARAJAN and SUBRAMANIAN 1986
		16	S India	RAO *et al.* 1986
I. tenuibracteata Y. L. Chen	9		Yunnan, China	present study

Taxon	Chrom. No.		Origin	References
	n	2*n*		
I. textori Miq.		20	Korea	LEE 1967
		20	?	FEDOROV 1969
I. thomsoni Hook. f.		14, 20	Himalaya	FEDOROV 1969
		12, 16	Himalaya	SHARMA and GHOSH 1976
I. tomentosa Heyne		16	S India	RAO *et al.* 1986
I. tongbiguanensis S. Akiyama et H. Ohba		18	Yunnan, China	SUGAWARA *et al.* 1994
		18	Yunnan, China	AKIYAMA *et al.* 1996a
I. tortisepala Hook. f.	10		Sichuan, China	present study
I. trichocepala Y. L. Chen	7		Yunnan, China	present study
I. tripetala Roxb.		14	Himalaya	FEDOROV 1969
	8		Meghalaya, India	SARKAR *et al.* 1980
I. uguenensis Warb.		16	Kenya	JONES and SMITH 1966
		16	Africa	ARISUMI 1987
I. uliginosa Franch.		18	Yunnan, China	SUGAWARA *et al.* 1994
		18	Yunnan, China	SUGAWARA *et al.* 1997
	9		Yunnan, China	present study
I. ulugurensis Warb	8		Tanzania	GILL and CHINNAPPA 1977
I. umbellata Heyne		20	S India	RAO *et al.* 1986
I. uncinata Wight	8		Tamil Nadu, India	BHASKAR 1976
		14	S India	RAO *et al.* 1986
I. uniflora Hayata	20		Taiwan, China	present study
I. urticifolia Wall.		18	Nepal	AKIYAMA *et al.* 1992
		36	Himalaya	AKIYAMA *et al.* 1993
I. usambarensis C. Grey-Wilson	8		Tanzania	MERLIN and GRANT 1985
		16	Tanzania	ZINOV'EVA-STAHEVITCH and GRANT 1982
		16	Tanzania	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. verticillata Wight		16	S India	RAO *et al.* 1986
		14	India	ARISUMI 1987
I. violaeflora Hook. f.		10, 12	Chiangmai, Thailand	LARSEN 1981
I. viscida Wight		16	Tamil Nadu, India	ZINOV'EVA-STAHEVITCH and GRANT 1982
	8	16	Tamil Nadu, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
	10		Tamil Nadu, India	ZINOV'EVA-STAHEVITCH and GRANT 1985
		16	S India	RAO *et al.* 1986
I. viscosa Bedd.	10		S India	BHASKAR and RAZI 1972-1973
		16	S India	RAO 1973
		32	Kerala, India	ZINOV'EVA-STAHEVITCH and GRANT 1984
I. walleriana Hook. f.		16	?	FEDOROV 1969
		16	Africa ?	SMITH 1934
		16	Tanzania	JONES and SMITH 1966
	10		Tanzania	GILL and CHINNAPPA 1977
	8	16	Tropical East Afria	ZINOV'EVA-STAHEVITCH and GRANT 1984
	8	16	?	ZINOV'EVA-STAHEVITCH and GRANT 1985
	8		E Africa	MERLIN and GRANT 1985
		16	S India	RAO *et al.* 1986
		16	S India	GOVINDARAJAN and SUBRAMANIAN 1986
		16	Africa	ARISUMI 1987
I. wuchengyihii S.Akiyama, H. Ohba et S. K. Wu		14	Yunnan, China	SUGAWARA *et al.* 1997
I. xanthina Comber	7		Yunnan, China	present study
I. yingjiangensis S. Akiyama et H. Ohba		16	Yunnan, China	SUGAWARA *et al.*, 1994
		16	Yunnan, China	AKIYAMA *et al.*, 1996a
	8		Yunnan, China	present study
I. zombensis Baker		16, 17	Malawi, Africa	STAHEVITCH 1995

posed a migration routes based on the above hypothesis. When the most frequent basic chromosome numbers of the diversity centers are mapped onto GREY-WILSON's migration map (Fig. 5), we can see that the basic numbers x = 7, 8 are predominantly shared by species from Africa, southern India, Sri Lanka and Southeast Asia, while the basic number x = 10 is predominantly distributed in the northern hemisphere, and the basic number x = 9 is shared only by the species from Himalayas and Southeast Asia. However, this pattern does not necessarily support GREY-WILSON's (1980a) hypothesis about the origin and migration of *Impatiens*, because assuming a Southeast Asian origin of *Impatiens* and subsequent radiations to all other areas including southern India, Sri Lanka, Africa and Madagascar (thus all the African and Madagascan species are derived from the Asian ancestors) can equally result in a such pattern. Traditional karyological studies alone may not be able to serve as a test of these alternative hypotheses. However, assuming GREY-WILSON's hypothesis implies an ascending dysploidy as chromosomal evolution, as higher basic numbers such as x = 9 or x = 10 are either infrequent or completely missing from Africa. Conversely, assuming a Southeast Asian origin of *Impatiens* implies more descending dysploidy. Our ongoing molecular phylogenetic studies on the family will hopefully give more insights on these controversies.

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