Cytological Study of *Begonia* Sect. *Coelocentrum* (Begoniaceae)

Yoshiko Kono^{1,2}, Ching-I Peng², Kazuo Oginuma^{1*}, Yan Liu³,
Wei-Bin Xu³, Hsun-An Yang² and Kuo-Fang Chung^{2*}

¹The Community Center for the Advancement of Education and Research at the University of Kochi, 5–15 Eikokuji-cho, Kochi 780–8515, Japan

²Research Museum and Herbarium (HAST), Biodiversity Research Center, Academia Sinica, 128 Academia Road, Section 2, Taipei 11529, Taiwan

³Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain, Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, Guilin, Guangxi, China

Received August 17, 2020; accepted August 31, 2020

Summary *Begonia* sect. *Coelocentrum* is a characteristic plant group in the limestone karsts of southern China and northern Vietnam and yet previous chromosome information is restricted to *ca.* 50 species and their karyotypes have never been investigated. Here we report the cytological investigations of 15 species of sect. *Coelocentrum*, including four karyotype analyses that are the first report in sect. *Coelocentrum*, ten species reported cytologically for the first time, and five species that were re-examined. Incorporating recent and present studies, chromosome numbers of 56 of the 82 species in sect. *Coelocentrum* are now available. Among the 56 species, 55 have a stable and common chromosome number of $2n=30$, with a few species showing aneuploidy numbers of $2n=31$, 32, 33, 35, 36, and a triploid number of $2n=45$. Karyotypic formula of the four investigated species are uniform as $2n=30=8m+22sm(st)$. Based on our and previous studies, the chromosome evolution in *Begonia* sect. *Coelocentrum* is discussed.

Keywords Chromosome number, Karyotype, *Begonia* sect. *Coelocentrum*.

Begonia L., one of the largest genera of angiosperms, is a pantropical genus of 1,980 described species in 70 sections distributed in Africa, America and Asia (Hughes *et al.* 2011 onward: <https://padme.rbge.org.uk/Begonia/home>, Moonlight *et al.* 2018). In terms of the number of species, *Begonia* is also the fastest growing plant genus (Moonlight *et al.* 2018), with more than 500 species added since Doorenbos *et al.* (1998)'s seminal work in which 1,400 species were recorded. The phenomenal recent growth of *Begonia* is particularly evident in Asia. For instance, the recircumscribed sect. *Baryandra* A.DC. grew from 49 (Rubite *et al.* 2013) to 76 species, sect. *Coelocentrum* Irmsch. from 12 to 82 species, sect. *Petermannia* (Klotzsch) A.DC. from 193 to 432 species, and sect. *Platycentrum* (Klotzsch) A.DC. from 96 to 177 species (Hughes *et al.* 2011 onward: <https://padme.rbge.org.uk/Begonia/home>, Liu *et al.* 2020).

Chromosomes of *Begonia* are small in size and difficult to stain by conventional methods, consequently, cytological investigations for *Begonia* are limited and restricted to a small number of species. Nevertheless, previous studies reveal a substantial variation in chromo-

some numbers within *Begonia*, including $2n=14$, 16, 18, 20, 22, 24, 26, 28, 30, 31, 32, 33, 34, 36, 38, 40, 42, 43, 44, 45, 46, 48, 52, 54, 56, 60, 64, 66, 70, 71, 72, 73, 74, 76, 78, 82, 84, and 156 (Heitz 1927, Matsuura and Okuno 1936, Hamel 1937, Bowden 1945, White *et al.* 1946, Sharma and Bhattacharyya 1957, 1961, Diers 1961, Piton 1962, Favarger and Huynh 1965, Legro and Doorenbos 1969, 1971, 1973, Sharma 1970, Kondo 1973, Sarkar 1974, 1989, de Wilde and Arends 1980, Peng *et al.* 1988, 2005a, b, c, Peng and Chen 1990, 1991, Arends 1992, Doorenbos *et al.* 1998, Peng and Sue 2000, Kokubugata and Madulid 2000, Oginuma and Peng 2002, Tian *et al.* 2002, Nakata *et al.* 2003, 2007, Ku *et al.* 2004, 2006, Ye *et al.* 2004, Li *et al.* 2005a, b, 2008, 2016, Fang *et al.* 2006, Ma and Li 2006, Liu *et al.* 2007).

By using improved methods, *i.e.*, enzymatic maceration method, reports of chromosome numbers have been increased especially for Asian *Begonia* in recent years (Ku *et al.* 2008, Peng *et al.* 2007, 2008a, b, 2010, 2012, 2013, 2014a, b, c, 2015a, b, c, 2017, Hughes *et al.* 2011, Kono *et al.* 2012, Nakamura *et al.* 2013, Ding *et al.* 2014, Rubite *et al.* 2015, Tseng *et al.* 2017, Han *et al.* 2018, Liu *et al.* 2020). However, among the 18 Asian sections, reports for chromosome numbers are still limited with low coverages: 22% for sect. *Baryandra*, 57% for sect. *Coelocentrum*, 14% for sect. *Diplocinium* and 28% for sect. *Platycentrum*.

*Corresponding author, e-mail: oginuma_kazuo@yahoo.co.jp; bochung@gate.sinica.edu.tw
DOI: 10.1508/cytologia.85.333

With 82 species, *Begonia* sect. *Coelocentrum* is richly represented in limestone karst areas across the Sino-Vietnamese bordering region (Chung *et al.* 2014, Hughes *et al.* 2011 onward: <https://padme.rbge.org.uk/Begonia/home>, Peng *et al.* 2015c, Moonlight *et al.* 2018, Liu *et al.* 2020). Nearly half of the species in the section were discovered in the past decade (Chung *et al.* 2014, Peng *et al.* 2013, 2014b, Liu *et al.* 2020), mostly from southern China.

In this paper, we provide the first report of karyotypes of four species of *Begonia* sect. *Coelocentrum*. We also report the first chromosome count for ten species and confirmed chromosome numbers of five species reported earlier. Based on the present results and previous chromosome reports for a total of 56 species, we also discuss the chromosome evolution in *Begonia* sect. *Coelocentrum*.

Materials and methods

The species of *Begonia* sect. *Coelocentrum* investigated are listed in Table 1 along with collection data. The sectional classification of *Begonia* followed Chung *et al.* (2014) and Moonlight *et al.* (2018). Root tips of 15 species were pretreated with 2 mM 8-hydroxyquinoline solution at 15–18°C for 6–8 h and then fixed overnight in ethanol-acetic acid (3:1) below 4°C. They were macerated in an enzyme mixture [2% Cellulase Onozuka R-10 (Yakult Honsha, Tokyo, Japan) and 1% Pectolyase (Sigma, St. Louis, MO, USA)] at 37°C for about 1 h. Chromosomes were stained in 2% Giemsa solution (Merck, Darmstadt, Germany). Categories of chromosome morphology based on the position of centromeres followed Levan *et al.* (1964).

Results

The chromosomal cytology of the following ten spe-

cies of *Begonia* sect. *Coelocentrum* was studied for the first time. Additionally, karyotypes of the first four species were analyzed, which are the first reports in sect. *Coelocentrum*.

The chromosome number of *Begonia auritistipula* Y. M. Shui & W. H. Chen at mitotic metaphase is $2n=30$ (Fig. 1a, b, i). The size of chromosomes varies gradually: the longest pair of chromosomes is about 1.6 μm long, and the shortest pair is about 0.8 μm long. Among the 30 chromosomes, eight chromosomes (Nos. 1–8 in Fig. 1i) have centromeres at median position (m-chromosome) and the other 22 chromosomes (Nos. 9–30 in Fig. 1i) have centromeres at submedian or subterminal position (sm- or st-chromosome). Eight m-chromosomes are small in size of about 0.8 to 1.2 μm long. Seven sm(st)-chromosomes (Nos. 9–14 and 23 in Fig. 1i) have the secondary constriction and/or small constriction (SC-chromosome). A satellite is observed at the distal region of the short arm of one sm-chromosome (No. 23 in Fig. 1i).

The chromosome number of *B. filiformis* Irmisch. at mitotic metaphase is $2n=30$ (Fig. 1c, d, j). The size of chromosomes varies gradually: the longest pair of chromosomes is about 1.8 μm long, and the shortest about 0.9 μm long. Among the 30 chromosomes, eight chromosomes (Nos. 1–8 in Fig. 1j) have centromeres at the median position and the other 22 chromosomes (Nos. 9–30 in Fig. 1j) have centromeres at the submedian or subterminal position. Eight m-chromosomes are small in size of about 0.9 to 1.2 μm long. Eight sm(st)-chromosomes (Nos. 9–16 in Fig. 1j) have the secondary constriction and/or small constriction. Satellite chromosomes are not observed (Fig. 1c, d, j).

The chromosome number of *B. leprosa* Hance at mitotic metaphase is $2n=30$ (Fig. 1e, f, k). The size of chromosomes varies gradually: the longest pair of chromosomes is about 1.7 μm long, and the shortest about 1.0 μm long. Among the 30 chromosomes, eight chro-

Table 1. Studied taxa and their collection data in *Begonia* sect. *Coelocentrum*.

Taxon	Collection ¹⁾	Chromosome number (2n)
<i>B. auritistipula</i> Y. M. Shui & W. H. Chen	China, Yunnan Prov., Peng 20532	30
<i>B. curvicarpa</i> S. M. Ku, C. I Peng & Yan Liu	China, Guangxi Prov., Peng 19850	30 ²⁾
<i>B. debaoensis</i> C. I Peng, Yan Liu & S. M. Ku	China, Guangxi Prov., Peng 22123	30 ²⁾
<i>B. filiformis</i> Irmisch.	China, Guangxi Prov., Peng 20332	30
<i>B. guangxiensis</i> C. Y. Wu	China, Guangxi Prov., Peng 19814	35 ³⁾
<i>B. lanternaria</i> Irmisch.	China, Guangxi Prov., Peng 22926	30
<i>B. leprosa</i> Hance	China, Guangxi Prov., Peng 20338	30
<i>B. lui</i> S. M. Ku, C. I Peng & Yan Liu	China, Guangxi Prov., Peng 21112	30
<i>B. ningmingensis</i> D. Fang, Y. G. Wei & C. I Peng var. <i>ningmingensis</i>	China, Guangxi Prov., Peng 22915	30 ²⁾
<i>B. phuthoensis</i> H. Q. Nguyen	Vietnam, Phu Tho Prov., Peng 21846	30
<i>B. picturata</i> Yan Liu, S. M. Ku & C. I Peng	China, Guangxi Prov., Peng 20387	30 ²⁾
<i>B. pseudodryadis</i> C. Y. Wu	China, Yunnan Prov., Peng 20530	30
<i>B. scabrifolia</i> C. I Peng, Yan Liu & C. W. Lin	China, Guangxi Prov., Peng 22197	30
<i>B. setulosopeltata</i> C. Y. Wu	China, Guangxi Prov., Peng 19830	30
<i>B. sinofloribunda</i> Dorr	China, Guangxi Prov., Leong 3401	30

¹⁾ All collections are kept at HAST.

²⁾ Chromosome number reported earlier

³⁾ New chromosome count for the species

Fig. 1. Somatic chromosomes at metaphase of four *Begonia* species in sect. *Coelocentrum*. (a and b) *B. auritistipula* ($2n=30$). (c and d) *B. filiformis* ($2n=30$). (e and f) *B. leprosa* ($2n=30$). (g and h) *B. phuthoensis* ($2n=30$). b, d, f, and h are drawings of a, c, e, and g, respectively. i, j, k, and l are chromosome arrangement of respective b, d, f, and h based on the karyotypic formulae. Scale bars in a–h = $5\mu\text{m}$ and in i–l = $2\mu\text{m}$.

mosomes (Nos. 1–8 in Fig. 1k) have centromeres at the median position and the other 22 chromosomes (Nos. 9–30 in Fig. 1k) have centromeres at the submedian or subterminal position. Eight m-chromosomes are small in size of about 1.1 to $1.3\mu\text{m}$ long. Six sm(st)-chromosomes (Nos. 9–14 in Fig. 1k) have the secondary constriction and/or small constriction. Satellite chromosomes are not observed (Fig. 1e, f, k).

The chromosome number of *B. phuthoensis* H. Q. Nguyen at mitotic metaphase is $2n=30$ (Fig. 1g, h, l). The size of chromosomes varies gradually: the longest pair of chromosomes is about $1.8\mu\text{m}$ long, and the shortest about $1.1\mu\text{m}$ long. Among 30 chromosomes, eight chromosomes (Nos. 1–8 in Fig. 1l) have centromeres at the median position and the other 22 chromosomes (Nos. 9–30 in Fig. 1l) have centromeres at the submedian or subterminal position. Eight m-chromosomes are small in size of about 1.1 to $1.3\mu\text{m}$ long. Seven sm(st)-chro-

mosomes (Nos. 9–14 and 23 in Fig. 1l) have the secondary constriction and/or small constriction. A satellite is observed in the distal region of the short arm of one sm-chromosome (No. 23 in Fig. 1l).

The chromosome number of *B. lanternaria* Irmisch. at mitotic metaphase is $2n=30$ (Fig. 2a). The size of chromosomes varies gradually: the longest pair of chromosomes is about $1.6\mu\text{m}$ long, and the shortest about $1.1\mu\text{m}$ long. Among the 30 chromosomes, the longest pair of chromosomes has centromeres at the submedian position, but the others are uncertain concerning exact positions of centromeres. Satellite chromosomes are not observed (Fig. 2a).

The chromosome number of *B. lui* S. M. Ku, C. I Peng & Yan Liu at mitotic metaphase is $2n=30$ (Fig. 2b). The size of chromosomes varies gradually: the longest pair is about $1.6\mu\text{m}$ long, and the shortest $0.8\mu\text{m}$ long. Among the 30 chromosomes, the longest pair of chromosomes

Fig. 2. Somatic chromosomes at metaphase of six *Begonia* species in sect. *Coelocentrum*. (a) *B. lanternaria* ($2n=30$). (b) *B. lui* ($2n=30$). (c) *B. pseudodryadis* ($2n=30$). (d) *B. scabrifolia* ($2n=30$). (e) *B. setulosopeltata* ($2n=30$). (f) *B. sinofloribunda* ($2n=30$). Scale bar = $5\mu\text{m}$.

has centromeres at the submedian position, but the others are uncertain concerning the exact positions of centromeres. Satellite chromosomes are not observed (Fig. 2b).

The chromosome number of *B. pseudodryadis* C. Y. Wu at mitotic metaphase is $2n=30$ (Fig. 2c). The size of chromosomes varies gradually: the longest pair of chromosomes is about $1.8\mu\text{m}$ long, and the shortest about $0.9\mu\text{m}$ long. Among the 30 chromosomes, the longest pair of chromosomes has centromeres at the submedian position, but the others are uncertain concerning exact positions of centromeres. Satellite chromosomes are not observed (Fig. 2c).

The chromosome number of *B. scabrifolia* C. I Peng, Yan Liu & C. W. Lin at mitotic metaphase is $2n=30$ (Fig. 2d). The size of chromosomes is bimodal: the longest pair of chromosomes is about $1.7\mu\text{m}$ long, and the others are about $0.8\text{--}1.3\mu\text{m}$ long. Among the 30 chromosomes, the longest pair of chromosomes has centromeres at the submedian position, but the others are uncertain concerning exact positions of centromeres. Satellite chromosomes are not observed (Fig. 2d).

The chromosome number of *B. setulosopeltata* C. Y. Wu at mitotic metaphase is $2n=30$ (Fig. 2e). The size of chromosomes is bimodal: the longest pair of chromosomes is about $1.6\mu\text{m}$ long, and the others are about $1.0\text{--}1.3\mu\text{m}$ long. Among the 30 chromosomes, the longest pair of chromosomes has centromeres at the submedian position, but the others are uncertain concerning exact positions of centromeres. Satellite chromosomes are not observed (Fig. 2e).

The chromosome number of *B. sinofloribunda* Dorr at mitotic metaphase is $2n=30$. The size of chromosomes

is bimodal: the longest pair of chromosomes is about $1.3\mu\text{m}$ long, and the others are about $0.8\text{--}1.0\mu\text{m}$ long. Among the 30 chromosomes, the longest pair of chromosomes has centromeres at the submedian position, but the others are uncertain concerning exact positions of centromeres. Satellite chromosomes are not observed (Fig. 2f).

For the following five species, their chromosome numbers were re-examined in the present study.

The chromosome number of *B. curvicarpa* S. M. Ku, C. I Peng & Yan Liu at mitotic metaphase is $2n=30$ (Fig. 3a), congruent with the previous report (Ku *et al.* 2004). The size of chromosomes varies gradually: the longest pair of chromosomes is about $1.3\mu\text{m}$ long, and the shortest about $1.0\mu\text{m}$ long. Among the 30 chromosomes, the longest pair of chromosomes has centromeres at the submedian position, but the others are uncertain concerning exact positions of centromeres. Satellite chromosomes are not observed (Fig. 3a).

The chromosome number of *B. debaoensis* C. I Peng, Yan Liu & S. M. Ku at mitotic metaphase is $2n=30$ (Fig. 3b), congruent with the previous report (Ku *et al.* 2006). The size of chromosomes varies gradually: the longest pair of chromosomes is about $1.3\mu\text{m}$ long, and the shortest about $0.8\mu\text{m}$ long. Among the 30 chromosomes, the longest pair of chromosomes has centromeres at the submedian position, but the others are uncertain concerning exact positions of centromeres. Satellite chromosomes are not observed (Fig. 3b).

The chromosome number of *B. guangxiensis* C. Y. Wu at mitotic metaphase is $2n=35$ (Fig. 3c), incongruent with $2n=36$ reported in Han *et al.* (2018). Its chromo-

Fig. 3. Somatic chromosomes at metaphase of five *Begonia* species in sect. *Coelocentrum*. (a) *B. curvicarpa* ($2n=30$). (b) *B. debaoensis* ($2n=30$). (c) *B. guangxiensis* ($2n=35$). (d) *B. ningmingensis* ($2n=30$). (e) *B. picturata* ($2n=30$). Scale bar = $5\mu\text{m}$.

some length is bimodal: the longest pair of chromosomes is about $1.8\mu\text{m}$ long, and the remainder is about 1.0 – $1.6\mu\text{m}$ long. Among the 35 chromosomes, the longest pair of chromosomes has centromeres at the submedian position, but others are uncertain concerning exact positions of centromeres. Satellite chromosomes are not observed (Fig. 3c).

The chromosome number of *B. ningmingensis* D. Fang, Y. G. Wei & C. I Peng var. *ningmingensis* at mitotic metaphase is $2n=30$ (Fig. 3d), congruent with the previous report (Fang *et al.* 2006). The length of the 30 chromosomes is bimodal: the longest pair of chromosomes is about $1.7\mu\text{m}$ long, and the others are about 1.0 – $1.3\mu\text{m}$ long. Among the 30 chromosomes, the longest pair of chromosomes has centromeres at the submedian position, but the others are uncertain concerning exact positions of centromeres. Satellite chromosomes are not observed (Fig. 3d).

The chromosome number of *B. picturata* Yan Liu, S. M. Ku & C. I Peng at mitotic metaphase is $2n=30$ (Fig. 3e), congruent with the previous report (Liu *et al.* 2005). The length of chromosomes varies gradually: the longest pair of chromosomes is about $1.4\mu\text{m}$ long, and the shortest about $1.0\mu\text{m}$ long. Among the 30 chromosomes, the longest pair of chromosomes has centromeres at the submedian position, but the others are uncertain concerning exact positions of centromeres. Satellite chromosomes are not observed (Fig. 3e).

Discussion

By adding the results of the present study, the re-

ported chromosome numbers in sect. *Coelocentrum* is increased to 56 (Table 2), or 68.3% of the 82 described species in the section. Except for *B. guangxiensis* ($2n=35$ and 36), 55 of the 56 species have at least one count of $2n=30$, congruent with the previous proposition that $2n=30$ is the dominant and thus basic chromosome set of sect. *Coelocentrum* (Chung *et al.* 2014, Han *et al.* 2018, Moonlight *et al.* 2018).

In addition to $2n=30$, chromosome numbers were reported in *B. guangxiensis* ($2n=36$; Han *et al.* 2018), *B. longgangensis* ($2n=45$; Peng *et al.* 2013, Han *et al.* 2018), *B. masoniana* ($2n=30+3f$; Legro and Doorenbos 1969), and *B. montaniformis* ($2n=31$, 32, and 33; Peng *et al.* 2015b), suggesting the role of chromosomal changes in the evolution of sect. *Coelocentrum*. The $2n=45$, along with $2n=30$ reported within the same population of *B. longgangensis*, was surmised to be a naturally occurring triploid (Peng *et al.* 2013). Based on fluorescence *in situ* hybridization (FISH) (Han *et al.* 2018), further hypothesized the triploid *B. longgangensis* represents an allotriploid originated from crossing between an unreduced $2n$ gamete and a normally segregated diploid species.

Legro and Doorenbos (1969) reported the presence of fragment chromosomes in *B. masoniana* ($2n=30+3f$). Also known as supernumerary or accessory chromosomes, fragment chromosomes were so categorized for their smaller sizes comparing to the standard chromosomes (*i.e.*, A-chromosomes) and are frequently (but not exclusively) heterochromatic and telocentric (Rieger *et al.* 1976). However, because chromosomes in *Begonia* are small in sizes, it is rather difficult to assure whether

Table 2. Chromosome data in *Begonia* sect. *Coelocentrum*.

Taxon	2n	Reference
<i>Begonia arachnoidea</i> C. I Peng, Yan Liu & S. M. Ku	30	Peng <i>et al.</i> (2008b)
<i>B. aurantiflora</i> C. I Peng, Yan Liu & S. M. Ku	30	Peng <i>et al.</i> (2008a)
<i>B. auritistipula</i> Y. M. Shui & W. H. Chen	30	Present study
<i>B. austroguangxinensis</i> Y. M. Shui & W. H. Chen	30	Han <i>et al.</i> (2018)
<i>B. bamaensis</i> Yan Liu & C. I Peng	30	Liu <i>et al.</i> (2007), Han <i>et al.</i> (2018)
<i>B. biflora</i> T. C. Ku	30	Han <i>et al.</i> (2018)
<i>B. cavalerieri</i> H. Lév.	30	Han <i>et al.</i> (2018)
<i>B. calciphila</i> C. I Peng,	30	Peng <i>et al.</i> (2015c)
<i>B. chongzuoensis</i> Yan Liu, S. M. Ku & C. I Peng	30	Peng <i>et al.</i> (2012), Han <i>et al.</i> (2018)
<i>B. circularis</i> C. I Peng & C. W. Lin	30	Peng <i>et al.</i> (2015b)
<i>B. cirrosa</i> L. B. Sm. & Wassh.	30	Han <i>et al.</i> (2018)
<i>B. curvicarpa</i> S. M. Ku, C. I Peng & Yan Liu	30	Ku <i>et al.</i> (2004), Present study
<i>B. daxinensis</i> T. C. Ku	30	Han <i>et al.</i> (2018)
<i>B. debaoensis</i> C. I Peng, Yan Liu & S. M. Ku	30	Ku <i>et al.</i> (2006), Han <i>et al.</i> (2018), Present study
<i>B. fangii</i> Y. M. Shui & C. I Peng	30	Peng <i>et al.</i> (2005a), Han <i>et al.</i> (2018)
<i>B. ferox</i> C. I Peng & Yan Liu	30	Peng <i>et al.</i> (2013)
<i>B. filiformis</i> Irmsch.	30	Present study
<i>B. guangxiensis</i> C. Y. Wu	36	Han <i>et al.</i> (2018)
	35	Present study
<i>B. guixiensis</i> Yan Liu, S. M. Ku & C. I Peng	30	Peng <i>et al.</i> (2014b)
<i>B. huangii</i> Y. M. Shui & W. H. Chen	30	Han <i>et al.</i> (2018)
<i>B. jingxiensis</i> D. Fang & Y. G. Wei	30	Han <i>et al.</i> (2018)
<i>B. kui</i> C. I Peng	30	Peng <i>et al.</i> (2007)
<i>B. langsonensis</i> C. I Peng & C. W. Lin	30	Peng <i>et al.</i> (2015b)
<i>B. lanternaria</i> Irmsch.	30	Present study
<i>B. leprosa</i> Hance	30	Present study
<i>B. leipingensis</i> D. K. Tian, L. H. Yang & C. Li	30	Li <i>et al.</i> (2016)
<i>B. liuyanii</i> C. I Peng, S. M. Ku & W. C. Leong	30	Peng <i>et al.</i> (2005b), Han <i>et al.</i> (2018)
<i>B. locii</i> C. I Peng, C. W. Lin & H. Q. Nguyen,	30	Peng <i>et al.</i> (2015b)
<i>B. longa</i> C. I Peng & W. C. Leong	30	Peng <i>et al.</i> (2014b)
<i>B. longgangensis</i> C. I Peng & Yan Liu	30, 45	Peng <i>et al.</i> (2013)
	45	Han <i>et al.</i> (2018)
<i>B. longiornithophylla</i> C. I Peng, W. B. Xu & Yan Liu	30	Liu <i>et al.</i> (2020)
<i>B. longistyla</i> Y. M. Shui & W. H. Chen	30	Han <i>et al.</i> (2018)
<i>B. lui</i> S. M. Ku, C. I Peng & Yan Liu	30	Present study
<i>B. luochengensis</i> S. M. Ku, C. I Peng & Yan Liu	30	Ku <i>et al.</i> (2004), Han <i>et al.</i> (2018)
<i>B. luzhaiensis</i> T. C. Ku	30	Han <i>et al.</i> (2018)
<i>B. masoniana</i> Irmsch.	30+3f	Legro and Doorenbos (1969)
	30	Doorenbos <i>et al.</i> (1998), Han <i>et al.</i> (2018)
<i>B. melanobullata</i> C. I Peng & C. W. Lin	30	Peng <i>et al.</i> (2015b)
<i>B. montaniformis</i> C. I Peng, C. W. Lin & N. H. Nguyen	30, 31, 32, 33	Peng <i>et al.</i> (2015b)
<i>B. morsei</i> Irmsch.	30	Han <i>et al.</i> (2018)
<i>B. ningmingensis</i> D. Fang, Y. G. Wei & C. I Peng var. <i>ningmingensis</i>	30	Fang <i>et al.</i> (2006), Present study
<i>B. ningmingensis</i> D. Fang, Y. G. Wei & C. I Peng var. <i>bella</i>	30	Fang <i>et al.</i> (2006)
<i>B. pengii</i> S. M. Ku & Yan Liu	30	Ku <i>et al.</i> (2008), Han <i>et al.</i> (2018)
<i>B. phuthoensis</i> H. Q. Nguyen	30	Present study
<i>B. picturata</i> Yan Liu, S. M. Ku & C. I Peng	30	Liu <i>et al.</i> (2005), Present study
<i>B. pseudodaxinensis</i> S. M. Ku, Yan Liu & C. I Peng	30	Ku <i>et al.</i> (2006), Han <i>et al.</i> (2018)
<i>B. pseudodryadis</i> C. Y. Wu	30	Present study
<i>B. pseudoleprosa</i> S. M. Ku, Yan Liu & C. I Peng	30	Han <i>et al.</i> (2018)
<i>B. retinervia</i> D. Fang, D. H. Qin & C. I Peng	30	Fang <i>et al.</i> (2006), Han <i>et al.</i> (2018)
<i>B. scabrifolia</i> C. I Peng, Yan Liu & C. W. Lin	30	Present study
<i>B. semiparietalis</i> Yan Liu, S. M. Ku & C. I Peng	30	Ku <i>et al.</i> (2006)
<i>B. setulosopeltata</i> C. Y. Wu	30	Present study
<i>B. sinofloribunda</i> Dorr	30	Present study
<i>B. subcoriacea</i> C. I Peng, Yan Liu & S. M. Ku	30	Peng <i>et al.</i> (2008b), Han <i>et al.</i> (2018)
<i>B. suboblata</i> D. Fang & D. H. Qin	30	Han <i>et al.</i> (2018)
<i>B. umbraculifolia</i> Y. Wan & B. N. Chang	30	Peng <i>et al.</i> (2008b)
<i>B. wangii</i> T. T. Yu	30	Han <i>et al.</i> (2018)
<i>B. zhuoyuniae</i> C. I Peng, Yan Liu & K. F. Chung	30	Han <i>et al.</i> (2018), Liu <i>et al.</i> (2020)

$2n=30+3f$ is a genuine case of the presence of fragment chromosomes. Alternatively, the reports of $2n=30$, 31, 32 and 33 in *B. montaniformis*, and $2n=35$ and 36 in *B.*

guangxiensis indicate the presence of aneuploidy in sect. *Coelocentrum*, suggesting the fragment chromosomes reported in *B. masoniana* might actually be a case of

aneuploid and aneuploidy could also be yet another important mechanism driving the evolution (Oginuma and Peng 2002) in sect. *Coelocentrum*.

In *Begonia*, karyotypes were previously only known from 14 species in two Asian sect. *Diploclinium* and *Platycentrum* (Oginuma and Peng 2002, Peng *et al.* 2014c, Peng *et al.* 2015c). In the present study, karyotypes of four species were analyzed, presenting the first report in sect. *Coelocentrum*. All four species showed the uniform karyotype of $2n=30=8m+22sm(st)$. Among the 22 *sm(st)*-chromosomes, 6–8 submedian SC-chromosomes were observed, accounting for 20–27% of the chromosome complements in sect. *Coelocentrum*. In the karyotypic analysis of Taiwan's *Begonia*, Oginuma and Peng (2002) identified the presence of 9% SC-chromosomes in two diploid species *B. palmata* and *B. aptera* (= *B. longifolia*) with $2n=22$, while in polyploids 23–63% are SC-chromosomes, suggesting that chromosome translocation and subsequent decrease in chromosome numbers that stabilized the genomes of polyploids have played a significant role in the evolution of Taiwan's polyploidy *Begonia*. Given this, the presence of 20–27% of SC-chromosomes in sect. *Coelocentrum* suggests that, in addition to polyploidy observed in *B. longganensis* and aneuploidy in *B. guangxiensis*, *B. masoniana*, and *B. montaniformis*, additional chromosomal changes could have played an important role in generating the high species diversity in *Begonia* sect. *Coelocentrum*. Further cytological investigation using approaches such as FISH (e.g., Han *et al.* 2018) would be informative in revealing how chromosome rearrangements such as chromosome fission and fusion have played in generating the remarkable diversity in *Begonia*.

Acknowledgements

The authors thank the staff of the Experimental Greenhouse, Biodiversity Research Center, Academia Sinica for maintaining the collection. YK, CIP, and KFC were supported by funding from Academia Sinica.

References

- Arends, J. C. 1992. Studies in Begoniaceae IV: Biosystematics of *Begonia squamulosa* Hook. f. and affiliated species in section *Tetraphila* A.DC. Wageningen Agric. Univ. Pap. **91**: 1–222.
- Bowden, W. M. 1945. A list of chromosome numbers in higher plants. I. Acanthaceae to Myrtaceae. Am. J. Bot. **32**: 81–92.
- de Wilde, J. J. F. E. and Arends, J. C. 1980. *Begonia* section *Squamibegonia* Warb. A taxonomic revision. Misc. Pap. Landbouwhogeschool **19**: 377–421.
- Chung, K. F., Leong, W. C., Rubite, R. R., Repin, R., Kiew, R., Liu, Y. and Peng, C.-I. 2014. Phylogenetic analyses of *Begonia* sect. *Coelocentrum* and allied limestone species of China shed light on the evolution of Sino-Vietnamese karst flora. Bot. Stud. **55**: e1.
- Diers, L. 1961. Der Anteil an Polyploidien in den Vegetationsgürteln der Westkordillere Perus. Zeitschr. Bot. **49**: 437–488.
- Ding, B., Nakamura, K., Kono, Y., Ho, M. J. and Peng, C.-I. 2014. *Begonia jinyunensis* (Begoniaceae, section *Platycentrum*), a new palmately compound leaved species from Chongqing, China. Bot. Stud. **55**: e62.
- Doorenbos, J., Sosef, M. S. M. and de Wilde, J. J. F. E. 1998. The Sections of *Begonia*. Agric. Univ. Wageningen Pap.
- Fang, D., Ku, S. M., Wei, Y. G., Qin, D. H. and Peng, C.-I. 2006. Three new taxa of *Begonia* (sect. *Coelocentrum*, Begoniaceae) from limestone areas in Guangxi, China. Bot. Stud. **47**: 97–110.
- Favarger, C. and Huynh, H. L. 1965. In: Löve, V. and Solbrig, O. T. (eds.). IOPB chromosome reports IV. Taxon **14**: 86–92.
- Hamel, J. L. 1937. Etudes caryologiques sur quelques Begoniacees. Rev. Cytol. Cytophysiol. Veg. **3**: 153–172.
- Han, Y. L., Tian, D. K., Fu, N. F., Xiao, Y., Li, Z. Y. and Han, Y. H. 2018. Comparative analysis of rDNA distribution in 29 species of *Begonia* sect. *Coelocentrum* Irmsch. Phytotaxa **381**: 141–152.
- Heitz, E. 1927. Über multiple und aberrante Chromosomenzahlen. Abhandl. Naturwiss. Vereins Hamburg **21**: 47–57.
- Hughes, M., Rubite, R. R., Kono, Y. and Peng, C.-I. 2011. *Begonia blancii* (sect. *Diploclinium*, Begoniaceae), a new species endemic to the Philippine island of Palawan. Bot. Stud. **52**: 203–209.
- Kokubugata, G. and Madulid, D. A. 2000. Chromosomal study of four plant-taxa in Batan Island, the Philippines and the Yaeyama group, Ryukyu Islands, Japan. In: Matsuura, K. (ed.). Proceedings of the First and Second Symposia in Asia. Natl. Sci. Mus. Monogr. **18**: 139–144.
- Kondo, K. 1973. Chromosome numbers of five taxa. Chromosome Inf. Serv. **15**: 33–34.
- Kono, Y., Chung, M. C. and Peng, C.-I. 2012. Identification of genome constitutions in *Begonia × chungii* and its putative parents, *B. longifolia* and *B. palmata*, by genomic *in situ* hybridization (GISH). Plant Sci. **185–186**: 156–160.
- Ku, S. M., Kono, Y. and Liu, Y. 2008. *Begonia pengii* (sect. *Coelocentrum*, Begoniaceae), a new species from limestone areas in Guangxi, China. Bot. Stud. **49**: 167–175.
- Ku, S. M., Liu, Y. and Peng, C.-I. 2006. Four new species of *Begonia* sect. *Coelocentrum* (Begoniaceae) from limestone areas in Guangxi, China. Bot. Stud. **47**: 207–222.
- Ku, S. M., Peng, C.-I. and Liu, Y. 2004. Notes on *Begonia* (sect. *Coelocentrum*, Begoniaceae) from Guangxi, China, with the report of two new species. Bot. Bull. Acad. Sin. **45**: 353–367.
- Legro, R. A. H. and Doorenbos, J. 1969. Chromosome numbers in *Begonia* 1. Neth. J. Agric. Sci. **17**: 189–202.
- Legro, R. A. H. and Doorenbos, J. 1971. Chromosome numbers in *Begonia* 2. Neth. J. Agric. Sci. **19**: 176–183.
- Legro, R. A. H. and Doorenbos, J. 1973. Chromosome numbers in *Begonia* 3. Neth. J. Agric. Sci. **21**: 167–170.
- Levan, A., Fredga, K. and Sandberg, A. A. 1964. Nomenclature for centromeric position of chromosomes. Hereditas **52**: 201–220.
- Li, H. Z., Guan, K. Y. and Ma, H. 2005a. Chromosome numbers of five species of *Begonia* from China. Acta Bot. Yunnan. **27**: 92–94.
- Li, H. Z., Ma, H., Guan, K. Y. and Peng, C.-I. 2005b. *Begonia rubinea* (sect. *Platycentrum*, Begoniaceae), a new species from Guizhou, China. Bot. Bull. Acad. Sin. **46**: 377–383.
- Li, H. Z., Ma, H., Zhou, Z. K. and Guan, K. Y. 2008. A new species of *Begonia* (Begoniaceae) from Guangxi, China. Bot. J. Linn. Soc. **157**: 83–90.
- Li, C., Yang, L. H., Tian, D. K., Chen, Y., Wu, R. J. and Fu, N. F. 2016. *Begonia leipingensis* (Begoniaceae), a new compound-leaved species with unique petiolule pattern from Guangxi of China. Phytotaxa **244**: 45–56.
- Liu, Y., Ku, S. M. and Peng, C.-I. 2005. *Begonia picturata* (sect. *Coelocentrum*, Begoniaceae), a new species from Guizhou, China. Bot. Bull. Acad. Sin. **46**: 367–376.
- Liu, Y., Ku, S. M. and Peng, C.-I. 2007. *Begonia bamaensis* (sect. *Coelocentrum*, Begoniaceae), a new species from Guizhou,

- China. Bot. Stud. **48**: 465–473.
- Liu, Y., Tseng, Y. H., Yang, H. A., Hu, A. Q., Xu, W. B., Lin, C. W., Kono, Y., Peng, C.-I. and Chung, K. F. 2020. Six new species of *Begonia* from Guangxi, China. Bot. Stud. **61**: e21.
- Ma, H. and Li, H. Z. 2006. *Begonia guianiana* (Begoniaceae), a new species from China. Ann. Bot. Fenn. **43**: 466–470.
- Matsuura, H. and Okuno, S. 1936. Cytogenetical studies on *Begonia*. I. The chromosome numbers. Jpn. J. Genet. **12**: 42–43.
- Moonlight, P. W. *et al.* 2018. Dividing and conquering the fastest-growing genus; Towards a natural sectional classification of the mega-diverse genus *Begonia* (Begoniaceae). Taxon **67**: 267–323.
- Nakamura, K., Rubite, R. R., Kono, Y., Callado, J. R. and Peng, C.-I. 2013. *Begonia tandangii* (Begoniaceae, section *Baryandra*), a new species from Luzon Island, the Philippines. Phytotaxa **145**: 27–37.
- Nakata, M., Guan, K., Godo, T., Lu, Y. and Li, J. 2003. Cytological studies on Chinese *Begonia* (Begoniaceae) I. Chromosome numbers of 17 taxa of *Begonia* collected in 2001 field studies in Yunnan. Bull. Bot. Gard. Toyama **8**: 1–16.
- Nakata, M., Guan, K., Li, J., Lu, Y. and Li, H. 2007. Cytotaxonomy of *Begonia rubropunctata* and *B. purpureofolia* (Begoniaceae). Bot. J. Linn. Soc. **155**: 513–517.
- Oginuma, K. and Peng, C.-I. 2002. Karyomorphology of Taiwanese *Begonia* (Begoniaceae): Taxonomic implications. J. Plant Res. **115**: 225–235.
- Peng, C.-I. and Chen, Y. K. 1990. *Begonia austrotaiwanensis* (Begoniaceae), a new species from southern Taiwan. J. Arnold Arbor. **71**: 567–574.
- Peng, C.-I. and Chen, Y. K. 1991. Hybridity and parentage of *Begonia buimontana* Yamamoto (Begoniaceae) from Taiwan. Ann. Mo. Bot. Gard. **78**: 995–1001.
- Peng, C.-I., Chen, Y. K. and Leong, W. C. 2005c. Five new species of *Begonia* (Begoniaceae) from Taiwan. Bot. Bull. Acad. Sin. **46**: 255–272.
- Peng, C.-I., Chen, Y. K. and Yen, H. F. 1988. *Begonia ravenii* (Begoniaceae), a new species from Taiwan. Bot. Bull. Acad. Sin. **29**: 217–222.
- Peng, C.-I., Hsieh, T. Y. and Ngyuen, Q.-H. 2007. *Begonia kui* (sect. *Coelocentrum*, Begoniaceae), a new species from Vietnam. Bot. Stud. **48**: 127–132.
- Peng, C.-I., Jin, X. H., Ku, S. M., Kono, Y., Huang, H. Y. and Yang, H. A. 2014a. *Begonia wuzhishanensis* (sect. *Diploclinium*, Begoniaceae), a new species from Hainan Island, China. Bot. Stud. **55**: e24.
- Peng, C.-I., Ku, S. M., Kono, Y., Chung, K. F. and Liu, Y. 2008b. Two new species of *Begonia* (sect. *Coelocentrum*, Begoniaceae) from limestone areas in Guangxi, China: *B. arachnoidea* and *B. subcoriacea*. Bot. Stud. **49**: 405–418.
- Peng, C.-I., Ku, S. M., Kono, Y. and Liu, Y. 2012. *Begonia chongzuoensis* (sect. *Coelocentrum*, Begoniaceae), a new calciphile from Guangxi, China. Bot. Stud. **53**: 283–290.
- Peng, C.-I., Ku, S. M. and Leong, W. C. 2005b. *Begonia liuyanii* (sect. *Coelocentrum*, Begoniaceae), a new species from limestone areas in Guangxi, China. Bot. Bull. Acad. Sin. **46**: 245–254.
- Peng, C.-I., Ku, S. M., Yang, H. A., Leong, W. C., Liu, Y., Nguyen, T. H., Kono, Y. and Chung, K. F. 2014b. Two new species of *Begonia* sect. *Coelocentrum*, *B. guixiensis* and *B. longa*, from Sino-Vietnamese limestone karsts. Bot. Stud. **55**: e52.
- Peng, C.-I., Lin, C. W., Repin, R., Kono, Y., Leong, W. C. and Chung, K. F. 2015a. Two new species of *Begonia*, *B. moneta* and *B. peridotica* (Begoniaceae) from Sabah, Malaysia. Bot. Stud. **56**: e7.
- Peng, C.-I., Lin, C. W., Yang, H. A., Kono, Y. and Nguyen, T. H. 2015b. Six new species of *Begonia* (Begoniaceae) from limestone areas in Northern Vietnam. Bot. Stud. **56**: e9.
- Peng, C.-I., Liu, Y. and Ku, S. M. 2008a. *Begonia aurantiflora* (sect. *Coelocentrum*, Begoniaceae), a new species from limestone areas in Guangxi, China. Bot. Stud. **49**: 83–92.
- Peng, C.-I., Liu, Y., Ku, S. M., Kono, Y. and Chung, K. F. 2010. *Begonia × breviscapa* (Begoniaceae), a new intersectional natural hybrid from limestone areas in Guanxi, China. Bot. Stud. **51**: 107–117.
- Peng, C.-I., Rubite, R. R., Lin, C.-W., Hughes, M., Kono, Y. and Chung, K.-F. 2017. Three new species of *Begonia* sect. *Baryandra* from Panay Island, Philippines. Bot. Stud. **58**: e28.
- Peng, C.-I., Shui, Y. M., Liu, Y. and Ku, S. M. 2005a. *Begonia fangii* (sect. *Coelocentrum*, Begoniaceae), a new species from limestone areas in Guangxi, China. Bot. Bull. Acad. Sin. **46**: 83–89.
- Peng, C.-I. and Sue, C. Y. 2000. *Begonia × taipeiensis* (Begoniaceae), a new natural hybrid in Taiwan. Bot. Bull. Acad. Sin. **41**: 151–158.
- Peng, C.-I., Wang, H., Kono, Y. and Yang, H. A. 2014c. *Begonia wui-senioris* (sect. *Platycentrum*, Begoniaceae), a new species from Myanmar. Bot. Stud. **55**: e13.
- Peng, C.-I., Yang, H. A., Kono, Y., Chung, K. F., Huang, Y. S., Wu, W. H. and Liu, Y. 2013. Novelties in *Begonia* sect. *Coelocentrum*: *B. longgangensis* and *B. ferox* from limestone areas in Guangxi, China. Bot. Stud. **54**: 44–52.
- Peng, C.-I., Yang, H. A., Kono, Y., Jung, M. J. and Nguyen, T. H. 2015c. Four new species of *Begonia* (Begoniaceae) from Vietnam: *B. abbreviata*, *B. calciphila*, *B. sphenantheroides* and *B. tamdaoensis*. Phytotaxa **222**: 83–99.
- Piton, F. 1962. Contribution à l'étude cytologique des Bégoniacées. Rev. Cytol. Biol. Veg. **24**: 165–216.
- Rieger, R., Michaelis, A. and Green, M. M. 1976. Glossary of Genetics and Cytogenetics. Springer-Verlag, New York.
- Rubite, R. R., Hughes, M., Alejandro, G. and Peng, C.-I. 2013. Recircumscription of *Begonia* sect. *Baryandra* (Begoniaceae): Evidence from molecular data. Bot. Stud. **54**: e38.
- Rubite, R. R., Hughes, M., Blanc, P., Chung, K. F., Yang, H. A., Kono, Y., Alejandro, G. J. D., De Layora, L. G., Virata, A. G. N. and Peng, C.-I. 2015. Three new species of *Begonia* endemic to the Puerto Princesa Subterranean River National Park, Palawan. Bot. Stud. **56**: e19.
- Sarkar, A. K. 1974. Evolution of species in the genus *Begonia*. Proc. Indian Sci. Congr. Assoc. **61** (IIIB): 32–33.
- Sarkar, A. K. 1989. Taxonomy of *Begonia* L. (Begoniaceae) as judged through cytology. Feddes Repert. **100**: 241–250.
- Sharma, A. K. 1970. Annual report 1967–1968. Res. Bull. Univ. Calcutta (Cytogenetics Lab.) **2**: 1–50.
- Sharma, A. K. and Bhattacharyya, U. C. 1957. Cytological studies in *Begonia*. I. Cellule **58**: 305–329.
- Sharma, A. K. and Bhattacharyya, U. C. 1961. Cytological studies in *Begonia*. II. Caryologia **14**: 279–301.
- Tian, D., Guan, K., Zhou, Q. and Gu, Z. 2002. Chromosome numbers of eight taxa of *Begonia* from Yunnan. Acta Bot. Yunnan. **24**: 245–249.
- Tseng, Y. H., Kim, Y. D., Peng, C.-I., Htwe, K. M., Cho, S. H., Kono, Y. and Chung, K. F. 2017. *Begonia myanmarica* (Begoniaceae), a new species from Myanmar, and molecular phylogenetics of *Begonia* sect. *Monopteron*. Bot. Stud. **58**: e21.
- White, O. E., Tayler, J. H. and Speese, B. M. 1946. *Begonia* species hybrids. J. Hered. **37**: 66–70.
- Ye, H. G., Wang, F. G., Ye, Y. S. and Peng, C.-I. 2004. *Begonia copitidifolia* (Begoniaceae), a new species from China. Bot. Bull. Acad. Sin. **45**: 259–266.