

Karyomorphology of three species in *Dipentodon* (Dipentodontaceae), *Perrottetia* (Celastraceae), and *Tapiscia* (Tapisciaceae) of the order Huerteales and their phylogenetic implications

Jing YANG Jiang-Chong WU Zhi-Jian GU*

(Kunming Botanical Garden, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650204, China)

Abstract The karyomorphology of three species in *Dipentodon* (Dipentodontaceae), *Perrottetia* (Celastraceae), and *Tapiscia* (Tapisciaceae), namely *Dipentodon sinicus*, *Perrottetia racemosa*, and *Tapiscia sinensis*, was investigated in the present study. Recent molecular research has discovered close relationships among these three genera, which has led to the establishment of the order Huerteales with *Perrottetia* being placed in Dipentodontaceae. Herein we report the chromosome numbers of *D. sinicus* and *P. racemosa* for the first time, and present their karyotype formulas as $2n = 34 = 22 \text{ sm} + 12 \text{ st}$ (*D. sinicus*), $2n = 20 = 11 \text{ m} + 9 \text{ sm}$ (*P. racemosa*), and $2n = 30 = 22 \text{ m(2SAT)} + 8 \text{ sm}$ (*T. sinensis*). Asymmetry of their karyotypes is categorized to be Type 3B in *D. sinicus*, Type 2A in *P. racemosa*, and Type 2A in *T. sinensis*. Each of the species shows special cytological features. Compared with *Perrottetia*, *Dipentodon* has a different basic chromosome number, a higher karyotype asymmetry, and different karyomorphology of its interphase nuclei, mitotic prophase, and metaphase. Thus, on the basis of these results, we have reservations regarding the suggestion of placing *Dipentodon* and *Perrottetia* together in the family Dipentodontaceae.

Key words chromosome number, *Dipentodon*, karyomorphology, *Perrottetia*, phylogenetic relationship, *Tapiscia*.

The angiosperm order Huerteales was described by Doweld (2001), but was rarely accepted by botanists until Stevens (2008) recognized and expanded it to contain three little known small families, namely Dipentodontaceae, Tapisciaceae, and Gerrardinaceae, based on Peng et al. (2003) and Zhang and Simmons (2006). Dipentodontaceae was first created for the genus *Dipentodon* Dunn, a monotypic genus distributed in south-west China and adjacent areas (Ma & Bartholomew, 2008; Yuan et al., 2008). Based on the work of Zhang and Simmons (2006), the genus *Perrottetia* Kunth was accepted by Stevens (2008) as another in Dipentodontaceae. *Perrottetia* contains 15 species distributed throughout tropical America, north-east Australia, China, Indonesia, Malaysia, New Guinea, the Pacific Islands, and the Philippines (Ma & Bartholomew, 2008). Tapisciaceae contains two genera: *Tapiscia* Oliv. and *Huerteia* Ruiz & Pav. *Tapiscia* is endemic to China, with two species distributed in south-east China. *Huerteia* contains four species and is distributed throughout the West Indies and northern South America (Li et al., 2008). The family Gerrardinaceae is a recently described family of Africa, containing only

one genus, *Gerrardina* Oliv., with two species (Alford, 2006).

In recent molecular studies, *Dipentodon* (Dipentodontaceae) was resolved as the sister group of *Tapiscia* (Tapisciaceae) based on DNA sequences analyses of *rbcL*, 18S, and *matR* genes by Peng et al. (2003). Zhang and Simmons (2006) studied the phylogeny and delimitation of Celastrales by analyzing nuclear (18S, internal transcribed spacer (ITS) 1, 26S ribosomal (r) DNA) and plastid (*atpB*, *matK*, *rbcL*, *trnL-F* spacer) genes. They found that *Perrottetia* (formerly in Celastraceae) was resolved as sister to *Dipentodon* (77% Jackknife (JK) support), and the clade comprising the two was further sister to *Tapiscia* (100% JK support). This led Zhang and Simmons (2006) to suggest that Dipentodontaceae contains two genera: *Dipentodon* and *Perrottetia*.

None of the three genera of Huerteales (i.e. *Dipentodon*, *Perrottetia*, and *Tapiscia*) investigated in the present study was previously well known. Although molecular studies have suggested new phylogenetic relationships among them as described above, more evidence is needed to evaluate and understand their relationships. For this purpose, we studied the karyomorphology of three species in these three genera. The aim of the present study was to analyze cytological data of the three related genera to gain an understanding of the cytotaxonomical features of *Dipentodon*,

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* Author for correspondence: E-mail: guzhijian@mail.kib.ac.cn; Tel: 0871-522-3627; Fax: 0871-521-8676.

Perrottetia, and *Tapiscia*. Two other genera in Huerteales, namely *Huertia* and *Gerrardina*, were not sampled in the present study.

1 Material and methods

All material for the present study was collected from China. Specifically, *Dipentodon sinicus* Dunn was collected from Zhaotong in Yunnan Province (voucher specimen KUN-0571257), *Perrottetia racemosa* (Oliv.) Loes. was from Emei Mountain in Sichuan Province (KUN-0668625), and *Tapiscia sinensis* Oliv. was from Xinning in Hunan Province (KUN-0577608).

For cytological observations, vigorous root tips were harvested and pretreated with a saturated solution of paradichlorobenzene for 1.5 h at approximately 20°C, before being fixed in Carnoy's fluid (3 : 1 ethanol and glacial acetic acid) at 0°C for 30 min. After maceration in a 1 : 1 mixture of 1 mol/L hydrochloric acid : 45% acetic acid at 60°C for 60 s, the material was stained with 1% aceto-orcin and then compressed for cytological observation. Descriptions of the positions of the centromeres on metaphase chromosomes were as specified by Levan et al. (1964). The classification of karyotype asymmetry was estimated according to Stebbins (1971).

Representative interphase nuclei were selected from undisturbed cells with large round nuclei. Mitotic prophase cells were selected where the distribution of the hetero- and euchromatin could be most clearly distinguished. The classification of interphase nuclei and the description of the condensation pattern of chromosomes during mitotic prophase follow Tanaka (1971, 1977).

2 Results

2.1 *Dipentodon sinicus* Dunn (Table 1; Figs. 1, 2A)

The interphase nuclei of *D. sinicus* possess approximately 40 round-shaped heterochromatic bodies. Karyomorphology at interphase is categorized to be the Round prochromosome type. The chromatin condensation of mitotic prophase is considered to be the Interstitial type.

In mitotic metaphase cells of *D. sinicus*, the chromosome number was counted as $2n = 34$ ($x = 17$). This is the first report of this information for *D. sinicus*. The chromosome length varied from 1.6 to 3.4 μm . Of the 34 chromosomes, 12 (chromosome no. 1, 2, 4, 5, 6, 7, 8, 15, 16, 17, 21, and 32) are subtelocentric and the remaining 22 chromosomes are submetacentric. Asymmetry of the karyotype is categorized to be Type 3B.

2.2 *Perrottetia racemosa* (Oliv.) Loes. (Table 1; Figs. 1, 2B)

The interphase nuclei of *P. racemosa* possess approximately 15 rod- or round-shaped heterochromatic bodies. Karyomorphology at interphase is categorized to be between the Rod-shaped prochromosome type and the Round prochromosome type. The chromatin condensation of mitotic prophase is considered to be the Gradient type.

In mitotic metaphase cells of *P. racemosa*, the chromosome number was counted as $2n = 20$ ($x = 10$). The present study is the first to report this information for *P. racemosa*. The chromosome length varied from 1.6 to 2.6 μm . Of the 20 chromosomes, nine (chromosome no. 1, 2, 5, 6, 7, 9, 10, 11, and 19) are submetacentric and the remaining 11 chromosomes are metacentric. Asymmetry of the karyotype is categorized to be Type 2A.

2.3 *Tapiscia sinensis* Oliv. (Table 1; Figs. 1, 2C)

The interphase nuclei of *T. sinensis* possess up to five round-shaped heterochromatic bodies. Karyomorphology at interphase is categorized to be the Round prochromosome type. The chromatin condensation of mitotic prophase is considered to be the Gradient type.

In mitotic metaphase cells of *T. sinensis*, we counted the chromosome number as $2n = 30$ ($x = 15$), identical to the count reported by Chen et al. (2007). However, this is the first report of the karyotype details for *T. sinensis*. The chromosome length varied from 0.9 to 1.7 μm . Of the 30 chromosomes, eight (chromosome no. 5, 6, 7, 8, 9, 10, 13, and 14) are submetacentric and the remaining 22 chromosomes are metacentric. A pair of satellites was located at the short arms of the chromosomes 19 and 20. Asymmetry of the karyotype is categorized to be Type 2A. The presence of one B-chromosome was observed.

3 Discussion

Dipentodon and *Perrottetia* were initially assigned to Celastraceae by Dunn (1911) and Kunth (1825). However, the systematic positions of both were questioned by researchers. *Dipentodon* has been moved into Samydaceae (which has the same range of variation in floral base numbers; Sprague, 1925) and Flacourtiaceae (including Samydaceae; Fischer, 1941; Loesener, 1942; Metcalfe & Chalk, 1950; Lobreau, 1969). Zhang and Gao (1995) supported its position in Celastraceae based on wood anatomy, whereas Merrill (1941) proposed the independent family Dipentodontaceae. Merr. Dipentodontaceae has been put into Rosales (Merrill, 1941), Olacales (Hutchinson 1959, 1973),

Table 1 Karyotype data of *Dipentodon sinicus*, *Perrottetia racemosa*, and *Tapiscia sinensis*

| <i>Dipentodon sinicus</i> | | | | | | | | <i>Perrottetia racemosa</i> | | | | <i>Tapiscia sinensis</i> | | | | | | | |
|---------------------------|--------|------|----|-----|--------|------|----|-----------------------------|--------|------|----|-----------------------------|--------|------|----|-----|--------|------|----|
| 2n = 34 = 22 sm + 12 st | | | | | | | | 2n = 20 = 11 m + 9 m | | | | 2n = 30 = 22 m(2SAT) + 8 sm | | | | | | | |
| No. | RL (%) | AR | CT | No. | RL (%) | AR | CT | No. | RL (%) | AR | CT | No. | RL (%) | AR | CT | No. | RL (%) | AR | CT |
| 1 | 4.28 | 3.07 | st | 21 | 2.74 | 3.88 | st | 1 | 6.10 | 1.92 | sm | 1 | 5.10 | 1.32 | m | 21 | 2.90 | 1.36 | m |
| 2 | 4.14 | 3.92 | st | 22 | 2.74 | 2.90 | sm | 2 | 6.10 | 2.18 | sm | 2 | 5.10 | 1.32 | m | 22 | 2.90 | 1.36 | m |
| 3 | 3.79 | 2.60 | sm | 23 | 2.74 | 2.25 | sm | 3 | 6.10 | 1.19 | m | 3 | 4.13 | 1.47 | m | 23 | 2.90 | 1.36 | m |
| 4 | 3.65 | 3.33 | st | 24 | 2.67 | 2.80 | sm | 4 | 6.10 | 1.19 | m | 4 | 3.87 | 1.32 | m | 24 | 2.90 | 1.36 | m |
| 5 | 3.65 | 3.33 | st | 25 | 2.60 | 2.70 | sm | 5 | 6.10 | 1.92 | sm | 5 | 3.69 | 2.00 | sm | 25 | 2.90 | 1.36 | m |
| 6 | 3.51 | 4.00 | st | 26 | 2.60 | 2.08 | sm | 6 | 5.92 | 1.83 | sm | 6 | 3.69 | 2.00 | sm | 26 | 2.90 | 1.36 | m |
| 7 | 3.37 | 3.80 | st | 27 | 2.60 | 2.70 | sm | 7 | 5.75 | 1.75 | sm | 7 | 3.69 | 2.00 | sm | 27 | 2.90 | 1.36 | m |
| 8 | 3.23 | 3.60 | st | 28 | 2.46 | 2.50 | sm | 8 | 5.57 | 1.67 | m | 8 | 3.69 | 2.00 | sm | 28 | 2.64 | 1.14 | m |
| 9 | 3.23 | 1.71 | sm | 29 | 2.32 | 1.75 | sm | 9 | 5.23 | 2.33 | sm | 9 | 3.43 | 1.79 | sm | 29 | 2.64 | 1.14 | m |
| 10 | 3.23 | 2.07 | sm | 30 | 2.32 | 1.75 | sm | 10 | 5.23 | 2.33 | sm | 10 | 3.43 | 1.79 | sm | 30 | 2.64 | 1.14 | m |
| 11 | 3.23 | 2.83 | sm | 31 | 2.18 | 2.88 | sm | 11 | 4.88 | 2.11 | sm | 11 | 3.43 | 1.44 | m | | | | |
| 12 | 3.23 | 2.83 | sm | 32 | 2.18 | 4.17 | st | 12 | 4.88 | 1.55 | m | 12 | 3.43 | 1.44 | m | | | | |
| 13 | 3.09 | 2.67 | sm | 33 | 2.18 | 2.10 | sm | 13 | 4.88 | 1.33 | m | 13 | 3.43 | 1.79 | sm | | | | |
| 14 | 2.95 | 2.50 | sm | 34 | 1.96 | 1.80 | sm | 14 | 4.70 | 1.45 | m | 14 | 3.16 | 1.77 | sm | | | | |
| 15 | 2.88 | 3.10 | st | | | | | 15 | 4.36 | 1.27 | m | 15 | 3.25 | 1.64 | m | | | | |
| 16 | 2.88 | 3.10 | st | | | | | 16 | 4.18 | 1.67 | m | 16 | 3.16 | 1.57 | m | | | | |
| 17 | 2.88 | 3.10 | st | | | | | 17 | 3.48 | 1.50 | m | 17 | 3.16 | 1.25 | m | | | | |
| 18 | 2.88 | 2.42 | sm | | | | | 18 | 3.48 | 1.50 | m | 18 | 3.16 | 1.25 | m | | | | |
| 19 | 2.88 | 2.42 | sm | | | | | 19 | 3.48 | 2.33 | sm | 19* | 2.90 | 1.36 | m | | | | |
| 20 | 2.81 | 3.00 | sm | | | | | 20 | 3.48 | 1.50 | m | 20* | 2.90 | 1.36 | m | | | | |

*, SAT-chromosome; AR, arm ratio; CT, chromosome type; RL, relative length.

Santalales (including Olacaceae; Melchior, 1964; Cronquist, 1981), and Violales (Dahlgren, 1980; Thorne, 1992; Takhtajan & Takhtadzian, 1997). Based on molecular evidence, Peng et al. (2003) suggested that Dipentodontaceae is closest to Malvales and Sapindales, which is the same conclusion reached by Peng (2001).

Perrottetia has long been considered an unusual genus in Celastraceae. All the characteristics of wood anatomy (Metcalf & Chalk, 1950; Boole, 1955), seed structure (Corner, 1976), leaf anatomy (den Hartog & Baas, 1978), flora structure (Matthews & Endress, 2005), and molecular analyses (Zhang & Simmons, 2006) show its deviation from classical Celastraceae genera. Dunn (1911) noticed some identical morphological characteristics between *Dipentodon* and *Perrottetia*, as did Liu and Cheng (1989) with wood anatomy. Based on the molecular evidence, Zhang and Simmons (2006) suggested that *Perrottetia* should be treated as another genus in Dipentodontaceae.

The systematic position of *Tapiscia* is also contentious. It was initially placed in Sapindaceae by Oliver (1890) and was then transferred to Staphyleaceae by Pax (1893). Furthermore, this family was subdivided into two subfamilies by Pax (1893): (i) the subfamily Staphyleoideae; and (ii) the subfamily Tapiscioideae (consisting of *Tapiscia* and *Huertia*). Dickson (1986, 1987) studied the floral morphology and leaf and nodal anatomy of Staphyleaceae, and pointed out that *Tapiscia* and *Huertia* deviated in a number of important respects from other genera of Staphyleaceae, which was

also the opinion of Krause (1942). Takhtajan (1987) suggested that *Tapiscia* should be in its own family: Tapisciaceae (Pax) Takht. with the genus *Huertia* included. Soltis et al. (2000) placed Tapisciaceae at the base of Brassicales–Malvales–Sapindales clade, concordant with Peng et al. (2003) and Ronse de Craene & Haston (2006).

Marked differences in the karyomorphology of these three species were observed in the present study. The basic chromosome numbers of *D. sinicus*, *P. racemosa*, and *T. sinensis* are $x = 17$ ($2n = 34$), $x = 10$ ($2n = 20$), and $x = 15$ ($2n = 30$), respectively. In addition, the karyotype of *D. sinicus* has a higher degree of asymmetry (Type 3B) with 22 submetacentric and 12 subtelocentric chromosomes, which distinguishes it from *P. racemosa* (Type 2A) and *T. sinensis* (Type 2A). Even though the interphase nuclei of these three species are all of the prochromosome type, the greater number of heterochromatic bodies in interphase nuclei of *D. sinicus* and its Interstitial-type mitotic prophase suggest distinct cytogenetic characteristics from *P. racemosa* and *T. sinensis*. Comparison of *P. racemosa* and *T. sinensis* revealed obvious deviation of *T. sinensis*, despite them sharing the same type of karyotype asymmetry (Type 2A). In the mitotic metaphase nuclei of *T. sinensis*, a pair of satellites was observed in the proximal regions of the short arms in the 10th pair of chromosomes, and the existence of a B-chromosome was also noted. Approximately five heterochromatic bodies in the interphase nuclei of *T. sinensis* could be seen, with an extremely short chromosome length ranging from 0.9

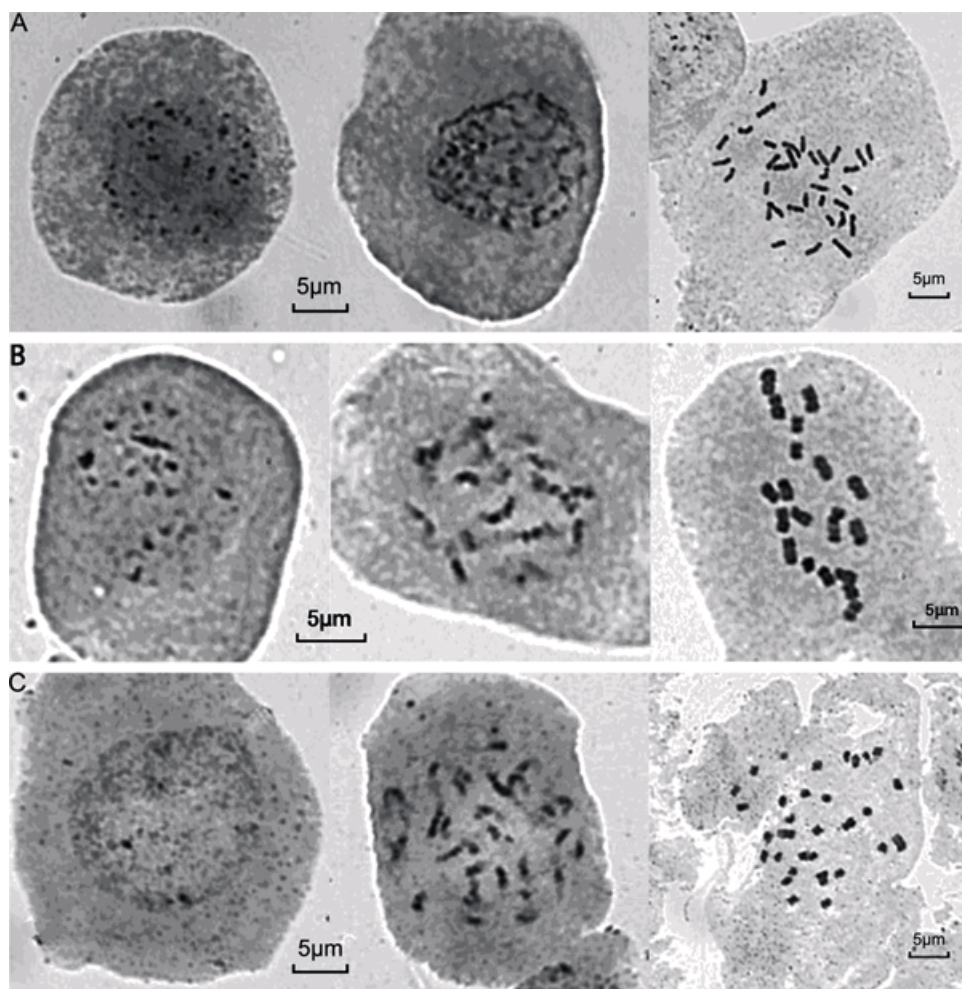


Fig. 1. Interphase nuclei, mitotic prophase nuclei, and metaphase chromosomes (left to right) of (A) *Dipentodon sinicus*, (B) *Perrottetia racemosa*, and (C) *Tapiscia sinensis*.

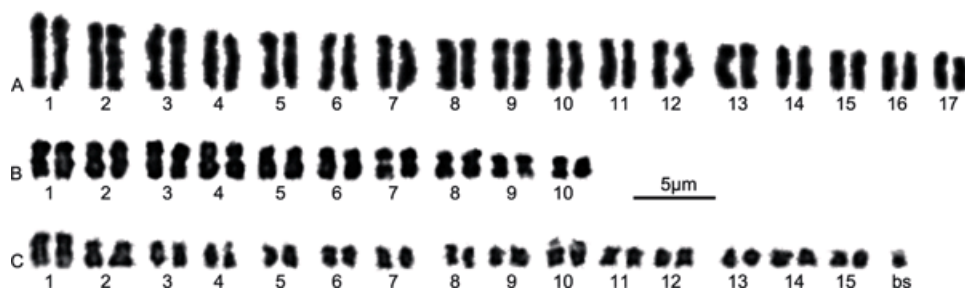


Fig. 2. Karyograms of (A) *Dipentodon sinicus*, (B) *Perrottetia racemosa*, and (C) *Tapiscia sinensis*.

to 1.7 μm. Given that the three species investigated in the present study showed distinct characteristics and basic chromosome numbers in karyomorphology, the findings may imply that they have independent phylogenetic positions. Wu et al. (2003) reported a different chromosome number of $2n = 24$ in *D. sinicus*. However, these

authors did not provide any evidence to support their data or any detailed information regarding karyotype. It is possible that the chromosome number reported by Wu et al. (2003) is a miscount.

Morphological differences between *Dipentodon* and *Perrottetia* are listed in Table 2 to better understand

Table 2 Different features of structures between *Dipentodon* and *Perrottetia*

| <i>Dipentodon</i> | <i>Perrottetia</i> |
|---|---|
| Shrubs or trees, bisexual flowers, semi-evergreen | Shrubs or small trees, dioecious, deciduous |
| Inflorescences abbreviated cymes in a pedunculate umbel | Inflorescence a raceme or panicle |
| Flowers yellowish green, 5–7-merous, pedicellate | Flowers usually 4- or 5-merous |
| Bracts 4 or 5, at the apex of the peduncle, caducous before anthesis | |
| Sepals and petals undifferentiated, 10–14, linear Disk flat cup-shaped, fleshy, with 5–7 yellow lobes opposite petals | Sepals and petals similar but petal margin more distinctly fimbriate and slightly wider, triangular |
| Stamens 5–7, attached outside disk margin, opposite sepals | Male flowers: stamens inserted on disk margin, filament subulate, anther subglobose or ellipsoid |
| | Female flowers: disk cup- or ring-shaped |
| Ovary connected with disk at base, 3-loculed basally but incompletely loculed apically | Ovary semi-immersed in disk, mostly 2-loculed |
| Ovules 2 per locule, all but 1 aborting before maturity, placentation axile at top of a free basal placentation | Ovules 2 per locule, basally attached, erect |
| Funicle and placenta developing into a seed stipe when mature | |
| Fruit a drupaceous capsule, 1-seeded Aril absent | Fruit a dry berry, 2–4-seeded Aril present, thin |

their relationships. Specialized features are shown in the flora organs in both genera. Based on differences in cytological and morphological characteristics that may have resulted from strong deviation in their speciation, there is some doubt as to the veracity of the conclusion that these two genera should be put in a family together.

With only morphological evidence, it is difficult to elucidate the relationships among *Dipentodon*, *Perrottetia*, and *Tapiscia*, or to understand the synapomorphies of Dipentodontaceae, *Perrottetia*, and Tapisciaceae (Stevens, 2008). The basic chromosome numbers are $x = 10$ in *P. racemosa*, $x = 17$ in *D. sinicus*, and $x = 15$ in *T. sinensis*. The latter two basic chromosome numbers are comparatively high. The basic chromosome number of $x = 17$ in *D. sinicus* may be have resulted from hybridization of its two related ancestors with basic chromosome numbers of $x = 8$ and $x = 9$, whereas the $x = 15$ in *T. sinensis* may be the result of diploidization of its paleopolyploid. Different basic chromosome numbers in these three genera could be the result of independent evolutionary histories. This may support treating them as comparatively independent families. Molecular analyses can elucidate potential relationships; however, caution should be exercised when deciding their phylogenetic positions, especially under the rank of family. With combined data from molecular, morphological, cytological, or other analyses, a more precise cladogram can be developed.

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