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Cytogenetics of *Cheniella* (Leguminosae: Cercidoideae) from China and Vietnam

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Abstract. The cytogenetics of *Cheniella*, a recently segregated genus of the early-diverging subfamily Cercidoideae of Leguminosae, remain understudied, hindering our understanding of the cytological evolution and the utilization of this important plant group. Here we conducted comparative cytogenetic studies on 11 species and one subspecies of *Cheniella* and one species of its sister genus *Phanera*. Unlike earlier reports which recovered $2n$=28 for two *Cheniella* species, we consistently observed chromosome counts of $2n$=26 for all 11 species of *Cheniella*, supporting the segregation of *Cheniella* from *Phanera*, which consistently exhibited $2n$=28 in this and previous studies. Our analyses, along with previous cytogenetic data, indicates that $2n$=14, $2n$=26 and $2n$=28 are the predominant chromosome numbers in the basal-most genus *Cercis*, *Cheniella* and the remainder genera, respectively. The ancestor of the subfamily is most probably a diploid with $2n$=14, with subsequent polyploidization followed by chromosome reduction events leading to $2n$=28 and $2n$=26 in the other lineages. Our results provide new insight into the cytotaxonomy and chromosome evolution of Cercidoideae, also lay the foundation for future genomics research.

Keywords: *Bauhinia* s.l., chromosome counts, cytology, Fabaceae, *Phanera*, Southeast Asia.

INTRODUCTION

The plant family Leguminosae Juss. (or Fabaceae Lindl.) is currently recognised by the Legume Phylogeny Working Group to consist of six subfamilies (LPWG, 2017), of which the Cercidoideae LPWG contains about 14 genera and 340 species distributed pantropically and in some subtropical regions. Various species of Cercidoideae are used for food, timber, dyes, ropes and medicine, and widely cultivated as ornamental trees in many areas of the world (Clark et al., 2017; Gu et al., 2024). The flowers of many Cerci-

doideae species are highly attractive and fragrant, with great value or potential as garden ornamental plants. The subfamily Cercidoideae currently contains 14 genera including *Adenolobus* (Harv. ex Benth. & Hook.f.) Torre. & Hillc., *Barklya* F.Muell., *Bauhinia* L., *Brenierea* Humbert, *Cercis* L., *Cheniella* R.Clark & Mackinder, *Gigasiphon* Drake, *Griffonia* Baill, *Lysiphyllum* (Benth.) de Wit, *Phanera* Lour., *Piliostigma* Hochst., *Schnella* Raddi; *Tournaya* A.Schmitz, and *Tylosema* (Schweinf.) Torre & Hillc. (Wunderlin, 1976; Lewis & Forest, 2005; LPWG, 2017; Clark et al., 2017; Sinou et al., 2020).

The initially diverged lineage of Cercidoideae, *Cercis*, exhibits a somatic chromosome number of 2*n*=14, whereas most other lineages in this subfamily were consistently reported to have a somatic chromosomal count of 2*n*=28, with a few exceptions of 2*n*=24, 2*n*=26, or even 2*n*=42, 2*n*=56 found in several species of *Barklya*, *Bauhinia*, *Gigasiphon*, *Lysiphyllum*, and *Piliostigma* (Table 1) (Sharma & Raju, 1968; Goldblatt, 1981; Yeh et al., 1986; Kumari & Bir, 1989). Intraspecific chromosomal variations are also observed. For example, *Bauhinia monandra* Kurz exhibits counts of 2*n*=24, 2*n*=28, and 2*n*=42 (Sharma & Raju, 1968; Gill & Husaini, 1982; Darlington & Wylie, 1955), *Bauhinia acuminata* L. has 2*n*=26 and 2*n*=28, and *Lysiphyllum hookeri* (F.Muell.) Pedley shows both 2*n*=26 and 2*n*=28 (Sharma & Raju, 1968; Singhal et al., 1980b; Goldblatt, 1981; Sarkar et al., 1982; Basumatari & Das, 2017).

Cheniella R.Clark & Mackinder, a recently segregated genus from *Bauhinia* s.l., contains 16 species and three subspecies, and is closely related to *Phanera* (Clark et al., 2017; Gu et al., 2024; Peng et al., 2024). The centre of diversity of *Cheniella* is in southern China, and its full distribution range extends westward to India and southeast through Indochina into Malesia (Clark et al., 2017). The genus is characterised as being tendrilled lianas with a deeply to slightly bilobed or emarginate leaf blade, elongate hypanthia, a fleshy disc on which the staminodes are mounted, glabrous or densly hirsute, oblong and compressed, indehiscent or tardily dehiscent pods with numerous seeds (Fig. 1). The chromosome numbers of two species in *Cheniella* have been previously reported, *C. corymbosa* (Roxb.) R.Clark & Mackinder and *C. quinnanensis* (Benth.) R.Clark & Mackinder, both with 2*n*=28 chromosomes (Sharma & Raju, 1968; Singhal et al., 1980a). It must be noted that the initial identifications of *C. corymbosa* and *C. quinnanensis* by Sharma & Raju (1968) and Singhal et al. (1980a) were *Bauhinia corymbosa* and (probably) *Bauhinia glauca* respectively, of which the former name was synonymised to *C. corymbosa* and the latter was probably erroneously identified, the correct name being *C. quinnanensis*. Beside the misidentification, the accuracy and reliability of the chromosome numbers in previous studies needed to be tested especially for those groups that were poorly studied or for those that have various chromosome counts reported.

To test the cytogenetics of *Cheniella*, we counted the chromosome numbers of 11 species and one subspecies of *Cheniella*, as well as one species of *Phanera*. By combining evidence from cytology and morphology, this study aims to provide the chromosomal data and cytotaxonomy of *Cheniella* and to compare these with other members of subfamily Cercidoideae.

MATERIALS AND METHODS

All seeds or transplanted living plants studied were collected in the field of southern and southwestern China and adjacent regions except for one sample was collected from Vietnam. Detailed collection information is shown in Table 1. The vouchers of all collections and permanent slides are deposited in the herbarium of South China Botanical Garden, Chinese Academy of Sciences (IBSC).

All cytological observations were made from root tip cells obtained either from seeds or from transplanted living individuals. All root tips were obtained from germinating seeds, mature and dry seeds were cut the seed coat and placed in petri dishes lined with moist filter paper and cultured at room temperature until 1–2 cm root sprouted. Root tips were pretreated in a saturated 1,4-dichlorobenzene solution for 150 min, then fixed with Carnoy's fluid (absolute alcohol: glacial acetic acid, 3:1, v/v) at 4 °C for at least 30 min. The fixed roots were hydrolysed in 1 N HCl solution at 60 °C for 4 min, stained with modified phenol magenta stain for 2 h and squashed for cytological observation. The best metaphase plates were photographed using a Nikon DS-Fi2 digital camera attached to the BX41 Olympus microscope. Permanent slides were made using the standard liquid nitrogen method.

RESULTS AND DISCUSSION

The interphase nuclei of 11 species from *Cheniella* and one species from *Phanera* studied in this paper show the similar shape and distribution pattern of chromatin, which are dispersed evenly throughout the nuclei (Fig. 1, A). According to Tanaka (1971, 1977), they can be categorised as the complex chromocentre type, which is characterised by darkly stained chromocentres of irregular shape and lightly stained chromatin threads. The

Table 1. Statistics on chromosome numbers in Cercidoideae.

Genus	Species	Chromosome number (2*n*)	Locality	Voucher	References	Notes
Adenolobus	*A. pechuelii* (Kuntze) Korcz. & Hillc.	28	Walvis Bay, Namibia	Seely *s.n.*	Goldblatt (1981)	
Barklya	*B. syringifolia* F.Muell.	26	Cult. in Australia	Pedley A1772 (MO)	Goldblatt (1981)	
Bauhinia	*B. acuminata* L.	28	-	-	Sharma & Raju (1968)	
		26	Uttar Pradesh, India	Singhal 23001	Singhal et al. (1980b)	*
		28	Howrah, India	CBLH 4512	Sarkar et al. (1982)	
		28	-	-	Kumari & Bir (1989)	
		28	-	-	Sinha & Singh (2013b)	
		28	Guwahati, Assam	-	Basumatari & Das (2017)	
	B. corniculata Benth.	28	-	-	Sharma & Raju (1968)	
	B. divaricata L.	28	-	-	Sandhu & Mann (1988)	
	B. forficata Link	28	-	-	Gill & Husaini (1986)	
		28	Paraná, Brazil	E. Biondo 303 (ICN)	Biondo et al. (2005)	
	B. lunarioides A.Gray ex S.Watson	28	-	Tharp 44159 (TEX)	Turner (1956)	
	B. galpinii N.E.Br.	28	-	-	Sharma & Raju (1968)	
		28	-	-	Paiva & Leitao (1989)	
		28	Uttar Pradesh, India	Singhal 23502	Singhal et al. (1990)	
	B. monandra Kurz	28	-	-	Sharma & Raju (1968)	
		24	-	-	Gill & Husaini (1982)	*
		42	-	-	Darlington & Wylie (1955)	*
	B. petersiana Bolle	28	-	-	Sharma & Raju (1968)	
	B. purpurea L.	28	-	-	Sharma & Raju (1968)	
		28	-	-	Yeh et al. (1986)	
		28	-	-	Kumari & Bir (1989)	
		28	-	-	Sinha & Singh (2013a)	
		28	-	-	Sinha & Singh (2013b)	
	B. racemosa Lam.	28	-	-	Sharma & Raju (1968)	
		28	-	-	Kumari & Bir (1989)	
		28	-	-	Sinha & Singh (2013b)	
	B. rufescens Lam.	28	-	-	Sharma & Raju (1968)	
		56	-	-	Sharma & Raju (1968)	*
	B. tomentosa L.	28	-	-	Sharma & Raju (1968)	
		28	-	-	Gill & Husaini (1982)	
		28	-	-	Kumari & Bir (1989)	
	B. ungulata L.	28	Belém, Brazil	Souza 14	Souza & Benko-Iseppon (2004)	

(Continued)

Table 1. (Continued).

Genus	Species	Chromosome number (2*n*)	Locality	Voucher	References	Notes
	B. variegata L.	28	-	-	Atchison (1951)	
		28	-	-	Sharma & Raju (1968)	
		28	-	-	Bir & Kumari (1979)	
		28	-	-	Sinha & Singh (2013a)	
		28	-	-	Sinha & Singh (2013b)	
		28	Sirmaur, India	56688 (PUN)	Rani et al. (2013)	
		28	Kangra, India	56276 (PUN)	Rani et al. (2013)	
		28	Nagaon, Assam	-	Basumatari and Das (2017)	
		28	Guangzhou, China	-	Zhong et al. (2022)	
	B.× blakeana Dunn	28	-	-	Sharma & Raju (1968)	
		28	-	-	Sinha & Singh (2013a)	
Cercis	*C. canadensis* L.	14	Cult. in USA	Curtis 101 (MO)	Curtis (1976)	
		14	-	-	Hill (1989)	
		14	-	-	Blackwell (1990)	
	C. chinensis Bunge	14	-	-	Yeh et al. (1986)	
		14	-	-	Chen et al. (2003)	
		14	Guangxi, China	-	Li et al. (2023)	
	C. chingii Chun	14	Jiangsu, China	-	Chen et al. (1991)	
	C. siliquastrum L.	14	-	-	Fernandes et al. (1975)	
		14	Prebalkan, Bulgaria	BK 73192	Kuzmanov (1975)	
Cheniella	*C. clemensiorum* (Merr.) R.Clark & Mackinder	26	Da Hang Pro, Vietnam	LBo779 (IBSC)	This study	
	C. corymbosa (Roxb.) R.Clark & Mackinder	26	Hainan, China	ZQB59 (IBSC)	This study	
		28	-	-	Sharma & Raju (1968)	*
	C. didyma (H.Y.Chen) R.Clark & Mackinder	26	Guangdong, China	TuTY4691 (IBSC)	This study	
	C. hupehana comb. nov. ined.	26	Hubei, China	ZQB68 (IBSC)	This study	
	C. longipes (Hosok.) S.R.Gu, T.Y.Tu & D.X.Zhang	26	Hainan, China	ZQB56 (IBSC)	This study	
	C. longistaminea S.R.Gu, T.Y.Tu & D.X.Zhang	26	Guangxi, China	ZengQB198 (IBSC)	This study	
	C. ovatifolia (T.C.Chen) R.Clark & Mackinder	26	Guangxi, China	TuTY4799 (IBSC)	This study	
	C. paraglauca sp. nov. nom. ined.	26	Guangdong, China	GuSR125 (IBSC)	This study	
	C. quinnanensis (T.C.Chen) R.Clark & Mackinder subsp. *quinnanensis*	26	Guangxi, China	TuTY4816 (IBSC)	This study	
		28	Uttar Pradesh, India	Singhal 22812	Singhal et al. (1980a)	*
	C. quinnanensis subsp. *villosa* R.Clark & Mackinder	26	Guangdong, China	TuTY4848 (IBSC)	This study	
	C. tenuiflora (Watt ex C.B.Clarke) R.Clark & Mackinder	26	Yunnan, China	GuSR021 (IBSC)	This study	
	C. tianlinensis × *ovatifolia*	26	Guangxi, China	ZQB32 (IBSC)	This study	
	C. touranensis (Gagnep.) R.Clark & Mackinder	26	Guangxi, China	TuTY4795 (IBSC)	This study	

(Continued)

Table 1. (Continued).

Genus	Species	Chromosome number (2*n*)	Locality	Voucher	References	Notes
Gigasiphon	*G. macrosiphon* (Harms) Brenan	26	Mua hills, Kenya	Gachathi *s.n.*	Goldblatt (1981)	
Lysiphyllum	*L. diphyllum* (Banks) de Wit	28	-	-	Sharma & Raju (1968)	
		28	-	-	Bir & Kumari (1979)	
		28	-	-	Kumari & Bir (1989)	
	L. hookeri (F.Muell.) Pedley	28	-	-	Sharma & Raju (1968)	
		26	-	-	Sharma & Raju (1968)	
		26	Cult. in Australia	Pedley A7771 (MO)	Goldblatt (1981)	
Phanera	*P. championii* Benth.	28	Taiwan, China	4728	Peng et al. (1986)	
		28	Guangxi, China	-	Lu et al. (2024)	
	P. integrifolia (Roxb.) Benth.	28	-	-	Sharma & Raju (1968)	
	P. roxburghiana (Voigt) Bandyop., Anand Kumar & Chakrab.	28	-	-	Sharma & Raju (1968)	
		28	Uttarakhand, India	Singhal 23281	Singhal et al. (1990)	
	P. semibifida (Roxb.) Benth.	28	-	-	Sharma & Raju (1968)	
	P. vahlii (Wight & Arn.) Benth.	28	-	-	Sandhu & Mann (1988)	
		28	Sirmaur, India	56004 (PUN)	Rani et al. (2013)	
	P. yunnanensis (Franch.) Wunderlin	28	Yunnan, China	GuSR097 (IBSC)	This study	
Piliostigma	*P. malabaricum* (Roxb.) Benth.	28	-	-	Sharma & Raju (1968)	
		28	-	-	Kumari & Bir (1989)	
	P. thonningii (Schumach.) Milne-Redh.	26	-	-	Yeh et al. (1986)	

* indicates the chromosome numbers should be interpreted with caution because they are different from other studies or from the usual perception.

similar pattern is consistent with the other reported Cercidoideae species.

Heterochromatin and euchromatin segments are clearly seen at mitotic prophase in all samples. The heterochromatin segments are located in the proximal regions that are deeply stained, indicating early condensation, while the euchromatin segments in the distal regions of chromosomes are lightly stained and extended, indicating late condensation (Fig. 1, B–C). According to Tanaka (1971, 1977), the prophase chromosomes of all species in this study are of the proximal type.

The prochromosomes in the pro-metaphase are curly and gradually arranged on the equator of the spindle with indistinct edges (Fig. 1, D). Paired sister chromatids are clearly visible during late metaphase stage (Fig. 1, E). Successful separation of daughter chromosomes is visible in late anaphase stage, moving from the equatorial plate to the poles of the spindle, but new nuclear membranes have not yet formed (Fig. 1, F).

There was little difference in size between the chromosomes in each species of *Cheniella* and *Phanera* (Fig. 1, G–T). Chromosomes in all species of *Cheniella* were rod-shaped or oblong in mitotic metaphase nuclei, whereas they were round or punctate in *Phanera yunnanensis* (Franch.) Wunderlin. The cell size and mitotic metaphase nuclei chromosome size of *P. yunnanensis* were smaller in comparison with *Cheniella*. Chromosomes in species of both *Cheniella* and *Phanera* are so small at mitotic metaphase nuclei that karyotypes cannot be clearly distinguished, but the number can be clearly counted. All studied *Cheniella* species have the same chromosome number $2n$=26 (Fig. 2, G–R), while the chromosome number of *P. yunnanensis* is $2n$=28 (Fig. 2, S–T). These results demonstrate the differences between *Cheniella* and *P. yunnanensis* in cytological characters. The chromosome count of *Cheniella* species is here determined to be $2n$=26, suggesting that the previous reported chromosome number of $2n$=28 (Singhal et al., 1980a; Sharma & Raju, 1968) might be erroneous. Consistency in chromosome numbers between different species within the genus indicates that speciation within *Cheniella* is not driven by polyploidy or chromosomal number variation.

The seeds of the artificial hybrid *Cheniella tianlinensis* × *ovatifolia* were harvested from the field, hand-pollinated and bagged, the mature legumes were collected for cytological analysis, revealing a chromosome number of $2n$=26 (Fig. 2, R). The maternal parent of the hybrid was *Cheniella tianlinensis* (T.C.Chen & D.X.Zhang) S.R.Gu, T.Y.Tu & D.X.Zhang and the paternal parent was *Cheniella ovatifolia* (T.C.Chen) R.Clark & Mackinder. Although chromosome counts for *C. tianlinensis* were not obtained, the chromosome number of *C. ovatifolia* was $2n$=26. Given the successful production of hybrid seeds with $2n$=26, it is reasonable to infer that *C. tianlinensis* also has a chromosome number of $2n$=26. These findings support the inclusion of *C. tianlinensis* within *Cheniella*, and are consistent with Gu et al. (2024).

Taxonomy of Cheniella *and* Phanera

Based on derived floral characters, palynology and previous molecular evidence, Clark et al. (2017) established the genus *Cheniella* to include 10 species and three subspecies. This was supported by the prior study of Hao et al. (2003) which presented a phylogenetic analysis of the nuclear ITS region, recovering a clade of five species later reassigned to *Cheniella*. However, in a phylogenetic study by Sinou et al. (2020) which sequenced *Legcyc1*, *Legcyc2*, *matK* and *trnL-F* for 17 liana species from Asia, a polytomy resulted, including *Cheniella* and *Phanera*. *Cheniella* appeared non-monophyletic, with sampled species dispersed in two clades, raising questions about the validity of the genus.

In contrast, Gu et al. (2024) analysed the concatenated sequences of 77 CDS, 103 IGS, 19 introns, and 4 rRNA genes, recovering two distinct clades for *Cheniella* and *Phanera*, and presenting a sister relationship between them. Unlike Sinou et al. (2020), *P. yunnanensis* grouped with other *Phanera* species rather than *Cheniella corymbosa*. Moreover, *P. yunnanensis* differs morphologically from *Cheniella* in characters that are informative at the generic level, having a raceme or simple cyme of two flowers, staminodes not joined at the base on a fleshy disc (Fig. 1, O–P), and a coriaceous legume that dehisces along both sutures.

In the treatment of Clark et al. (2017), *P. tianlinensis* was not included in *Cheniella* due to its pubescent legumes and rarity in herbaria. Gu et al. (2024) found that the fruit traits and flower structures of *P. tianlinensis* align with *Cheniella*. Additionally, *P. tianlinensis* also cluster with the *Cheniella* clade phylogenetically. Intergrating evidence of the morphological and molecular studies, Gu et al. (2024) concluded that *Cheniella* is a natural group that includes *P. tianlinensis*.

In the present study, all *Cheniella* species exhibited rod-shaped or oblong chromosomes in mitotic metaphase nuclei, unlike *Phanera yunnanensis*, which displayed round or punctate chromosomes. Additionally, cell size and mitotic metaphase chromosome size in *P. yunnanensis* were smaller in comparison with *Cheniella*. All examined *Cheniella* species possessed a chromosome number of $2n$=26, whereas *P. yunnanensis* had a chromosome number of $2n$=28, which consistent with numbers reported from other studies of *Phanera* (Sharma & Raju, 1968; Peng et

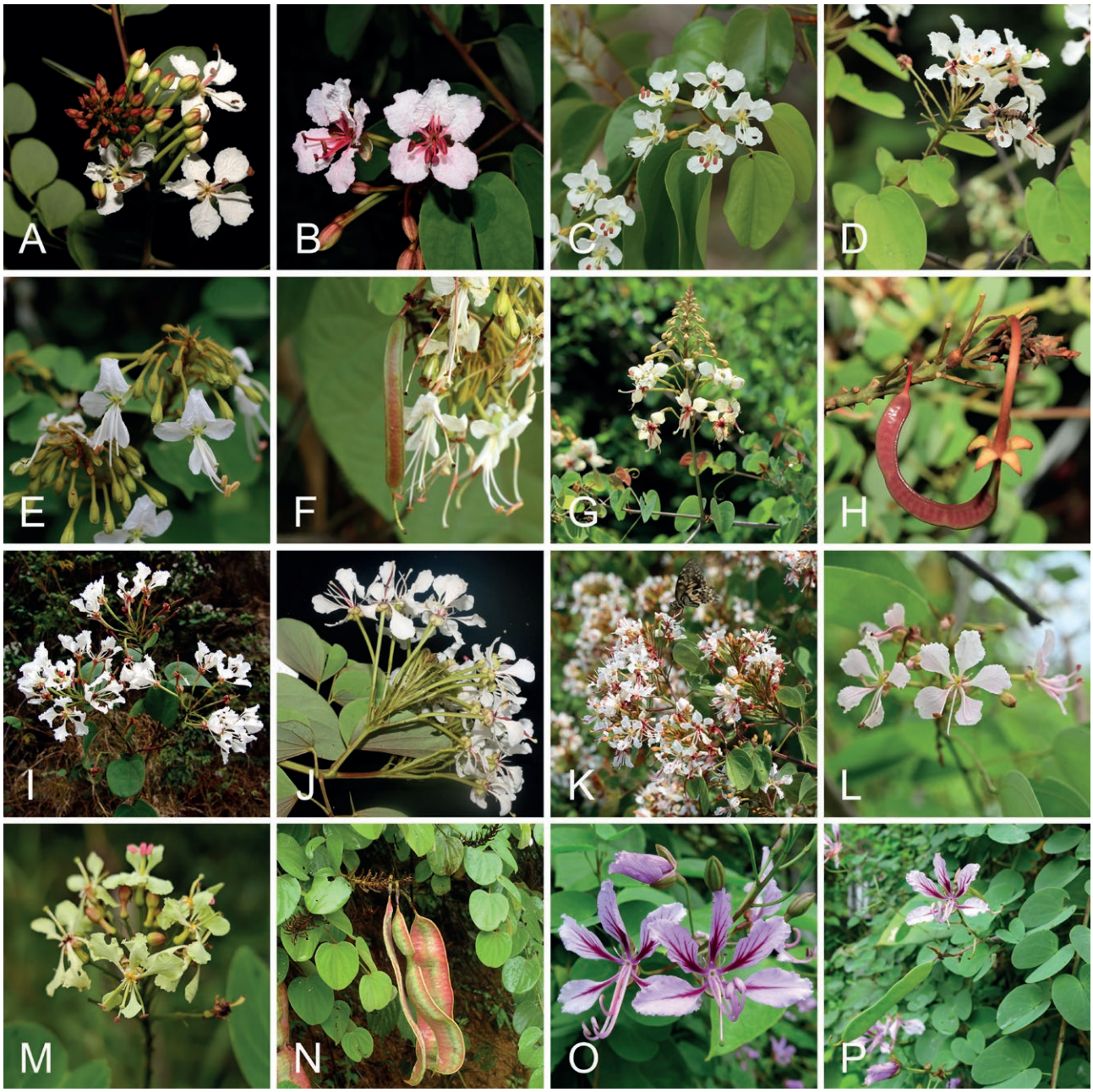

Figure 1. Morphological diversity in *Cheniella* and comparison with *Phanera*. A: *Cheniella didyma*; B: *C. corymbosa*; C: *C. quinnanensis* subsp. *villosa*; D: *C. quinnanensis* subsp. *quinnanensis*; E–F: *C. longistaminea*; G–H: *C. longipes*; I: *C. ovatifolia*; J: *C. tenuiflora*; K: *C. paraglauca* sp. nov. nom. ined.; L: *C. hupehana* comb. nov. ined.; M: *C. touranensis*; N: *C. clemensiorum*; O–P: *Phanera yunnanensis*. Photos: A, G–H & O–P, Qiu-Biao Zeng; B–F & I, Tie-Yao Tu; J & K, Shi-Ran Gu; L, Yi-Chen Zhang; M, Kai-Wen Jiang; N, Bo Li.

al., 1986; Singhal et al., 1990; Lu et al., 2024). *Cheniella tianlinensis* has a chromosome number of 2*n*=26, as it can hybridize with *C. ovatifolia* (2*n*=26), producing offspring with chromosome number of 2*n*=26. These findings highlight the differences between *Cheniella* and *Phanera*, and confirm that *C. tianlinensis* belongs to *Cheniella*.

Chromosome number evolution within Cercidoideae

The subfamily Cercidoideae of Leguminosae contains 14 genera and a diverse array of species, many of which exhibit significant intraspecific or interspecific variability in chromosome numbers, 2*n*=14, 24, 26, 28

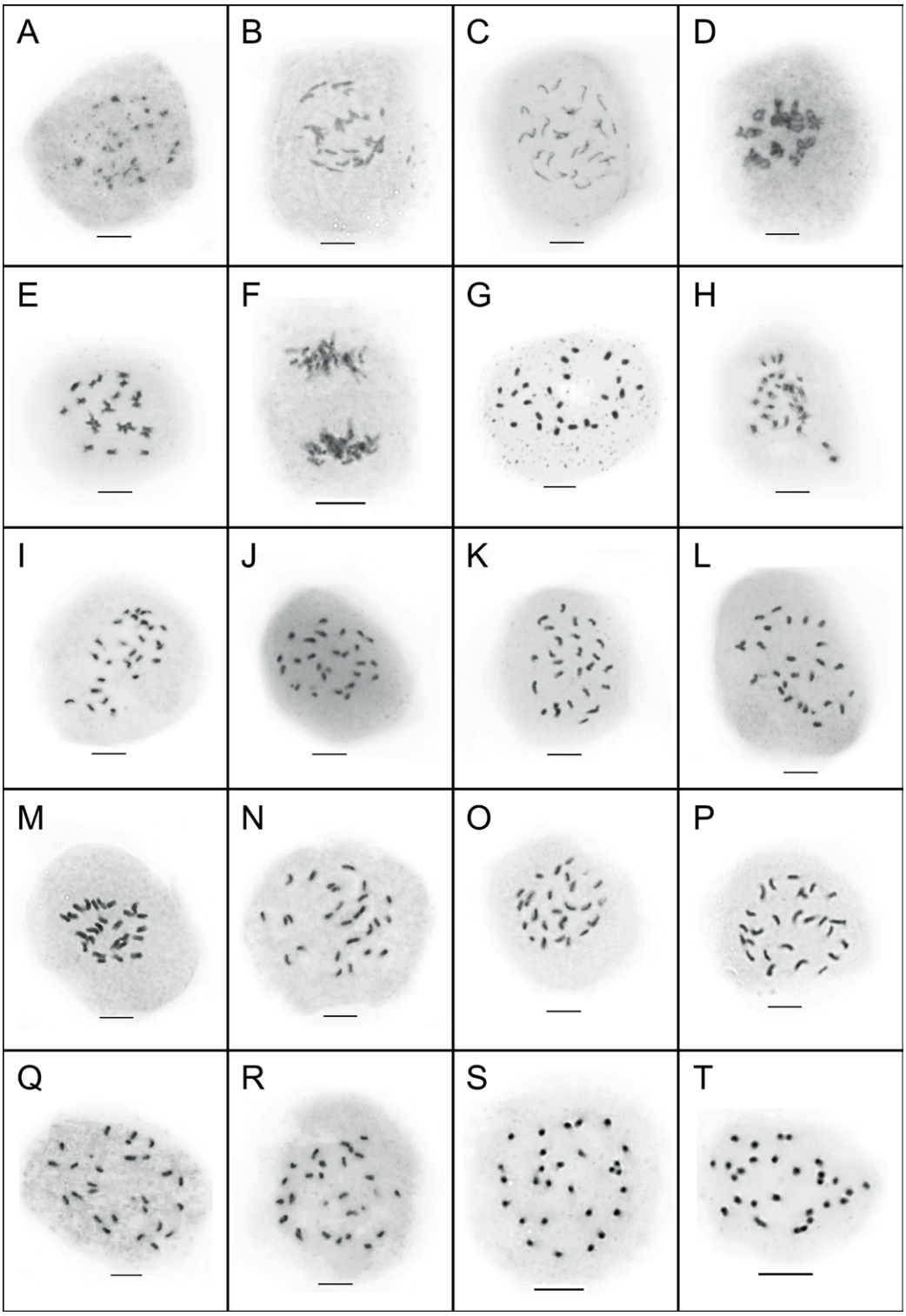

Figure 2. Comparative cytological features between *Cheniella* and *Phanera*. Scale bars=2 μm. A: Mitotic interphase of *Cheniella didyma*. B: Early prophase of *C. ovatifolia*. C: Late prophase of *C. corymbosa*. D: Pro-metaphase of *C. quinnanensis* subsp. *villosa*. E: Late metaphase of *C. longistaminea*. F: Mitotic anaphase of *Phanera yunnanensis*. G–T: Mitotic metaphases, G: *C. longipes*, 2*n*=26; H: *C. touranensis*, 2*n*=26; I: *C. hupehana* comb. nov. ined., 2*n*=26; J: *C. clemensiorum*, 2*n*=26; K: *C. longistaminea*, 2*n*=26; L: *C. corymbosa*, 2*n*=26; M: *C. paraglauca* nom. ined., 2*n*=26; N: *C. quinnanensis* subsp. *villosa*, 2*n*=26; O: *C. ovatifolia*, 2*n*=26; P: *C. quinnanensis*, 2*n*=26; Q: *C. tenuiflora*, 2*n*=26; R: *Cheniella tianlinensis* × *ovatifolia*, 2*n*=26; S–T: *P. yunnanensis*, 2*n*=28.

(42, 56) (Doyle, 2012; Steven et al., 2015; Roberts & Werner, 2016; LPWG, 2017). The earliest diverging lineage within Cercidoideae, *Cercis*, has a somatic chromosome number of 2*n*=14, whilst most other lineages in this subfamily share the chromosome number 2*n*=28, including *Adenolobus*, *Griffonia*, *Phanera*, *Piliostigma*, and most species of *Bauhinia* (Table1). Our study has confirmed that *Cheniella* possesses a somatic chromosome number of 2*n*=26, which is the same as several species of *Barklya*, *Bauhinia*, *Gigasiphon*, *Lysiphyllum*, and *Piliostigma* (Table1). Exceptions to the predominant chromosome numbers have been observed occasionally in *B. monandra* (2*n*=24 and 2*n*=42) and *B. rufescens* (2*n*=56) (Darlington & Wylie, 1955; Sharma & Raju, 1968; Gill & Husaini, 1982).

Given the basal-most phylogenetic position of *Cercis* within Cercidoideae (Hao et al., 2003; LPWG, 2017; Gu et al., 2019; Sinou et al., 2020; Gu et al., 2024), it is reasonable to infer that the ancestral state of chromosome number for this subfamily was likely a diploid with 2*n*=14. *Cercis* retains the characteristics of the diploid ancestors, whereas the ancestor of the sister clade of Cercis, which comprises all the remaining genera experienced a whole genome duplication event, resulting in the chromosome number of 2*n*=28, with probably a few undergoing further duplications to achieve higher chromosome numbers. This was followed by at least three independent aneuploidy chromosomal variation events, reducing the chromosome numbers to 2*n*=26. Reported chromosome counts of 2*n*=24, 2*n*=42 and 2*n*=56 in certain genera or species should be interpreted with caution. Understanding chromosomal evolution within this group is crucial for elucidating the broader evolutionary patterns that shape its biodiversity.

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