Chromosome Studies in Gomidesia, Marlierea, Myrceugenia and Myrcia (Myrtaceae, Subtribe Myrciinae)

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Chromosome studies in *Gomidesia*, *Marlierea*, *Myrceugenia* and *Myrcia* (*Myrtaceae*, subtribe *Myrciinae*)

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Summary. In this paper we describe the chromosome numbers of several species of *Myrtaceae* (subtribe *Myrciinae*) from south-eastern Brazil, in order to help determine the circumscription and limits of this group. The chromosomal counts of 20 species were obtained, 17 of which are new. The number 2n = 22 occurs in almost all of species and genera analysed except for the polyploid species *Gomidesia gaudichaudiana* and two species of *Myrcia*, with 2n = 44. With these results, our knowledge of the chromosome number in the subtribe *Myrciinae* increased from 12 (2.2%) to 29 species (5.4%). The occurrence of 2n = 22 in species of the four genera analysed did not help resolve taxonomic questions relating to the distinction between *Myrcia*, *Marlierea* and *Gomidesia*. Although less frequent in *Myrciinae*, polyploidy appears to have had an important role in the evolution of this family, with high frequency in *Eugeniinae* (22.5% of *Eugenia* species) and *Myrtinae* (50% of the species, 75% in *Psidium*).

Key words. Chromosome number, *Myrtaceae*, *Myrtoideae*, polyploidy.

Introduction

The family *Myrtaceae* is widespread in tropical, subtropical and temperate regions of Australia (Cronquist 1981), with 133 genera and > 3800 species (Wilson *et al.* 2001). According to Niedenzu (1893), this family is divided into two large subfamilies, *Myrtoideae* (with bacoid fruits and opposite leaves) and *Leptospermoideae* (capsular fruits and alternate leaves). Schmid (1980) reinstated another subfamily, *Chamelaucioideae* (with indehiscent capsular fruits). All neotropical *Myrtaceae* are placed in the subfamily *Myrtoideae*, except the genus *Tepualia* (*Leptospermoideae*) (Landrum & Kawasaki 1997). The species of *Myrtoideae* form a single tribe, *Myrteae* (McVaugh 1968). Berg (1855 – 56, 1857 – 59) divided *Myrteae* into three subtribes: *Eugeniinae* (globose embryos with a short distint radicle), *Myrciinae* (embryos with foliar cotyledons and a long radicle) and *Myrtinae* (originally named *Pimentiinae*, reduced cotyledons and a long radicle) (Landrum & Kawasaki 1997).

The subtribe *Myrciinae* is exclusively neotropical whereas *Myrtinae* and *Eugeniinae* are paleotropical and reach the Mediterranean (Landrum 1981). In a recent analysis based on *ITS* and *psbA-trnH* sequence data, Lucas *et al.* (2005) found *Myrciinae* to be monophyletic, whereas the *Eugeniinae* and *Myrtinae* are paraphyletic.

The *Myrciinae* generally have pentamerous flowers (tetramerous in *Myrceugenia*) that are isolated or variously arranged in collateral pairs, racemes, thyrses, thyrsoids or terminal or subterminal panicles. The floral bud opens by detachment of the calyptre (*Calyptranthes*) or by irregular tearing of the calyx lobes (*Marlierea*). It can also be opened with calyx lobes that are distinct before anthesis (*Myrcia*, *Gomidesia* and *Myrceugenia*). The seed coat is membranous or chartaceous and the embryo has two separated and generally foliar cotyledons, with a long radicle (Landrum & Kawasaki 1997).

Taxonomic background of *Myrciinae*

The circumscription of *Myrciinae* has undergone numerous modifications. De Candolle (1828 in McVaugh 1968) recognised only two genera of *Myrciinae*, *Calyptranthes* and *Myrcia*. Berg (1857 – 59), in his treatment of Brazilian *Myrtaceae*, accepted the genera previously described but added eight new genera (*Aulomyrcia*, *Calyptromyrcia*, *Cerquierea*, *Eugeniopsis*, *Gomidesia*, *Marlierea*, *Myrceugenia* and *Rubachia*). Most of these genera have since been synonymised (Table 1). McVaugh (1968) grouped the entire family into six informal groups and recognised six of the genera described by Berg (1855 – 56, 1857

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– 59) as "*Myrcioid genera*", in addition to accepting the genus *Nothomyrcia* Kausel (today *Myrceugenia*). Briggs & Johnson (1979) added the genus *Mitranthes* to the "*Myrcia* alliance". In a recent synopsis of Brazilian species, Landrum & Kawasaki (1997) recognised three genera of *Myrtaceae*: *Calyptranthes*, *Myrceugenia* and *Myrcia*, with the latter including *Marlierea* and *Gomidesia* (Table 1).

Myrceugenia O. Berg has tetramerous flowers with an open calyx and ovary with 2 – 4 locules and 2 – 20 ovules per locule. This genus presents a myrcioid embryo and floral characters inherent to the *Eugeniinae* (McVaugh 1968). According to Landrum (1981), *Myrceugenia* is sometimes considered the most primitive genus in *Myrciinae* with an undefined phylogenetic position (Landrum 1981; Lucas *et al.* 2005).

Myrcia DC. ex Guill. *sensu* Landrum & Kawasaki (1997) is the largest genus of the subtribe *Myrciinae*. These species have paniculate inflorescences and pentamerous flowers. According to Landrum & Kawasaki (1997), the distinction among the genera *Marlierea*, *Gomidesia* and *Myrcia* is complex, because their circumscription is based entirely on certain floral characters, such as the coalition of the hypanthium and anther dehiscence. According to Berg (1855 – 56, 1857 – 59) and McVaugh (1968), *Marlierea* has closed floral buds with anthesis occurring by a longitudinal tearing of the calyx, while *Gomidesia* has a pentamerous calyx and tetralocular anthers, with pollen sacs showing different degrees of development and a sigmoid dehiscence. McVaugh (1968) accepted the separation between *Marlierea*, *Gomidesia* and *Myrcia*, but considered the distinction between *Myrcia* and *Marlierea* to be arbitrary, based on hyphanthium development and floral bud rupture. Anthers of *Gomidesia* show sigmoid dehiscence, which is the only consistent distinction between *Gomidesia* and *Myrcia* (which has a rimose dehiscence). The phylogenetic relationships between *Marlierea* and *Myrcia* are still unclear whereas *Gomidesia* may be monophyletic (Lucas *et al.* 2005).

Chromosome studies

In general, *Myrtaceae* show little variation in chromosome number, with n = 11 occuring in most genera across different subfamilies or tribes (Rye 1979). Most chromosome studies have been carried out on Australian species (subfamilies *Leptospermoideae* and *Chamelaucioideae*). Atchinson (1947) studied 47 introduced species cultivated in California (mainly *Eucalyptus* species), while Rye (1979) analysed 150 species in western Australia. Although chromosome data have been reported for only a few species of *Myrtoideae*, polyploidy apparently is an important evolutionary process, since species and cytotypes with multiples of x = 11 have been identified (Atchinson 1947; Costa 2004; Rye 1979). Costa & Forni-Martins (2006a) suggested that the difficulty in identifying Brazilian *Myrtaceae* is due to hybridisation and polyploidy during speciation, since intermediate characters occur between related taxa.

Chromosome numbers are known for only 12 species of *Myrciinae* in three genera (*Myrcia*, *Myrceugenia* and *Luma*). The genus *Luma* has no defined limits and was considered primitive by Landrum (1981) because of its embryo characters that show similarities to both *Eugeniinae* and *Myrciinae*. Forni-Martins & Martins (2000) reported the gametic chromosome number (*n*) of two *Myrciinae* species, *Myrcia bella* and *M. lingua* to be n = 11 and presented the first records for *Myrcia*. Landrum (1981), in a revision of neotropical

Table 1. Circumscription of the subtribe *Myrciinae*. Genera currently considered synonyms are listed in parentheses.

De Candolle (1828)	Berg (1857) "*Myrcioideae* subtribe"	McVaugh (1968) "Myrcioid genera"	Briggs & Johnson (1979) "*Myrcia alliance*"	Landrum & Kawasaki (1997) (Brazilian genera)
	Aulomyrcia O. Berg (*Myrcia*)			
Calyptranthes Sw.	*Calyptranthes*	*Calyptranthes*	*Calyptranthes*	*Calyptranthes*
	Calyptromyrcia O. Berg (*Myrcia*)			
	Cerquierea O. Berg (*Gomidesia*)		*Mitranthes* O. Berg	
	Eugeniopsis O. Berg (*Marlierea*)			
	Gomidesia O. Berg	*Gomidesia*	*Gomidesia*	*Myrcia*
	Marlierea Cambess.	*Marlierea*	*Marlierea*	*Myrcia*
	Myrceugenia O. Berg	*Myrceugenia*	*Myrceugenia*	*Myrceugenia*
Myrcia DC.	*Myrcia*	*Myrcia*	*Myrcia*	*Myrcia*
	Rubachia O. Berg (*Marlierea*)	*Nothomyrcia* Kausel (*Myrceugenia*)	*Nothomyrcia* (*Myrceugenia*)	

Table 2. Species analysed and details of voucher specimens.

Genera/Species – State, Municipality, Habitat (*Collector* & no.)
Gomidesia
G. gaudichaudiana (DC.) O. Berg — MG, Conceição do Mato Dentro, "*campo rupestre*"(*I. R. Costa* 448)
G. eriocalyx O. Berg — MG, Conceição do Mato Dentro, "*campo rupestre*" (*C. F. Verola* 46)
G. spectabilis (DC.) O. Berg — SP, Sete Barras, Tropical Rain Forest (*I. R. Costa* 520)
Gomidesia sp. — SP, Atibaia, Rocky outcrop (*I. R. Costa* 481)
Marlierea
M. clausseniana (O. Berg) Kiaersk. — MG, Conceição do Mato Dentro, "*campo rupestre*" (*I. R. Costa* 451)
M. tomentosa Cambess. — SP, Ubatuba, Tropical Rain Forest (*K. Matsumuto* 800)
M. warmingiana Kiaersk. — SP, Ubatuba, Tropical Rain Forest (*K. Matsumoto* 836)
Myrceugenia
M. myrcioides (Cambess.) O. Berg — MG, Camanducaia, Cloud Forest (*I. R. Costa* 474)
M. ovata Landrum — MG, Camanducaia, Cloud Forest (*I. R. Costa* 475)
Myrcia
M. bella Cambess. — SP, Itirapina, Cerrado *sensu stricto* (*I. R. Costa* 423)
M. fallax (DC.) O. Berg — SP, Atibaia, Rocky outcrop (*I. R. Costa* 460)
M. formosiana DC. — SP, Cananéia, Tropical Rain Forest (*C. Urbanetz* 171)
M. laruotteana Cambess. — SP, Itirapina, Cerrado *sensu stricto* (*I. R. Costa* 466)
M. lingua DC. — SP, Itirapina, Cerrado *sensu stricto* (*I. R. Costa* 430)
M. multiflora (Lam.) DC. — SP, Atibaia, Rocky outcrop (*I. R. Costa* 479)
M. rostrata DC. — SP, Mogi Guaçu, Cerrado *sensu stricto* (*I. R. Costa* 482)
Myrcia sp. 1 — MG, Conceição do Mato Dentro, "*campo rupestre*" (*C. F. Verola* 33)
Myrcia sp. 2 — SP, Ubatuba, Tropical Rain Forest (*K. Matsumoto* 833)
Myrcia sp. 3 — RJ, Rezende, Tropical Rain Forest (*L. Freitas* 897)
Myrcia sp. 4 — MG, Ouro Preto, Gallery Forest (*K. Matsumoto* 776)

Myrceugenia, determined the chromosome number of six Brazilian species (*M. bracteosa*, *M. brevipedicellata*, *M. euosma*, *M. miersiana*, *M. ovata* var. *gracilis* and *M. pilotantha* var. *major*) and one Chilean species (*M. exsucca*), all of which had 2n = 22. Apart from these only two other species, *M. fernandeziana* and *M. schultzei*, both Chilean with n = 11, have been recorded (Sanders *et al.* 1983). For *Luma apiculata*, Landrum (1981) found 2n = 22 and n = 10 was reported by Tschishow (1956 in Landrum 1986). Until now, chromosome data has not been available for *Calyptranthes*, *Marlierea* and *Gomidesia*.

McVaugh (1956) considered the American *Myrtaceae* a complex group in need of extensive systematic studies. Barroso (1991) also highlighted the need to combine biosystematic studies with regional surveys in order to define the taxa.

The aim of this work is to determine chromosome numbers in species of *Myrciinae* as part of an investigation to establish the taxonomic relationships among these taxa.

Material and Methods

Twenty species of *Myrciinae* (*Myrtaceae*) were collected in different habitats, including cerrado *sensu stricto*, "campos rupestres" and forests (tropical rainforest, semideciduous forest and gallery forest) in southeastern Brazil (Table 2). Species and populations were chosen based on the availability of suitable material (floral buds and mature fruits with seeds). Species were identified by comparison with specimens in herbaria and literature reports and confirmed by specialists (Marcos Sobral – UFMG and Eve Lucas MSc. – RBG Kew). The generic division of Berg (1855 – 1856, 1857 – 1859) and McVaugh (1968), who considered the genera *Marlierea* and *Gomidesia* to be valid, was followed. Voucher specimens were deposited in the Herbarium at the Universidade Estadual de Campinas (UEC) (Table 2).

For meiotic studies, floral buds were fixed in Farmer solution (ethanol:acetic acid, 3:1, v/v) for 24 h and stored in 70% alcohol at -20°C. The cytological preparations were obtained by squashing the anthers in acetocarmine 1.2% (Medina & Conagin 1964).

To obtain mitotic metaphases, seeds were germinated at a temperature of 28° – 30°C. The radicular meristems were pre-treated with 2 mM 8-hydroxiquinoline for 24 h, at 8°C. The roots were fixed in Farmer solution, stored in 70% alcohol, and stored at -20°C until slide preparations were made, stained with Giemsa (Guerra 1983).

Slides were examined using light microscopy and well-spread metaphase cells were photographed.

Results

Chromosome numbers of 20 species of *Myrciinae* are presented (Table 3, Fig. 1). In *Gomidesia*, three of the four species analysed were diploid with 2n = 22, one species, *G. gaudichaudiana*, was polyploid, with 2n = 44 (Table 3). In *Marlierea*, three species were diploid, i. e. 2n = 22 (Table 2, Fig. 1B, C, D). In *Myrceugenia*, both *M. ovata* and *M. myrcioides* had 2n = 22 (Table 3). In *Myrcia* nine species were diploid with 2n = 22 and two were polyploid with 2n = 44 (Table 3, Fig. 1J). In only two species, *M. bella* and *M. fallax*, was it possible to confirm both the gametic (n = 11) and somatic (2n = 22) chromosome numbers (Table 3).

Discussion

According to Landrum & Kawasaki (1997), who included *Gomidesia* and *Marlierea* in *Myrcia*, the *Myrciinae* in Brazil consists of about 540 species. Chromosome numbers were previously known for only 12 (2.2%) of these. This investigation has increased this percentage to c. 5.4% (29 species), and included *Gomidesia* and *Marlierea* for the first time (Table 3).

A constant number of 2n = 22 was observed in all species and genera analysed, except for the polyploids, which had multiples of x = 11. These results confirm the base chromosome number of x =

Table 3. Gametic (*n*) and somatic (*2n*) chromosome numbers for *Myrtaceae* species (subtribe *Myrciinae*). * and ** signify first count for the species and genus, respectively.

Genus/Species	*n*	*2n*	References
Gomidesia			
G. eriocalyx (DC.) O. Berg	–	22**	This work
G. gaudichaudiana O. Berg	–	44**	This work
G. spectabilis O. Berg	11**	-	This work
Gomidesia sp.	–	22**	This work
Luma			
Luma apiculata (DC.) Burret		22	Landrum 1981
Marlierea			
M. clausseniana (Berg) Kiaersk.	11**	–	This work
M. tomentosa Cambess.**	–	22**	This work
M. warmingiana Kiaersk.**	–	22**	This work
Myrceugenia			
M. bracteosa (DC.) Legrand & Kausel	–	22	Landrum 1981
M. brevipedicellata (Burret) Legrand & Kausel	11	–	Landrum 1981
M. euosma (O. Berg) Legrand	–	22	Landrum 1981
M. exsucca (DC.) O. Berg	–	22	Landrum 1981
M. fernandeziana (Hook. & Arn.) Johow	11	–	Sanders *et al.* 1983
M. miersiana (Gardner) Legrand & Kausel	–	22	Landrum 1981
M. myrcioides (Cambess.) O. Berg	–	22*	This work
M. ovata var. *gracilis* (Burret) Landrum	11	22	Landrum 1981
	11	–	This work
M. pilotantha var. *major* (Legrand) Landrum	11	–	Landrum 1981
M. schultzei Johow	11	–	Sanders *et al.* 1983
Myrcia			
M. bella Cambess.	11	22	This work
	11	–	Forni-Martins & Martins 2000
M. fallax (DC.) O. Berg	11*	–	This work
M. formosiana DC.	–	22*	This work
M. laruotteana Cambess.	–	22*	This work
M. lingua DC.	11	22	This work
	11	–	Forni-Martins & Martins 2000
M. rostrata DC.	11*	–	This work
M. multiflora (Lam.) DC.		22*	This work
Myrcia sp. 1	–	22*	This work
Myrcia sp. 2	–	44*	This work
Myrcia sp. 3	–	44*	This work
Myrcia sp. 4	–	22*	This work

11 for *Myrtaceae* (Atchinson 1947; Raven 1975), even though these authors had based their conclusions principally on subfamilies *Leptospermoideae* and *Chamelaucioideae* since only a few species of *Myrtoideae* had previously been studied.

The basic chromosome number in *Myrtaceae* differs from that of most families in the order *Myrtales* (*sensu* APG 2003). According to Costa (2004), families that are phylogenetically closer to *Myrtaceae* such as *Vochysiaceae* and *Heteropixidaceae*, have similar chromosome numbers, with species groups of 2n = 22 and 2n = 24, whereas more distantly-related families (e.g. *Melastomataceae*, *Lythraceae* and *Combretaceae*) possess different basic chromosome numbers such as x = 8, 9, 10, 12, 13 and 14 (Costa 2004).

For *Myrceugenia*, records are available for six Brazilian and three Chilean species (Landrum 1981; Sanders *et al.* 1983), all of which are diploid with 2n = 22 (Table 3). For *M. ovata* 2n = 22 was reported by Landrum (1981) for the *gracilis* variety (also used here), while the record of 2n = 22 in *M. myrcioides* is new. So far, there are no reports of polyploid species in this genus.

In *Marlierea* (three species) and *Gomidesia* (three species), all species were diploid with 2n = 22 (Table 3, Fig. 1), except for *Gomidesia gaudichaudiana* (2n = 44), a species whose distribution is restricted to the Cadeia do Espinhaço, Minas Gerais.

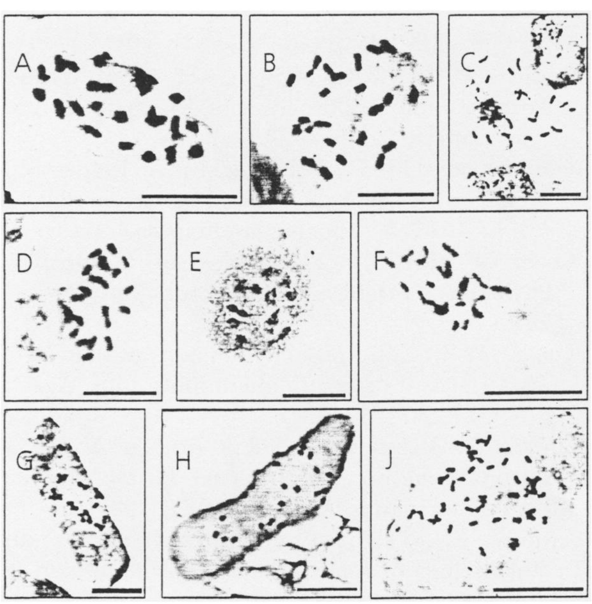

Fig. 1. Chromosomes in species of *Myrciinae*. **A** *Gomidesia* sp. (2n = 22); **B** *Marlierea clausseniana* (2n = 22); **C** *Marlierea warmingiana* (2n = 22); **D** *Marlierea tomentosa* (2n = 22); **E** *Myrcia bella* (n = 11); **F** *Myrcia formosiana* (2n = 22); **G** *Myrcia* sp. 4 (2n = 22); **H** *Myrcia* sp. 1 (2n = 22); **J** *Myrcia* sp. 2 (2n = 44). Scalebars: 5 μm.

In *Myrcia*, the gametic number of n = 11 for *M. bella* and *M. lingua* was previously reported by Forni-Martins & Martins (2000) and confirmed here for mitotic cells with 2n = 22 (Table 3). The same chromosome number (2n = 22) was found in nine other species studied, except for two unindentified polyploid species with 2n = 44 (Table 3).

The occurrence of polyploid species in the *Myrciinae* supports the suggestion of Rye (1979) that polyploidy is frequent in *Myrtoideae*, as also emphasised by Costa & Forni-Martins (2006a). Polyploidy may have played an important role in evolution of *Myrtoideae* (Atchinson 1947; Andrade & Forni-Martins 1998; Costa & Forni-Martins 2006a; Rye 1979). According to Costa & Forni-Martins (submitted a), the frequency of polyploid species in the other subtribes is even higher. In *Eugeniinae*, c. 22.5% of species of *Eugenia* studied are polyploid, whereas in *Myrtinae*, c. 50% of species studied are polyploids. In *Psidium* 75% of the species studied are polyploids (Costa & Forni-Martins 2006b).

The constant chromosome number and the small size of the chromosomes (Atchinson 1947; Costa 2004; Forni-Martins & Martins 2000; Rye 1979; Vijayakumar & Subramanian 1985), limits the usefulness of chromosome numbers as taxonomic characters in the subfamily *Myrtoideae*. The occurrence of 2n = 22 in all species of four genera analysed does not allow a clear taxonomic distinction among genera *Myrcia*, *Marlierea* and *Gomidesia*, as previously suggested by several authors (Legrand 1958, 1962; McVaugh 1968; Barroso 1991), nor does it support the unification of these genera (Landrum & Kawasaki 1997). The occurrence of polyploid species in genera of *Myrciinae* such as *Myrcia* and *Gomidesia*, is of little taxonomic significance at the generic level. This conclusion differs from that of Landrum (1981), who stated that genera might be differentiated by their degree of ploidy.

In *Leptospermoideae*, variation in chromosome number has been reported in *Actinidium* (n = 6), *Beaufortia* (n = 8, 10), *Darwinia* (n = 6, 7, 9, 12, 14), *Verticordia* (n = 6, 7, 8, 9, 11, 12, 16, 22) and *Thryptomene* (n = 9, 10, 11 and 22), and has been considered a useful taxonomic character in these genera (Rye 1979). Although less frequent in *Leptospermoideae*, intrageneric polyploidy was observed by Rye (1979) in *Calytrix* (2n = 22, 44), *Chamelaucium* (2n = 22, 44, 66), *Darwinia* (2n = 10, 12, 14, 18, 22, 24, 28, 36, 42) and *Verticordia* (2n = 12, 14, 16, 18, 22, 24, 32, 44). Brighton & Ferguson (1976) also found polyploid species in *Melaleuca*, with a diploid number of 2n = 22, 33, 44 and 66. In *Leptospermoideae*, numerical variation is mainly due to disploidy (Atchinson 1947; Rye 1979).

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