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ORIGINAL ARTICLE

Dysploidy and polyploidy trigger strong variation of chromosome numbers in the prayer-plant family (Marantaceae)

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Abstract

Karyotype analyses in species of the family Marantaceae (550 species, 31 genera) were conducted to shed light on the reported strong variation of chromosome number and size and the occurrence of polyploidy. Special attention was paid to the alterations in basic chromosome numbers, karyotypes and ploidy levels. Taxon sampling covered the whole distribution area of Marantaceae in Africa, Asia and America. We applied mitotic chromosome counting using conventional rapid squash techniques in 43 accessions (39 species, 16 genera), evaluated literature records for 51 species and conducted karyotype analyses. Eleven different somatic chromosome numbers were found ($2n = 20$, 22, 24, 26, 28, 33, 44, 36, 52, 65, 72). Based on the presumed basic chromosome numbers of $x = 9$, 10, 11, 12, 13, 14, this may correspond to diploid, triploid, tetraploid, pentaploid and octoploid levels, respectively. Dysploid variation, polyploidy and, to a lesser extend, hybridization may be the main factors in chromosome number evolution of the family. Our results also point to a certain degree of association with species diversification and geographical patterns.

Keywords Chromosome evolution · Dysploidy · Hybridization · Karyotype variability · Marantaceae · Polyploidy

Introduction

Changes in chromosome number and structure are important processes that often reflect speciation events as they can establish crossing barriers between populations (e.g. Lowry and Willis 2010; Ouyang and Zhang 2013; Winterfeld et al. 2014, 2016; Baack et al. 2015; Wölk et al. 2015). Chromosome variations such as polyploidy, hybridization or dysploid change may provide the cytological basis for ecological differentiation, adaptation and isolation. The phylogenetic effects in chromosome variations, their ecological significance and their impact on speciation and diversification are the subject of many studies in major angiosperm families (e.g. Knight et al. 2005; Peruzzi et al. 2012; Grabowska-Joachimiak et al. 2015; Carta et al. 2018 and references therein).

An outstanding system to study the role of chromosomal changes in species diversification is the pantropically distributed monocot family Marantaceae which, on the one hand, exhibits a geographically uneven distribution of high species diversity and, on the other hand, provides a remarkable variation in morphological traits and chromosome number. Marantaceae is the second largest family of Zingiberales (Kennedy 1978a, b, 2000; Dhetchuvi 1996; Andersson 1998; Suksathan and Borchsenius 2005; Jongkind 2008; Ley and Claßen-Bockhoff 2011) and comprises approximately 550 species in 31 genera (Stevens 2001 onwards, Prince and Kress 2006; Al-Gharaibeh 2017). The plants are perennial herbs and lianas from the understorey and gaps of tropical lowland rainforest and are distributed throughout tropical and warm temperate parts of the world (Andersson 1998). Their diversity centre is in the New World, where they are represented by ca. 450 species in 13 genera. Ca. 50 species in 11 genera are found in Africa including Madagascar and ca. 50 species in 6 genera in Asia (Prince and Kress 2006; Al-Gharaibeh 2017).

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Available chromosome counts reveal a strong variation of chromosome number in Marantaceae. Some chromosome numbers were recurrently found, but in general there seems to be a swarm of possibly aneuploid forms as reviewed by Bisson et al. (1968) and Mahanty (1970). While the sister family Cannaceae is characterized by a uniform basic number of $x=9$, Marantaceae seems to have monoploid numbers ranging from as low as 4 up to 13. Since the beginning of karyological studies in Marantaceae (Venkatasubban 1946; Mangenot and Mangenot 1957, 1958; Sharma and Bhattacharyya 1958; Sato 1960; Bisson et al. 1968; Mahanty 1970; Mukhopadhyay and Sharma 1987), there has been continuous discussion on the partly conflicting results and the ancestral states in the chromosomal evolution of the family.

Some authors (Venkatasubban 1946; Sato 1948, 1960; Bisson et al. 1968) suggested that basic numbers of $x=9$, 10, 11, 12, 13 were the derivatives of the original $x=4$ (in the following: $p=4$ according to Peruzzi 2013). However, $2n=8$ was reported in only two species (Table 1), for which higher numbers were recorded by other authors (e.g. Venkatasubban 1946) that makes this assumption questionable. Further, there was a strong geographical and taxonomic bias since the early chromosome surveys were restricted to a couple of genera, especially *Goeppertia* (under *Calathea*) and *Maranta*, which are mainly American, while Old World taxa had not been considered so far. Subsequently $p=11$, which is found in several species of the American genus *Goeppertia* (Venkatasubban 1946; Sato 1948; Sharma and Bhattacharyya 1958), as suggested as ancestral in Marantaceae (Sharma and Bhattacharyya 1958). The other numbers should have been derived from $p=11$ by ascending or descending dysploidy. Mahanty (1970) worked on the Malayan and primarily African genera *Stachyphryium*, *Marantochloa*, and *Thalia* and emphasized that geographical distribution may have played a role in the evolution of Marantaceae and their different basic numbers. Based on the assumption that the origin of the family was tropical America (Holttum 1951), migration to the Far East and the African tropics might have been linked with the acquisition of 'derived' chromosomal character states. Mahanty (1970) suggested that $x=13$ as frequently found in African Marantaceae is a secondary basic number, which became established in Old World genera. Recent molecular phylogenetic and morphological investigations (Andersson and Chase 2001; Prince and Kress 2006), however, point to an origin of Marantaceae in the Old World. This means that the presumed cytogeographical pattern of 'original' monoploid chromosome numbers in the New and 'derived' ones in the Old World must be called into question. In addition to the varying basic numbers, also high chromosome numbers being based on polyploidy were reported in the American genera *Maranta* and *Stromanthe* (Venkatasubban 1946; Bisson et al. 1968; Sharma and Mukhopadhyay 1984; Hanson et al. 1999; see Table 1). Polyploidy was suggested to be related to the vegetative mode of propagation, which is important in the whole family Marantaceae. In this way, chromosomal 'biotypes', which otherwise would become extinct, would be preserved (Mahanty 1970).

Some chromosome numbers reported in the literature for the Marantaceae should be treated with caution, due to shortcomings in some of the chromosome techniques employed and also with regard to the fact that the plant specimens were partly unreliably identified. Up to now, chromosome counts are available from only a relatively small number of species. Therefore, reliable conclusions cannot be drawn on the actual range of chromosomal variation in Marantaceae, not to speak of chromosomal and genome evolution in this family.

The present study aimed at providing a detailed survey of chromosome variation in Marantaceae. In particular, (1) we determined chromosome numbers and made karyotype analyses of 43 accessions, focussing on taxa that were not examined before, in which available information seemed to be doubtful or several different chromosome numbers have been reported; (2) we critically examined the numerical variation in monoploid chromosome sets, checked for different ploidy levels and possible aneuploid forms to explain the enormous variation in somatic chromosome numbers; and (3) we chose taxa from all major tropical regions (Africa, America, Asia) to find out whether there are trends in karyotype evolution that can be associated with the diversification of evolutionary lineages in Marantaceae and/or biogeography.

Materials and methods

Plant material

In total, 43 plant accessions belonging to 16 genera were included in the chromosome survey, of which 37 were identified to species level. The species of *Hypselodelphys* (M69) could not have been identified. One accession is cf. *Sarcophrynium* (M63). For *Ctenanthe burle-marxii, Goeppertia bella* and *G. zebrina* two different provenances could be investigated. Root tips were excised from Marantaceae plants of the living collection of the Botanical Garden of the Martin Luther University of Halle-Wittenberg. Voucher specimens are deposited in the herbarium HAL. For 51 further species, data from the literature were evaluated. The taxa studied, collection and voucher details and references are listed in Table 1.

Table 1 Voucher information of the Marantaceae samples, sorted alphabetically, with collection details, somatic chromosome number ($2n$) of this study in bold numerals with [number of counts] and data from literature (* see below the table), ploidy level (pl), basic chromosome number (x), karyological parameter: *MCL* mean chromosome length, *TML* total monoploid length of chromosome set, M_{CA} mean centromeric asymmetry, CV_{CL} interchromosomal asymmetry; for calculations see "Materials and methods" section

Taxon	Provenance/distribution, accession number (BGH, LEY), voucher specimen (HAL) and handling number (M)	$2n$	pl	x	MCL (µm)	TML (µm)	M_{CA}	CV_{CL}
Ctenanthe burle-marxii H.Kenn	Brazil, BGH 6712/1, HAL124131, M22	**20** [11]	2*x*	10	1.6	15.7	15.0	22.5
Ctenanthe burle-marxii var. *obscura* H.Kenn.	Brazil, BGH 13144/1, HAL124132, M77	**20** [14]	2*x*	10	1.7	17.0	22.1	16.2
Ctenanthe dasycarpa K.Schum.	Panama/Colombia, BGH 13147/1, HAL124134, M79	**72** [4]	8*x*	9	1.2	10.4	19.4	19.5
Ctenanthe kummeriana (É.Morren) Eichl.		20 + 2B*[1]						
Ctenanthe lubbersiana Eichl.		20*[1,2]						
Ctenanthe oppenheimiana (É.Morren) K.Schum.		18*[3,4]						
Ctenanthe setosa Eichl.	Brazil, BGH 6713/1, HAL124150, M25	**36** [5]	4*x*	9	1.6	14.5	22.8	26.0
Donax canniformis K.Schum.	Asia, BGH 13145/1, HAL146503, M80	**22** [4]	2x	11	1.8	19.6	20.4	28.1
Goeppertia albertii (L.H.Bailey & Raffill) Borchs. & S.Suárez		18*[1]						
Goeppertia argyrophylla (Linden ex K.Koch) Borchs. & S.Suárez		27*[1]						
Goeppertia bachemiana (É.Morren) Borchs. & S.Suárez	Brazil, BGH 13149, HAL124122, M75	**26** [3], 26*[5,6]	2*x*	13	1.4	18.6	19.9	37.2
Goeppertia bella (W.Bull) Borchs. & S.Suarez	Brazil, BGH 6707/3, HAL146201 + 146202, M9	**26** [2], 28*[2]	2*x*	13	1.2	16.1	22.2	29.3
	Brazil, BGH 6707/1b, HAL124121, M73	**26** [3]	2*x*	13	–	–	–	–
Goeppertia concinna (W.Bull) Borchs. & S.Suárez		8*[7]						
Goeppertia cylindrica (Roscoe) Borchs. & S.Suárez		16*[1]						
Goeppertia flavescens (Lindl.) Borchs. & S.Suárez		24*[8]						
Goeppertia lancifolia (Boom bis) Borchs. & S.Suárez	Brazil, BGH 6705/2, HAL124123 M4	**26** [4], 22*[3], 26*[9], 28*[5,6]	2*x*	13	–	–	–	–
Goeppertia leucostachys (Hook.f.) Borchs. & S.Suárez		26*[1]						
Goeppertia lindeniana (Wallis) Borchs. & S.Suárez		26*[2,8]						
Goeppertia majestica (K.Schum.) Borchs. & S.Suárez		22*[7], 24*[5,6,9]						
Goeppertia makoyana (E.Morren) Borchs. & S.Suárez		26*[2,8], 24*[10]						

Table 1 (continued)

Taxon	Provenance/distribution, accession number (BGH, LEY), voucher specimen (HAL) and handling number (M)	2*n*	pl	*x*	MCL (µm)	TML (µm)	M_{CA}	CV_{CL}
Goeppertia mediopicta (E.Morren) Borchs. & S.Suárez		22*[8]						
Goeppertia nigricans (Gang-nep.) Borchs. & S.Suárez		22*[1]						
Goeppertia ornata (Linden) Borchs & S.Suarez	Guyana, Colombia, BGH 6708/1, HAL124125, M10	**24** [1]**, 26** [4], **27** [1], 28*[2,*5], 26*[7]	2*x*	13	1.1	14.4	24.7	38.6
Goeppertia ovandensis (Matuda) Borchs. & S.Suárez,		25*[11]						
Goeppertia picturata (K.Koch & Linden) Borchs. & S.Suárez	Brazil, BGH 6709/1, HAL124126, M13	**28** [12], 24*[1], 26*[9]	2*x*	14	1.4	20.1	23.4	16.5
Goeppertia taeniosa (Joriss.) Borchs. & S.Suárez		52*[3,*4]						
Goeppertia undulata (Linden & André) Borchs. & S.Suárez	Brazil, Peru, BGH 6710/2, HAL124127 and 145213, M17	**26** [3], 22*[2], 24*[5,*6]	2*x*	13	1.0	13.5	24.3	23.6
Goeppertia veitchiana (J.H.Veitch ex Hook.f.) Borchs. & S.Suárez		8*[3], 26*[8]						
Goeppertia virginalis (Linden ex Regel) Borchs. & S.Suárez		26*[2]						
Goeppertia warscewiczii (Lem.) Borchs. & S.Suarez	Costa Rica, BGH 6711/1, HAL124128, M19	**26** [3]	2*x*	13	1.3	16.8	19.8	37.2
Goeppertia wiotii (E.Morren) Borchs. & S.Suárez,		26*[1]						
Goeppertia zebrina (Sims) Lindl.	Brazil, LEY 13148/1, HAL124129, M71	**26** [4], 22*[7], 24*[8], 26*[4,*5,*6,*8]	2*x*	13	1.3	16.3	26.9	24.1
	Brazil, LEY 13146/1, HAL124130, M72	**26** [5]	2*x*	13	1.0	12.7	19.0	11.7
Halopegia azurea K.Schum.	DR Congo, Kifundi, LEY 13151/1, HAL124135, M65	**26** [4]	2*x*	13	1.2	15.4	22.2	20.3
Hypselodelphys sp. (K. Schum.) Milne-Redh.	DR Congo, Kifundi, LEY 13152, HAL124136, M69	**21** [1], **22** [10], **24** [1],	2*x*	11	1.5	16.9	21.7	23.2
Ischnosiphon bambusaceus (Poepp. & Endl.) Koernicke		42*[2]						
Maranta arundinacea L.	South America, BGH 6714/2, HAL124137, M29	**49** [1], **50** [1], **52** [6], 18*[3,*4], 46*[8], 48*[5,*12]	4*x*	13	0.8	10.0	19.2	12.7
Maranta bicolor Ker Gawl.	Brazil, BGH 6715/3, HAL124138, M32	**52** [2], 24*[8], 32*[4], 52*[6,*13]	4*x*	13	1.0	12.4	19.4	22.1
Maranta depressa E.Morren		48*[2]						
Maranta gibba Sm.		40*[11]						
Maranta leuconeura var. *erythroneura* G.S.Bunting	Brazil, BGH 6716/1, HAL124139, M33	**49** [2], **52** [3]	4*x*	13	0.9	12.3	14.1	17.3
Maranta leuconeura var. *kerchoviana* Peters	Brazil, BGH 6717/3, HAL124140, M38	**52** [3]	4*x*	13	0.9	11.3	11.8	15.7
Maranta leuconeura var. *massangeana* E.Morren		52*[2]						
Maranta leuconeura var. *mediovariegata* E.Morren		52*[10]						

Table 1 (continued)

Taxon	Provenance/distribution, accession number (BGH, LEY), voucher specimen (HAL) and handling number (M)	2*n*	pl	*x*	MCL (µm)	TML (µm)	M_{CA}	CV_{CL}
Maranta leuconeura E.Morren		26*[7,*14], 52*[9]						
Maranta lietzei (E.Morren) C.H.Nelson, Sutherl. & Fern.Casas.		24*[5,*6], 26*[8]						
Maranta noctiflora Regel & Körn.	Brazil, BGH 4316/1, HAL124141, M39	**52** [3], **56** [1]	4*x*	13	0.9	12.1	13.5	23.7
Maranta picta W.Bull		26*[7]						
Maranta sanguinea hort. ex Planch.		24*[15]						
Maranta striata Veitch.		26*[3,*4]						
Marantochloa conferta (Benth.) A.C.Ley	DR Congo, Kifundi, LEY 12850/1, HAL124142, M54	**25** [2], **26** [6]	2*x*	13	1.0	13.6	20.2	13.3
Marantochloa cordifolia (K.Schum.) Koechlin	DR Congo, Kinshasa, LEY 12857/1, HAL124146, M56	**34** [1], **36** [4]	4*x*	9	1.6	14	26.8	24.3
Marantochloa congensis (K.Schum.) J.Léonard & Mullend.	Gabon, LEY 12849/1, HAL124143, M58	**65** [11]	5x	13	1.0	13.5	23.4	16.2
Marantochloa cuspidata Milne-Redh.		28*[2]						
Marantochloa flexuosa (Benth.) Hutch.				13*[1]				
Marantochloa leucantha (K.Schum.) Milne-Redh.	Ivory Coast, BGH 6747/1, HAL124145, M42	**26** [6], 28*[16]	2*x*	13	1.2	16	17.1	16.8
Marantochloa mannii (Benth.) Milne-Redh.	Africa, BGH 12855/1, HAL124148, M70	**26** [5]	2*x*	13	1.2	15	15.5	12.7
Marantochloa purpurea (Ridl.) Milne-Redh.	Africa, BGH 12852/1, HAL124149, M60	**21** [1], **22** [1], **24** [1], **26** [5]	2*x*	13	1.1	13.7	17.9	17.9
Megaphrynium macrostachyum (Benth.) Milne-Redh.	Africa, BGH 12854/1, HAL124151, M63	**34** [2], **36** [4], **38** [2]	4*x*	9	1.9	17.5	18.4	16.9
Monotagma smaragdinum (Linden & André) K.Schum.		27*[3]						
Phacelophrynium interruptum K.Schum.	Asia, BGH 13573, HAL145212, M87	**22** [5]	2*x*	11	1.7	19.1	24.8	25.4
Phrynium imbricatum Roxb.	SE Asia, BGH 333 03BI, HAL145211, M90	**22** [4]	2*x*	11	1.6	17.3	19.6	30.9
Phrynium pedunculiferum D.Fang	SE Asia, BGH 289 03BI, HAL145215, M92	**22** [4]	2*x*	11	1.5	16.7	16.4	15.6
Phrynium pubinerve Blume	SE Asia, BGH 334 03BI, HAL145209, M82	**22** [4]	2*x*	11	1.6	17.4	18.3	25.0
Phrynium terminale Ridl.	SE Asia, BGH 331 03BI, HAL145210, M94	**22** [5]	2*x*	11	1.4	15.2	18.7	37.1
Pleiostachya pruinosa K.Schum.	Central America, BGH 6721/2, AL1325, HAL124152, M48	**24** [4]	2*x*	12	1.3	15.6	12.8	20.4
Sarcophrynium brachystachyum (Körn.) K.Schum.	Africa, BGH 6722, HAL124153, M49	**26** [4], 28*[17, *18, *19]	2*x*	13	1.2	15	14.1	11.5
Sarcophrynium prionogonium (K.Schum.) K.Schum.		28*[19]						

Table 1 (continued)

Taxon	Provenance/distribution, accession number (BGH, LEY), voucher specimen (HAL) and handling number (M)	2*n*	pl	*x*	MCL (µm)	TML (µm)	M_{CA}	CV_{CL}
Sarcophrynium schweinfurthianum (Kuntze) Milne-Redh.	DR Congo, Bandundu forest, BGH 13704c, HAL145208, M95	**26** [5]	2*x*	13	1.2	15	14.1	11.5
Stachyphrynium griffithii K.Schum.				13*[1]				
Stachyphrynium placentarium (Lour.) Clausager & Borchs.	SE Asia, BGH 1783 70HD, HAL145214, M85	**26** [13]	2*x*	13	1.3	17.4	21.5	22.2
Stachyphrynium latifolium (Blume) K.Schum.	SE Asia, BGH 339 03BI, HAL145216, M86	**26** [3]	2*x*	13	1.8	22.8	15.0	18.1
Stromanthe amabilis Hort.		48*[2]						
Stromanthe macrochlamys (Woodson & Standl.) H.Kenn. & Nicolson		c.60, 63*[11]						
Stromanthe porteana A.Griseb.		22*[2]						
Stromanthe sanguinea Sond.	Brazil, BGH 6723, HAL146504, M50	**44** [7], 24*[15], 36*[1,*4], 44*[6,*8,*13]	4*x*	11	1.4	15.2	18.5	24.5
Thalia dealbata L.		12*[15]						
Thalia geniculata L.	Africa, BGH 5396, HAL124155, M51	**29** [1], **32** [1], **33** [7], **35** [1], 18*[20], 26*[1]	3*x*	11	1.1	12.6	12.4	29.6
Thaumatococcus daniellii (Benn.) Benth. ex Eichl.	Gabon, BGH 6796/2, HAL124156, M53	**20** [3], 20*[17,*18]	2*x*	10	1.7	17	17.2	28.8
Trachyphrynium braunianum Baker	Gabon, BGH 12853/1, HAL124154 M61	**22** [6], **24** [3], 22*[18]	2*x*	11	1.8	19.7	15.7	20.1

BGH Culture of Botanical Garden Halle; *LEY* collected by A.C. Ley; *HAL* Vouchers are deposited at the herbaria of the University of Halle-Wittenberg; *M* handling number

*[1]Mahanty (1970), *[2]Bisson et al. (1968), *[3]Sato (1948), *[4]Sato (1960), *[5]Sharma and Mukhopadhyay (1984), *[6]Mukhopadhyay and Sharma (1987), *[7]Sharma and Bhattacharyya (1958), *[8]Venkatasubban (1946), *[9]Eksomtramage et al. (2007), *[10]Mukherjee (1981), *[11]Vovides and Lascurain (1995), *[12]Simmonds (1954), *[13]Hanson et al. (1999), *[14]Bharathan et al. (1994), *[15]Suessenguth (1921), *[16]Cave (1960), *[17]Mangenot and Mangenot (1957), *[18]Mangenot and Mangenot (1962), *[19]Gadella (1982), *[20]Miege (1960)

Chromosome counting, karyotyping and regression analysis

Chromosome numbers were counted in actively growing root tips. They were washed with tap water a few times, treated in 8-hydroxyquinoline (0.002 M aqueous solution) at 21 °C for 3 h to accumulate metaphases, fixed in absolute ethanol/glacial acetic acid (3:1) at 21 °C for 3 h and stored in absolute ethanol at -20 °C until preparation. Enzyme-treated root tips (Schwarzacher et al. 1980) were squashed on slides in a drop of 45% propionic acid with 2% carmine and covered with a coverslip. Photographs of metaphase chromosomes were taken on a Zeiss Axiophot microscope using a computer-assisted cooled CCD camera (Zeiss Axiocam HRC) employing Zeiss Axiovision software. A total of 4–20 metaphase plates were used for chromosome counts.

For karyotyping, one metaphase plate with sharp contours of individual chromosomes was chosen. Karyotypes were reconstructed in all species except for *Goeppertia bella* (M73) and *G. lancifolia* (M4), in which only chromosome numbers could be retrieved. Chromosomes were arranged and measured in CorelDraw Graphics Suite—X8 by hand. They were grouped as pairs or groups of putative homologues or homoeologues according to their similarities in chromosome length and position of centromeres and/or secondary constrictions. Selected metaphase plates and karyograms of each taxon studied are shown in Figs. 1, 2, 3 and 4, respectively. Calculations of karyological parameters, done with Excel, are as follows Paszko (2006) and Peruzzi and Eroğlu (2013): TML = total length of monoploid chromosome set [= (L + S)/ploidy level, L = total length of long arms, S = total length of short arms]; M_{CA} = mean centromeric asymmetry [= (L − S)/

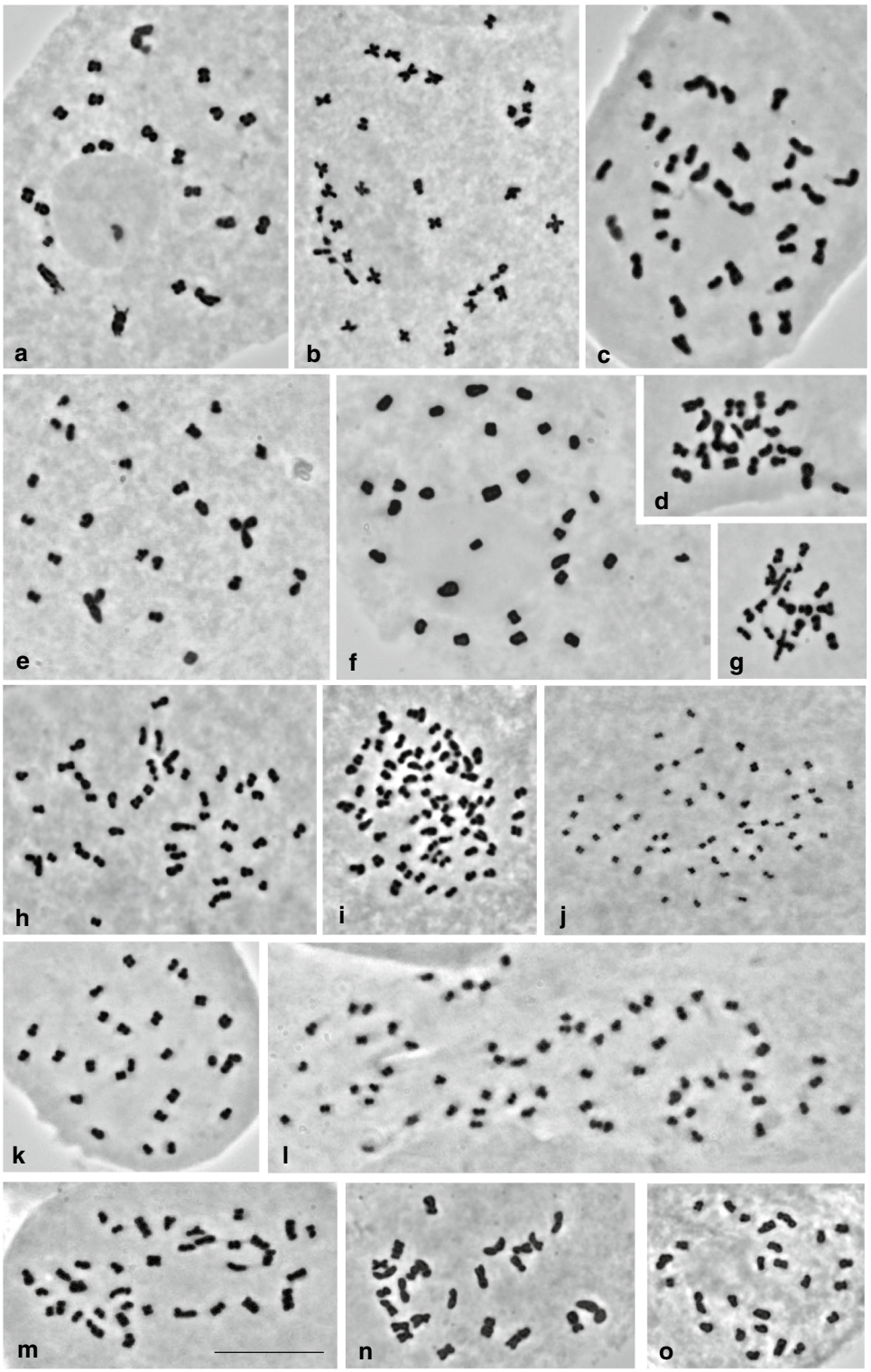
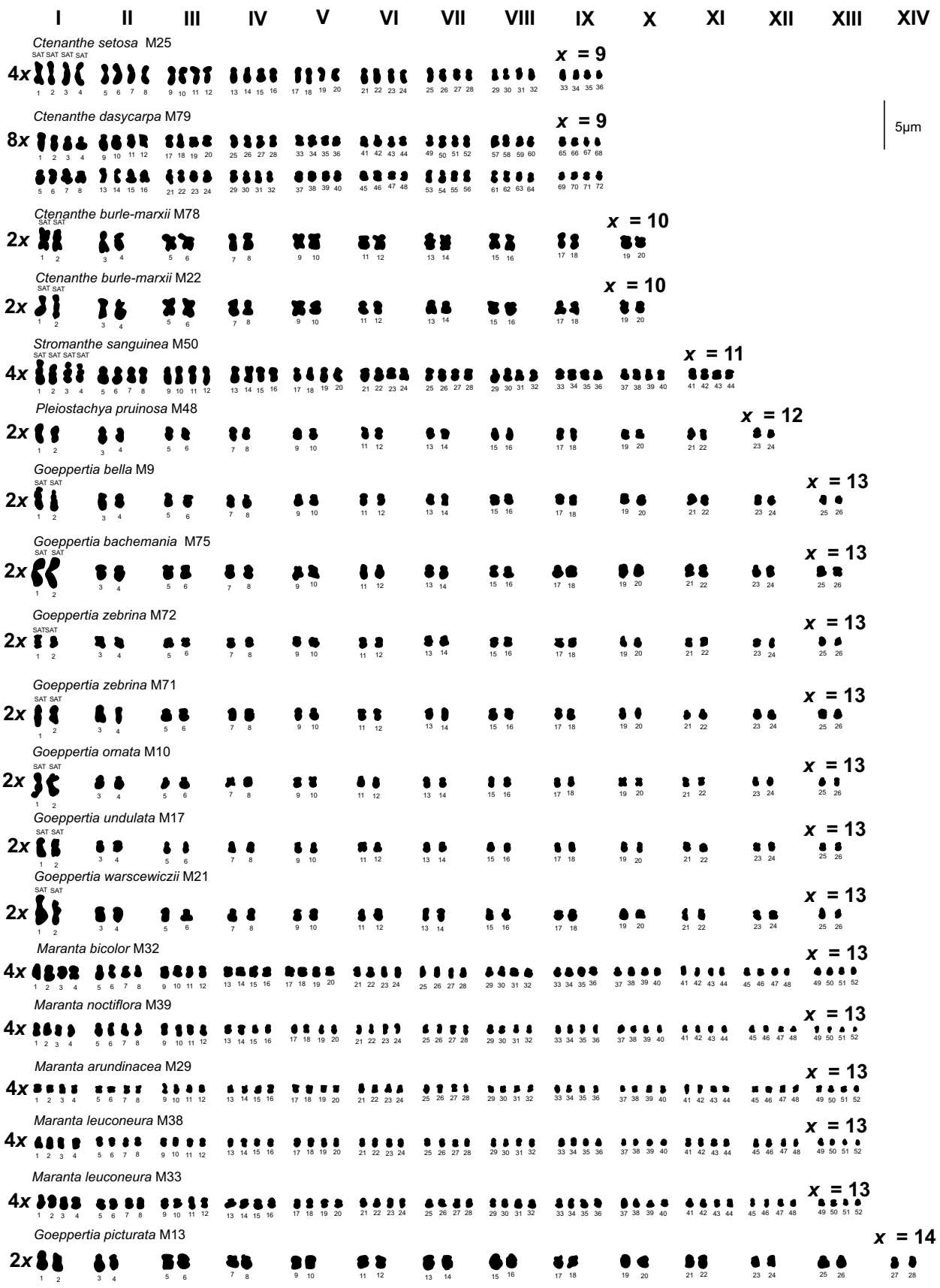


Fig. 1 Somatic metaphase plates. **a** *Phrynium terminale* ($2n=22$); **b** *Thalia geniculata* M51 ($2n=33$); **c** *Megaphrynium macrostachyum* M63 ($2n=36$); **d** *Trachyphrynium brauneanum* M62 ($2n=22$); **e** *Goeppertia bachemiana* M75 ($2n=26$); **f** *Goeppertia picturata* M13 ($2n=28$); **g** *Thaumatococcus danielii* M53 ($2n=20$); **h** *Stromanthe sanguinea* M50 ($2n=44$); **i** *Ctenanthe dasycarpa* M79 ($2n=72$); **j** *Maranta arundinacea* M29 ($2n=52$); **k** *Marantochloa conferta* M54 ($2n=26$); **l** *Marantochloa congensis* M58 ($2n=65$); **m** *Marantochloa cordifolia* M56 ($2n=36$); **n** *Stachyphrynium latifolium* M86 ($2n=26$) and **o** *Stachyphrynium placentarium* M85. Scale bar 10 µm

$(L+S)\times 100$]; CV_{CL} = interchromosomal asymmetry [= (sCL/MCL) × 100, sCL = standard deviation of chromosome length in a chromosome complement, MCL = mean chromosome length].

For regression analysis, linear models were calculated between the four dependent variables MCl, TML, M_{CA} and CV_{CL} and the three predictor variables chromosome number ($2n$), ploidy level (pl) and basic chromosome number (x) using the software R (R Core Team 2014). Because a


I II III IV V VI VII VIII IX X XI XII XIII XIV
Ctenanthe setosa M25
4x
x = 9
Ctenanthe dasycarpa M79
8x
x = 9
5µm
Ctenanthe burle-marxii M78
2x
x = 10
Ctenanthe burle-marxii M22
2x
x = 10
Stromanthe sanguinea M50
4x
x = 11
Pleiostachya pruinosa M48
2x
x = 12
Goeppertia bella M9
2x
x = 13
Goeppertia bachemania M75
2x
x = 13
Goeppertia zebrina M72
2x
x = 13
Goeppertia zebrina M71
2x
x = 13
Goeppertia ornata M10
2x
x = 13
Goeppertia undulata M17
2x
x = 13
Goeppertia warscewiczii M21
2x
x = 13
Maranta bicolor M32
4x
x = 13
Maranta noctiflora M39
4x
x = 13
Maranta arundinacea M29
4x
x = 13
Maranta leuconeura M38
4x
x = 13
Maranta leuconeura M33
4x
x = 13
Goeppertia picturata M13
2x
x = 14

◂**Fig. 2** Karyograms of diploid to octoploid taxa of American Marantaceae. Chromosomes are arranged into groups of presumed homologues or homoeologues according to chromosome size and position of centromeres and secondary constrictions if present (SAT)

phylogenetic hypothesis including the species studied for their chromosomes is still lacking, we are using ordinary regression analysis instead of regressions on phylogenetic independent contrasts. It has been shown that results from the two types of analysis produce very similar results (Ricklefs and Starck 1996).

Results

Chromosome counts, basic numbers and ploidy levels

Chromosome counts in 43 accessions are listed in Table 1, along with information on previous reports for 51 taxa. For 24 species and for genus *Hypselodelphys*, chromosome numbers are reported for the first time. In 32 accessions, all cells studied consistently had the same chromosome number. Variable chromosome numbers, the most frequent being underlined in the following, occurred in eleven accessions, i.e. *Goeppertia ornata* ($2n = 24$, 26, 27), *Hypselodelphys* sp. ($2n = 21$, 22, 24), *Maranta arundinacea* ($2n = 49$, 50, 52; Fig. 1j), *M. leuconeura* ($2n = 49$, 52), *Marantochloa conferta* ($2n = 25$, 26; Fig. 1k), *M. purpurea* ($2n = 21$, 22, 24, 26), *Megaphrynium macrostachyum* ($2n = 34$, 36, 38; Fig. 1c), *Thalia geniculata* ($2n = 29$, 32, 33, 35; Fig. 1b) and *Trachyphrynium brauneanum* ($2n = 22$, 24; Fig. 1d). Numerical variation within the same individual was infrequently observed in *Maranta noctiflora* ($2n = 52$ counted in three cells, $2n = 56$ in one cell) and *Marantochloa cordifolia* ($2n = 36$ in four cells, $2n = 34$ in one cell).

The most likely basic chromosome numbers and ploidy levels were as follows: $x = 9$ in *Ctenanthe setosa*, *Marantochloa cordifolia*, *Megaphrynium macrostachyum*, all of which had $2n = 4x = 36$, and *Ctenanthe dasycarpa* with $2n = 8x = 72$ (Fig. 1c, i, m). $x = 10$ occurred in *Ctenanthe burle-marxii* (accessions M22 and M77) and *Thaumatococcus danielii*, both $2n = 2x = 20$ (Fig. 1g). $x = 11$ was found in *Donax canniformis*, *Hypselodelphys* sp., *Phacelophrynium interruptum*, *Phrynium imbricatum*, *P. pedunculiferum*, *P. pubinerve*, *P. terminale* and *Trachyphrynium brauneanum*, all of which had $2n = 2x = 22$, *Thalia geniculata* with $2n = 3x = 33$ and *Stromanthe sanguinea* with $2n = 4x = 44$ (Fig. 1a, b, d, h). $x = 12$ with $2n = 2x = 24$ had only *Pleiostachya pruinosa*. The most frequent basic number of $x = 13$ was consistently found in nine of ten accessions of genus *Goeppertia*, in *Halopegia azurea*, *Sarcophrynium brachystachyum*, *S. schweinfurthianum*, *Stachyphrynium placentarium* and *S. latifolium*, all of which had $2n = 2x = 26$ (Fig. 1e, n, o). It occurred also in the five studied species of *Maranta*, which had $2n = 4x = 52$ (Fig. 1j), in five of the six species of genus *Marantochloa* (*M. conferta*, *M. leucantha*, *M. mannii*, *M. purpurea*), which had $2n = 2x = 26$ (Fig. 1k, m) and $2n = 5x = 65$ (only *M. congensis*; Fig. 1l). $x = 14$ occurred only in *Goeppertia picturata*, which had $2n = 2x = 28$ (Fig. 1f).

Infrageneric variation in basic chromosome numbers was encountered in *Ctenanthe*, *Goeppertia* and *Marantochloa*. Species of *Ctenanthe* had $x = 9$ or $x = 10$ and of *Goeppertia* $x = 13$ or $x = 14$ (see above). Although $x = 13$ was the most common basic number in *Marantochloa*, *M. cordifolia* had $x = 9$ with $2n = 4x = 36$.

Karyotypes

In the karyograms of Figs. 2, 3 and 4 usually one or two chromosome pairs of the complements show secondary constrictions and/or are almost twice as large as the other chromosomes. They were designated in the following as satellite chromosomes (SAT). Two of such pairs were present in three Asian accessions of the $x = 11$ diploids *Phrynium* and *Phacelophrynium* as well as in African $x = 9$ tetraploid *Marantochloa cordifolia*. One pair was present in $x = 11$ Asian diploid *Donax canniformis,* African triploid *Thalia geniculata*, $x = 13$ Asian diploids *Stachyphrynium placentarium* and *S. latifolium*, American $x = 9$ tetraploid *Ctenanthe setosa*, $x = 11$ tetraploid *Stromanthe sanguinea*, $x = 13$ diploids of *Goeppertia* and African *Halopegia azurea*, African $x = 9$ tetraploid *Megaphrynium macrostachyum*, $x = 10$ diploid *Thaumatococcus danielii* as well as $x = 11$ diploid *Trachyphrynium brauneanum* and *Hypselodelphys* sp. In the karyograms of all other accession, no chromosomes with clearly visible satellites could be verified with the method used.

Karyotype analyses with detailed measurements are presented in Table 1. Chromosomes of Marantaceae are small. Mean chromosome lengths (MCL) varied from 0.8 µm in 4*x Maranta arundinacea* to 1.9 µm in 4*x Megaphrynium macrostachyum*. The total monoploid lengths (TML) ranged from 10.0 µm in 4*x Maranta arundinacea* to 22.8 µm in 2*x Stachyphrynium latifolium*. Mean centromeric asymmetry (M_{CA}) varied from 12.4 in 3*x Thalia geniculata* (symmetrical chromosomes) to 26.8 in 4*x Marantochloa cordifolia* with more asymmetrical chromosomes. Interchromosomal asymmetry (CV_{CL}), indicating the variation of chromosome lengths within the whole complement, was lowest in *Sarcophrynium schweinfurthianum* (CV_{CL} 11.5) and highest in *Goeppertia ornata* (CV_{CL} 38.6).

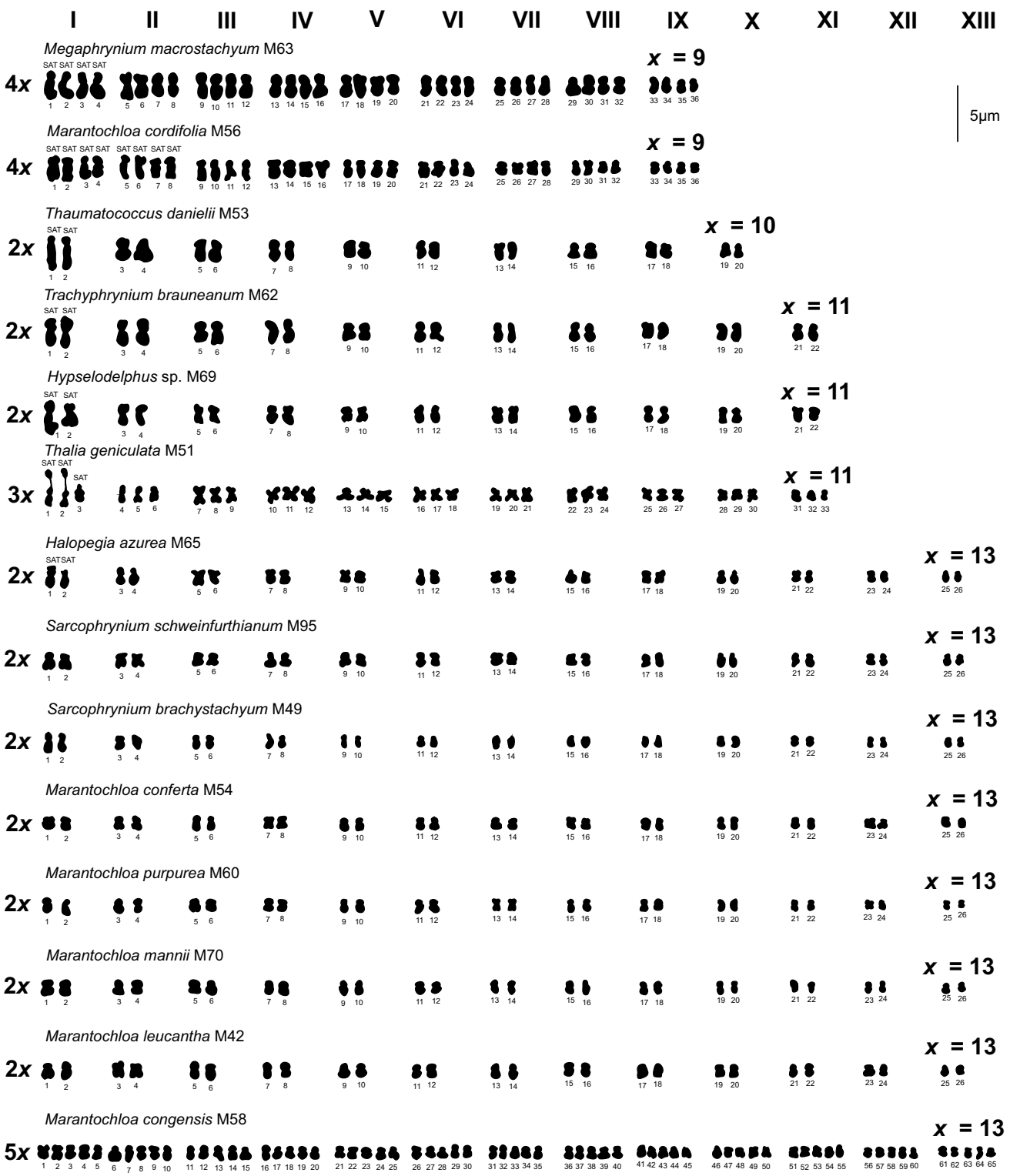


Fig. 3 Karyograms of diploid to pentaploid taxa of African Marantaceae. Chromosomes are arranged into groups of presumed homologues or homoeologues according to chromosome size and position of centromeres and secondary constrictions if present (SAT)

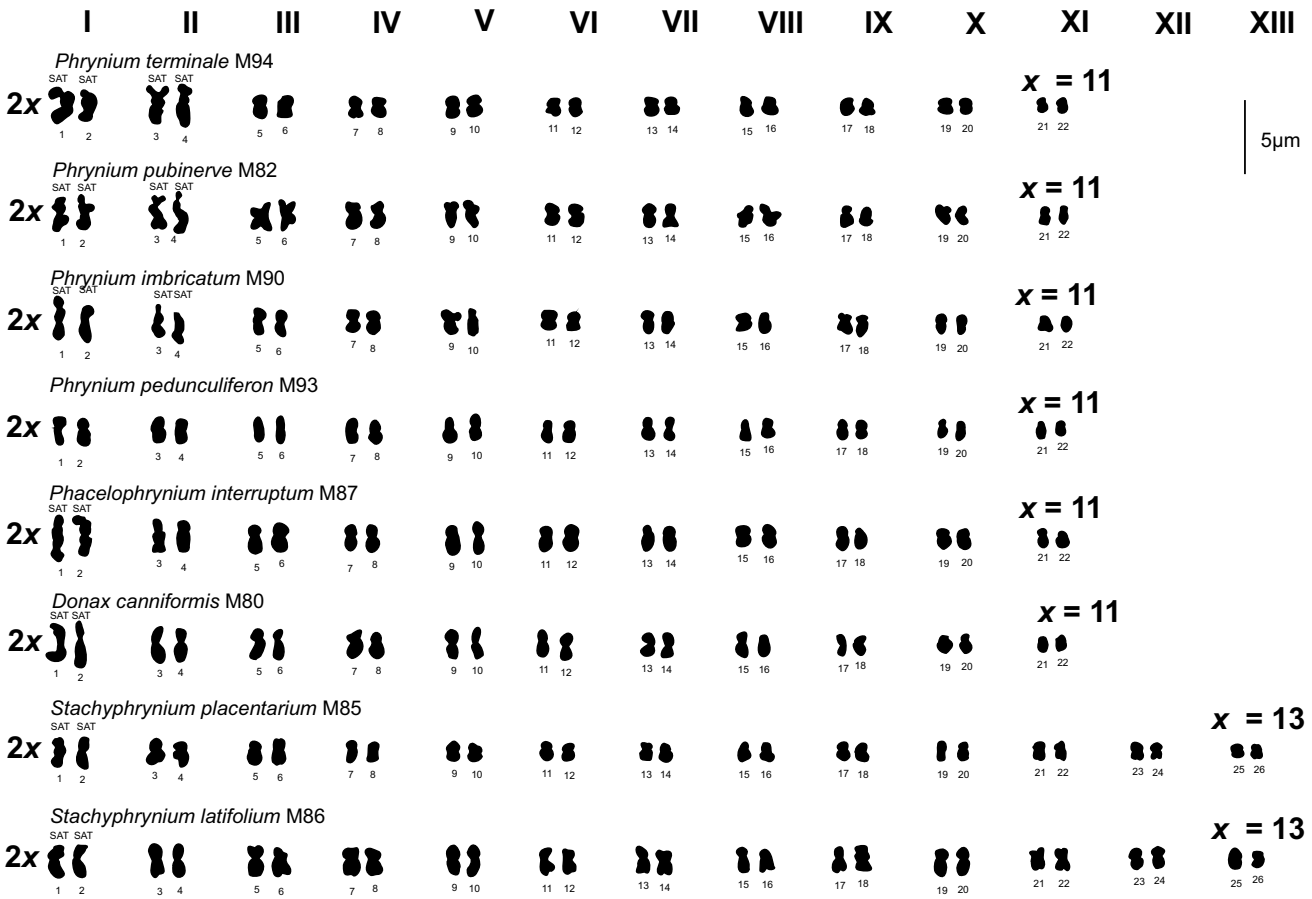


Fig. 4 Karyograms of Asian taxa of Marantaceae. Chromosomes are arranged as pairs of presumed homologues according to chromosome size and position of centromeres and secondary constrictions if present (SAT)

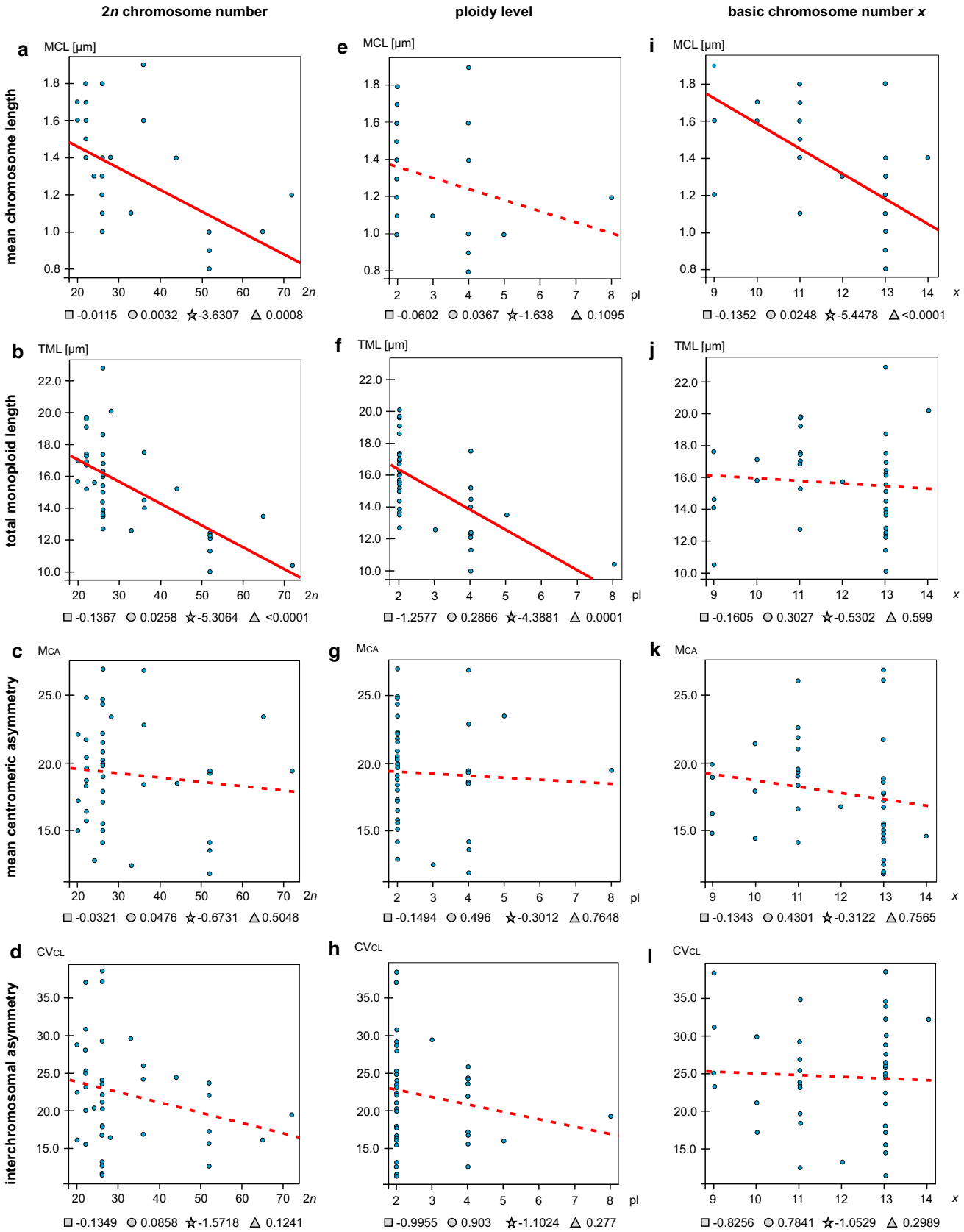
Regression analysis

In Fig. 5, the results for the linear regression models are presented as scatter plots, which refer to the dependent (MCL, TML, M_{CA}, CV_{CL}) and independent variables ($2n$, pl, x). Calculations are listed under each plot with the following parameters: an estimate of the regression slope, its standard error, the t test statistic and the two-sided significance level for the null hypothesis of regression slopes equal to zero. Solid lines in A, B, F and I show significant linear regression, and dotted lines in the other plots represent not significant correlations. The four significant regression models in A, B, F and I had p values < 0.0008 that were significant after adjusting the p value for multiple testing, e.g. by the conservative Bonferroni correction, which divides the p value by the number of comparisons ($0.05/12 = 0.004$).

Discussion

Variation of chromosome numbers in Marantaceae

Chromosome counts in 43 accessions, along with information on previous reports for 51 taxa (15 of them were the same species; Table 1), reveal consistencies in eight species. In seven species, we found deviating chromosome numbers. In our study, a consistent somatic chromosome number occurred in 32 out of the 43 investigated accessions. Aberrations were rather the exception than the rule. Variation of chromosome numbers was found in only eleven accessions. In nine of them, two to four different chromosome numbers were observed (Table 1). In these instances, we consider the most frequently occurring somatic number of the respective taxon to establish the monoploid chromosome number


2n chromosome number
ploidy level
basic chromosome number x
a
MCL [µm]
mean chromosome length
-0.0115 0.0032 -3.6307 0.0008
e
MCL [µm]
-0.0602 0.0367 -1.638 0.1095
i
MCL [µm]
-0.1352 0.0248 -5.4478 <0.0001
b
TML [µm]
total monoploid length
-0.1367 0.0258 -5.3064 <0.0001
f
TML [µm]
-1.2577 0.2866 -4.3881 0.0001
j
TML [µm]
-0.1605 0.3027 -0.5302 0.599
c
MCA
mean centromeric asymmetry
-0.0321 0.0476 -0.6731 0.5048
g
MCA
-0.1494 0.496 -0.3012 0.7648
k
MCA
-0.1343 0.4301 -0.3122 0.7565
d
CVCL
interchromosomal asymmetry
-0.1349 0.0858 -1.5718 0.1241
h
CVCL
-0.9955 0.903 -1.1024 0.277
l
CVCL
-0.8256 0.7841 -1.0529 0.2989

◂**Fig. 5** Regression analysis of chromosome data (2*n* chromosome number, ploidy level, basic chromosome number *x*) versus karyomorphology data (*MCL* mean chromosome length, *TML* total length of monoploid chromosome set, M_{CA} mean centromeric asymmetry, CV_{CL} interchromosomal asymmetry) in Marantaceae taxa. Parameter: *circle* an estimate of regression slope, *star* standard error, *triangle t* test statistic, *square* two-sided significance level for null hypothesis of regression slopes equal to zero. *Regular lines* significant-, *dotted lines* not significant linear regression

and ploidy level (2*x*, 3*x*, 4*x*). Plants with different somatic chromosome numbers in root tip cells often have uniform euploid chromosome numbers at meiosis (Joachimiak et al. 2001) and mostly form bivalents during meiotic prophase (Armstrong 1981, 1984 and references therein). Possibly due to the rarity of flowering in green house cultures of Marantaceae species, reliable information on meiosis is scarce and the literature records are restricted to only a few species of the genera *Calathea, Stromanthe, Maranta* (Bisson et al. 1968; Mahanty 1970). In the light of our findings, we suppose that the chromosome numbers are rather stable at least within the generative tissues.

Somatic variation in chromosome numbers has been observed in root tips of many angiosperm species (e.g. Fedorov 1969; Kula 1999; Winterfeld et al. 2015). It was suggested that it is either a result of chromosome rearrangements such as fusion or split after recent polyploidization (Smulders et al. 1994; Mishiba and Mii 2000) or a result of defective chromosome segregation as a consequence of meiotic disturbances caused by somatic irregularities, namely lagging and late separation of chromosomes (polysomaty and aneusomaty; Kula 1999; Mishiba and Mii 2000; Orr et al. 2015).

Our study did not verify far-reaching inconsistencies of chromosome numbers in Marantaceae species that were reported by previous investigations (Table 1; Sharma and Bhattacharyya 1958; Bisson et al. 1968). Hence, we suppose that such findings are due to artefacts from preparation, misidentification of the specimens studied or the use of outdated genus and species concepts, and will allow far-reaching quantification of chromosome number variation (Peruzzi et al. 2014) and to test their phylogenetic and adaptional effects (Carta et al. 2018) in the future.

Dysploidy and polyploidy caused the extensive chromosome number variation

Our study validates the occurrence of considerable somatic chromosome number variation in Marantaceae. The presumed basic chromosome numbers and the inferred ploidy levels of the studied taxa are specified in Table 1. Our chromosomal survey revealed eleven different somatic chromosome numbers, namely $2n = 20$, 22, 24, 26, 28, 33, 36, 44, 52, 65 and 72, which are considered as multiples of $x = 9$, 10, 11, 12, 13 and 14 as the possibly genuine basic chromosome numbers of the taxa investigated. Consequently, plants with these particular somatic chromosome numbers described above may correspond to diploids, triploids, tetraploids, pentaploids and octoploids, respectively.

Bisson et al. (1968) provided an explanation for the wide variation of chromosome numbers in the family Marantaceae by invoking frequent hybridization of taxa with different basic numbers. He presented a network spanning nearly all arithmetically possible chromosome numbers. However, it should be considered that in general only species with similar karyotypes are easily capable to produce hybrids, whereas species with different karyotypes are usually not able to cross (Baltisberger and Hörandl 2016). Despite this, hybridization is rather frequent in Marantaceae as shown by recent phylogenetic (interspecific) and phylogeographic (intraspecific) studies (Ley and Claßen-Bockhoff 2011; Ley and Hardy 2013, 2014, 2017). However, due to the facts that species of Marantaceae (1) propagate mainly by vegetative means, (2) seed setting after flowering is very rare (Sharma and Bhattacharyya 1958) and (3) the origin of such chromosomal biotypes through sexual reproduction is fairly impossible (Mahanty 1970), we suppose that hybridization plays also, but only an ancillary role in the chromosome evolution of Marantaceae species in our investigation. Few verifiable instances form the triploid *Thalia geniculata* and pentaploid *Marantochloa congensis*, in which meiotic disturbances cannot be excluded. For the taxa of Marantaceae, it is more likely that dysploidy, through gains and losses of single chromosomes or fission and/or fusion of chromosome segments, is the most common mechanism of karyotypic change in the family. Polyploidy, due to the initiation of reproductive isolation between diploids and the established polyploids, is considered the most common mechanism of sympatric plant speciation (Stace 2000; Husband and Sabara 2003; Bolnick and Fitzpatrick 2007; Rieseberg and Willis 2007; Wood et al. 2009; Ramsey 2011). It played seemingly a significant, but not dominant, role in the evolution and diversification of Marantaceae (e.g. potentially in the separation of *Marantochloa congensis,* from its sister species *M. sulphurea* and *M. monophylla*; see Ley and Hardy 2014).

The broad variation of presumed basic chromosome numbers and the relatively low proportion of polyploid taxa found in our study (Table 1, Figs. 2, 3, 4) support the evolutionary significance of karyotype changes through dysploidy, which may have comparatively longer-term persistence over evolutionary time than polyploid changes that fail in many cases to persist (Escudero et al. 2014). Our observations in Marantaceae are in contrast to the attention polyploidy and dysploidy usually received in the literature. While the evolutionary role of polyploidy has been stressed in many reviews, chromosomal change via dysploidy was less regarded. Only a few studies suggested the prevalence of dysploidy in

species diversification among angiosperms so far (e.g. Ray and Chisaki 1957; Grant 1981; Lee and Namai 1993; Vickery 1995; Soltis et al. 2001; Church 2003; Mandakova and Lysak 2018; Winterfeld et al. 2018).

Chromosome structure and trends in chromosome evolution

Data on chromosome morphology are important to understand the variation in chromosome numbers and to identify potentially different genomes within a plant family. So far, karyotype studies of only a few species of Marantaceae have been published (Sharma and Bhattacharyya 1958; Mahanty 1970; Mukhopadhyay and Sharma 1987; Eksomtramage et al. 2007). Our detailed karyotype analyses reveal that the chromosomes are overall comparatively small (< 2 µm in length), and complement lengths (TML) are comparatively short. Mean centromeric asymmetry (M_{CA}) and variation of chromosome lengths (CV_{CL}) within the whole complements are variable. All in all, karyotypes of the studied taxa reveal considerable variation, but it is rather continuous.

Regression analyses of chromosome number (2*n*), ploidy level (pl) and basic chromosome number (*x*) versus karyotype data, such as mean chromosome length (MCL), total length of a monoploid chromosome set (TML), mean centromeric asymmetry (M_{CA}) and interchromosomal asymmetry (CV_{CL}), respectively, were conducted (Fig. 5). The following trends in karyotype evolution were retrieved: There is a linear correlation between 2*n* chromosome number and MCL/TML (Fig. 5a, b; significant in both), meaning that an increase in 2*n* is linked with a decrease in MCL/TML. An increase in 2*n* is coupled with polyploidy as seen in the ploidy-level graph (Fig. 5e, f; significant in f). There are no correlations between 2*n* and M_{CA} (Fig. 5c) as well as between ploidy level and M_{CA} (Fig. 5g). 2*n* and CV_{CL} showed a weak interrelation (Fig. 5d), which is caused mainly by polyploidization (Fig. 5h). Thus, chromosomes of a complement seem to converge in their length after whole-genome duplication. Basic number *x* and MCL revealed a significant linear correlation (Fig. 5i). Some hypotheses were developed for the explanation of chromosome number variation in various angiosperm species (Fusion-, Fission-, Modal-Hypothesis; White 1973; Todd 1970, 1975; Matthey 1973) and to interpret the observed patterns in chromosome morphology and behaviour (e.g. Schubert and Lysak 2011; Lysak et al. 2006; Escudero et al. 2014).

However, the direction of dysploidy change cannot be fully determined in Marantaceae. There are two possibilities: either increasing dysploidy accompanied by decreasing chromosome length (MCL) or, alternatively, decreasing dysploidy accompanied by increasing chromosome length. The latter process leads to fewer and larger chromosomes and is a frequent pattern in monocots following polyploidization (Carta et al. 2018). To reveal its role in diploid and polyploidy Marantaceae and to determine the original basic number in the family, however, a comparison of chromosome data with a molecular phylogenetic framework would be essential, which is not yet available. There is no significant correlation or trend visible for change in *x* and TML, M_{CA} and CV_{CL} values (Fig. 5j, k, l).

Biogeographic differentiation

Variation of chromosome and karyotype characters was analysed in relation to the main distribution areas (America, Africa, Asia) and their species diversity (Fig. 6). All in all, the strongest variation occurred in the taxa of tropical America. They displayed eight different 2*n* chromosome numbers, three ploidy levels and six different basic chromosome numbers. We sampled 17 of about 450 species in this region. Lower variation with six different 2*n* numbers, two ploidy levels (except for triploid and pentaploid hybrids) and four different basic numbers were characteristic of tropical Africa, a region with ca. 50 species, of which we sampled 14 species. The lowest variation occurred in the Asian taxa, of which we studied eight of about 50 species. They had only two different chromosome numbers, two different ploidy levels and were consistently diploid. Mean centromeric asymmetry (M_{CA}) was similar in taxa from all continents. African taxa stood out by low interchromosomal asymmetry (CV_{CL}). Interestingly, high rates of chromosomal variation are characteristic of taxa with low chromosome sizes, both MCL and TML, as typically found in the American taxa (MCL 1.2 µm, TML 14.5 µm; Fig. 6). The lowest chromosomal variation occurred in the Asian taxa having the largest chromosomes (MCL 1.6 µm, TML 18.5 µm). African taxa were intermediate (MCL 1.3 µm, TML 15.5 µm). One explanation would be the fact that smaller genomes might have improved evolvability through benefiting from raising general genome flexibility (Puttick et al. 2015).

If we accept the suggestion of Africa as the original home of the family (Mahanty 1970; Andersson and Chase 2001; Prince and Kress 2006), a karyotype with $x = 13$ could possibly be the phylogenetically ancestral state as hypothesized by Mahanty (1970). Decreasing dysploidy would have led to basic numbers of $x = 11$, 10 and 9. Diploids prevail, and tetraploids occur sporadically such as triploid and pentaploid hybrids (Fig. 6). The relatively low species diversity in Africa is possibly due to higher extinction rates as a result of shrinking lowland tropical forests during the tertiary (Maley 1996; Prince and Kress 2006).

Following Prince and Kress (2006), the New World tropics were reached secondarily by dispersal events from Africa. The enormous species richness in America and higher chromosomal diversity (basic chromosome numbers of $x = 9$, 10, 11, 12, 13, 14; diploid, tetraploid and octoploid

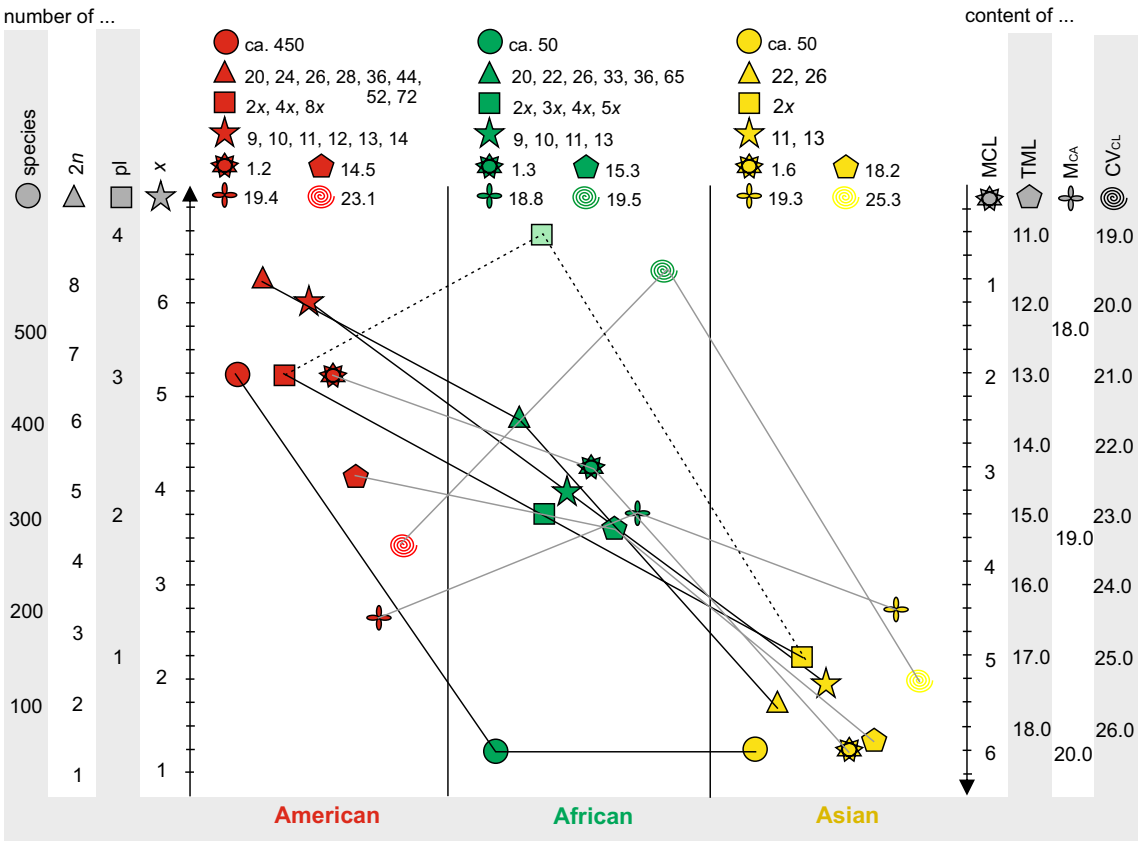


Fig. 6 Relations between chromosome and karyotype data and species diversity in American, African and Asian Marantaceae. Number of different 2*n* chromosome numbers, *pl* ploidy levels, *x* basic chromosome numbers and species number are on the left-hand side. Mean values of karyotype parameters: *MCL* mean chromosome length, *TML* total length of monoploid chromosome set, M_{CA} mean centromeric asymmetry, CV_{CL} interchromosomal asymmetry, are on the right-hand side. The lines between the symbols are only ledger lines for better visualizing of common chromosome parameters from the three areas. The highest variability of chromosome data occurred in America (red), lower variability in Africa and the lowest variability in Asia, which corresponds widely with the respective species diversity

ploidy levels) thus would reflect a secondary radiation and not indicate the original home of the family in America as proposed by Holttum (1951).

The Asian tropics were considered under all scenarios to be colonized secondarily by Marantaceae. On the basis of the present knowledge, the species have a low variation of chromosome features and chromosomes are larger than in the other regions, which might support their status as phylogenetically rather derived.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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