Review of chromosome cytology in *Moraea* (Iridaceae: Irideae): what chromosomes reveal about the evolution of the genus

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ABSTRACT

A review of the chromosome cytology of the African and Eurasian geophytic genus *Moraea* Mill. (currently 214 spp.); including 51 new counts, many for taxa poorly known cytologically or not counted before, that shows that 167 species, representing 78% of the total, have been counted from one or more populations. The inferred ancestral base number is $x = 10$. Polyploidy is relatively rare; available counts indicate that both Eurasian species are tetraploid, but that, among the sub-Saharan species, just nine species (less than 5%) are exclusively polyploid and an additional 15 (7%) have diploid and polyploid populations. Chromosome rearrangement leading to reduced base numbers has occurred in subg. *Polyanthes* ($x = 10$), in which four sections have a base number of $x = 6$. Three subgenera, *Grandiflorae*, *Homeria* and *Vieusseuxia*, also have $x = 6$, but have different karyotypes. Several species and one subspecies are dysploid, all but one with haploid numbers lower than in related species, and are neodysploids. Except for *M. virgata* subsp. *karooica*, dysploidy is interpreted as descending. Fourteen species have diploid and polyploid populations, notably *M. crispa* (subg. *Polyanthes)* and *M. cookii* (subg. *Homeria*), in which the distribution of populations with $2n = 12$, 24 and 36 is correlated with geography. Seven species have euploid and dysploid populations at the diploid level and *M. inclinata* has populations with $2n = 12$ and 22. Differences in chromosome number within species are not normally reflected in external morphology. Compared to most other genera of Iridaceae in sub-Saharan Africa, chromosome number and karyotype are unusually variable so that sampling of multiple populations of species is required to establish these characters. Although many species remain to be examined cytologically, those uncounted are mostly in the species-rich subg. *Grandiflorae* and subg. *Vieusseuxia*, both of which exhibit little variation in chromosome number and karyotype. Chromosome rearrangement and polyploidy appear to have been important in the early evolution of the genus as well as in recent speciation.

INTRODUCTION

The cytology of the Afro-Mediterranean geophytic genus *Moraea* Mill. (currently 214 spp.) of Iridaceae, subfamily Iridoideae, has been the subject of extensive investigation because of the unusually wide variation in chromosome number and karyotype that closely correlate with morphological variation. *Moraea* also exhibits one of the most extensive dysploid reduction series in flowering plants. The correlation between karyology and morphology led Goldblatt (1976a) to propose an infrageneric classification using cytology as a major factor in circumscribing subgenera and sections. The circumscription of *Moraea* was subsequently expanded to include the related genera *Barnardiella* Goldblatt, *Galaxia* Thunb., *Gynandriris* Parl., *Hexaglottis* Vent., *Homeria* Vent. and *Roggeveldia* Goldblatt. These genera were reduced to synonymy in *Moraea* on the basis of inferred morphological, and in some instances cytological, synapomorphies with species groups within *Moraea* (Goldblatt 1998). A molecular DNA-based phylogenetic study of *Moraea* subsequently confirmed Goldblatt's conclusion that *Moraea* is paraphyletic without the inclusion of these genera, thus endorsing its expanded circumscription (Goldblatt *et al*. 2002). That study and a second, more extensive one (Schnitzler *et al*. 2011)

also showed that Goldblatt's (1976a) infrageneric classification of *Moraea* needed extensive revision. Although most of the more distinctive species clusters are monophyletic, subg. *Moraea* included disparate elements and required major revision. In addition, some species or species clusters did not fall in the subgenera or sections to which they had been assigned. Our new classification based on phylogenetic principles and integrating molecular and morphological data recognizes 11 subgenera (Goldblatt *et al*. 2013) and provides a framework for interpreting cytological evolution in the genus. Here we provide a review of chromosome cytology in *Moraea* following this new classification. We include 51 new chromosome reports, several for species known until now from a single count and five for species previously unknown cytologically. Chromosome numbers have now been reported for 167 of the 214 species of *Moraea* currently recognized, representing 78% of the genus, a significant albeit incomplete survey.

MATERIALS AND METHODS

Data on chromosome numbers in *Moraea* were extracted from Goldblatt's (1971) review of the cytology of southern African Iridaceae and from indexes to plant chromosome numbers that included chromosome numbers published after that time (Moore 1974, 1977; Goldblatt 1981c, 1984c, 1985a, 1987a; Goldblatt & Johnson 1990, 1994, 1996, 2000, 2003, 2006, 2010). Counts are tabulated following the revised, phylogenetic infrageneric classification (Goldblatt *et al*. 2013), with species names corrected to reflect current nomenclature and taxonomy. Original sources were consulted for all counts.

We interpret patterns of change in chromosome number and karyotype in light of the plastid DNA-based

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phylogeny, also published in *Bothalia* 43(1), which includes a phylogenetic tree that may be consulted as companion to this review (Goldblatt *et al.* 2013). We then relate the patterns to established hypotheses for interpreting these phenomena by Stebbins (1950, 1971), Jones (1970) and Raven (1975). Briefly, polyploid sequences always proceed from lower to higher numbers by doubling. Stepwise changes, rather than doubling of base numbers are, we believe, largely descending in a process involving translocation of chromosome material to a second chromosome, accompanied by loss of a centromere, some heterochromatin and those genes associated with cell division. The process is here and throughout the text referred to as dysploidy. Descending dysploid reduction sometimes results in translocation of a long chromosome arm of an acrocentric chromosome to the short arm of another and loss of the centromere portion of the donor chromosome, resulting in a large metacentric chromosome and a lower base number, a process often called chromosome fusion or Robertsonian translocation. Translocation of the long chromosome arm of a short acrocentric chromosome to the distal end of the long arm of a second chromosome and loss of the centromere of the donor chromosome yields a longer, acrocentric chromosome.

Original counts

For original counts, root tips of newly sprouted corms were harvested in mid-morning and prepared according to a root tip squash method described by Goldblatt & Takei (1993). Vouchers are housed at the Missouri Botanical Garden Herbarium (MO) and Compton Herbarium (NBG). Counts are based on samples of three to four individuals unless otherwise stated and, following widespread practice in plant cytology, are assumed to represent entire populations.

RESULTS

Chromosome number

The most parsimonious interpretation of the available data shows ancestral basic chromosome number in *Moraea* is $x = 10$. This was first established by outgroup comparison, where $x = 10$ is the base number (and only chromosome base number) for the related genera *Bobartia* L., *Dietes* Salisb. ex Klatt and *Ferraria* Burm. ex Mill. (Goldblatt 1971, 1981c; Goldblatt & Takei 1997). Subsequent DNA sequence-based phylogenetic analyses (Goldblatt *et al.* 2002; Schnitzler *et al.* 2011; Goldblatt *et al.* 2013) are congruent with this hypothesis—species with base numbers of $x = 10$ are consistently retrieved as ancestral to species with other base numbers.

A base of $x = 10$ characterizes the monospecific subg. *Plumarieae*, five (of eight) species counted in subg. *Visciramosae*, and seven (of eight) species counted in subg. *Umbellatae* (Table 1). The three subgenera are collectively sister to the remaining species of *Moraea* [see phylogenetic tree in Goldblatt *et al.* (2013)]. Counts for all but two species are diploid, $2n = 20$, but the two counts for *M. margaretae* (subg. *Umbellatae*) are tetraploid, $2n = 40$. The single count for *M. linderi* is $2n = 30$, thus triploid, but only two individuals of this extremely rare species were available for study and it

seems likely that the species is normally diploid. Subgenera *Acaules*, *Monocephalae* and *Moraea* also have $x = 10$. Two species of subg. *Moraea* are dysploid: *M. indecora* has $2n = 16$ and, as circumscribed at present, *M. papilionacea* has southern populations with $2n = 18$ and a northern Cedarberg population has $2n = 16$ (Goldblatt 1971; 1976a).

In subg. *Acaules*, *Moraea tricolor* has dysploid populations in the west of its range (three populations documented with $2n = 18$), but two pink-flowered populations from the Caledon District (the eastern part of its range) have $2n = 20$. In *M. ciliata* two of ten counts, both from the Caledon District, are tetraploid, $2n = 40$; and one population from Glenlyon, Nieuwoudtville, includes both euploid and dysploid individuals (Goldblatt 1976a). Based on available counts, these six subgenera together have 26 species exclusively diploid, one exclusively tetraploid, one heteroploid, two dysploid at the diploid level, and one (*M. tricolor*) with dysploid and euploid populations.

The specialized, acaulescent subg. *Galaxia*, with all but two of 17 species counted, has $x = 9$. This is the only base number in ser. *Galaxia* (Table 1) and also in the monospecific ser. *Unguiculatae* (sister to ser. *Eurystigma* and *Galaxia*). Ser. *Eurystigma*, in contrast, exhibits an extended dysploid series, $n = 8$, 7, and 6. *M. versicolor* of ser. *Eurystigma* has most populations with $n = 8$ but populations from the northern Cape Peninsula have $n = 7$. *M. galaxia* (ser. *Galaxia*) is heteroploid, with most populations $2n = 36$, thus tetraploid, but one population in the eastern part of its range is diploid, $2n = 18$, and another from the northern end of its range has $2n = 54$, thus hexaploid. Three counts for *M. stagnalis* are also tetraploid, $2n = 36$. Counts for all members of ser. *Eurystigma* are at the diploid level except *M. citrina*, in which three populations counted are diploid with $2n = 16$, one is tetraploid and one dysploid with $2n = 14$ (Goldblatt 1979a).

Subg. *Polyanthes*, now including several species previously assigned to subg. *Moraea* (Goldblatt 1976a) has $x = 10$ in sects. *Deserticola* and *Serpentinae* (Table 1). The four remaining sections all have the derived base of $x = 6$. In the *M. fugax* complex (sect. *Deserticola*), *M. gracilenta* and *M. macrocarpa* have exclusively $2n = 20$ (five populations counted) but races of *M. fugax* have $n = 10$, 9, 8, 7, 6 and 5. Closely allied *M. filicaulis* (also treated as a subspecies of *M. fugax*), has diploid numbers of $2n = 12$ and 10. As noted elsewhere (Goldblatt 1986b), this dysploid series in *M. fugax* is remarkable for a single species, albeit a variable one with distinct morphological races. Outgroup comparison compels us to interpret the series as descending. Significantly, populations of *M. fugax* with $2n = 10$ have about the same genome size as species with $2n = 20$ based on measurements of chromosome length (Goldblatt *et al.* 1986b; Goldblatt & Takei 1997). This independently supports our inference that the pattern in *M. fugax* represents descending dysploidy. An early count of $2n = 28$ in *M. fugax* by Sakai (1952) must be seen as an error: most likely his study material was misidentified.

The remaining four sections of subg. *Polyanthes* (Table 1) have $x = 6$. Sect. *Polyanthes* has exclusively

Table 1.—Chromosome numbers in *Moraea* with collection data for new counts. Unless stated to the contrary, vouchers are at the Missouri Botanical Garden (MO). Herbarium acronyms are abbreviated according to Holmgren *et al.* (1990) and are indicated in parentheses after collection number. Subgenera and sections are arranged in phylogenetic sequence following in Goldblatt *et al.* (2013), but species are arranged alphabetically. For the sake of brevity, collection data for past counts are not included. Abbreviations: S. Africa = South Africa; E. Cape = Eastern Cape; KZN = KwaZulu-Natal, N. Cape = Northern Cape, W. Cape = Western Cape, n/v = no voucher.

Species	Diploid no. 2*n* (number of populations)	Collection data or reference for published counts
Subg. *Plumariae* Goldblatt & J.C.Manning		
M. lugubris (Salisb.) Goldblatt	20 (1)	(Goldblatt 1976a)
Subg. *Visciramosae* Goldblatt		
(uncounted: *M. simplex* Goldblatt & J.C.Manning; *M. vespertina* Goldblatt & J.C.Manning; *M. saldanensis* Goldblatt & J.C.Manning)		
M. bubalina Goldblatt	20 (1)	S. Africa, N. Cape, Soutpan road, *Goldblatt 7074*
M. bituminosa (L.f.) Ker Gawl.	20 (1)	(Goldblatt 1976a)
M. elsiae Goldblatt	20 (2)	(Goldblatt 1976a; Goldblatt & Takei 1997)
M. inconspicua Goldblatt	20 (1)	(Goldblatt 1976a, as *M. viscaria* (L. f.) Ker Gawl.
M. viscaria (L.f.) Ker Gawl.	20 (2)	(Goldblatt 1971; 1976a, as *M. odorata* G.J. Lewis)
Subg. *Umbellatae* Goldblatt & J.C.Manning		
(uncounted *M. intermedia* Goldblatt & J.C. Manning)		
M. cooperi Baker	20 (1)	(Goldblatt 1971)
M. linderi Goldblatt	30 (1)	S. Africa, W. Cape, Cold Bokkeveld, *Goldblatt 8031*
M. longiflora Ker Gawl.	20 (1)	S. Africa, N. Cape, Kamiesberg, *Goldblatt 4317*
M. margaretae Goldblatt	40 (2)	(Goldblatt 1976a)
M. maximiliani (Schltr.) Goldblatt	20 (1)	(Goldblatt 1980a, as *Rheome maximiliani* (Schltr.) Goldblatt)
M. nana (L.Bolus) Goldblatt	20 (3)	(Goldblatt 1987b, as *Hexaglottis nana* L. Bolus); S. Africa, N. Cape, Spektakel Mtns, *Goldblatt 6669.*
M. umbellata Thunb.	20 (1)	(Goldblatt 1987b, as *Rheome umbellata* (Thunb.) Goldblatt)
	30 (3)	(Goldblatt 1980a, 1987b, as *Rheome umbellata* (Thunb.) Goldblatt)
Subg. *Moraea*		
M. gariepensis Goldblatt	20 (1)	(Goldblatt 1986a then undocumented: Namibia), *Goldblatt 7153*
M. gawleri Spreng.	20, 24 (2)	(Goldblatt 1971—latter count now believed to be 20 + 4B)
	20 (2)	S. Africa, W. Cape, Hout Bay, *Goldblatt 4972*; Swellendam to Bontebok Park, *Goldblatt s.n.* n/v
M. indecora Goldblatt	16 (1)	(Goldblatt1986a then undocumented: S. Africa, W. Cape, *Goldblatt 3053*)
M. namaquamontana Goldblatt	20 (1)	(Goldblatt 1986a then undocumented: S. Africa, W. Cape, *Oliver et al. 627*)
M. nubigena Goldblatt	20 (1)	(Goldblatt 1986a then undocumented: S. Africa, W. Cape, *Goldblatt 4208*)
M. papilionacea (L.f.) Ker Gawl.	18 (3)	(Goldblatt 1971; 1976a)
	16 (1)	S. Africa, W. Cape, Cedarberg, *Goldblatt 5136*
M. ramosissima (L.f.) Ker Gawl.	20 (2)	(Sakai 1952; Goldblatt 1971)
M. vegeta L.	20 (3)	(Fernandes & Neves 1961; Goldblatt 1971 as *M. juncea* L.); S. Africa, W. Cape, Hout Bay, *Goldblatt 4973*
M. vlokii Goldblatt	20 (1)	(Goldblatt 1992)
Subg. *Galaxia* (Thunb.) Goldblatt Ser. *Galaxia*		
(uncounted: *M. vuvuzela* J.C.Manning & Goldblatt)		
M. albiflora (G.J.Lewis) Goldblatt	18 (5)	(Goldblatt 1979a, as *G. albiflora* G.J. Lewis)
M. angulata Goldblatt	18(27) (1)	(Goldblatt 1979a, as *G. alata* Goldblatt)
	27 (1)	
M. fugacissima (L.f.) Goldblatt	15 (5)	(Goldblatt 1979a, as *G. fugacissia* (L.f.) Druce)
	16 (1)	(Goldblatt 1971, later corrected to 18)
M. kamiesensis Goldblatt	18 (1)	(Goldblatt 1979a, as *G. grandiflora* Andrews)
M. luteoalba (Goldblatt) Goldblatt	18 (2)	(Goldblatt 1979a, as *G. luteoalba* Goldblatt)
	27 (1)	
M. galaxia Goldblatt & J.C.Manning (all as *Galaxia ovata* Thunb.)	18 (2)	(Goldblatt 1979a)
	36 (5)	
	54 (1)	(Goldblatt 1984a)
	16 (1)	(Goldblatt 1971, later corrected to 18)
M. pilifolia Goldblatt	18 (2)	(Goldblatt 1979a, as *G. ciliata* Pers.)
M. stagnalis (Goldblatt) Goldblatt	36 (3)	(Goldblatt 1979a, as *G. stagnalis* Goldblatt)
Ser. *Eurystigma* (Goldblatt) Goldblatt		

Species	Diploid no. 2*n* (number of populations)	Collection data or reference for published counts
(uncounted: *M. fenestralis* (Goldblatt & E.G.H.Oliver) Goldblatt)		
M. barnardiella Goldblatt	16 (4)	(Goldblatt 1979a, 1984a, as *G. barnardii* Goldblatt)
M. citrina (G.J.Lewis) Goldblatt	16 (3) 34 (1) 14 (1)	(Goldblatt 1971, 1979a, as *G. citrina* G. J. Lewis)
M. melanops Goldblatt & J.C. Manning	16 (1)	(Goldblatt 1979a, as *G. barnardii* Goldblatt)
M. minima Goldblatt	12 (1)	Goldblatt 1984a, as *G. parva* Goldblatt)
M. variabilis (G.J.Lewis) Goldblatt	14 (5)	(Goldblatt 1979a, as *G. variabilis* G. J. Lewis)
M. versicolor (Salisb. ex Klatt) Goldblatt	16 (3) 14 (3)	(Goldblatt 1979a, as *G. versicolor* Salisb. ex Klatt)
Ser. *Unguiculatae* Goldblatt & J.C.Manning		
M. kamiesmontana (Goldblatt) Goldblatt	18 (1)	(Goldblatt 1984a, as *G. kamiesmontana* Goldblatt)
Subg. *Macrocephalae*		
(uncounted: *M. vallisavium* Goldblatt)		
M. angusta (Thunb.) Ker Gawl.	20 (2)	(Goldblatt 1971; Goldblatt & Takei 1997)
M. anomala G. Lewis	20 (1)	(Goldblatt & Takei, 1997)
M. neglecta G.J. Lewis	20 (2)	(Goldblatt 1971, 1976a; Goldblatt & Takei 1997)
Subg. *Acaules*		
(uncounted: *M. longipes* Goldblatt & J.C. Manning)		
M. ciliata (L.f.) Ker Gawl.	20 (7)	(Goldblatt 1971, 1976a; Johnson & Brandham 1997); S. Africa, W. Cape, Cold Bokkeveld, *Goldblatt s.n.* n/v; Nardouwsberg, *Goldblatt 2195*; Cedarberg, Middelberg, *Goldblatt 5131*
	20, 18	(Goldblatt 1976a)
	40 (2)	(Goldblatt 1976a); S. Africa, W. Cape, Bredasdorp Poort, *Goldblatt 6933*
M. falcifolia Klatt	20 (2)	(Goldblatt 1976a)
M. macronyx G.J.Lewis	20 (2)	(Goldblatt 1971; 1976a)
M. tricolor Andrews	18 (3)	(Goldblatt 1976a, as *M. ciliata*); S. Africa, W. Cape, Camphill Village road, *Goldblatt 2178*; Tinnie Versfeld Reserve, Darling, *Goldblatt s.n.* n/v)
	20 (2)	S. Africa, W. Cape, Drayton Siding, *Goldblatt 2516*; W. Cape, near Eseljacht Pass, *Goldblatt s.n.* n/v
Subg. *Polyanthes* (Goldblatt) Goldblatt & J.C.Manning Sect. *Serpentinae* Goldblatt & J.C.Manning		
M. serpentina Baker	20 (4)	(Goldblatt 1971, as *M. framesii* L. Bolus; Goldblatt 1976a)
M. tortilis Goldblatt	20 (1)	(Goldblatt 1976a)
Sect. *Deserticola*		
M. bolusii Baker	20 (1)	(Goldblatt 1976a)
M. filicaulis Baker	12 (4) 10 (3)	(Goldblatt 1971 as *M. diphylla* Baker; 1980b as *M. fugax* subsp. *filicaulis* (Baker) Goldblatt)
M. fugax (D.Delaroche) Jacq.	20 (3) 18 (7) 16 (1) 14 (3) 12 (4) 10 (8)	(Goldblatt 1971; 1986b as *M. fugax* or subsp. *fugax*)
M. gracilenta Goldblatt	20 (2)	(Goldblatt 1976a, as *M. fugax* var. *gracilis* Baker; 1986b)
M. graniticola Goldblatt	20 (1)	(Goldblatt 1986c)
M. herrei (L. Bolus) Goldblatt	20 (3)	(Goldblatt 1976c; Goldblatt & Takei 1997) (as *Barnardiella spiralis* (N.E.Br.) Goldblatt)
M. hexaglottis Goldblatt	20 (1)	(Goldblatt 1986c)
M. macrocarpa Goldblatt	20 (3)	(Goldblatt 1986c)
M. macgregorii Goldblatt	20 (1)	(Goldblatt 1976a)
M. namibensis Goldblatt	20 (1)	(Goldblatt & Takei 1997)
M. rigidifolia Goldblatt	20 (1)	(Goldblatt 1986c)
M. saxicola Goldblatt	20 (1) 20 (1)	(Goldblatt 1976a) S. Africa, N. Cape, Garies–Bitterfontein, *Goldblatt 4257*

Species	Diploid no. 2*n* (number of populations)	Collection data or reference for published counts
Sect. *Hexaglottis* (Vent.) Goldblatt		
M. brevituba (Goldblatt) Goldblatt	24 (1)	(Goldblatt 1987b, as *H. brevituba* Goldblatt)
M. lewisiae (Goldblatt) Goldblatt	12 (4)	(Goldblatt 1987b, as *H. lewisiae* Goldblatt)
M. longifolia (Jacq.) Pers.	24 (2)	(Goldblatt 1987b, as *H. longifolia* (Jacq.) Salisb.)
M. namaquana (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1987b, as *H. namaquana* Goldblatt)
M. riparia (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1987b, as *H. riparia* Goldblatt)
M. virgata Jacq. subsp. *virgata*	12 (5) 10 (4)	(Goldblatt 1987b, as *H. virgata* (Jacq.) Sweet) (Goldblatt 1971, 1987b)
subsp. *karooica* (Goldblatt) Goldblatt	14 (2)	(Goldblatt 1987b, as *H. virgata* subsp. *karooica* Goldblatt)
Sect. *Polyanthes*		
(uncounted: *M. tanquana* Goldblatt & J.C.Manning)		
M. bipartita L. Bolus	12 (3)	(Goldblatt & Takei 1997); S. Africa, W. Cape, near Lemoenshoek, *Goldblatt 4187*; Attaquas Kloof, *Vlok s.n*
M. deserticola Goldblatt	12 (1)	(Goldblatt & Takei 1997)
M. polyanthos Thunb.	12 (8)	(Goldblatt 1971, as *Homeria lilacina* L. Bolus); (Goldblatt 1980a; Goldblatt & Takei 1997); S. Africa, W. Cape, Little Brak River, *Goldblatt 4919*; near Albertinia, *Goldblatt 4954*
M. polystachya (L.f.) Ker Gawl.	12 (5)	(Riley 1962; Goldblatt 1971, Goldblatt 1976a)
M. speciosa (L. Bolus) Goldblatt	12 (2)	Goldblatt 1980a
M. venenata Dinter	12 (1)	(Goldblatt 1976a, as *M. polystachya, Tölken 3985* (BOL)).
Sect. *Pseudospicatae* Goldblatt & J.C.Manning		
(uncounted: *M. afro-orientale* Goldblatt, *M. iringensis* Goldblatt, *M. pearsonii* Goldblatt & J.C.Manning, *M. marginata* J.C.Manning & Goldblatt)		
M. alpina Goldblatt	12 (1)	Lesotho, top of Sani Pass, *Hilliard & Burtt 8773* (E)
M. callista Goldblatt	12 (2)	(Goldblatt & Takei 1997)
M. carsonii Baker	12 (2)	(Goldblatt 1976a; Goldblatt & Takei 1997)
M. crispa Thunb.	12 (6) 24 (4) 36 (1)	(Goldblatt 1980a); S. Africa, W. Cape, near Beaufort West *Esterhuysen s.n.*; N. Cape, Roggeveld, Quaggasfontein, *Goldblatt s.n.* (Goldblatt 1980a); S. Africa, W. Cape, Cedarberg, Krom R., *Goldblatt 5126*; Cedarberg, Eikeboom, *Goldblatt 5128*; N. Cape, near Nieuwoudtville, *Goldblatt s.n.* n/v S. Africa, W. Cape, near Gydo Pass, *Goldblatt 5124*
M. elliotii Baker	12 (2) 24 (1)	(Lewis 1966; Goldblatt 1976a) (Goldblatt 1976a)
M. exiliflora Goldblatt	12 (1)	S. Africa, W. Cape, *Esterhuysen 36122*
M. fistulosa (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1979b, as *Roggeveldia fistulosa* Goldblatt)
M. inclinata Goldblatt	12 (1) 22 (1)	S. Africa, E. Cape, Mhlahlane, *Goldblatt 7595* S. Africa, KZN, Cobham Forest Station, *Hilliard & Burtt 9694* (E)
M. monticola Goldblatt	24 (1)	(Goldblatt 1992, as *Roggeveldia montana* Goldblatt)
M. natalensis Baker	12 (2)	(Lewis 1966, as *M. erici-rosenii* Fries); Zimbabwe, *Goldblatt 5935*
M. pseudospicata Goldblatt	12 (1)	(Goldblatt 1986c)
M. stricta Baker	24 (2) 36 (1) 48 (1) 60 (1)	(Goldblatt 1971, as *M. trita* N.E. Br.); S. Africa, Gauteng, Blyvooruitzicht, *Goldblatt s.n.* no voucher (Goldblatt 1976a) (Goldblatt 1977) Malawi, Nyika Plateau, *Pawek 12942*
M. thomsonii Baker	12 (2)	(Chimphamba 1974); S. Africa, Mpumalanga, Mt. Sheba, *Davidson s.n.* (J)
M. verecunda Goldblatt	12 (1)	S. Africa, N. Cape, Nieuwoudtville, *Holmes s.n.*
Sect. *Gynandriris*		
(uncounted: *M. contorta* Goldblatt)		
M. australis Goldblatt	12 (1)	(Goldblatt 1980b, as *G. australis* Goldblatt)
M. cedarmontana (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1980b, as *G. cedarmontana* Goldblatt)
M. hesperantha (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1980b, as *G. hesperantha* Goldblatt)
M. mediterranea Goldblatt	24 (4)	(Goldblatt 1980b, as *G. monophylla* Boiss. & Heldr. ex Klatt)
M. pritzeliana Diels	12 (3)	(Goldblatt 1971; 1980b, as *G. pritzeliana* (Diels) Goldblatt)
M. setifolia (L.f.) Druce	12 (4)	(Goldblatt 1971; 1980b, as *G. setifolia* (L.f.) R.C.Foster)
M. simulans Baker	24 (1) 36 (1)	(Goldblatt 1980b, as *G. simulans* (Baker) R.C.Foster
M. sisyrinchium (L.) Ker Gawl.	24 (19)	(Goldblatt 1980b and references therein, as *G. sisyrinchium* (L.) Parl.)

Species	Diploid no. 2*n* (number of populations)	Collection data or reference for published counts
Subg. *Vieusseuxia* (D.Delaroche) Baker Sect. *Integres* Goldblatt & J.C.Manning		
M. thomasiae Goldblatt	12 (1)	(Goldblatt 1976a)
Sect. *Vieusseuxia* (D.Delaroche) Goldblatt & J.C.Manning		
(uncounted: *M. albicuspa* Goldblatt; *M. cantharophila* Goldblatt & J.C.Manning; *M. deltoidea* Goldblatt & J.C.Manning; *M. decipiens* Goldblatt & J.C.Manning; *M. dracomontana* Goldblatt; *M. hainebachiana* Goldblatt & J.C.Manning; *M. helmei* Goldblatt & J.C.Manning; *M. lilacina* Goldblatt & J.C.Manning; *M. longiaristata* Goldblatt; *M. modesta* Killick; *M. ogamana* Goldblatt & J.C.Manning; *M. pubiflora* N.E.Br.; *M. rivulicola* Goldblatt & J.C.Manning; *M. vigilans* Goldblatt & J.C.Manning)		
M. algoensis Goldblatt	12 (3)	(Goldblatt 1976a); S. Africa, W. Cape, Karoo Garden,Worcester, *Olivier 138* (NBG); E. Cape, near Hankey, *Goldblatt 4934*
M. amabilis Diels	12 (4)	(Goldblatt 1971 as *M. tripetala*; Goldblatt & Manning 2012)
M. aristata (D.Delaroche) Asch. & Graebn.	12 (1)	(Goldblatt 1976a)
M. atropunctata Goldblatt	12 (1)	(Goldblatt 1982)
M. barkerae Goldblatt	12 (1)	(Goldblatt 1976b)
M. barnardii L.Bolus	12 (1)	(Goldblatt 1976a)
M. bellendenii Ker Gawl.	12 (1)	(Goldblatt 1971)
M. brevistyla (Goldblatt) Goldblatt	12 (1)	S. Africa, KZN, Giants Castle, *Goldblatt & Manning s.n.*
M. caeca Goldblatt	12 (1)	(Goldblatt 1976a)
M. cuspidata Goldblatt & J.C.Manning	12 (1)	(Goldblatt 1976a, as *M. tripetala*)
M. debilis Goldblatt	12 (2)	(Goldblatt 1976a); S. Africa, W. Cape, Caledon District, *Goldblatt 2495*
M. fergusoniae L.Bolus	20 (1) 12 (4)	(Goldblatt 1971—evidently for another species) (Goldblatt & Takei 1997)
M. grandis Goldblatt & J.C.Manning	12 (2)	(Goldblatt 1976a; Goldblatt & Manning 2012)
M. incurva G. Lewis	12 (1)	(Goldblatt & Takei 1997)
M. insolens Goldblatt	12 (1)	(Goldblatt 1976a)
M. lurida Ker Gawl.	12 (3)	(Goldblatt 1971; 1976a)
M. marionae Baker	12 (1)	S. Africa, Mpumalanga, Mt. Sheba, *Davidson 3227* (J)
M. *mutila* (C.H.Bergius ex Eckl.) Goldblatt & J.C.Manning	12 (2)	(Goldblatt & Manning 2012)
M. tricuspidata Goldblatt	12 (1) 24 (4)	(Goldblatt 1976a) (Goldblatt 1976a); S. Africa, E. Cape, Humansdorp, *Goldblatt 4928*; near Grahamstown, *Goldblatt 5129*; W. Cape, Cedarberg, near Eikeboom, *Goldblatt 5129*
M. trifida R.C.Foster	12 (1)	(Goldblatt 1986a)
M. tripetala Goldblatt	12 (5)	(Goldblatt 1976a; Goldblatt & Manning 2012)
M. unguiculata Ker Gawl.	12 (6)	(Goldblatt 1976a, as *M. tenuis* Ker Gawl.; Goldblatt & Takei 1997); S. Africa, N. Cape, near Middelpos, *Goldblatt 6124*; W. Cape, road to Jonas Kop, *Goldblatt 5865*
M. worcesterensis Goldblatt	12 (1)	(Goldblatt 1986c)
Sect. *Villosae* Goldblatt & J.C.Manning		
M. calcicola Goldblatt	12 (1)	(Goldblatt 1982)
M. gigandra L.Bolus	12 (1)	(Goldblatt 1976a)
M. loubseri Goldblatt	12 (1)	(Goldblatt 1976a)
M. tulbaghensis L.Bolus	24 (1) 12 (2)	(Goldblatt 1976a) (Goldblatt & Takei 1997); (Goldblatt 1976a, as *M. neopavonia* R.C.Foster)
M. villosa (Ker Gawl.) Ker Gawl.		
subsp. *villosa*	24 (2)	(Goldblatt 1971))
subsp. *elandsmontana* Goldblatt	12 (1)	(Goldblatt 1982)
Subg. *Grandiflora*		
(uncounted: *M. angolensis* Goldblatt, *M. ardesiaca* Goldblatt, *M. balundana* Goldblatt, *M. bovonei* R.C.Foster, *M. brevifolia* Goldblatt, *M. carnea* Goldblatt, *M. clavata* Goldblatt, *M. hiemalis* Goldblatt, *M. inyangani* Goldblatt, *M. muddii* N.E.Br., *M. reticulata* Goldblatt, *M. robusta* (Goldblatt) Goldblatt, *M. textilis* Baker, *M. unibracteata* Goldblatt, *M. upembana* Goldblatt, *M. verdickii* De Wild.)		
M. alticola Goldblatt	12 (1)	(Goldblatt 1976a)
M. bella Harms	12 (1)	(Goldblatt & Takei 1997)
M. galpinii Baker) N.E.Br.	12 (1)	S.Africa, Mpumalanga, Mt. Sheba, *Murday 1159* (J)
M. graminicola Oberm.	12 (1) 12 (1)	(Goldblatt 1971) S. Africa, KZN, Cobham, *Hilliard & Burtt 9420A* (E)

Species	Diploid no. 2*n* (number of populations)	Collection data or reference for published counts
M. huttonii (Baker) Oberm.	12 (3)	(Goldblatt 1976a); S. Africa, KZN, Umzimonti Valley *Hilliard & Burtt 9405* (E); Free State, NE of Van Reenen, *Hilliard & Burtt 9405* (E)
M. macrantha Baker	12 (3)	(Goldblatt 1977; 1976a as *M. textilis* Baker)
M. moggii N.E.Br.	12 (1)	(Goldblatt 1971)
M. schimperi (Hochst.) Pic.Serm.	12 (5)	(Goldblatt 1976a; Goldblatt & Takei 1997)
M. spathulata (L.f.) Klatt	12 (6)	(Riley 1962; Lewis 1966, as *M. spathacea*; Goldblatt 1971)
M. tanzanica Goldblatt	12 (1)	(Goldblatt 1977)
M. aff. ventricosa Baker	12 (1)	(Goldblatt 1977)
Subg. *Homeria*		
M. aspera Goldblatt	12 (2)	(Goldblatt 1980a, as *H. spiralis* L. Bolus)
M. autumnalis (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1981b, as *H. autumnalis* Goldblatt)
M. bifida (L.Bolus) Goldblatt	12 (4) 12 + 4B (1) 24 (1)	(Goldblatt 1980a, as *H. bifida* L. Bolus)
M. brachygyne (Schltr) Goldblatt	12 (3)	(Goldblatt 1971; 1980a, as *H. brachygyne* Schltr.)
M. britteniae (L.Bolus) Goldblatt	12 (1) 24 (1)	(Goldblatt 1980a, as *H. britteniae* L. Bolus)
M. bulbillifera (G.J.Lewis) Goldblatt	12 (5) 12 +1B (1) 18 (1) 24 (1)	(Goldblatt 1980a, as *H. bulbillifera* G.J. Lewis)
M. cedarmonticola Goldblatt	12 (3)	(Goldblatt 1980a; 1981b, as *H. cedarmontana* Goldblatt)
M. collina Thunb.	24 (11)	(Goldblatt 1980a, as *H. collina* (Thunb.) Salisb.)
M. comptonii (L.Bolus) Goldblatt	12 (5)	(Goldblatt 1980a, as *H. comptonii* L. Bolus)
M. cookii (L.Bolus) Goldblatt	12 (2) 24 (1) 24 (3) 36 (2)	(Goldblatt 1980a; 1992, as *H. cookii* L. Bolus) (Goldblatt 1971, as *H. pallida* Baker) (Goldblatt 1980a)
M. demissa Goldblatt	10 (2) 9 (5) 8 (1)	(Goldblatt 1980a; 1981b, as (as *H. tenuis* Schltr.) (Goldblatt 1981b)
M. elegans Jacq.	12 (3)	(Goldblatt 1980a, as *H. elegans* (Jacq.) Sweet)
M. fenestrata (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1980a, as *H. fenestrata* Goldblatt)
M. flaccida Sweet	24 (2) 36 (7)	(Goldblatt 1980a; 1992, as *H. flaccida* (Sweet) Steud.)
M. flavescens (Goldblatt) Goldblatt	9 (2)	(Goldblatt 1980b, as *H. flavescens* Goldblatt)
M. flexicaulis Goldblatt	12 (1)	(Goldblatt 1982, as *Moraea flexuosa* Goldblatt)
M. fragrans Goldblatt	12 (2)	(Goldblatt 1980a, as *H. odorata* L. Bolus).
M. fuscomontana (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1981b, as *H. fuscomontana* Goldblatt)
M. karooica Goldblatt	12 (3)	(Goldblatt 1980a, as *H. tricolor* G.J.Lewis)
M. knersvlaktensis Goldblatt	12 (1)	(Goldblatt 1980a, as *H. ramosissima* Schltr.)
M. longistyla (Goldblatt) Goldblatt	12 (6)	(Goldblatt 1980a, as *H. longistyla* Goldblatt)
M. louisabolusiae Goldblatt	12 (1)	(Goldblatt 1981b, as *H. bolusiae* Goldblatt)
M. marlothii (L.Bolus) Goldblatt	24 (1)	(Goldblatt 1980a, as *H. marlothii* L. Bolus)
M. miniata Andrews	12 (10) 24 (1)	(Goldblatt 1980a; 1981b, as *H. miniata* (Andrews) Sweet)
M. minor Eckl.	12 (7)	(Goldblatt 1980a; 1992, as *H. minor* (Eckl.) Goldblatt)
M. ochroleuca (Salisb.) Drapiez	12 (2) 24 (2) 24 + 2–3B (1)	(Goldblatt 1980a, as *H. ochroleuca* Salisb.)
M. patens (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1981b, as *H. patens* Goldblatt)
M. pallida (Baker) Goldblatt	12 (2) 8 (4)	(Goldblatt 1971, as *H. glauca* (Wood & Evans) N.E.Br. and *H. pura* N.E. Br.) (Goldblatt 1981b as *H. pallida* Baker)
M. pendula (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1980a, as *H. pendula* Goldblatt)
M. pyrophila Goldblatt	12 (2) 24 (1)	(Goldblatt 1981b; 1992 as *H. galpinii* L. Bolus) (Goldblatt 1980a, as *H. galpinii* L. Bolus)
M. radians (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1984b, as *Sessilistigma radians* Goldblatt)
M. reflexa Goldblatt	12 (1)	(Goldblatt & Takei 1997 as *H. hantamensis* Goldblatt & J.C.Manning)
M. schlechteri (L.Bolus) Goldblatt	12 (5)	(Goldblatt 1980a; 1992, as *H. schlechteri* L. Bolus)
M. serratostyla (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1992, as *H. serratostyla* Goldblatt)
M. vallisbelli (Goldblatt) Goldblatt	12 (2)	(Goldblatt 1980a, as *H. vallisbelli* Goldblatt)

$2n = 12$ in six (of seven) species counted. In sect. *Hexa-glottis*, four of the six species are diploid, $2n = 12$. The remaining two species, *Moraea brevituba* and the auto-gamous *M. longifolia*, are polyploid, $2n = 24$ (Goldblatt 1987b as *Hexaglottis*). Among the diploid species of the section, the widespread *M. virgata* subsp. *virgata* has $2n = 12$ over most of its range but $2n = 10$ in the immediate southwestern Cape populations, these evidently derived from the ancestral $x = 6$ for the section. Subsp. *karooica* of *M. virgata* is evidently also dysploid but has $2n = 14$ in two populations counted (of three known at present). Two very small chromosomes account for the extra pair. The pattern in sect. *Gynandriris* is more complex (Table 1). The two Mediterranean–Middle Eastern species, *M. sisyrinchium* and *M. mediterranea*, are tetraploid, $2n = 24$, for the many populations counted (at least 19 records for *M. sisyrinchium*) (Goldblatt 1980b), and the southern African *G. simulans* is evidently also polyploid, based on two populations sampled, one $2n = 24$ and the other $2n = 36$. Counts for five of the remaining six southern African species, all from the winter-rainfall region of the subcontinent, are exclusively diploid, $2n = 12$, but *M. contorta* remains uncounted.

Largest section of subg. *Polyanthes*, sect. *Pseudo-spicatae* with 13 of 18 species counted, has nine spe-cies exclusively diploid, all $2n = 12$, and two, *M. elliottii* and *M. inclinata*, with diploid and tetraploid populations (Table 1). The latter has $2n = 22$ in the one polyploid population so far recorded, thus hypopolyploid. The widespread *M. stricta,* the range of which extends from Stutterheim in Eastern Cape, South Africa to Ethiopia, has southern populations tetraploid and hexaploid, $2n = 24, 48$, and a population in Malawi, pentaploid, $2n = 60$. Lastly, the comparatively widespread *M. crispa* has diploid, tetraploid and hexaploid populations, all based on $n = 6$. The six Great Karoo and Roggeveld popula-tions sampled are diploid, four Cedarberg populations are tetraploid, and the single Cold Bokkeveld popula-tion, the southernmost sampled, is hexaploid, thus $2n = 36$. The only count for *M. monticola* is tetraploid, thus $2n = 24$, in one of its two known populations.

For subg. *Polyanthes* as a whole, 34 (77%) of the spe-cies counted are exclusively diploid (including diploid level dysploids), seven (16%) are exclusively polyploid, and three (7%) have diploid and polyploid populations.

The remaining subgenera, *Grandiflora*, *Homeria* and *Vieusseuxia* all have $x = 6$ (Table 1). Although the molecular phylogeny (see phylogenetic tree in Goldblatt *et al.* 2013) retrieves them as possibly sharing a com-mon ancestor (with weak statistical support), each has a different karyotype, suggesting that $x = 6$ may have been achieved independently in each. The majority of species are diploid. For subg. *Grandiflora*, cytologically least well known of the subgenera, 11 of 28 species have been counted: all are diploid, $2n = 12$, and have an almost identical karyotype (Goldblatt 1971; Goldblatt & Takei 1997). In subg. *Vieusseuxia*, 28 of 42 species are known from at least one count. Of these 25 are exclusively dip-loid and just three, *M. tricuspidata*, *M. tulbaghensis* and *M. villosa*, have diploid and tetraploid populations. No species is exclusively polyploid.

The cytology of subg. *Homeria* is particularly inter-esting for its diversity: 21 of the 35 species (all counted)

are exclusively diploid with $2n = 12$. Dysploid reduction at the diploid level has been documented in *Moraea pal-lida*, which has its easternmost populations diploid, $2n = 12$, and the western populations $2n = 8$. The latter are complex heterozygotes forming chromosome rings at meiosis (Goldblatt 1980c). In western South Africa, *M. demissa* has $2n = 10, 9$ and 8; and the only number so far known for *M. flavescens* (two populations sampled) is $2n = 9$. These last two species, like unrelated *M. pal-lida*, are also complex heterozygotes, forming various patterns of chromosome rings at meiosis (Goldblatt 1986c). Both are autogamous and produce full cap-sules of normal-looking viable seeds. Seven species, *M. bifida*, *M. britteniae*, *M. bulbillifera*, *M. cookii*, *M. miniata*, *M. ochroleuca* and *M. pyrophila*, have diploid and tetraploid populations (just one each of the several populations counted for *M. bifida* and *M. miniata*). The particularly widespread *M. cookii* has diploid, tetraploid and hexaploid populations and a pattern with a clear geographical component, with diploids occurring in the Western Karoo, tetraploids in the mountains of the Great Karoo, and hexaploids in the interior mountains of West-ern Cape. *M. flaccida* has both tetraploid and hexaploid populations and several counts for *H. collina* and the only one for *M. marlothii* are tetraploid, $2n = 24$. Thus on available data, only three (8%) of the 35 species of subg. *Homeria* counted, are exclusively polyploid.

Genome size

Chromosomes of all *Moraea* species, and most other members of Iridoideae, are relatively large compared with those of other subfamilies of Iridaceae (Goldblatt 1971; Goldblatt & Takei 1997), directly reflecting larger genome sizes. Total DNA per cell in most diploid spe-cies is in the range 15–27 pg (Goldblatt *et al.* 1984c) using the correction factor determined by Goldblatt & Takei (1997). *Dietes* and *Ferraria*, the other African members of tribe Irideae (to which *Moraea* belongs), have a similar genome size and comparably large chro-mosomes. In *Moraea*, chromosomes of subg. *Galaxia* are the smallest in the genus (Goldblatt 1971), evidently a derived condition: the one diploid species sampled, *M. fugacissima*, has just 4.8 pg per cell, somewhat less than half that in other subgenera. In subg. *Vieusseuxia*, species of sect. *Villosae* have particularly large chro-mosomes and a genome size of $\pm$ 27 pg in the diploid *M. calcicola* and $\pm$ 54 pg in polyploid samples of *M. tulbaghensis* and *M. villosa*. The single species of sect. *Vieusseuxia* sampled, *M. unguiculata*, has a genome size of $\pm$ 19.7 pg, thus consistent with most other subgen-era. Genome size in subg. *Grandiflorae* is evidently the largest in the genus, as determined by chromosome size alone. Comparing chromosome volume (not length), Goldblatt (1971) showed that *M. spathulata* ($2n = 12$) (subg. *Grandiflorae*) has about twice as much chromo-some material as *M. ramosissima* (subg. *Moraea*) and *Dietes*, both $2n = 20$. By extension, we infer a genome size in subg. *Grandiflorae* of about twice that for diploid species of other subgenera, excluding *Vieusseuxia* sect. *Villosae*.

Karyotype morphology

Although not clear from early illustrations made using sections of root tips (e.g. Goldblatt 1971), the *x*

= 10 karyotypes appear moderately bimodal under root tip squash methods (Goldblatt 1976a; Goldblatt & Takei 1997). The chromosome complements consist of three long acrocentric chromosome pairs and seven medium to short ± acrocentric pairs about half the length of the long pairs, e.g. in *M. elsiae* (subg. *Visciramosae*), *M. anomala* (subg. *Monocephalae*) and even in *M. herrei* (Goldblatt 1976c as *Barnardiella spiralis*) and *M. namibensis* (subg. *Polyanthes*). Karyotypes in *Ferraria*, sister to *Moraea*, are comparable, as are those for *Dietes* (Goldblatt 1971, 1981a; De Vos 1979), sister to *Ferraria + Moraea* (Goldblatt *et al*. 2002; Schnitzler *et al*. 2011). Most species have small satellites on the distal end of one of the longest chromosome pairs but satellite position is variable and satellites are located in different positions in several species.

Each of the three subgenera in which *x* = 6 is ancestral are characterized by somewhat different karyotypes, thus consistent with a hypothesis that the reduced base number evolved independently in each. In subg. *Grandiflorae* karyotypes are strongly conserved and are fairly symmetric, with all chromosomes acro- to subtelocentric. Size differences are minimal in all species counted (Goldblatt 1971) but the longest and fourth longest pairs are consistently acrocentric. Satellites are located on the short arm of a long telocentric chromosome pair (third longest pair of the complement) in most species counted.

Karyotypes in subg. *Homeria* are also conserved and symmetric in all species with *x* = 6. The complement comprises six nearly equal acrocentric pairs, with a small satellite located on the distal end of the short arm of one of the two longest pairs (Goldblatt 1971, 1980a). In the three species with lower numbers, 2*n* = 10, 9 and 8, karyotypes are asymmetric and include one or more pairs of very long metacentric chromosomes ± twice the length of the acrocentrics.

Subg. *Vieusseuxia* exhibits some variation in its karyotypes, but in general the largest chromosome pair is metacentric or almost so and there are two additional, smaller metacentric or submetacentric pairs. The position of satellites is especially variable, but small satellites are located on the short arm of a long, acrocentric chromosome pair in the majority of species examined cytologically (*Moraea algoensis, M. amabilis, M. barnardii, M. caeca, M. calcicola, M. cuspidata, M. loubseri, M. marionae, M. tricuspidata, M. unguiculata, M. worcesterensis*). A notable exception is *M. tripetala*, in which a large satellite is present on the short arm of a nearly telocentric chromosome pair (Goldblatt & Manning 2012). This feature readily separates it from close allies, which have different karyotypes, most of them typical of the subgenus.

Other notably different karyotypes in subg. *Vieusseuxia* include very large satellites on the short arm of an acrocentric chromosome pair in *Moraea insolens* and *M. lurida*, a closely allied species pair, and small satellites in the longest, metacentric pair in *M. bellendenii, M. mutabilis, M. tulbaghensis* and *M. villosa*. Particularly unusual for the subgenus, the karyotype of the taxonomically isolated *M. thomasiae* has five acrocentric chromosome pairs, one submetacentric pair, and unusually large satellites on the short arm of a long acrocentric pair, a feature reminiscent of the karyotype of *M. tripetala*. *M. fergusoniae*, the only species of the subgenus with multiple leaves (and referred in the past to subg. *Moraea*) has a karyotype comparable to that of *M. thomasiae* with large satellites on a long acrocentric chromosome pair, but the smallest chromosome pair is metacentric (Goldblatt 1971, 1976a and unpublished). Evidently chromosome rearrangement, often involving the position of the satellite, has been important in the evolution of the subgenus, and is sometimes a useful indicator of phylogenetic relationship among species. Karyotypes are, as far as known, consistent within a species but most (with the exception of *M. fergusoniae, M. tripetala* and *M. amabilis*) are known from only one or two counts, rendering this conclusion open to verification.

In subg. *Polyanthes*, karyotypes of sect. *Polyanthes* and *Pseudospicatae*, with *x* = 6, are comparable and differ mainly in the position of the satellites. The longest and one other pair are submetacentric and the remaining pairs are acrocentric. The karyotype of *M. polystachya* documented by Goldblatt (1976a) has a small satellite at the distal end of the long arm of the longest acrocentric pair, the same karyotype as in *M. venenata* (published as *M. polystachya* and not illustrated). Other species examined have small satellites on a small acrocentric pair. Satellite position is evidently variable, even with the same species (e.g. in *M. crispa* and *M. polyanthos*) and evidently without taxonomic significance (Goldblatt 1980a, 1986c). One of two populations of the Tanzanian *M. callista* examined is structurally heterozygous with one long and one short metacentric chromosome (Goldblatt & Takei 1997), the significance of which remains to be established.

In sect. *Hexaglottis* the ancestral karyotype consists of six nearly equal acrocentric pairs, with a small satellite present on the distal end of the short arm of one of the two longest pairs (Goldblatt 1987b). *Moraea lewisiae* subsp. *secunda* has a distinctive karyotype for the group, with the longest chromosome pair metacentric and with a small satellite located at the distal end of the shortest chromosome pair. As discussed in more detail below, in *M. virgata* (*x* = 6), southwestern Cape populations of subsp. *virgata* have 2*n* = 10 and *M. virgata* subsp. *karooica* has 2*n* = 14, thus both one subspecies is dysploid and the other has dysploid populations. The basic karyotype in the section recalls that in subg. *Homeria*, evidently the result of convergence.

The karyotype in sect. *Gynandriris* is the most distinctive in subg. *Polyanthes,* consisting of one long metacentric pair, one small metacentric pair and four moderate-sized acrocentrics, one or sometimes two of which have large satellites on their short arms. The polyploid *M. monophylla* and *M. sisyrinchium* have the same karyotype with two sets of chromosome pairs otherwise matching the diploid karyotypes. Evidence is consistent with an independent origin of *x* = 6 in sect. *Gynandriris* and a shared origin of that base in sect. *Polyanthes* and sect. *Pseudospicatae*, but possibly not for sect. *Hexaglottis*.

Dysploidy

There are six known dysploid species in *Moraea*: *M. indecora* and *M. papilionacea* (subg. *Moraea*), *M. variabilis* and *M. minima* (subg. *Galaxia*), and *M. demissa* and *M. flavescens* (subg. *Homeria*). Several more have euploid and dysploid populations. In addition, subg. *Galaxia* is itself dysploid, as is ser. *Eurystigma* of subg. *Galaxia*. Subgenera *Grandiflora, Vieusseuxia* and *Homeria*, all $x = 12$, are dysploid as are four of six sections of subg. *Polyanthes*. Dysploidy in populations of otherwise euploid species is associated with no visible morphological changes except in *M. virgata*. Here the taller, larger-flowered subsp. *karooica* has an extra pair of small chromosomes, thus $2n = 14$ (vs. $2n = 12$ in 5 populations of subsp. *virgata* and $2n = 10$ in four more) and is sufficiently distinct in morphology to merit taxonomic separation. All but one of these examples clearly represents descending dysploidy.

Among the dysploid species two different patterns of chromosome rearrangement are evident. The first is exemplified by *M. indecora* ($2n = 16$), which has two large metacentric pairs (plus one long acrocentric pair bearing a small satellite on the short arm and five short ± acrocentric pairs) whereas its relatives with $2n = 20$ have only acrocentric chromosomes. The reduction in base number is best explained by fusion of small chromosome pairs, the probable result of Robertsonian translocation (the product of unequal reciprocal translocation and loss of a pair of centromeres, *fide* Jones 1970). In *M. papilionacea*, which has populations with $2n = 18$ and $2n = 16$, there are one or two pairs of large metacentric chromosomes respectively (Goldblatt 1971 and unpublished).

In subg. *Galaxia* both this and a second pattern, the absence of metacentric chromosomes in the dysploid derivatives, are evident. The subgenus has a basic karyotype with the derived $2n = 18$ and consists of 9 pairs of acrocentric chromosomes. Base number in ser. *Eurystigma* is $x = 8$, again derived, and consisting only of acrocentric chromosome pairs. However, dysploid populations of *M. versicolor* with $n = 7$ have a pair of large metacentric chromosomes. *M. variabilis* is also dysploid, $n = 7$, but the karyotype consists only of acrocentric pairs (Goldblatt 1979a).

In the most striking example of descending dysploidy, *Moraea fugax* displays a sequence of diploid chromosome numbers from the ancestral $2n = 20$ to 10 (Goldblatt 1986b). In the blue- or white- or pink-flowered morph, karyotypes with $n = 10$, 9 and 8 have exclusively acrocentric chromosomes but the $n = 7$ morphs have the largest pair metacentric and one $n = 6$ morph has two large metacentric chromosome pairs. In the yellow-flowered morph of the species with $n = 8$, 7 and 5, the $n = 8$ population has the largest pair metacentric, the $n = 7$ population has two large metacentric pairs and the $n = 5$ pair has the three largest pairs metacentric.

In these examples, the dysploid populations or taxa thus exhibit both patterns of karyotype change with about equal frequency.

DISCUSSION

In *Moraea*, only narrowly endemic species can be confidently predicted to have a single chromosome number. In more widespread species, multiple counts for different populations across their ranges are needed to establish chromosome number. Of 166 species counted, no less than 14 species have diploid and polyploid populations and another seven have euploid and dysploid populations at the diploid level and one at the polyploid level (*M. inclinata*). Chromosome number and karyotype in *Moraea* are unusually variable compared to most other genera of Iridaceae in sub-Saharan Africa, which mostly display very conservative karyotypes. However, in *Lapeirousia* and *Romulea* (subfam. Crocoideae) at least, dysploidy and subsequent polyploidy have been involved in their evolution and speciation (Goldblatt & Takei 1993, 1997). Although many species of *Moraea* remain to be examined cytologically, uncounted species are mostly in the species-rich subg. *Grandiflorae* and subg. *Vieusseuxia*, both of which to date have exhibited no variation in chromosome base number and, in subg. *Vieusseuxia,* only moderate variation in karyotype.

Polyploidy

Although believed to be a significant mode of speciation in many floras (Stebbins 1950, 1971; and see review by Soltis *et al*. 2010), polyploidy appears relatively unimportant in the rich geophytic flora of sub-Saharan Africa, and of particularly the Greater Cape flora. Just 11 of the 166 species of *Moraea* for which we have counts are exclusively polyploid, thus less than 7%, and 15 more (9%) have diploid and polyploid populations. Of the polyploid species, two are Eurasian, thus only 9 of 164 sub-Saharan (African) species of *Moraea* counted (5.5%), are exclusively polyploid. This is consistent with a low frequency of neopolyploidy in other sub-Saharan geophytic monocot families.

For example, in Hyacinthaceae, which are particularly well represented in southern Africa, available counts in subfam. Hyacinthoideae show that 16 of 101 counted species (16%) of *Eucomis* L'Herit, *Lachenalia* J.Jacq. ex Murray and *Massonia* Thunb. ex Houtt. are exclusively polyploid, and a further 18 (18%) have diploid and polyploid populations (Goldblatt *et al.* 2012). However, five genera, including *Eucomis*, have polyploid base numbers, and are thus evidently palaeopolyploid. In sub-Saharan members of subfam. Ornithogaloideae (Goldblatt & Manning 2011), only one of the 24 species of *Ornithogalum* L. and three of 23 species of *Albuca* L. subg. *Albuca* counted are exclusively polyploid. In subfamily Urgineoideae only one of 14 counted sub-Saharan species of *Drimia* Jacq. is exclusively polyploid (7%). In contrast, polyploidy is relatively frequent in Eurasian species of *Ornithogalum, Drimia* and most of the larger genera of Hyacinthoideae. Among southern African Amaryllidaceae and Colchicaceae, both smaller geophyte families, there are no recorded polyploid species.

In other Iridaceae, only five of 70 (7%) sub-Saharan species of *Gladiolus* L. sampled cytologically so far have polyploid populations whereas all 10 to 12 Eurasian species are exclusively polyploid (Goldblatt *et al.*

1993). Among other sub-Saharan genera of Iridaceae subfam. Crocoideae with at least 10 species the frequency of neopolyploidy ranges from 0% (*Babiana* Ker Gawl., *Crocosmia* Planch., *Freesia* Klatt, *Hesperantha* Ker Gawl., *Tritonia* Ker Gawl.), to 3–6% (*Romulea* Maratti, *Sparaxis* Ker Gawl., *Watsonia* Mill.) to 8–12% (*Geissorhiza* Ker Gawl., *Ixia* L.) based on current, moderate sampling (Goldblatt 1971, 1985b; Goldblatt & Takei 1997).

Dysploidy provides a means of reproductive isolation in populations in the same way as polyploidy; and thus appears to have played almost as much a role in evolution and, by inference, speciation in *Moraea* as has polyploidy. Five species and one subspecies are what may be called neodysploids (dysploid at and below species rank) vs. 11 neopolyploids. More important, four subgenera (*Galaxia, Grandiflorae, Homeria* and *Vieusseuxia*) are palaeodysploid, as are ser. *Eurystigma* of subg. *Galaxia* and also sections *Hexaglottis, Gynandriris, Polyanthes* and *Pseudospicatae* of subg. *Polyanthes*. Dysploidy appears to be largely unidirectional in *Moraea*, with all but one example of dysploidy most parsimoniously inferred as descending. There is just one instance of ascending dysploidy, in *M. virgata* subsp. *karooica*, in which the karyotype has one small additional chromosome pair in both of the two populations examined (of three currently known).

Moraea is therefore one of the relatively few genera of flowering plants in which polyploid changes in chromosome number and chromosome rearrangement leading to dysploidy have been established as important factors in its early diversification and subsequent more recent speciation. Considerations of the determinants of speciation need to take these phenomena into account as much as geography and ecological factors such as shifts in soil, habitat and climate preferences, and reproductive and pollination biology. Chromosome rearrangement and polyploidy have played important roles in the evolution of the genus as well as in recent speciation.

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