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## Review

# A review of chromosome cytology in Hyacinthaceae subfamilies Urgineoideae and Hyacinthoideae (tribes Hyacintheae, Massonieae, Pseudoprosperae) in sub-Saharan Africa

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**Abstract**

The chromosome cytology of subfamilies Hyacinthoideae and Urgineoideae of the monocot family Hyacinthaceae are reviewed for their centres of diversity in sub-Saharan Africa within the framework of a recent molecular-based classification. We also provide some new chromosome counts for genera or species that are unknown or poorly known cytologically. We conclude that the ancestral basic chromosome number for Hyacinthoideae is  $x=10$  but tribe Pseudoprosperae evidently has  $x=9$ , the most likely base in Hyacintheae. Tribe Massonieae has five of the nine (out of 10) genera counted apparently ancestrally tetraploid with  $2n=40$  and we infer a basic chromosome number for the tribe of  $x=10$  based on patterns within the tribe and by outgroup comparison. An extensive descending dysploid series is present in *Lachenalia*, ranging from a possible ancestral base of  $x=10$  to  $n=5$ , and several species are polyploid or have diploid and polyploid populations. Basic number in Urgineoideae is also  $x=10$  and the subfamily exhibits little divergence from that base among sub-Saharan species. Polyploidy at species rank is relatively rare among the sub-Saharan members of both subfamilies. Based on available data just 7% of species of Urgineoideae and 15% of sub-Saharan Hyacinthoideae are species level polyploids but several more have diploid and polyploid populations. This conforms to the pattern of low level of polyploidy in subfamily Ornithogaloideae of Hyacinthaceae and other sub-Saharan families of geophytic plants.

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**Keywords:** Africa; Base numbers; Chromosome cytology; Hyacinthaceae; Hyacintheae; Hyacinthoideae; Massonieae; Pseudoprosperae; Urgineoideae**Contents**

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## 1. Introduction

Recent, molecular-based classifications of Hyacinthaceae recognize four subfamilies: the monogeneric South American Oziroëoideae and the three much larger Old World Hyacinthoideae, Ornithogaloideae and Urgineoideae (Manning et al., 2004). Subfamily Hyacinthoideae is subdivided into three tribes, the species-rich Eurasian Hyacintheae, the monospecific southern African Pseudoprosperae, and the predominantly sub-Saharan African Massonieae with 10 genera and  $\pm 104$  species in Africa and southern Asia. Urgineoideae are largely sub-Saharan African with several species in Eurasia as far east as India. Massonieae has a similar distribution but with a marked secondary radiation in Eurasia. This review complements the similar study in Ornithogaloideae (Goldblatt and Manning, 2011) and completes our cytological review for the family in sub-Saharan Africa.

Chromosome counts for Hyacinthoideae and Urgineoideae are widely scattered in the literature, many of them published under genera and species that are now relegated to synonymy. We assemble here all published counts for the two subfamilies excluding Hyacintheae (none of which occur in sub-Saharan Africa), under their current names and arranged according to the most recent infrafamilial classification (Manning et al., 2004). We also provide some new chromosome counts for genera and species uncounted or poorly known. We analyze the patterns of variation in chromosome number in relation to the molecular phylogeny, infer basic numbers for genera and sections, and highlight important gaps in our knowledge of the cytology of the subfamilies. These gaps limit a deeper understanding of the chromosomal evolution in some lineages of Hyacinthoideae but we infer an ancestral base for both Hyacinthoideae and Urgineoideae of  $x=10$ , which we also identified as the likely base number in the sister clade Ornithogaloideae (Goldblatt and Manning, 2011).

## 2. Materials and methods

### 2.1. Published counts

Data on chromosome number in genera of Hyacinthoideae and Urgineoideae were extracted from indexes to plant chromosome numbers covering the years since chromosome numbers were first made available in accessible compilations (Bolkhovskikh, 1969; Goldblatt, 1981; Goldblatt and Johnson, 1990; Moore, 1973, 1974, 1977, etc.; see Tables 2 and 3). We tabulate counts according to the current subfamilial classification, with species names corrected to reflect current nomenclature and taxonomy (Manning et al., 2004). Original sources were consulted for most

counts, especially those we had reason to question. We had hoped to check voucher specimens for questionable counts but those for the important contribution by De Wet (1957) could not be located at PRE where they had been deposited (C. Archer pers. comm. 2009). Most papers published before the 1980s do not list voucher specimens. There is no precedent for ignoring chromosome counts not linked to voucher specimens and we see no reason to do so here. Examples of doubtful identification are discussed in the text and noted in Table 3.

Patterns of change in chromosome number and karyotype are inferred using established hypotheses for these phenomena (Jones, 1970; Raven, 1975; Stebbins, 1950, 1971). Polyploid sequences are interpreted as proceeding from lower to higher numbers by doubling. Dysploid (aneuploid) sequences, i.e. stepwise changes rather than doubling of base numbers, are widely believed to be largely descending in a process involving translocation of chromosome material to a second chromosome and loss of a centromere plus those genes associated with cell division. Descending dysploid reduction frequently results in translocation of a long arm of an acrocentric chromosome to the short arm of another and loss of the centromere of the donor chromosome, resulting in a large metacentric chromosome (and lower base number), a process often called chromosome fusion or Robertsonian translocation.

We do not list authorities for species in the text as these are included in Tables 2 and 3.

### 2.2. Original counts

Material for the original counts reported here (Fig. 2; Table 1) was prepared according to the protocol described by Goldblatt and Takei (1993). The vouchers are housed at the Missouri Botanical Garden Herbarium (MO) and Compton Herbarium (NBG). Counts are based on samples of three to four individuals and are assumed to represent entire populations, following widespread practice in plant cytology.

Table 1

New chromosome counts in Massonieae and Urgineae. Vouchers are housed at the Missouri Botanical Garden (MO) and Compton (NBG) Herbaria.

Species	Diploid number, $2n$	Voucher data
<i>Daubenyia aurea</i>	32	South Africa, N Cape, Roggeveld Plateau west of Sutherland, Hall 3269 (NBG)
<i>Drimia capensis</i>	60	South Africa, N Cape, Nieuwoudtville, Goldblatt 6537 (MO)
<i>Massonia depressa</i>	18	South Africa, N Cape, Nieuwoudtville, Goldblatt 6097 (MO)
<i>M. echinata</i>	22	South Africa, N Cape, Bushmanland, Goldblatt & Manning 13042 (MO)

### 3. Results

The results of our review of the literature and our original counts are presented in Tables 1–3. Postulated ancestral numbers are plotted on Fig. 1. Karyotypes for three of the four species counted for this study are illustrated in Fig. 2.

### 4. Discussion

#### 4.1. *Urgineoideae*

*Urgineoideae* comprise the two genera *Bowiea* (1 sp.) and *Drimia* (including *Litanthus*, *Rhadamanthus*, *Rhodocodon*,

Table 2

Chromosome numbers in *Drimia* (*Urgineoideae*) circumscribed after Manning et al. (2004). Numbers were culled from the *Atlas of Chromosome Numbers of Flowering Plants* (Bolkhovskikh, 1969) and *Index to Plant Chromosome Numbers* (Goldblatt, 1981, 1984, 1985, 1987; Goldblatt and Johnson, 1990, 1991, 1994, 1996, 1998, 2000, 2003, 2006, 2010; Moore, 1973, 1974, 1977). Original counts are indicated in bold type. *Urginea langii* Brem., reported by (De Wet, 1957) to have  $2n=20$ , is *Albuca seineri* (Engl. & Krause) J.C.Manning & Goldblatt and we discuss the significance of the count in the text.

<i>Bowiea</i> Harv. ex Hook.f. [1 sp.]	
<i>B. volubilis</i> Harv.	$2n=20$ (Schnarf and Wunderlich, 1939; D'Amato, 1949; De Wet, 1957; Jones and Smith, 1967, and as <i>B. kilimandscharica</i> Mildbr.; Bruyns and Vosa, 1987; Stedje and Nordal, 1987, as <i>B. kilimandscharica</i> )
<i>Drimia</i> Jacq. (including <i>Litanthus</i> Harv., <i>Rhadamanthus</i> Salisb., <i>Schizobasis</i> Baker, <i>Tenicroa</i> Raf., <i>Thuranthos</i> C.H.Wright, <i>Urginea</i> Steinh.) [ $\pm 100$ spp.; 36 counted]	
<i>D. elata</i> Jacq.	$2n=18$ (De Wet, 1957; Fernandez and Neves, 1962, as <i>D. alta</i> R.A.Dyer; Bruyns and Vosa, 1987, as <i>D. ciliaris</i> Jacq. ex Willd.)
<i>D. altissima</i> (L.f.) Ker Gawl.	$2n=20$ (De Wet, 1957; Jones and Smith, 1967, as <i>Urginea altissima</i> Baker); Stedje and Nordal, 1987) (counts of $2n=32$ by De Wet, 1957 as <i>U. epigaea</i> R.A.Dyer must be for another species)
<i>D. calcarata</i> (Baker) Stedje	$2n=22$ (Oyewole, 1975, as <i>U. altissima</i> ) $2n=20$ (De Wet, 1957, as <i>Urginea tenella</i> Baker) $2n=40$ (De Wet, 1957 as <i>Urginea pretoriensis</i> ) $2n=40$ plus 2 fragments (De Wet, 1957 as <i>Urginea rubella</i> )
<i>D. capensis</i> (Burm.f.) Wijnands	$2n=60$ (new count, Table 1)
<i>D. congesta</i> (Wight) Stearn	$2n=20$ (Yadav and Dixit, 1990, as <i>Urginea congesta</i> Wight)
<i>D. convallarioides</i> (Salisb.) J.C.Manning & Goldblatt	$2n=20$ (De Wet, 1957, as <i>Rhadamanthus convallarioides</i> Salisb.)
<i>D. delagoensis</i> (Baker) Jessop	$2n=32$ (De Wet, 1957, as <i>Urginea lydenburgensis</i> R.A.Dyer)
<i>D. depressa</i> (Baker) Jessop	$2n=20$ (De Wet, 1957, as <i>Urginea depressa</i> Baker)
<i>D. exigua</i> Stedje	$2n=20$ (Stedje and Nordal, 1987)
<i>D. fugax</i> (Moris) Stearn var. <i>fugax</i>	$2n=20+0-8B$ (Battaglia and Guanti, 1968, as <i>Urginea fugax</i> (Moris) Steinh.) $2n=20$ (Talavera et al., 1995, <i>U. fugax</i> (Moris) Steinh. var. <i>fugax</i> ) $2n=20$ (Talavera et al., 1995, as <i>U. fugax</i> var. <i>major</i> Lit. & Maire ex Maire)
<i>D. fugax</i> var. <i>major</i> Maire	$2n=20$ (De Wet, 1957)
<i>D. haworthioides</i> Baker	$2n=18$ (Bruyns and Vosa, 1987)
<i>D. hesperia</i> (Webb. & Berth.) J.C.Manning & Goldblatt	$2n=28$ (Bramwell et al., 1972, as <i>Urginea hesperia</i> Webb. & Berth.)
<i>D. indica</i> (Roxb.) Jessop	$2n=20$ (Raghavan and Venkatasubban, 1940; Jha, 1989; Boraiah and Khaleel, 1970; Naik, 1976, all as <i>Urginea indica</i> Kunth; Stedje and Nordal, 1987 and many other counts) $2n=20, 40, 60$ (Jha and Sen, 1983, as <i>Urginea indica</i> Kunth) $2n=20$ (Watters and Ornduff, 1985, as <i>Schizobasis intricata</i> Baker) $2n=18$ (Bruyns and Vosa, 1987, as <i>S. intricata</i> )
<i>D. intricata</i> (Baker) Baker	$2n=20$ (De Wet, 1957, as <i>Thuranthos macranthum</i> (Baker) C.H.Wright)
<i>D. macrantha</i> (Baker) Baker	$2n=20+4B$ (Stedje, 1996)
<i>D. macrocarpa</i> Stedje	$2n=20, 40, 60, 60+1B, 60+2B$ (as <i>Urginea maritima</i> L.: Boscaiu et al., 2001; Fernández et al., 2001; Talavera et al., 1995; Oberprieler and Vogt, 1994 and many more counts indexed)
<i>D. maritima</i> (L.) Stearn	$2n=20$ (Battaglia, 1957)
<i>D. maura</i> Maire	$2n=20$ (De Wet, 1957, as <i>Urginea multisetosa</i> Baker)
<i>D. multisetosa</i> (Baker) Jessop	$2n=20$ (Oyewole, 1988, as <i>Urginea pauciflora</i> (Baker) Baker)
<i>D. pauciflora</i> Baker	$2n=20$ (Bruyns and Vosa, 1987, as <i>Rhadamanthus platyphyllus</i> B.Nord.)
<i>D. platyphylla</i> (B.Nord.) J.C.Manning & Goldblatt	$2n=20$ (Kamble and Ansari, 1976; Yadav and Dixit, 1990, both as <i>Urginea polyantha</i> Blatt.)
<i>D. polyantha</i> (Blatt. & McCann) Stearn	$2n=20, 30$ (Raghavan and Venkatasubban, 1940, as <i>Urginea polyphylla</i> Hook.f.)
<i>D. polyphylla</i> (Hook.f.) M.Y.Ansari & Sundararagh	$2n=20$ (Yadav and Dixit, 1990, as <i>Urginea razii</i> (M.Y.Ansari) Deb & Dasgupta)
<i>D. razii</i> M.Y.Ansari	$2n=20$ (De Wet, 1957; Jones and Smith, 1967, as <i>Urginea burkei</i> Baker)
<i>D. sanguinea</i> (Schinz) Jessop	$2n=20$ (Bruyns and Vosa, 1987, as <i>Litanthus pusillus</i> Harv.)
<i>D. uniflora</i> J.C.Manning & Goldblatt	$2n=20$ (Martinoli, 1954; Battaglia, 1957; Bartolo et al., 1984, all as <i>Urginea undulata</i> (Desf.) Steinh; Valdes-Bermejo, 1980)
<i>D. undata</i> Stearn	$2n=20$ (Jones and Smith, 1967, as <i>Schizobasis</i> sp.)
<i>D. sp.</i>	$2n=40$ (Naik, 1973; Naik, 1976; Dixit and Yadav, 1989, all as <i>Urginea coromandeliana</i> Hook.f.)
<i>D. sp.</i>	$2n=22$ (Oyewole, 1975, as <i>Urginea gigantea</i> (Jacq.) Oyewole)
<i>D. sp.</i>	$2n=20$ (Boraiah and Khaleel, 1970, as <i>Urginea govindappae</i> Boraiah and Fathima)
<i>D. sp.</i>	$2n=20$ (Boraiah and Fathima, 1972, as <i>Urginea govindappensis</i> Boraiah & Fathima)
<i>D. sp.</i>	$2n=40$ (Satô, 1942, as <i>Urginea scilla</i> Steinh.)
<i>D. sp.</i>	$2n=60$ (Miege, 1960, as <i>Urginea nigritana</i> Baker)
<i>D. sp.</i>	$2n=20$ (Martinoli, 1954; Battaglia, 1957; Bartolo et al., 1984, all as <i>Urginea undulata</i> (Desf.) Steinh.)
<i>D. sp.</i>	$2n=20$ (Oyewole, 1988, as <i>Urginea ensifolia</i> (Thonn.) Hepper)
<i>D. sp.</i>	$2n=22$ (Oyewole, 1975, as <i>Urginea viridula</i> Baker)

Table 3

Chromosome numbers in Massonieae arranged following the classification of Manning et al. (2004). Numbers were culled from the *Atlas of Chromosome Numbers of Flowering Plants* (Bolkhovskikh, 1969) and *Index to Plant Chromosome Numbers* (Goldblatt, 1981, 1984, 1985, 1987; Goldblatt and Johnson, 1990, 1991, 1994, 1996, 1998, 2000, 2003, 2006, 2010; Moore, 1973, 1974, 1977). *Namophila* U.Müll.-Doblies & D.Müll.-Doblies (1 sp.), is uncultured. Original counts are indicated in bold type; doubtful counts are marked \* and listed in parentheses after accepted counts.

<i>Daubenya</i> Lindl. [10 spp., 4 counted]	
<i>D. capensis</i> (Schltr.) A.M. Van der Merwe & J.C.Manning	2n=34 (Brandham, 1990a, as <i>Androsiphon capense</i> Schltr.)
<i>D. aurea</i> Rendle	2n=32 (Wetschnig and Pfosser, 2003) 2n=32 (new count, Table 1)
<i>D. stylosa</i> (Barker) A.M. Van der Merwe & J.C.Manning	2n=32 (Brandham, 1990b; Johnson and Brandham, 1997, as <i>Amphisiphon stylosa</i> Barker)
<i>D. zeyheri</i> (Kunth) J.C.Manning & A. Van de Merwe	2n=34 (Wetschnig and Pfosser, 2003, as <i>Massonia zeyheri</i> Kunth.)
<i>Eucomis</i> L'Her. [11 spp.; 10 counted, 1 estimated for ploidy level]	
<i>E. autumnalis</i> (Mill.) Chitt.	2n=60 (Satô, 1942; Riley, 1962; Reyneke and Liebenberg, 1980) 2n=30 (Delay, 1947, as <i>E. undulata</i> L'Hér.) 2n=60 (Satô, 1942; Fernandez and Neves, 1962, both as <i>E. undulata</i> L'Hér.)
<i>E. bicolor</i> Baker	2n=30 (Matsuura and Sutô, 1932) 2n=30–32 (Reyneke and Liebenberg, 1980)
<i>E. comosa</i> (Houtt.) Wehrh.	2n=30, 60 (Reyneke and Liebenberg, 1980) 2n=30 (Matsuura and Sutô, 1932; Satô, 1942, as <i>E. punctata</i> L'Hér.) 2n=60 (Riley, 1962, as <i>E. punctata</i> L'Hér.)
<i>E. grimshawii</i> Duncan & Zonn.	diploid, based on genome size, number not established (Zonneveld and Duncan, 2010)
<i>E. humilis</i> Baker	2n=60 (Reyneke and Liebenberg, 1980)
<i>E. montana</i> Compton	2n=60 (Reyneke and Liebenberg, 1980)
<i>E. pallidiflora</i>	2n=60 (Satô, 1942) [*De Wet's (1957) report of 2n=50 for the species as <i>E. pole-evansii</i> N.E.Br. indicates tetraploidy but the count is evidently inaccurate] 2n=60 (Satô, 1942)
<i>E. regia</i> (L.) L'Hér.	2n=30 (De Wet, 1957; Reyneke and Liebenberg, 1980) 2n=60 (Riley, 1962)
<i>E. schiffii</i> Reyneke	2n=30–32 (Reyneke and Liebenberg, 1980)
<i>E. vandermerwei</i> I.Verdc.	2n=30 (Reyneke and Liebenberg, 1980) [*the count of 2n=20 by De Wet (1957) is clearly an error]
<i>E. zambesiaca</i> Baker	2n=30–32 (Reyneke and Liebenberg, 1980)
<i>Lachenalia</i> J.Jacq. ex Murr. [±120 spp.; 86 counted] see text	
<i>Ledebouria</i> Roth [±45 spp.; 22 counted]	
<i>L. apertiflora</i> (Baker) Jessop	2n=24 (Fernandez and Neves, 1962, as <i>Scilla linearifolia</i> Baker) 2n=26 (Venter, 1993)
<i>L. barteri</i> (Baker) J.C.Manning & Goldblatt	2n=20 (Kootin-Sanwu, 1969, as <i>Drimiopsis barteri</i> Baker) 2n=22, 44 (Stedje and Nordal, 1987, as <i>D. barteri</i> )
<i>L. botryoides</i> (Baker) J.C.Manning & Goldblatt subsp. <i>botryoides</i>	2n=44, 55, 66 (Stedje and Nordal, 1987; Stedje, 1994, 1996, as <i>Drimiopsis botryoides</i> Baker subsp. <i>botryoides</i> ) 2n=20 (De Wet, 1957, as <i>Drimiopsis crenata</i> Van der Merwe) 2n=64 (Gill, 1978, as <i>L. volkensii</i> Baker) 2n=22 (Stedje, 1994, 1996)
<i>L. botryoides</i> subsp. <i>prostrata</i> Stedje	2n=22 (Stedje, 1994, 1996)
<i>L. burkei</i> (Baker) J.C.Manning & Goldblatt subsp. <i>burkei</i>	2n=44 (Lebatha et al., 2003, as <i>Drimiopsis burkei</i> Baker subsp. <i>burkei</i> )
<i>L. burkei</i> subsp. <i>stolonissima</i> (U.Müll. Doblies & D.Müll. Doblies) J.C.Manning & Goldblatt	2n=40 (Lebatha et al., 2003, as <i>Drimiopsis burkei</i> subsp. <i>stolonissima</i> U.Müll. Doblies & D.Müll. Doblies)
<i>L. camerooniana</i> (Baker) Speta	2n=46 (Giménez-Martin, 1959, as <i>Scilla camerooniana</i> Baker)
<i>L. concolor</i> (Baker) Jessop	n=18 (Jessop, 1972b)
<i>L. cooperi</i> (Hook.f.) Jessop	n=12, 14, ca. 22 (Jessop, 1970) n=10, 13, 15 (Jessop, 1972b)
<i>L. ensifolia</i> ((Eckl.) S.Venter & T.J.Edwards)	2n=30 (Venter, 1993)
<i>L. floribunda</i> (Baker) Jessop	n=18 or 19 (Jessop, 1970) n=10, 11, 17, 30 (Jessop, 1972b)
<i>L. humifusa</i> (Baker) J.C.Manning & J.C. Manning & Goldblatt	2n=10 (Wetschnig and Pfosser, 2003, as <i>Resnova humifusa</i> (Baker) U.Müll. Doblies & D.Müll. Doblies) 2n=20 (De Wet, 1957, as <i>Drimiopsis saundersii</i> Baker)
<i>L. hyacinthina</i> Roth.	2n=20 though often with irregular meiosis (summary of many published counts by Wetschnig et al., 2007)
<i>L. kirkii</i> (Baker) Stedje & Thulin	2n=60 (Vij et al., 1982, as <i>Drimiopsis kirkii</i> Baker) 2n=66 (Sharma, 1970; Sen, 1973a, 1973b, as <i>D. kirkii</i> ) 2n=68 (Mahalakshma and Sheriff, 1970, as <i>D. kirkii</i> )
<i>L. luteola</i> Jessop	n=46 (Jessop, 1972b)
<i>L. marginata</i> (Baker) Jessop	n=13 (Jessop, 1972b)
<i>L. nossibeensis</i> (H.Perr.) J.C. Manning & Goldblatt	2n=30 (Wetschnig et al., 2007)
<i>L. petiolata</i> J.C. Manning & Goldblatt	2n=60 (Fernandez and Neves, 1962, as <i>Drimiopsis maculata</i> Lindl.) n=15, ca. 26 (Jessop, 1972a, as <i>D. maculata</i> ) 2n=64 (Satô, 1942; Delay, 1947, both as <i>D. maculata</i> )
<i>L. pusilla</i> (U.Müll. Doblies & D.Müll. Doblies) J.C. Manning & Goldblatt	2n=44 (Lebatha et al., 2003, as <i>Drimiopsis pusilla</i> U.Müll. Doblies & D.Müll. Doblies)

(continued on next page)



Table 3 (continued)

<i>Daubenya</i> Lindl. [10 spp., 4 counted]	
<i>L. revoluta</i> (L.f.) Jessop	$n=15$ (Jessop, 1970) $n=9, 10, 11$ (22), 12, 13, 15 16, 17 (Jessop, 1972b) $2n=28$ (Stedje, 1996)
<i>L. socialis</i> (Baker) Jessop	$n=13, 15$ (Jessop, 1972b)
<i>L. somaliensis</i> (Baker) Stedje & Thulin	$2n=30$ (Stedje, 1996)
<i>L. undulata</i> (Jacq.) Jessop	$n=18, 18$ or 19 (Jessop, 1970) $n=10, 13, 14, 15$ (Jessop, 1972b) $2n=30$ (Giménez-Martin, 1959, as <i>Scilla undulata</i> Baker) $2n=20$ (Stedje, 1996)
<i>L. urceolata</i> Stedje	
<i>Massonia</i> [ $\pm 9$ spp., 4 counted]	
<i>M. bifolia</i> (Jacq.) J.C.Manning & Goldblatt	$2n=40$ (Wetschnig and Pfosser, 2003, as <i>Whiteheadia bifolia</i> (Jacq.) Baker) $2n=26^*$ (Johnson and Brandham, 1997) [*perhaps a misidentification] $2n=18$ (new count, Table 1)
<i>M. depressa</i> Houtt.	$2n=18$ (Johnson and Brandham, 1997) $2n=22$ (new count, Table 1)
<i>M. echinata</i> L.f.	$2n=22$ (Johnson and Brandham, 1997)
<i>M. pustulata</i> Jacq.	$2n=22$ (Johnson and Brandham, 1997)
<i>Merwillia</i> Speta [3 or 4 spp.; 1 sp. counted]	
<i>M. plumbea</i> (Lindl.) Speta ( <i>krausii</i> form)	$2n=40$ (Wetschnig and Pfosser, 2003, as <i>M. krausii</i> (Baker) Speta)
( <i>natalensis</i> form)	$2n=32$ (De Wet, 1957, as <i>Scilla natalensis</i> Planch.) $2n=40$ (Giménez-Martin, 1959, as <i>Scilla natalensis</i> Planch.) $n=20$ (or 21) (Ratter and Milne, 1973, as <i>Scilla</i> aff. <i>natalensis</i> Planch.)
<i>Schizocarphus</i> Van der Merwe [1 sp.]	
<i>S. nervosus</i> (Burch.) Van der Merwe	$2n=40$ (Wetschnig and Pfosser, 2003) $2n=42$ (Jessop, 1970) [*counts of $2n=28$ for the species and $2n=56$ for its synonym <i>S. gerrardii</i> (Baker) Van der Merwe by De Wet (1957) are evidently for another plant] $2n=38$ (Chaudhuri and Sen, 2001)
<i>Spetaea</i> Wetschnig & Pfosser [1 sp.]	
<i>S. lachenaliiflora</i> Wetschnig & Pfosser	$2n=20$ (Wetschnig and Pfosser, 2003)
<i>Veltheimia</i> Gled. [2 spp.]	
<i>V. bracteata</i> Harv. ex Baker.	$2n=40$ (Coleman, 1940; Delay, 1947, both as <i>V. viridiflora</i> Jacq.)
<i>V. capensis</i> (L.) DC.	$2n=40$ (Satô, 1942, as <i>V. glauca</i> (Aiton) Jacq.; Nordenstam, 1969)

*Schizobasis*, *Tenicroa*, *Thuranthos*, *Urginea* and a few more,  $\pm 100$  spp.) (Manning et al., 2004). The majority of species counted are diploid with  $2n=20$  (Table 2). Polyploidy is recorded

in the only count for the western South African *D. capensis*,  $2n=60$  and thus hexaploid, and both counts for *U. coromandeliana* (the combination in *Drimia* remains to be made),  $2n=40$  and thus

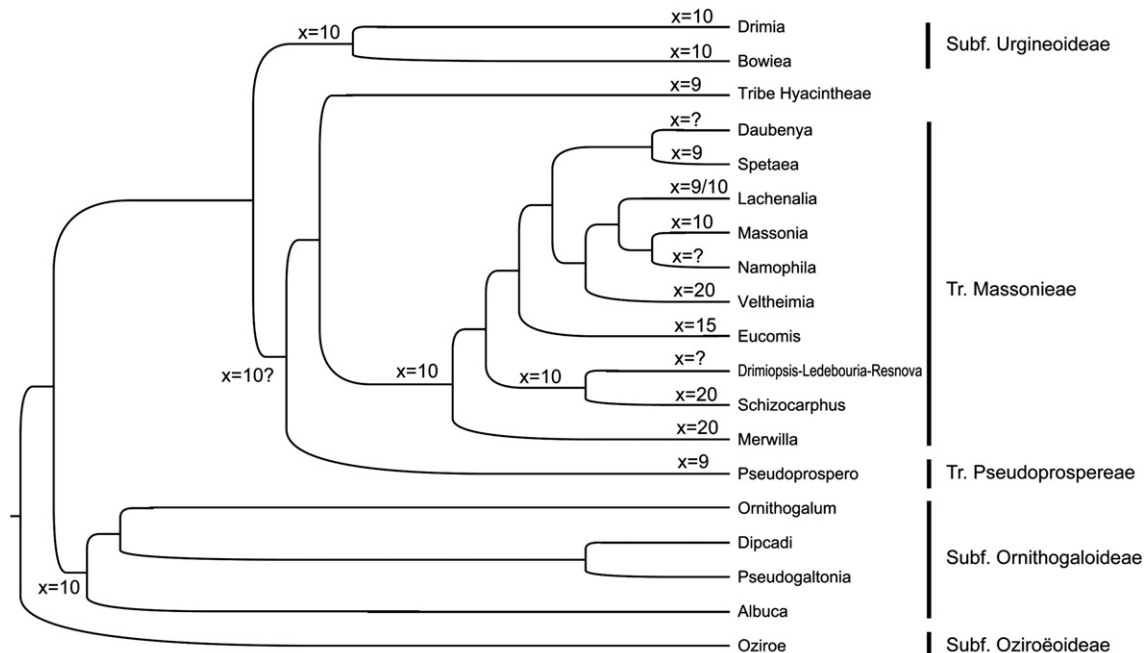


Fig. 1. Phylogeny of Hyacinthaceae with genera of Massonieae and Urgineoideae, showing the relationships of subgenera and sections, with inferred basic chromosome numbers indicated on branches of the tree (adapted from Manning et al., 2009).

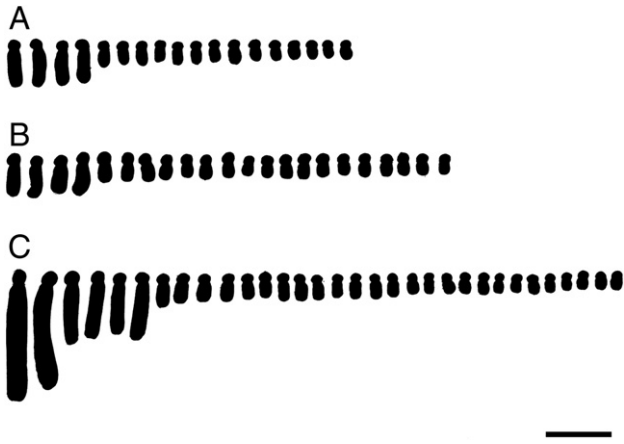


Fig. 2. Karyotypes of *Massonia depressa* (A), *M. echinata* (B) and *Daubenya aurea* (C). Scale bar=10  $\mu$ m.

tetraploid. The Eurasian *D. maritima* has races with  $2n=20$ , 40 and 60, occasionally with B chromosomes. Most counts for *D. indica* are  $n=20$ , but there are also reports of  $n=40$  and 60 for the species. The two counts for *D. elata* are both  $2n=18$  and we regard this as a dysploid species. The karyotype consists of one long metacentric pair plus two longer acrocentric and six short pairs (De Wet, 1957), a pattern consistent with fusion of two short chromosomes. Two counts are available for *D. intricata*, one  $2n=20$  and the other  $2n=18$ . If correct this last count represents a dysploid population within the species. In light of the overwhelming predominance of  $x=10$  in the subfamily, the single count of  $2n=28$  for *D. hesperia* is puzzling and should be confirmed. Karyotypes in *Drimia*, as in many Hyacinthaceae, are bimodal. Our karyotype (Table 1 but not illustrated) for *D. capensis* included 12 long acrocentric chromosome pairs and a balance of small acrocentric to submetacentric pairs half to less than half as long as the long pairs. In southern Africa, *Drimia calcarata* stands out in having diploid and polyploid counts, evidently in different populations.

Total DNA content per cell in Urgineoideae is established only for *Bowiea volubilis*,  $1C=4.63$  pg (Bennett and Smith, 1976).

Although there are no formally published counts for the *Tenicroa/Sypharissa* group of *Drimia* (Table 2), Speta (1998) indicated that *Tenicroa* has  $2n=20$ , without references and without listing the species counted. This is consistent with Urgineoideae. Numbers cited by Speta (1998) for three other generic synonyms of *Drimia*, again without referencing sources or species counted, are more problematic, namely those for *Rhadamanthopsis* ( $2n=18$ , 16 and 12), *Rhadamanthus* ( $2n=18$ ) and *Urgineopsis* (including only *D. salteri* (Compton) J.C.Manning & Goldblatt,  $2n=14$ ). In light of all other published chromosome numbers in *Drimia*, these counts are questionable, and require full documentation. In comparison, published counts for two species of *Rhadamanthus* (now included in *Drimia*) are both  $2n=20$  (Table 2).

*Urginea langii* Brem., counted by De Wet (1957), is a synonym of *Albuca seineri* (Engl. & Krause) J.C.Manning & Goldblatt (Ornithogaloideae). De Wet's count of  $2n=20$  for the species is consistent with our suggested base number of  $x=10$

for *Albuca* subg. *Namibiogalum*, to which *A. seineri* was referred by Goldblatt and Manning (2011). The only other published count for *A. seineri* is  $2n=24$  (Vosa, 1980). When discussing the cytological evolution of *Albuca* we were unable to explain the significance of Vosa's (1980) count and the strongly bimodal karyotype, which was inconsistent with that of *A. donaldsonii* Rendle ( $2n=20$ ), only other member of subg. *Namibiogalum* counted. The karyotype of *A. donaldsonii* described by Stedje and Nordal (1984) [as *Ornithogalum donaldsonii*] is moderately asymmetric but not bimodal. The karyotype illustrated by De Wet (1957) accords broadly but not exactly with *A. donaldsonii*. We conclude that Vosa's (1980) count is more likely for another species, possibly for a member of *Albuca* subgen. *Urophyllon* in which *A. seineri* (as *Ornithogalum*) was included at the time of Vosa's count (Obermeyer, 1978) and in which karyotypes are consistently bimodal.

Based on the scenario above it seems reasonable to hypothesize that the basic, ancestral chromosome number in *Bowiea* and *Drimia*, and thus for Urgineoideae as a whole, is  $x=10$  (Fig. 2), not  $x=5$  as suggested by De Wet (1957). On available data, just one of the 14 counted species of *Drimia* in sub-Saharan Africa is exclusively polyploid, representing 7% of those species that have been examined cytologically.

#### 4.2. Hyacinthoideae

Based on the two available counts, *Pseudoprospero firmifolium* (Baker) Speta, only species of tribe Pseudoprosperaeae, has  $2n=18$  (De Wet, 1957; Jessop, 1970 [as *Scilla firmifolia* Baker]). The karyotype illustrated by De Wet (1957) consists of a graduated series of relatively large chromosomes, both acrocentric and metacentric. This suggests a base number for Pseudoprosperaeae of  $x=9$ . The genus and tribe are thus evidently dysploid and derived from our hypothetical ancestral base of  $x=10$  as found in the outgroup Urgineoideae (Fig. 2).

We have not examined the cytology of the largely Eurasian Hyacintheae (12–20 genera, for which there are numerous counts) in detail but the following observations are relevant to our review. Wetschnig and Pfosser's (2003) phylogeny of Hyacintheae places *Barnardia scilloides* Lindl. (= *Scilla scilloides* (Lindl.) Druce) as sister to the remaining members of the tribe included in their study. *B. scillararis* may have  $x=9$ , although the cytology of the species is complex, with numbers of  $2n=16$ , 18, 34 and 36, sometimes with B chromosomes (e.g. Araki, 1972; Bang and Choi, 1993; Haga, 1962; Haga and Noda, 1956). *B. numidica* (Poir.) Speta (= *Scilla numidica* Poir.), which has not been sequenced for phylogenetic study, has  $2n=18$  (Cardona, 1991) but no other species of the genus appear to have been studied cytologically. We offer a preliminary hypothesis that  $x=9$  is ancestral for Hyacintheae, which seems at least plausible given the phylogenetic position of *Barnardia* in the tribe and the base numbers in related tribes but we refrain from further speculation (Fig. 2).

In Massonieae, the only counts for *Merwillia*, sister to the remainder of Massonieae, are  $2n=40$  (Table 3) (we ignore De Wet's report of  $2n=32$  for *M. plumbea* [as *Scilla natalensis*] as it is obviously erroneous). The taxonomically isolated

*Schizocarphus* also has  $2n=40$  (again we question De Wet's report of  $2n=28$  and 56 in this genus). The count of  $2n=38$  for the genus by Chaudhuri and Sen (2001) may represent dysploid plants. Their calculation of total DNA per cell of  $4C=16.18$  pg ( $1C=4.03$ ) appears inconsistent with polyploidy because *Veltheimia*, with the same diploid chromosome number, has  $1C$  values of 9.99 and 10.73 pg (see below). Although cross genus comparisons of  $C$  value cannot always be relied to produce valid inferences of homology and ploidy level this merits mention here. Additional counts are needed to establish that there are no diploid populations in these two genera, both of which are relatively widespread.

All counts for both species of *Veltheimia*, sister to *Massonia* plus the uncounted *Namophila* (Fig. 2), are also  $2n=40$  (Table 3). Total DNA for both species, determined by Zonneveld et al. (2005), are  $1C=9.99$  and 10.73 pg (chromosome numbers not recorded for either sample), which is consistent with polyploidy when compared to  $1C$  values for *Massonia* (mean value for three species  $1C=3.20$  pg) and for *Bowiea volubilis* ( $1C=4.63$  pg;  $2n=20$ ). Like *Merwillia* and *Schizocarphus*, *Veltheimia* must be inferred, on available data, to be ancestrally tetraploid.

In *Massonia* the only count for *M. bifolia* (= *Whiteheadia bifolia*), sister to the remaining species of *Massonia*, is  $2n=40$ , thus evidently tetraploid, but other species of *Massonia* (Fig. 2, Table 3) appear to be ancestrally diploid, with  $2n=18$  and 22. The report of  $2n=26$  for *M. depressa* by Johnson and Brandham (1997) may be for some other species. Karyotypes in the genus are moderately bimodal. In our sample of *M. depressa* we recorded two long and seven shorter chromosome pairs, and for *M. echinata* two long and nine short pairs (Fig. 2). Total DNA per cell is known for three species, *M. depressa* ( $1C=3.36$  pg), *M. pustulata* ( $1C=3.19$  pg) and *M. sp.* ( $1C=3.05$  pg) (Zonneveld et al., 2005). Although chromosome numbers were not recorded for these samples we provisionally assume that each was diploid as this is the only ploidy level recorded for the two named species. Despite the limitations of cross genus comparisons, we note that genome size in these *Massonia* species (mean  $1C=3.20$  pg for the three species examined) is consistent with ancestral diploidy when compared with genome size in *Bowiea* (Urgineoideae) ( $1C=4.63$  pg). Additional counts in *Massonia*, in which only half the species have been counted, will be helpful in interpreting the cytological evolution of the genus. Based on available data, we hypothesize an ancestral base for *Massonia* of  $x=10$ , with *M. bifolia* interpreted as tetraploid, although this is based on a single count and possibly a single plant (Table 3). Records of  $2n=22$  in *Massonia* may represent the presence of B chromosomes or ascending dysploidy.

*Lachenalia*, with  $\pm 120$  spp., is the largest of the sub-Saharan genera of Hyacinthaceae (Goldblatt and Manning, 2000), and sister to the *Namophila*–*Massonia* clade (Fig. 2). It is cytologically complex (e.g. Hamatani et al., 2004; Ornduff and Waters, 1978; Spies et al., 2009) and we do not list the numerous published counts for the genus, in which some 86 species have been counted. A descending dysploid series is evident, with diploid numbers of  $2n=20, 18, 16, 14, 12$  and 10, with  $2n=14$  the most common number (in 30 spp.). Notably *L. mutabilis* has populations with  $2n=7, 6$  and 5. Some 18 species have  $2n=16$

and nine species have  $2n=18$ . Two species, *L. comptonii* and *L. undulata*, have  $2n=20$  and seven have  $2n=11$ . Of the species counted, 15 are exclusively polyploid, most on secondary base numbers of  $x=14$  or 11; and 14 more have diploid and polyploid populations. Just one species of the *Polyxena/Periboea* group, which is deeply nested in *Lachenalia*, has been counted, *L. ensifolia* (Thunb.) J.C. Manning & Goldblatt, with  $2n=24$  and 26 (Johnson and Brandham, 1997). The species may be tetraploid on a secondary base. Most available cytological studies do not illustrate karyotypes (or at least not accurately enough), preventing comparisons of total chromosome length among species with different numbers as a crude estimate of ploidy level.

We hypothesize an ancestral base of  $x=10$  or 9 for *Lachenalia* as most likely in light of our inferred base number of  $x=10$  for the sister clade, *Veltheimia* and *Massonia* (plus the uncounted *Namophila*). Evolution and classification of *Lachenalia* should be viewed with this hypothesis in mind. Measurements of total chromosome length (or total DNA) would help refine our understanding of which species are polyploid, and hence establish more reliably the ancestral base for the genus. According to our hypothesis of an ancestral base of 10 or 9, species with base numbers lower than  $n=10$  would be derived and those with base numbers above  $n=10$  would be polyploid. Little more can be said of the cytological situation here until a molecular-based phylogeny of the genus is available but cytology appears likely to be useful in determining relationships and evolution within *Lachenalia*.

For the *Spetaea/Daubenya* clade (Fig. 2), the monospecific *Spetaea* has  $n=10$  (Table 3) and a remarkable bimodal karyotype consisting of one pair of very large chromosomes, one medium-sized pair, and the remainder very small chromosomes (Wetschnig and Pfosser, 2003). In *Daubenya* two of the four species counted have  $2n=32$  and the other two have  $2n=34$ . As in *Spetaea*, karyotypes are bimodal. The karyotype in the population of *D. aurea* that we examined (Fig. 2) consisted of three long and 13 very short chromosome pairs (less than one third the length of the long chromosomes) and is clearly not directly polyploid.

Total chromosome length, a proxy for total DNA content, is 230 mm in our preparations in *Daubenya aurea* compared with 116 mm in *Massonia* species with diploid numbers of  $2n=18$  or 22 (measured in millimetres on metaphase karyotypes using the same preparation method). Provisionally, based on available counts and total chromosome length measurements, it seems most reasonable to conclude that *Daubenya* is palaeotetraploid. Although this is the most parsimonious conclusion for ploidy level in *Daubenya*, other explanations cannot be excluded, although we are unaware of any that accord with the data. Accordingly we suggest as a possible hypothesis dysploid reduction in the ancestors of the *Daubenya* clade to  $n=9$  or 8, followed by polyploidization and subsequent secondary dysploid reduction to  $n=17$  and 16. Additional counts for the genus, in which only four of the 10 species have been examined cytologically, are needed to expand and refine our understanding of its cytological evolution.

The phylogenetically isolated genus *Eucomis* (11 spp.) has  $x=15$  (Table 3). [If *E. autumnalis* subsp. *amaryllidifolia* is



recognized as a separate species on the basis of its diploid status in an otherwise tetraploid species, as suggested by Zonneveld and Duncan (2010), the genus has 12 species]. Four species (or five if *E. amaryllidifolia* is recognized) are exclusively diploid,  $2n=30$ , and four (or five) are exclusively tetraploid (depending on the status of *E. autumnalis* subsp. *amaryllidifolia*). Most counts for *E. regia* are diploid,  $2n=30$ , but there is one of  $2n=60$  (Riley, 1962) suggesting a polyploid population. Records of  $2n=30$ – $32$  may indicate the presence of B chromosomes or merely difficulty in obtaining an exact count. Karyotypes are markedly bimodal, some with three pairs of long acrocentric (macro-) chromosome pairs in diploid species, but the karyotypes of *E. bicolor* and *E. zambesiaca* each have a prominent metacentric pair, possibly an indication of unequal reciprocal translocations in the populations examined (Reyneke and Liebenberg, 1980). In an extensive examination of genome size in *Eucomis*, Zonneveld and Duncan (2010) show that diploid species (chromosome numbers not determined) have genome sizes of between  $1C=10.2$ – $15.1$  pg, with *E. grimshawii* having the lowest values and *E. regia* the highest in the range. Tetraploid species (again chromosome numbers not determined) have  $1C=20.3$ – $30.2$  pg.

We offer the hypothesis that *Eucomis* is polyploid on a derived, dysploid base. Genome size measurements provide support for the hypothesis of ancestral polyploidy for the genus based on the following argument. *Eucomis* is nested in a clade with base number  $x=10$  and diploid species of *Eucomis* have almost the same  $1C$  values as *Veltheimia*, also tetraploid ( $2n=20$ ). Genome size in these two genera is about three times that in ancestrally diploid *Massonia* species (mean value for three species examined for genome size is  $1C=3.20$  pg). As noted earlier, cross genus comparisons of genome size may not always be reliable indicators of ploidy levels.

In the isolated *Ledebouria* clade (including *Drimiopsis* and *Resnova*) two species have  $2n=20$  and three more have  $2n=20$  plus other numbers. The *L. hyacinthina/revoluta* group, including the Madagascan *L. nossibeensis*, is unusual in having a range of numbers from  $n=9$ – $15$ . Karyotypes in the group are strongly bimodal, e.g. *L. nossibeensis* ( $2n=30$ ) has two large chromosome pairs with a balance of much smaller chromosome pairs, the same pattern reported for *L. somaliensis* by Stedje (1996). Despite the high chromosome number in these species, however, the karyotypes are not consistent with direct polyploidy. The karyotype of *L. urceolata*,  $n=10$ , does not exhibit the bimodality evident in species with higher base numbers. According to current data *L. humifusa* (= *Resnova humifusa*) has  $2n=10$  but there is also a count of  $2n=20$  for the species under the synonym *Drimiopsis saundersii* (Table 3), with a karyotype of four long and six shorter pairs. No other members of the *Resnova* group have been counted (although *L. nossibeensis* was at one time included in *Resnova*). Polyploidy and dysploidy are frequent in *Ledebouria* and if species identifications are correct then many are heteroploid. Meiotic studies by Jessop (1972b) are particularly confusing—different accessions of some species have a range of haploid numbers but are said to exhibit no meiotic abnormalities. Total DNA per cell (Zonneveld et al., 2005) has been determined

for three species, *L. cooperi* ( $1C=5.60$  pg), *L. petiolata* (as *Drimiopsis maculata*) ( $1C=3.75$  pg) and *L. socialis* ( $1C=5.85$  pg) but these estimates do not include the chromosome number of the samples examined, rendering assessments of ploidy levels impossible.

The diploid count of  $2n=10$  in *Ledebouria humifusa* defies easy explanation. Sometimes segregated in the genus *Resnova* with several other species (e.g. Lebatha et al., 2006), *L. humifusa* is deeply nested within the *Ledebouria* clade in molecular-based phylogenies (Ali et al., 2011; Wetschnig et al., 2007) and a second count of  $2n=20$  for the species is consistent with many counts in the remainder of the genus. We cannot discount the possibility that *L. humifusa* is a dysploid derivative and that the count of  $2n=20$  represents neopolyploidy (polyploidy at species rank or lower). The karyotype of the  $2n=20$  plants examined by De Wet (1957) could be interpreted as tetraploid: there are 5 pairs of more or less like chromosomes in the haploid karyotype.

Based on the count of  $2n=10$  for *Ledebouria humifusa* Wetschnig and Pfosser (2003) suggested a base number of  $x=5$  for *Ledebouria* and other genera of Massonieae. In this scenario counts based on  $n=10$  would be tetraploid and those with  $n=15$  hexaploid. Given the karyotypes this seems unlikely: few species, even within *Ledebouria*, show an expected four or six sets of like chromosomes. Indeed, the karyotype of the monospecific *Spetaea* ( $n=10$ ) includes one long, one medium, and one moderately short chromosome pairs (plus seven pairs of very short chromosome pairs), thus generally inconsistent with polyploidy. If the genus is in fact polyploid then considerable chromosome repatterning must have occurred.

Given the hypothetical base number of  $x=10$  for Massonieae, Urgineoideae and also Ornithogaloideae, the base in the phylogenetically isolated *Ledebouria* clade is most parsimoniously inferred to be  $x=10$ , with some species polyploid, heteroploid or dysploid. We suggest that the typical vegetative reproduction common in populations of the alliance makes it possible for chromosomal aberrations (non-coding fragments, B chromosomes) to accumulate, perhaps tolerated in species or populations that reproduce mainly vegetatively. Hence the range of numbers mostly above  $n=10$ , the most common number in the genus, that have been reported, notably by Jessop (1970, 1972a, 1972b).

#### 4.3. Summary

We infer an ancestral basic chromosome number of  $x=10$  for Urgineoideae. This is the only base number for almost all species of the two genera in the subfamily, the same base was postulated for Ornithogaloideae (Goldblatt and Manning, 2011), sister to Hyacinthoideae plus Urgineoideae (Manning et al., 2004). We infer the same ancestral base of  $x=10$  for Massonieae, in part by outgroup comparison (Fig. 1) and because the pattern within the tribe seems to us most consistent with this hypothesis. The striking, decreasing dysploid series in *Lachenalia* is notable for Massonieae, indeed for all sub-Saharan Hyacinthaceae, and merits detailed investigation in combination with systematic and molecular phylogenetic study. Similar extensive dysploid sequences are known in another geophytic



southern African family, Iridaceae, especially in *Lapeirousia* (Goldblatt and Takei, 1993), *Romulea* (De Vos, 1972) and *Moraea* (Goldblatt, 1971, 1976, 1986).

In Hyacinthoideae, Pseudoprosperae evidently has  $x=9$ . Originally placed as one element in a trichomy with Massonieae and Hyacintheae (Wetschnig and Pfosser, 2003; Manning et al., 2004), Pseudoprosperae has more recently been resolved as basal in the subfamily, i.e. sister to Massonieae+Hyacintheae (Buerki et al., 2012). All topologies support a postulated ancestral base of  $x=9$  for Hyacintheae.

Neopolyploidy is relatively uncommon among sub-Saharan Hyacinthoideae. According to available counts, one species of *Massonia* out of four counted is tetraploid. For *Lachenalia*, 86 species or almost three quarters of the total in the genus have been counted. Available counts show that 15 species are exclusively polyploid and a further 14 have diploid and polyploid populations. Assuming a total of 11 species in *Eucomis*, four are tetraploid and two have diploid and tetraploid populations. Among these three genera, just 20 species out of 101 species counted are exclusively polyploid. In contrast, 16 species have diploid and polyploid populations.

The modest level of neopolyploidy in sub-Saharan Hyacinthoideae is consistent with the pattern in Ornithogaloideae (Goldblatt and Manning, 2011) in which just one of 24 species of sub-Saharan *Ornithogalum* and three of 23 species of *Albuca* subgen. *Albuca* are exclusively polyploid. Other families of sub-Saharan geophytes show the same pattern of low polyploid frequency. In *Gladiolus* (Iridaceae) just five of 70 (7%) sub-Saharan species sampled so far have polyploid populations whereas all six Eurasian species are exclusively polyploid (Goldblatt et al., 1993). In *Moraea* (Iridaceae) the two Eurasian species are tetraploid, only nine of 164 (<5%) species of sub-Saharan Africa counted are exclusively polyploid and 15 more species have diploid and polyploid populations (Goldblatt, 1976; Goldblatt and Manning, 2011). As in *Ornithogalum*, polyploidy is relatively frequent in Eurasian genera of Hyacinthoideae, judging from records in the cytological literature.

In contrast to the low frequency of neopolyploidy in African Hyacinthoideae, five of the nine genera of the subfamily in sub-Saharan Africa for which we have chromosome counts appear palaeopolyploid (polyploid at generic rank or higher). All counts for *Merwillia*, *Schizocarphus* and *Veltheimia* are tetraploid,  $2n=40$ . For *Eucomis* ( $x=15$ ) and *Daubinya* the best explanation we can offer, based on outgroup comparison and genome size estimates, is that both are hypotetraploid.

The situation in *Ledebouria* is less clear, given the infraspecific variation in chromosome number in almost all species. Only two counted species have exclusively  $2n=20$  and several more have populations evidently with  $2n=20$  as well as other numbers. Numbers not multiples of 10 may represent the presence of B chromosomes but the frequency of plants or populations with dysploid numbers is remarkable. Several *Ledebouria* species frequently reproduce asexually and some exhibit meiotic abnormalities, rarely producing viable seeds (Jessop, 1972a, 1972b). We suggest that frequent asexual reproduction via bulbils may allow abnormal karyotypes to persist in the wild.

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