A review of chromosome cytology in Hyacinthaceae subfamily Ornithogaloideae (Albuca, Dipcadi, Ornithogalum and Pseudogaltonia) in sub-Saharan Africa

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Abstract

The chromosome cytology of Hyacinthaceae subfamily Ornithogaloideae is reviewed within the framework of a recent molecular-based classification, with particular emphasis on its center of diversity in sub-Saharan Africa. We also provide new chromosome counts for sections that are unknown or poorly known cytologically. Albuca subgen. Namibiogalum (9 spp.) probably has an ancestral base number of x=10 but subgen. Albuca (±70 spp), subgen. Monarchos (9 spp.) and subgen. Osmyne (36 spp.) have x=9. The pattern in subgen. Urophyllon (3 spp.) is remarkable: although x=6 is likely, the species in the section exhibit a range of 2n=12, 10, 8, 6 and 4 (exclusive of polyploidy). All karyotypes have three large chromosome pairs and a variable number of small chromosomes. Pseudogaltonia (2 spp.) has x=9 and Dipcadi (26 spp.) possibly x=9 in series Uropetalum and x=6 in series Dipcadi, which exhibits a pattern of descending dysploidy leading to n=3 in D. marlothii. In Ornithogalum (±130 spp.) chromosome numbers are known for only 24 of the ±84 sub-Saharan species, mostly from subgen. Aspasia and subgen. Ornithogalum sect. Linaspasia, both of which have x=6, and from subgen. Galtonia, which has x=8. In contrast, x=7 is basic for the Eurasian sects. Honoritus and Melophis, and x=18 seems likely for sect. Cathissa. Sect. Ornithogalum, the cytology of which we does not examine in detail, may have x=9. Polyploidy is apparently rare in the sub-Saharan African ornithogaloids, in marked contrast to the high frequency of polyploidy among Eurasian species. In Albuca just 3 or possibly 4 sub-Saharan species (9% or 13% of those counted) are exclusively polyploid and 5 more have diploid and polyploid races; and in sub-Saharan Ornithogalum, only the tropical O. gracillimum is exclusively polyploid, and the western southern African O. hispidum has diploid and polyploid races.

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1. Introduction

Phylogenetic relationships in Hyacinthaceae subfamily Ornithogaloideae have been intensively studied using molecular sequence data (Manning et al., 2009a,b; Martínez-Azorín et al., 2011), providing a framework for assessing cytological patterns in the subfamily. The recent classification of Ornithogaloideae by Manning et al. (2009a,b) recognizes four genera in the subfamily: Albuca with ±135 species, mostly in sub-Saharan Africa; Dipcadi with 26 species in Africa and Eurasia as far east as India; Ornithogalum with 84 species in sub-Saharan Africa and ±56 species in Eurasia; and the southern African Pseudogaltonia with two species. An alternative generic classification, based on essentially the same topology, recognizes nineteen genera (Martínez-Azorín et al., 2011).

Chromosome counts for the subfamily 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 Ornithogaloideae except Eurasian sect. Ornithogalum (±70 spp) under their current names and arranged according to the infrafamilial classification proposed by Manning et al. (2009a,b), and provide some new chromosome counts for groups 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 subfamily.

These gaps limit a deeper understanding of the chromosomal evolution in Ornithogaloideae, but we tentatively postulate an ancestral base for the subfamily of $n=10$, which is the base number in the most closely related subfamilies (De Wet, 1957; Jones and Smith, 1967). This number is probably basic for Albuca subgen. Namibiogalum, with descending dysploid evidently playing the primary role in the cytological evolution in the genus, leading to $x=9$ in subgen. Albuca and subgen. Osmyne, although subgen. Urophylloc has $x=6$. A base number of $x=9$ is likely for Pseudogaltonia–Dipcadi. In Ornithogalum, subgen. Galtonia has a base number of $x=8$, subgen. Avonsera has $x=7$, and subgen. Aspasia has $x=6$. The sub-Saharan members of subgen. Ornithogalum also have $x=6$ (sects. Linaspasia and Neopatersonia) but the Eurasian members of the subgenus have base numbers of $x=7$ (sects. Honoriius and Melomphis), $x=18$ or 16 (sect. Cathissa), and a secondary base of $x=9$ seems most likely for sect. Ornithogalum.

2. Materials and methods

2.1. Published counts

Data on chromosome number in genera of Ornithogaloideae were extracted from indexes to plant chromosome numbers covering the years since chromosome numbers were first made available (Bolkhovskikh, 1969; Goldblatt, 1981, etc.; Goldblatt and Johnson, 1990, Moore, 1973, 1974, 1977; etc. see Table 2). We tabulate counts according to the current subfamilial classification, with species names corrected to reflect current nomenclature and taxonomy (Manning et al., 2007, 2009a,b; Obermeyer, 1978). Original sources were consulted for most counts, especially those we had reason to question. We had hoped to examine 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 and these probably do not exist. When localities for plants sampled are provided in some papers we were able to infer current names according to current taxonomy.

Specifically, counts published as Ornithogalum lacteum forma from the western Karoo with $2n=10$ (Pienaar, 1963) refer to plants that are now treated as O. corticatum (Manning et al., 2007); and counts for O. lacteum from sites in the southwestern Cape almost certainly refer to the morphologically similar O. conicum, and we feel justified in correcting the species name even though vouchers are not available. Other name corrections simply follow current taxonomy. It seems more useful to include these counts under current names than to disregard them entirely. There is no precedent for ignoring chromosome counts in the literature when they are not linked to voucher specimens and we see no reason to do so. Examples of doubtful identification are discussed in the text below.

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

2.2. Original counts

Material for the original counts reported here 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. Following widespread practice in plant cytology, these are assumed to represent entire populations.

3. Results

In Albuca, our own counts for A. unifolia (subgen. Monarchos, until now uncounted), A. decipiens and A. fragrans (both subgen. Albuca sect. Falconera) and A. glandulifera and A. suaveolens (both subgen. Osmyne) are all \(2n=18\) (Table 1).

Karyotypes consist of 3 longer and 6 much shorter chromosome pairs, closely matching those described elsewhere (e.g. Pienaar, 1963). The only previous count in subgen. Osmyne, for A. suaveolens, can now be interpreted as tetraploid, \(2n=36\). Our new counts thus establish a likely base of \(x=9\) for the subgenus and show the widespread \(A. suaveolens\) to be heteroploid as currently circumscribed.

In Ornithogalum, O. xanthochlorum (not before counted) has \(2n=16\), which accords with other counts for subgen. Galtonia (Table 2). In contrast, O. filicaule (=Neopatersonia namaquensis G.J. Lewis) (subgen. Ornithogalum sect. Neopatersonia) has \(2n=12\), thus with a base number \(x=6\). This is the most common base among the African members of the genus and is ancestral for subgen. Ornithogalum. The karyotype in this species consists of three large and three smaller chromosome pairs about half as long as the longer pairs, and matches relatively closely that of the \(2n=12\) cytotype of \(O. graminifolium\) (Pienaar, 1963).

We also recorded \(2n=8\) for \(O. graminifolium\) (subgen. Ornithogalum) (Table 1), a count that differs from past reports of \(2n=12\) and 10 for the species (Table 2). The \(2n=8\) karyotype consists of one large acrocentric pair, one large subtelocentric pair and two pairs of somewhat smaller, subtelocentric pairs. We assume that it is derived from populations with higher diploid numbers and telocentric chromosomes as illustrated by Pienaar (1963), which shows three medium-sized and three small telocentric chromosome pairs. Pienaar’s comment that the count of \(2n=10\) for \(O. graminifolium\) might be for what is now \(A. virens\) may be correct, as the karyotype published by Therman (1951) shows the characteristic three long and a variable number of much short chromosome pairs of that species (in this case two short pairs).

4. Discussion

4.1. Albuca

The pattern in Albuca subgen. Namibiogalum, sister to the rest of the genus, is puzzling. Albuca donaldsonii has \(2n=20\) based on two accessions of the species (Stedje and Nordal, 1984; Stedje, 1996) but A. seineri has \(2n=24\) (Vosa, 1980) (Table 2). The karyotype of \(O. donaldsonii\) is moderately asymmetric but not bimodal, whereas that of \(O. seineri\) is strongly bimodal, with nine long and three small (less than half as long), acrocentric pairs, as in subgen. Albuca and Urophyllon. The karyotype in \(A. donaldsonii\) is not obviously polyploid — it does not consist of sets of two pairs of like chromosomes. Vosa (1980) suggested that the karyotype of \(A. seineri\) might be hexaploid on a base of \(x=4\) but in light of the higher base numbers for \(Albuca\) and other tribes of Hyacinthaceae we find this hypothesis hard to accept. Nevertheless, we are unable to offer an alternative explanation for the karyotype in the species.

It is premature to comment on the pattern in subgen. Namibiogalum but we note that the most likely base number for subfam. Oziroëoideae, sister to the remaining Hyacinthaceae, is \(x=10\) (Fernandez and Daviña, 1991). A base number of \(x=10\) is also the most likely for Urgineoideae, immediate sister to Ornithogaloideae (De Wet, 1957). The base number in \(A. donaldsonii\) might then be basic for Ornithogaloideae, with other numbers in subgen. Namibiogalum which is the result of descending dysploidy and secondary polyploidy.

Our count for \(Albuca unifolia\) is the first for subgen. Monarchos and both the base number, \(x=9\), and the karyotype of three long and six small chromosome pairs accord exactly.

| Species         | Diploid number, \(2n\) | Voucher data                                                                 |
|-----------------|------------------------|------------------------------------------------------------------------------|
| A. decipiens    | 18                     | South Africa, W Cape, near Trawal, Goldblatt & Manning 13059 (NBG)           |
| A. fragrans     | 18                     | South Africa, W Cape, Cape Town, Manning 3124 (NBG)                           |
| A. glandulifera | 18                     | South Africa, N Cape, Bushmanland, Goldblatt & Manning 13042                 |
| A. suaveolens   | 18                     | South Africa, W Cape, Vanrhyns Pass, Goldblatt & Manning 13057 (NBG)         |
| A. unifolia     | 18                     | South Africa, N Cape, near Steinkopf, Goldblatt & Manning no voucher         |
| O. filicaule    | 12                     | South Africa, N Cape, south of Springbok, Goldblatt & Manning 11369 (NBG)   |
| O. graminifolium| 8                      | South Africa, N Cape, Nieuwoudtville, Goldblatt 6537 (MO)                    |
| O. xanthochlorum| 16                     | South Africa, W Cape, Tanqua Karoo, Snijsman 2227 (NBG)                      |
Table 2
Chromosome numbers in *Albuca, Dipcadi, Ornithogalum and Pseudogaltonia* arranged following the classification of Manning et al. (2009a,b). Numbers were culled from the *Atlas of Chromosome Numbers of Flowering Plants* (Bolkhovskikh, 1969) and *Index to Plant Chromosome Numbers* (Moore, 1971, 1972, 1974; Goldblatt, 1981, 1985, 1987; Goldblatt and Johnson, 1990, 1991, 1994, 1996, 1998, 2000, 2003, 2006). *Ornithogalum nathoanum* U.Müll.-Doblies & D.Müll.-Doblies, unplaced in this classification, is uncounted. Original counts are indicated in bold type.

*Albuca* L. (±120 species, 31 counted)

Subgen. *Namibialbum* (U.Müll.-Doblies & D.Müll.-Doblies) J.C. Manning & Goldblatt (9 spp., 2 counted)

* A. donaldsonii Rendle

A. seineri (Engl. & Krause) J.C. Manning & Goldblatt

2n=24 (Vosa, 1980 as *Ornithogalum seineri* (Engl. and Krause) Oberm.)

Subgen. *Monarchos* (U.Müll.-Doblies & D.Müll.-Doblies) J.C. Manning & Goldblatt (±10 spp., 1 counted)

A. unfoliala (Retz.) J.C. Manning & Goldblatt

2n=18 (new count, Table 1)

Goldblatt

Subgen. *Urophyllon* (Salish.) J.C. Manning & Goldblatt (3 spp.; all counted)

A. bracteata (Thunb.) J.C. Manning & Goldblatt

2n=18, ±36 (Piennaar, 1963; 54 (Therman, 1951 as *Ornithogalum caudatum* Jacq.))

A. virens (Lindl.) J.C. Manning & Goldblatt

subsp. virens

2n=6 (Piennaar, 1963 as *O. virens* Lindl.)

2n=10 (Piennaar, 1963 as *O. flavovirens* Baker, *O. ecklonii* Schidl.)

2n=12, 10, 8, 16, 6, 4 (Stedje, 1998, Vosa, 1997 as *O. tenuifolium* Delaroche)

2n=12 (Piennaar, 1963 as *O. pretoriense* Baker)

2n=20 (De Wet, 1957, as *O. inconspicuum* Baker)

subsp. arida Oberm.

2n=12, 8 (Piennaar, 1963 as *O. setifolium* sensu F.M. Leight.)

subsp. sordida (Baker) Stedje

2n=12 (Stedje, 1998)

subsp. robusta Stedje

2n=16 (Stedje, 1998) possibly 2n=16 (Stedje and Nordin, 1984, as *O. gracillimum*)

A. volubilis (H.Perr.) J.C. Manning & Goldblatt

2n=12 (Wetschnig et al., 2007 as *Iigeria volubilis* (H. Perr.) Speta)

Subgen. *Osmyne* (Salish.) J.C. Manning & Goldblatt (±28 spp., 2 counted)

A. glandulifera J.C. Manning & Goldblatt

2n=18 (new count, Table 1)

A. suaveolens (Jacq.) J.C. Manning & Goldblatt

2n=18 (new count, Table 1)

2n=36 (De Wet, 1957)

Subgen. *Albuca*

Sect. *Pallastema* (Salish.) J.C. Manning & Goldblatt (±13 spp.; 7 counted)

A. abyssinica Jacq.

2n=18, 36 (Paiva and Leitao 1989 as *A. melleri* Baker; Stedje, 1996; Jones and Smith, 1967; Jong, 1991 as *A. angolensis* Dryand.; Jones and Smith, 1967 as *A. melleri* and *A. wakefieldii* Baker; Gill and Abubakar, 1975, as *A. wakefieldii*)

2n=16 (Jones and Smith, 1967)

2n=20 (De Wet, 1957 as *A. bainesii* Baker)

A. fibrotunicata Gledhill & Oyewole

2n=36 (Oyewole, 1972)

A. nigritana Baker

2n=36, 54 (Jones and Smith, 1967; Oyewole, 1972, also as *A. scabromarginata* De Wild.)

A. pendula B. Mathew

2n=16, 14 (Johnson, 1999)

A. sudanica A. Chev.

2n=36 (Oyewole, 1972)

A. tenuis Knudtzon

2n=18 (Knudtzon and Stedje, 1986; Stedje, 1996)

A. transvaalensis Mogg

2n=20 (De Wet, 1957; Maekawa, 1962)

Sect. *Branciona* (Salish.) J.C. Manning & Goldblatt (10–30 spp.; 10 counted)

A. aurea Jacq.

2n=18 (Jong, 1991)

A. batteniana Hilliard & B.L. Burtt

2n=18 (Jong, 1991)

A. fastigiata Dryand.

2n=18 (De Wet, 1957; Maekawa, 1962; Jones and Smith, 1967; Zakhryeva and Makushenko, 1969)

2n=54 (Müller, 1912 — possibly for *A. setosa*)

A. humilis Baker

2n=18 (Jong, 1991)

A. kirki (Baker) Brennan

2n=18 (Knudtzon and Stedje, 1986)

A. nelsonii N.E.Br.

2n=18 (Satō, 1942; Jong, 1991); 20 (De Wet, 1957)

A. setosa Jacq.

2n=18 (Jong, 1991); also as *A. pachylamys* Baker (Paiva and Leitao, 1989)

2n=40 (De Wet, 1957 as *A. pachylamys*)

A. nyakensis Baker

2n=18 (Paiva and Leitao, 1989)

A. polypylla Baker

2n=18 (Jong, 1991 and as *A. macowanii* Baker)

A. rupestris Hilliard & B.L. Burtt

2n=18 (Jong, 1991)

Sect. *Falconera* (Salish.) J.C. Manning & Goldblatt (18 spp.; 4 counted)

A. decipiens U.Müll.-Doblies

2n=18 (new count, Table 1)

A. fragrans Jacq.

2n=18 (new count, Table 1)

A. shawii Baker

2n=18 (Jong, 1991)
Table 2 (continued)

**Subgen. Albuca**

| Sect. Albuca (19 spp.: 3 counted) | 2n=18 (Nordenstam, 1969; De Wet, 1957; Zakhryeva and Makushenko, 1969, as *A. altissima* Dryand.) |
|-----------------------------------|--------------------------------------------------------------------------------------------------|
| *A. canadensis* (L.) Leight.      | 2n=18 (Nordenstam, 1969; De Wet, 1957; Zakhryeva and Makushenko, 1969, as *A. altissima* Dryand.) |
| *A. flaccida* Jacq.              | 2n=18 (De Wet, 1957; Maekawa, 1962, also as *A. canadensis*)                                    |
| *A. xanthochodon* Hilliard & B.L. Burtt | 2n=18 (Jong, 1991)                                                                              |

**Pseudogaltonia** (Kuntze) Engl. (2 spp., 1 counted)

| *P. clavata* (Mast.) Phill.      | 2n=18 (Jong, 1991; Speata, 1985, as *Lindernia clavata* (Mast.) Speata) [De Wet’s (1957) count of 2n=24 is probably for another species] |

**Dipcadi Medik.** [26 spp.; 13 counted]

**Northern hemisphere species** [all series Dipcadi]

| *D. biflorum* S.A. Ghazanfar    | 2n=12 (Ghazanfar, 1996)                                                                 |
| *D. concanense* (Dalzell) Baker | 2n=12 (Dixit et al., 1992; Kanmani, 1975)                                                |
| *D. erythraeum* Webb & Berthel. | 2n=22 (Khatoon and Ali, 1993; Jakh et al., 1994)                                           |
| *D. montanum* (Dalzell) Baker   | 2n=20 (Mahabale and Cheenaveeraih, 1954)                                                   |
|                                 | 2n=21, 22 (Vijayavalli and Mathew, 1988)                                                     |
|                                 | 2n=10, 12, 20 (Naik, 1974)                                                                 |
| *D. saxorum* Blatter            | 2n=12 (also 12+2B) (Mahabale and Cheenaveeraih, 1954; Naik, 1974)                          |
| *D. serotinum* (L.) Medik.      | 2n=8 (Corsi et al., 1996; Quieros, 1983; Valdes-Bermejo et al., 1978; Ruiz Rejon, 1978)    |
|                                 | 2n=32 (Humphries et al., 1978)                                                             |
| *subsp. lividum* (Pers.) Maire & Weiller | 2n=28 (Delay and Petit, 1971)                                                                |
| *D. ursulae* Blatter            | 2n=20 (Mahabale and Cheenaveeraih, 1954)                                                   |

**Southern African species**

**Series Uropetalon** (Burch. ex Ker Gawl.) J.C. Manning & Goldblatt (9 spp.: 2 counted)

| *D. ciliare* (Zeyh. ex Harv.) Baker | 2n=21, 22 (Vijayavalli and Mathew, 1990, as *D. reedit* (Baker) Baker)                     |
| *D. glaucum* (Burch. ex Ker Gawl.) Baker | 2n=18 (De Wet, 1957).                                                                         |
| *D. viride* (L.) Moench            | 2n=12 (De Wet, 1957, Fernandez and Neves, 1962; Stedje and Nondal 1984; Raimondo et al., 2000, also as *D. tacczezum* Baker) |

**Series Dipcadi**

| *D. gracilimum* Baker             | 2n=12 (Jones and Smith, 1967)                                                                |
| *D. longifolium* (Lindl.) Baker   | 2n=24 (Oyewole, 1988); n=6 (Rao and Mwasumbi, 1981)                                          |
| *D. marlothii* Engl.              | 2n=6 (Ratter and Milne, 1973)                                                                |

**Ornithogalum** (±84 sub-Saharan species, 24 counted)

**Subgen. Avonsera** (Speta) J.C. Manning & Goldblatt (1 sp.)

| *O. convallarioides* H. Perr. (H. Perr.) | 2n=14 (Wetschnig et al., 2007, as *Avonsera convallarioides* Speta)                         |

**Subgen. Galtonia** (Decne.) J.C. Manning & Goldblatt

**Sect. Xanthochlorum** (U.Müll.-Doblies & D.Müll.-Doblies) J.C. Manning & Goldblatt (3 spp., 2 counted)

| *O. prasinum* Ker Gawl.            | 2n=16 (Pienaar, 1963); 2n=14, 12 (De Wet, 1957 — plants possibly unidentified)               |
| *O. xanthochlorum* Baker           | 2n=16 (new count, Table 1)                                                                    |

**Sect. Galtonia** (5 spp., all counted)

| *O. candidans* (Baker) J.C. Manning & Goldblatt | 2n=16 (Forrest and Jong, 2004 as *Galtonia candidans* (Baker) Decene.)                     |
| *O. princeps* (Baker) J.C. Manning & Goldblatt | 2n=16 (De Wet, 1957; Forrest and Jong, 2004) as *G. princeps* (Baker) Decene.               |
| *O. regalis* (Hilliard & B.L. Burtt) J.C. Manning & Goldblatt | 2n=16 (Forrest and Jong, 2004 as *G. regalis* Hilliard & B.L. Burtt)                       |
| *O. saundersiae* Baker             | 2n=14 (Pienaar, 1963)                                                                         |
|                                 | 2n=12 (de Wet, 1957)                                                                          |
| *O. viridiflorum* (I. Verd.) J.C. Manning & I. Verd. Goldblatt | 2n=16 (De Wet, 1957; Forrest and Jong, 2004) as *G. viridiflora*                           |

**Subgen. Aspasia** (Salish.). U.Müll.-Doblies & D.Müll.-Doblies

**Sect. Aspasia** (12 spp. 9 counted)

| *O. cerestium* F.M. Leighton.      | 2n=12 (Pienaar, 1963)                                                                        |
| *O. conicum* Jacq.                | 2n=12 (De Wet, 1957, Pienaar, 1963 also as *O. lacteum* Jacq. from SW Cape sites)          |
| *O. corticatum* Mart.-Azorin       | 2n=10 (Pienaar, 1963 as *O. lacteum*)                                                        |
| *O. dubium* Houtt.                | 2n=12 (18) (De Wet, 1957, as *O. flavissimum* Jacq., *O. alticolum* F. Leight; Pienaar, 1963, as *O. alticolum* F. Leight, *O. fergusonii* L. Bol., *O. filiromarginatum* F. Leight., *O. flavissimum* Jacq., *O. leipoldtii* L. Bol., *O. minutum* Jacq.) |
|                                 | 2n=10 (De Wet, 1957, as *O. leipoldtii* L. Bol.)                                             |
| *O. maculatum* Jacq.             | 2n=14 (De Wet, 1957)                                                                         |
|                                 | 2n=12 (24) (Pienaar, 1963)                                                                   |
| *O. pruinosum* F.M. Leight.       | 2n=12 (Pienaar, 1963)                                                                        |

(continued on next page)
with records for the large subgen. *Albuca*, which has \(x=9\) (Table 2) and a nearly identical karyotype across all four sections (Pienaar, 1963; Jong, 1991).

We agree with Jong (1991) that early counts by De Wet (1957) of \(2n=20\) or 40 in subgenus *Albuca*, for *A. transvaalensis* and *A. setosa*, must be discounted as errors, probably for \(2n=18\) and 36 respectively. Jong’s extensive cytological survey of *Albuca* subgen. *Albuca* makes it clear that \(x=9\) is the ancestral base number. The counts of \(2n=2\) to 18 in the subgenus, for *A. abyssinica* (Jones and Smith, 1967) (also \(2n=18\)) and *A. pendula* (Johnson, 1999) (also \(2n=14\)), evidently represent examples of dysploid reduction from the ancestral \(2n=18\) but it is not clear whether these dysploid counts represent single isolated individuals in cultivation or entire populations.

The counts for two species of the exclusively southern African *Albuca* subgen. *Osmyne*, \(2n=18\) for *A. glandulifera* and \(2n=18\) for *A. suaveolens*, confirm \(x=9\) for the section. The only previous count for the subgenus is \(2n=36\), also for *A. suaveolens*, indicating that the species is heteroploid. The karyotype of three long and six short chromosome pairs matches that in subgen. *Albuca* and *Monarchos*. The number in subgen. *Osmyne* is consistent with its close relationship to *Albuca* and supports its transfer to *Albuca* from *Ornithogalum* (Manning et al., 2009a,b) — the sub-Saharan African species of *Ornithogalum* have \(x=8\) or 6, rarely 7 or numbers lower than 6.

Of the 23 species of subgen. *Albuca* that have been counted thus far, 17 are diploid, three have diploid and polyploid populations, and three species are exclusively polyploid. All of the variably or consistently polyploid species are from subtropical and tropical Africa. Thus *A. abyssinica* has diploid and tetraploid populations, *A. nigrina* has tetraploid and hexaploid populations, and *A. setosa* has diploid and tetraploid populations. An early count of \(2n=54\) for *A. fastigiata* (sect. *Branciona*) (Müller, 1912) is unlikely for that species, which otherwise has \(2n=18\). Species identifications in this section are extremely difficult and Müller’s counts may well be for the morphologically similar *A. setosa*, which is known to have diploid and tetraploid populations. Significantly, *A. fibrotunicata*, *A. nigrina* and *A. sudanica* all have \(2n=36\) and if these species, which are closely allied to *A. abyssinica* (sect. *Pallastemma*), are recognized as distinct from it, then exclusive polyploidy is restricted to subgen. *Albuca*.

Despite the stability in chromosome base number evident in *Albuca* subgen. *Albuca*, *Monarchos* and *Osmyne*, we emphasize that only 24% of the species have been counted, with only three species each known cytologically in sects. *Falconera* and *Albuca*.  

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**Table 2 (continued)**

| Subgen. | Aspasia (Salish.) | U.Müll.-Doblies & D.Müll.-Doblies |
|---------|------------------|-----------------------------------|
| Sect.   | Aspasia (12 spp. 9 counted) |
| O. rupestre L.f. | \(2n=12\) (Pienaar, 1963, as *O. ranunculoides* L. Bol.) |
| O. synanthifolium F.M. Leight. | \(2n=12\) (De Wet, 1957; Pienaar, 1963, also as *O. lacteum* from E Cape) |
| O. thyrsoides Jacq. | \(2n=12\) (18) (Pienaar, 1963, also as *O. hermannii* F. Leight.) |

| Sect. Hispidespasia | U.Müll.-Doblies & D.Müll.-Doblies (18 spp.: 2 counted) |
|---------------------|--------------------------------------------------------|
| O. hispidum Hornem. | \(2n=12\) (De Wet, 1957, also as *O. karroicum* F. Leight.) |
| O. thermophilum F.M. Leight. | \(2n=12\) (De Wet, 1957) |

| Subgen. | Ornithogalum |
|---------|--------------|
| Sect.   | Neopatersonia (Schönland) | J.C. Manning & Goldblatt (4 spp., 1 uncounted) |
| O. filicaule J.C. Manning & Goldblatt | \(2n=12\) (new count, Table 1) |

| Sect. Elsia (F.M. Leight.) | J.C. Manning & Goldblatt (1 sp., uncounted) |
|---------------------------|---------------------------------------------|

| Sect. Linaspasia | U.Müll.-Doblies & D.Müll.-Doblies (40 spp: 4 counted) |
|-------------------|--------------------------------------------------------|
| O. flexuosum (Thumb.) U.Müll.-Doblies | \(2n=12\) (14) (De Wet, 1957 as *O. zeyheri* Baker) |

| O. gracilimum R.E. Fries | \(2n=24\) (Stedje and Nordal, 1984) |
|--------------------------|-----------------------------------|
| O. graminifolium Thumb.  | \(2n=12\) (Pienaar, 1963 also as *O. attenuatum* F. Leight.) |
|                          | \(2n=10\) (Satô, 1953; Theran, 1951) |
|                          | \(2n=8\) (new count, Table 1) |
| O. juncifolium Jacq.     | \(2n=12\) (Pienaar, 1963 as *O. leptophyllum* Baker) |
|                          | \(2n=10\) (Pienaar, 1963 as *O. subulatum* Baker) |

| Sect. Cathissa (Salish.) | J.C. Manning & Goldblatt (3 spp., all counted) |
|--------------------------|---------------------------------------------|
| O. broteroi M. Lainz     | \(2n=34\) (Moret, 1987); 34 (35) (Neves, 1952) |
| O. concinnum | \(2n=36\) (Neves, 1950, 1952) |
| O. reverchonii Lange ex Willk. | \(2n=32\) (Fernandez et al., 1985; Johnson and Brandham, 1997) |
|                          | \(2n=36\) (32+4B?) (Fernandez Casas and Garcia Guardia, 1978) |

| Sect. Melonophis (Raf.) | J.C. Manning & Goldblatt (1 sp.) |
|-------------------------|---------------------------------|
| O. arabricum L.         | \(2n=14\), 28, and other numbers (Lauber, 1947) |

| Sect. Honorius (S.F. Gray) | J.C. Manning & Goldblatt (2 spp. or more, 2 counted) |
|-----------------------------|--------------------------------------------------------|
| O. boucheanum Aschers.      | \(2n=28\) (Agapova, 1977; Lauber, 1947) |
|                            | \(2n=56\) (Dalgic and Ozhatay, 1997) |
| O. nutans L.                | \(2n=14\), 15, 40, 41 (Cullen and Rattert, 1967). [Counts of \(2n=16\), 30 in the literature may be incorrect or include B chromosomes] |

| Sect. Ornithogalum (species±70 spp.: counts not reviewed here) | |
The pattern in the three species of *Albuca* subgen. *Urophyllon*, the remaining subgenus, is puzzling (Table 2). The Madagascan *A. volubilis* has $2n=12$ but the widespread African *A. virens* (=*Ornithogalum tenuifolium* Redoute and to be distinguished from *O. tenuifolium* Guss.) as circumscribed by Obermeyer (1978) has a striking range of numbers (Table 2). It is noteworthy that plants associated with the segregate species that were regarded as synonyms of *A. virens* (=*O. tenuifolium*) by Obermeyer (1978) have differing numbers: thus *O. virens* has consistently been reported as having $2n=6$ (see Pienaar, 1963), and a karyotype of three medium-sized chromosome pairs; plants identified as *O. setifolium* and *O. ecklonii* and *O. flavovirens* Baker $2n=10$; and those as *O. pretoriense* Baker $2n=12$. Illustrations of karyotypes provided by Pienaar (1963) show that diploid populations of *A. virens* consistently have three medium, subtelocentric chromosome pairs and a variable number of very small telocentrics. The differences in number obviously cannot be explained by polyploidy. The Madagascan *Albuca volubilis*, $2n=12$, has a similar karyotype to populations of *A. virens* with that number.

Plants referred to *Albuca virens* subsp. *virens* sensu Obermeyer (1978) have been also reported as having $2n=6$, 8, 10 and 12 by Vosa (1997) with the same unusual, asymmetric, bimodal karyotypes. In East Africa, plants of *A. virens* subsp. *robusta* (as *O. tenuifolium* subsp. *robustum*) also have $2n=12$ (with three medium and three short pairs), but
subsp. *sordida* has \(2n = 16\) with one long metacentric, four medium pairs and three short pairs (Stedje and Nordal, 1984). In a more detailed study, Stedje (1989) examined *A. virens* (as *O. tenuifolium*) across tropical Africa, and reported \(2n = 4, 6, 12, 16\) and 26 in the species. The \(2n = 16\) karyotype is most easily explained as derived from \(2n = 18\) by fusion of a pair of telocentric chromosomes (Robertsonian translocation) in a polyploid derivative. The \(2n = 26\) count is polyploid, but plants with \(2n = 4, 6, 12\) and 16 are evidently all diploid, according to Stedje’s measurements of chromosome length and total DNA content.

The remaining species of subgen. *Urophyllon*, *Albuca bracteata* (= *O. caudatum*, *O. longibracteatum*) most likely has \(x = 9\), based on several counts, including \(2n = 18\) (Pienaar, 1963), and \(2n = 54\) (Neves, 1959; Therman, 1951). In the phylogenetic tree presented by Manning et al. (2009a, b) the species is nested in *Albuca*. We note that total chromosome length in the species is about twice as long as some cytotypes of *A. virens* (e.g. plants identified as *O. flavovirens* Baker with \(2n = 10\)), which suggests polyploidy, but it also has three long chromosome pairs (as do all diploid cytotypes of *A. virens*) and six short pairs, so that if it is polyploid then extensive chromosome rearrangement must have followed polyploidization.

In contrast, Stedje’s (1989) comparisons of DNA content show amounts of DNA per cell that are only about 50% more in populations with \(2n = 12\) (3M + 3S) than in those with \(2n = 6\) (3M = 1S), which evidently excludes polyploidy as an explanation for the difference in chromosome number, as does the karyotype itself, differing as it does only in the number of small chromosomes. Stedje (1989) has postulated that \(x = 6\) is basic for *A. virens* and that lower numbers are derived by unequal reciprocal translocation of chromat from small to large chromosomes and loss of the centromeric portions of the small chromosomes, ultimately leading to the \(2n = 6\) karyotype. This hypothesis finds additional support from the phylogeny obtained by Manning et al. (2009a, b), in which *P. volubilis*, \(2n = 12\), was retrieved as sister to *A. virens* plus *A. bracteata*.

The karyotype in the single \(2n = 4\) population of *Albuca virens* from southern Mozambique that was examined by Stedje (1989), has one long metacentric and one medium sub-telocentric chromosome pair, the metacentric pair evidently the result of further chromosome fusion in this cytologically unstable species complex.

For subgen. *Urophyllon* then, we accept the hypothesis that \(x = 6\) is the ancestral basic chromosome number. As noted by Knudtzon and Stedje (1986), the strongly bimodal karyotypes in most populations of *A. virens* (and for that matter in *A. bracteata* and *P. volubilis*) are not unlike those in some species of subgen. *Albuca*, its sister taxon. We postulate that this derived base number is the result of chromosome fusion from an ancestral base \(x = 9\).

For *Albuca* as a whole, we tentatively suggest an ancestral base of \(x = 10\), as postulated for subgen. *Namibiogaltonia*. The subgenera *Albuca*, *Monarchos* and *Osmyne* thus have the derived base \(x = 9\) and very similar karyotypes but subgen. *Urophyllon* has \(x = 6\), if our interpretation of the patterns outlined above is correct. Within subgen. *Albuca*, dysploid reduction is rare and mostly confined to populations of species that also have the ancestral base number. Available counts for *A. pendula*, \(2n = 16\) and 14, make this the only dysploid species of subgen. *Albuca*. In contrast, dysploidy is a characteristic of subgenus *Urophyllon*, with *A. virens* presenting an extreme example of intraspecific dysploidy, the phenomenon often associated with a strongly bimodal karyotype.

Based on available data, *Albuca* has a frequency of 9–13% polyploidy in sub-Saharan Africa, compared with a frequency of 21% for tropical Africa alone. The evident low incidence of polyploidy in *Albuca* in southern Africa and its higher incidence in tropical Africa are consistent with the low frequency of polyploidy in other geophytic families in the region (Goldblatt, 1971; Goldblatt and Takei, 1997). The unconventional cytological situation in *A. virens*, although remarkable, is not without precedent: in the geophytic genus *Moraea* (Iridaceae), *M. jugax* (D. Delaroche) Ker Gawl. has diploid numbers ranging from \(2n = 20, 18, 16\) to 14, 12 to 8. The base number in close relatives is \(2n = 20\) and Goldblatt (1986) has interpreted the situation as a descending dysploid series, with no polyploidy. Nevertheless, such a complex phenomenon is rare and most species of *Albuca* have a single base number, the majority of these either exclusively diploid or tetraploid.

### 4.2. *Dipcadi* and *Pseudogaltonia*

*Pseudogaltonia clavatum* has been reported as having \(2n = 24\) (De Wet, 1957) but both Speta (1985) and Jong (1991) report \(2n = 18\) for the species (Table 1). We suspect an error of some kind by De Wet (1957) — perhaps his plant was misidentified, for it seems unlikely that the species has populations with \(x = 12\) and 9. De Wet’s voucher specimen for this count could not be located at PRE, where it was housed, and is presumed lost. Provisionally we suggest a basic chromosome number of \(x = 9\) for *Pseudogaltonia*. The phylogenetic placement by Martínez-Azorín et al. (2011) of *Dipcadiaceae* as sister to *Albucesceae* receives further support from this interpretation.

*Dipcadi* has counts at the diploid level of \(2n = 12, 10, 8\) and 6 (Table 2). We infer a base number of \(x = 6\) for the genus, with descending dysploidy and subsequent polyploidisation in some species. Following this hypothesis, *D. biflorum*, *D. concanense*, *D. gracillimum*, *D. longifolium*, *D. saxorum* and *D. viride* share the ancestral number for the genus. *Dipcadi longifolium* and *D. montanum*, \(2n = 10\) and 20 (also 21, 22 in the latter), *D. serotinum*, \(2n = 8, 28, 32\), and 8 plus a variable number of B chromosomes, *D. unicolor*, \(2n = 8\), and *D. marlothii*, \(2n = 6\), are hypodiploids. Polyploidy has been recorded in *D. serotinum* (Humphries et al., 1978), \(2n = 12, 28, 32, 64* subsp. *lividum* (Delay and Petit, 1971), \(2n = 28\) (possibly \(24 + 4B\) or the result of descending dysploidy), and also in *D. longifolium* (Oywolwe, 1988) and *D. montanum* (Mahabale and Cheenaveeraiah, 1954). The only number so far reported for *D. urssaeae* is tetraploid, \(2n = 20\) (Mahabale and Cheenaveeraiah, 1954).

The different base numbers in the two genera *Dipcadiacea*, \(x = 9\) in *Pseudogaltonia* and \(x = 6\) in *Dipcadi* (Table 2), are consistent with patterns in Omithogaloideae. In this light we offer the hypothesis that the range of numbers in
subgen. *Dipcadi* is the result of early dysploid reduction with the establishment of $n=6$, the most common base in the subgenus. Further dysploid reduction and polyploid increase obviously played an important role in its evolution, leading to $2n=6$ in *D. marlothii*. Variation in chromosome number in *D. montanum* is surprising and misidentification of plants studied is possible.

Polyploidy is frequent in *Dipcadi*. Of the seven Eurasian species that have been counted, three are exclusively diploid, two are exclusively polyploid, and the remaining two are heteroploid. Three of the six southern African species counted, *D. ciliare*, *D. glaucum* and *D. longifolium*, are tetraploid.

### 4.3. *Ornithogalum*

*Ornithogalum* subgen. *Avonsera* has $2n=14$ (Table 2). Four species of subgen. *Galtonia* sect. *Galtonia* have $2n=16$ (Forrest and Jong, 2004) and the fifth, *O. saundersii*, has $2n=14$ (Pienaar, 1963). The karyotypes are bimodal and consist of eight large and eight much smaller chromosomes, except in *O. saundersii*, which has a karyotype of ten large and four smaller chromosomes. In subgen. *Galtonia* sect. *Xanthochlorum*, both *O. xanthochlorum* and *O. prasinum* also have $2n=16$ [the latter possibly also with $2n=14$ and 12 if counts by De Wet (1957) for that species are correct, although we suspect that the counts are for other species since the karyotype illustrated by De Wet (1957) is quite unlike that reported by Pienaar (1963)]. Karyotypes in subgen. *Galtonia* are strongly asymmetrical and bimodal, with four large and four small chromosome pairs. Base number for the subgenus is clearly $x=8$. No instances of polyploidy have been reported in subgen. *Galtonia* and *O. saundersii*, $n=7$, is evidently a hypodiploid.

Subgen. *Aspasia* sects. *Aspasia* and *Hidaspasia* are moderately well known cytologically and have $x=6$. In subgen. *Ornithogalum*, the sub-Saharan sects. *Linaspasia* and *Neopatersonia* also have $x=6$ but both are inadequately sampled (Table 2), and sect. *Elsiea* (1 sp.) is uncounted. The majority of counts in the four sections are diploid, $2n=12$, as is the only species of sect. *Neopatersonia* counted. Only occasional instances of dysploidy, $2n=10$, and of triploidy, $2n=18$, have been recorded (Pienaar, 1963). Populations of *O. corticatum* [reported as *O. lacteum* from the Western Karoo, South Africa by Pienaar (1963)] appear to consistently have $2n=10$ and it is, on available evidence, a dysploid species. *O. juncifolium* has $2n=12$ as well as dysploid races with 10, and *O. graminifolium* has $2n=12$, 10 and 8, a striking exception to the rule in the genus. The karyotype of *O. corticatum* has a pair of very long metacentric chromosomes, a likely product of chromosome fusion and elimination of a pair of centromeres (Robertsonian translocation sensu Jones 1970). The recognition of *O. corticatum* as distinct by Manning et al. (2007) is supported by the cytological difference from related species. Similar chromosomal rearrangements characterize the dysploid races of *O. juncifolium*.

As is the case with *Albuca* subgen. *Albuca*, relatively few species of sub-Saharan species of *Ornithogalum* have actually been studied cytologically. All five species of subgen. *Galtonia* sect. *Galtonia* have been counted, some of them several times, but for the larger subgen. *Aspasia* (30 spp., 11 counted) and subgen. *Ornithogalum* (45 spp, 4 counted) our knowledge base is modest, and just 24 of an estimated total 84 species have actually been counted. Available evidence, nevertheless, strongly points to $x=6$ as basic for both subgen. *Aspasia* and subgen. *Ornithogalum* in sub-Saharan Africa. Apart from the few isolated examples of dysploidy mentioned above, triploidy, $2n=18$, has been recorded in one otherwise diploid species (Pienaar, 1963). Only *O. hispidum* is currently known to have diploid and tetraploid populations, and one more, the tropical African *O. gracillimum*, is evidently tetraploid, $2n=24$. According to Stedje (1996), who made this count, this was the first for the species and we thus infer that the count of $2n=16$ listed as for *O. gracillimum* (Stedje and Nordal, 1984) was for another species, perhaps what is now *Albuca virens*, under which we provisionally list it (Table 2). No higher levels of polyploidy have been reported and only *O. gracillimum* is thus far exclusively polyploid.

The frequency of polyploidy in sub-Saharan *Ornithogalum* is surprisingly low, just 1 of 24 species so far counted (4%), especially in light of the contrary situation in the Eurasian members of subgen. *Ornithogalum* (sects. *Cathissa*, *Honorius*, *Melophis* and *Ornithogalum*). Sects. *Melophis* and *Honorius* have $x=7$, and those species that have been counted are heteroploid or exclusively tetraploid. Sect. *Cathissa*, however, appears paleotetraploid with a likely base number of $x=16$ or possibly $x=18$ (Table 2). Sect. *Ornithogalum* likely has $x=9$ but both dysploidy and polyploidy have clearly been involved in its radiation. We lack a deep understanding of the taxonomy of sect. *Ornithogalum* and are unable to reliably estimate the frequency of polyploidy here. Nevertheless, the high frequency of polyploidy evident in the Eurasian sections of subgen. *Ornithogalum* stands in marked contrast to its near absence sub-Saharan Africa. This pattern is mirrored in other geophytic genera that occur in both Africa and Eurasia. In *Gladiolus* (Iridaceae), only five of 70 sub-Saharan species sampled so far have polyploid populations (7%) but all six Eurasian species are polyploid (Goldblatt et al., 1993). In *Moraea* (Iridaceae) the two Eurasian species are tetraploid, and only 8 of 162 species counted are exclusively polyploid (5%), and 18 more species have diploid and polyploid populations (Goldblatt, 1976 and unpublished).

### 4.4. Summary

In *Albuca* we hypothesize that subgen. *Namibiogalum* probably has $x=10$, whereas subgen. *Albuca*, *Osmyne* and *Monarchos* all have $x=9$. The pattern in subgen. *Urophyllophon* is remarkable: although a base number of $x=6$ is likely, its three constituent species exhibit a range of $2n=12, 10, 8, 6$ and 4 (exclusive of polyploidy). All karyotypes have three large chromosome pairs and a variable number of very small chromosomes. Polyploidy is rare in the southern African species of *Albuca*: following current taxonomy, just 9% (alternatively 13%) of sub-Saharan species are polyploid and another 16% have both diploid and polyploid races, a common
situation in that flora (Goldblatt, 1971). In tropical Africa, the frequency of polyploidy for \textit{Albuca} is over 20%.

\textit{Pseudogaltonia} has \(x=9\) and \textit{Dipcadi} possibly \(n=6\) in subgen. \textit{Dipcadi} but \textit{D. serotinum}, probably highly derived among the Eurasian species according to an unpublished molecular phylogeny (F. Forest unpublished data), has \(n=4\). The remaining species show a pattern of descending dysploidy leading to \(n=3\) in the southern African \textit{D. marlothii}.

Chromosome numbers are known for just 24 of the estimated 84 species of sub-Saharan \textit{Ornithogalum}, mostly from sects. \textit{Aspasia} and \textit{Linaspasia}, in which \(x=6\) is basic. In contrast, \(x=9\) seems the likely ancestral base number for the Eurasian species of sect. \textit{Ornithogalum}. Both sections of \textit{Ornithogalum} subgen. \textit{Galtonia} have \(x=8\). Polyploidy is also rare in southern and tropical African species of \textit{Ornithogalum}, but both polyploidy and dysploidy are frequent among the Eurasian species of sects. \textit{Cathissa} and \textit{Ornithogalum}. Above species rank, the only taxon of \textit{Ornithogalum} that remains uncounted is sect. \textit{Elsiea} (1 sp.) of subgen. \textit{Ornithogalum}.

The cytological scenario we have outlined for subfam. \textit{Ornithogaloideae} envisages repeated instances of descending dysploidy from higher ancestral base numbers (Fig. 1). Base numbers seem to have stabilized in \textit{Albuca} at \(x=9\) except in subgen. \textit{Urophyllon}. A lower base of \(x=6\) was established independently in multiple lineages in sub-Saharan \textit{Ornithogalum} although subgen. \textit{Avonsera} has \(x=7\) and subgen. \textit{Galtonia} has \(x=8\). The major pattern in the cytological evolution of the subfamily is decreasing dysploidy, and polyploidy appears to have played a minimal role except in \textit{Dipcadi}, in which both dysploidy and polyploidy appear important in its radiation (Fig. 1).

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