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KARYOTYPE ASYMMETRY IN *GALTONIA* AND *PSEUDOGALTONIA* (*HYACINTHACEAE*)[a]

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The karyotype of a recently described species of *Galtonia* (*Hyacinthaceae*), *G. regalis*, is described and its cytotaxonomic relationship to other members of the genus examined. Since conflicting cytological patterns for the genus exist in the literature, the chromosome compositions of the three other species, *G. candicans*, *G. princeps* and *G. viridiflora*, are re-investigated. This study demonstrates that the karyotype of *Galtonia* is uniformly asymmetrical and distinctively trimodal, with $2n = 16$. Also included in this investigation is the allied monotypic genus *Pseudogaltonia*. Its karyotype is also asymmetrical, but differs from *Galtonia* in its chromosome number of $2n = 18$, and in certain other features.

Keywords. Bimodality, *Galtonia*, *Galtonia regalis*, karyotype asymmetry, *Ornithogalum*, polymodality, *Pseudogaltonia*, trimodality.

INTRODUCTION

Galtonia Decne. (*Hyacinthaceae*), a small genus of four species, occurs in SE Africa, i.e. southernmost Gauteng (Transvaal), Lesotho, Orange Free State, KwaZulu Natal, Transkei and Eastern Cape, from 60 to 2700m altitude (Hilliard & Burtt, 1988). Hilliard and Burtt's revision of the genus (1988) includes *G. regalis* Hilliard & Burtt, which they described in 1986 as clearly distinct from the other three species: *G. princeps* (Baker) Decne., *G. candicans* (Baker) Decne. and *G. viridiflora* Verdoorn.

Very different karyotypes have been published for the genus, the most recent being for *G. princeps* and *G. viridiflora* by de Wet (1957), who depicted the complements as being symmetrical, the chromosomes showing a gentle gradation in length. This contrasts sharply with karyotypes reported earlier by other authors, for example Newton (1924) and Sato (1942). Newton observed in *G. candicans* and *G. princeps*, and Sato in the latter only, complements that were asymmetrical, composed of chromosomes of two strikingly distinct size classes. This paper aims to shed some light on the problem of this conflicting information, and to determine

[a] If the generic circumscriptions in *Hyacinthaceae*, proposed by Manning, Goldblatt & Fay on p. 533 of this issue, are followed, then *Galtonia* and *Pseudogaltonia* would be treated as groups of species within an enlarged *Ornithogalum*.

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where the karyotype of *G. regalis* fits. This necessitated a cytological re-examination of the other three species. For comparison, *Pseudogaltonia* (Kunze) Engl. was also included in this study; the only species, *P. clavata* (Mast.) E. Phillips from Namibia and Namaqualand, was formerly in *Galtonia* as *G. clavata* Mast.

Materials and methods

Except for the single collection of *G. candicans*, more than one accession of each of the other three species were sampled. Only a single accession of *Pseudogaltonia clavata* was available. Accession details are summarized in Table 1. Root tips were pretreated either in 0.025% colchicine for 2.5–3 hours at room temperature (c.20°C) or in 0.002M 8-hydroxyquinoline for 4–6 hours (6 hours preferred) at 13°C and fixed in 3:1 ethanol:propionic acid. Both pretreatments were satisfactory, as were staining

Table 1. Details of *Galtonia* and *Pseudogaltonia* accessions investigated

Name	RBGE accession no.	Collector name and no.	Locality
G. regalis	19820246	*Hilliard & Burtt* 15382	KwaZulu Natal: Royal Natal National Park, Tugela Gorge
	19850404	*Hilliard & Burtt* 18120	KwaZulu Natal: Mpendhle District, Upper Loteni Valley, above Ashcave, c.1981m
	19850424	*Hilliard & Burtt* 18179	KwaZulu Natal: Mpendhle District 2929 AD, Upper Loteni Valley
	19850623	*Small, W*	KwaZulu Natal: Upper Hlatimba Valley, 1981m
G. candicans	19694472	Not of wild origin	
G. princeps	19831314	*Hilliard & Burtt* 16349	E Cape: Umtata, NW, 1525m
	19831316	*Hilliard & Burtt* 16746	KwaZulu Natal: Harding District, c.655–915m
	19831317	*Hilliard & Burtt* 16750	KwaZulu Natal: Harding District, about 3km from *Hilliard & Burtt* 16746, c.655–915m
G. viridiflora	19830123	*Hilliard & Burtt* 16181	KwaZulu Natal: Drakensberg Highmoor Forest Reserve
	19790335	*Hilliard & Burtt* 12077	Lesotho: Nr Molimo Nthuse Pass
P. clavata	19871188	*Long & Rae* 790	Namibia: Gobabis District, 10km E of Witvlei, c.1430m

RBGE, Royal Botanic Garden Edinburgh.
m = metres above sea level.

in lacto-propionic-orcein (after Dyer, 1963) or Feulgen reagent (after Fox, 1969). Some useful metaphase spreads were also obtained after pretreatment in saturated aqueous α-bromonaphthalene for 3 hours at room temperature, or overnight at about 5–6°C, but the results were somewhat erratic. Flower buds for meiotic study were fixed in 3:1 ethanol:propionic acid and stained in lacto-propionic orcein or Snow's acid-alcoholic carmine. For protocol used see Jong (1997).

RESULTS

Galtonia regalis: $2n = 2x = 16$ (as in other species in the genus, see Table 2; Figs 1 and 4).

The karyotype is strongly bimodal, consisting of a group of eight very long chromosomes and a group of eight short ones. The long chromosome group (L) consists of six acrocentrics, i.e. with subterminal centromeres, which are type *t* according to the terminology of Levan *et al*. (1964); the other two, apparently with terminal centromeres, are type *T*, the chromosomes terminating in a narrow point or tiny 'pimples'. Among the eight short chromosomes can be recognized one subgroup of four distinctly longer chromosomes (S_l), one pair of which is acrocentric, type *t*, each member bearing a satellite distal to the short arm. Variation in size and

TABLE 2. Chromosome number and satellite size variation in *Galtonia* and *Pseudogaltonia* accessions investigated

Name	Accession no.	Collector name and no.	2*n*	*n*	
G. regalis	19820246	*Hilliard & Burtt* 15382	16	8	Heteromorphic
	19850404	*Hilliard & Burtt* 18120	16		Homomorphic
	19850424	*Hilliard & Burtt* 18179	16	8	Homomorphic
	19850623	*Small, W*	16		
G. viridiflora	19790335	*Hilliard & Burtt* 12077	16		Heteromorphic
	19830123	*Hilliard & Burtt* 16181	16		Homomorphic
G. princeps	19831314	*Hilliard & Burtt* 16349	16	8	Heteromorphic? satellites minute, often heterochromatic
	19831316	*Hilliard & Burtt* 16746	16		Homomorphic? satellites slightly larger than *Hilliard & Burtt* 16349
	19831317	*Hilliard & Burtt* 16750	16	8	
G. candicans	19694472		16	8	Heteromorphic, one satellite sometimes heterochromatic
P. clavata	19781188	*Long & Rae* 790	18		Heteromorphic

? indicates satellites very small: hard to tell if they differ in size.

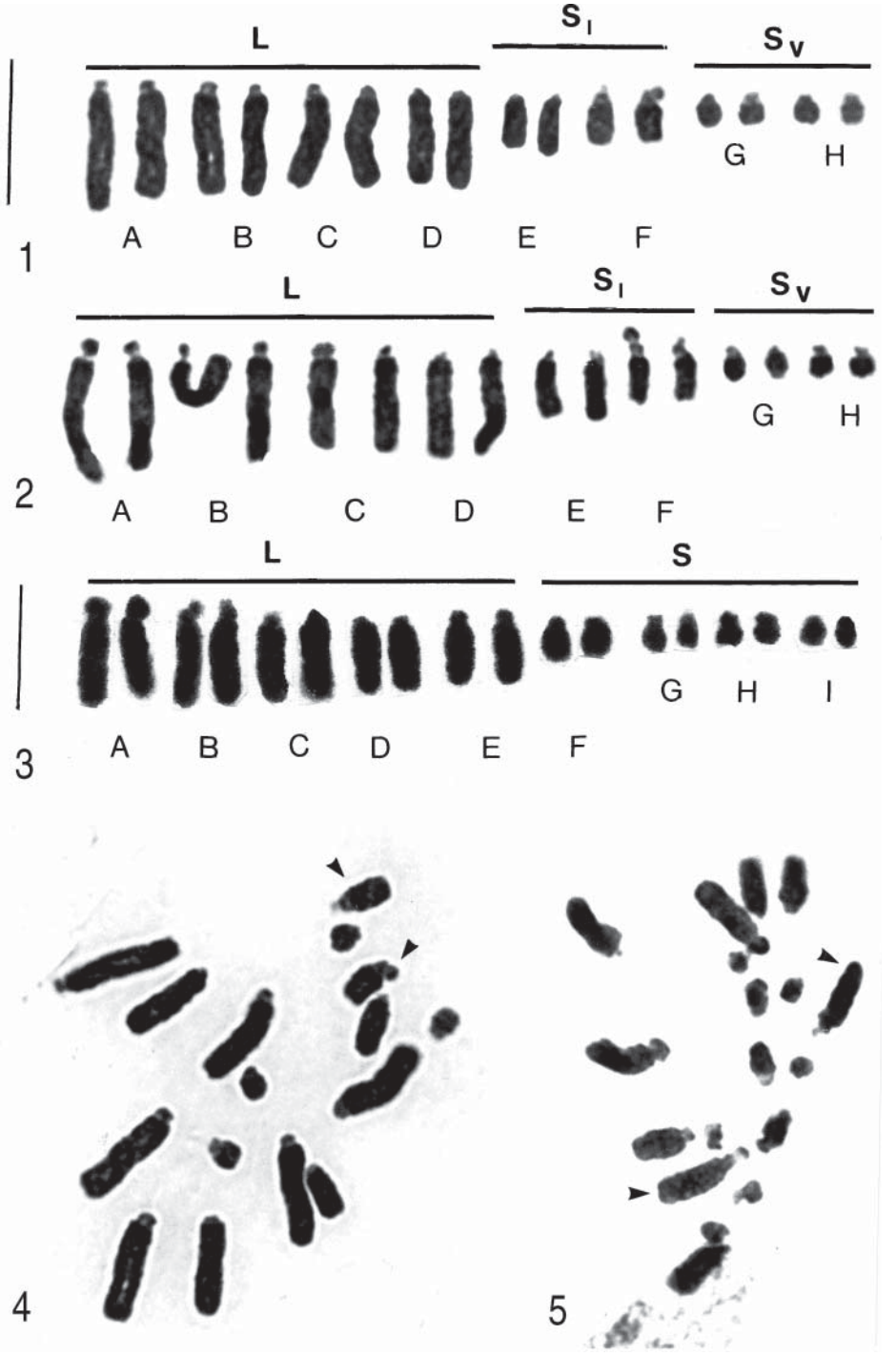

L
S I
S V
A B C D E F G H
1
L
S I
S V
A B C D E F G H
2
L
S
A B C D E F G H I
3
4
5

TABLE 3. Mean total chromosome length (μm) in *Galtonia regalis* (*Hilliard & Burtt* 15382) based on six well-spread, colchicine-pretreated root tip metaphases

Chromosome pair/no.		Mean total length	Chromosome pair/no.		Mean total length
A	1	9.6	E	9	4.6
	2	9.4		10	4.4
B	3	8.9	F	11	4.2
	4	8.5		12	4.0
Mean of 1–4		**9.1**	Mean of 9–12		**4.3**
C	5	8.0	G	13	2.5
	6	7.9		14	2.5
D	7	7.7	H	15	2.6
	8	7.3		16	2.4
Mean of 5–8		**7.7**	Mean of 13–16		**2.5**

Group L: pairs A to D; Group S_I: pairs E & F; Group S_V: pairs G & H.

euchromaticity of the satellite occurs between members of this SAT-chromosome pair (Figs 1 and 4) and between accessions, being heteromorphic in *Hilliard & Burtt* 15382, and homomorphic in *Hilliard & Burtt* 18120 (see Table 2). The second pair of chromosomes in this subgroup has no discernible small arm, and the centromere is interpreted as being terminal, and thus of type *T*. The second subgroup of four short chromosomes (S_V) consists of very much smaller acrocentrics, where the centromeres are often indistinct. The karyogram in Fig. 1 is based on the metaphase in Fig. 4.

Table 3 gives the mean total lengths derived from six well-spread metaphases, ranging from the mean of the longest pair (c.9.5μm) to the mean of the shortest pair (2.5μm), with a relative length difference of about 26% between the longest and

FIGS 1–3. Karyograms.

1: *Galtonia regalis*, based on Fig. 4 (*Hilliard & Burtt* 15382). Karyotype formula $8L+4S_I+4S_V$; L = long chromosomes (A to D); S = short chromosomes: S_I = intermediate subgroup E & F (F with satellites); S_V = very short subgroup G & H.

2: *G. viridiflora* (*Hilliard & Burtt* 12077). Karyotype formula as for Fig. 1. Note prominent small arms in pair A; SAT-chromosomes F are clearly heteromorphic.

3: *Pseudogaltonia clavata* (*Long & Rae* 790). Karyotype formula 10L + 8S. Note prominent small arm in longest pair A, much larger than any in *Galtonia*; second longest pair (B) with satellites. Among the S group, one pair (F) is longer than the rest.

Scale bars = 10μm; bar in Fig. 1 applies also to Fig. 2 (and Figs 4 and 5); bar in Fig. 3 applies there only.

FIGS 4–5. Somatic metaphases from colchicine-pretreated root tips.

4: *G. regalis* (*Hilliard & Burtt* 15382), $2n = 16$, SAT-chromosomes heteromorphic.

5: *P. clavata* (*Long & Rae* 790), $2n = 18$, SAT-chromosomes heteromorphic, the smaller satellite often faintly stained.

Scale bar as in Fig. 1. Arrows indicate SAT-chromosomes.

shortest of the complement. Bimodality of the karyotype is even more strikingly demonstrated in meiotic metaphases (Fig. 9). In fact, the karyotype may be more appropriately described as trimodal, as there exists a sharp discontinuity in size not only between the L chromosome group and the rest, but also between the intermediate (S_I) chromosomes and the very small ones (S_V) within the small chromosome group, namely, 4.3μm compared with 2.5μm, a difference of some 58%.

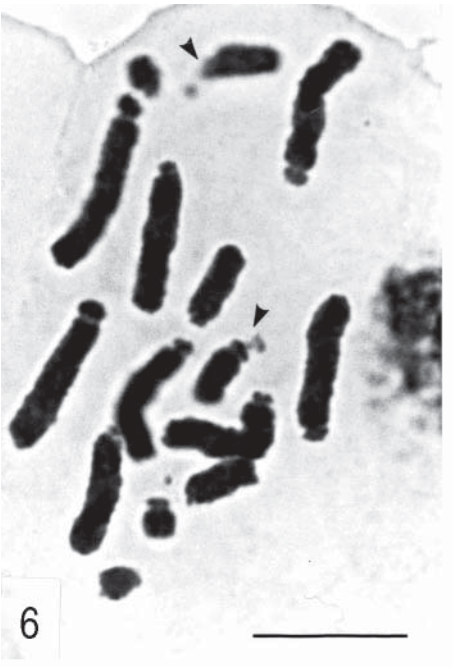
The karyotypes of the other three species, *G. princeps*, *G. candicans* and *G. viridiflora*, are very similar to each other and to that of *G. regalis* (cf. Fig. 2 and Fig. 1). Thus the karyotypic pattern of *Galtonia* may be represented by the formula $8L+4S_I+4S_V$, with the S chromosome group comprising two distinct sizes: S_I = short, S_V = very short. Newton (1924) described the S_I group as of intermediate length in *G. candicans* and *G. princeps*, as did Sato (1942) for *G. candicans.* As in *G. regalis*, a satellite occurs on the second longest pair of the S_I chromosomes, and differences in size and stainability are often observed between members (Table 2). Of special note is the short arm of the longest chromosomes of *G. viridiflora* which is consistently more prominent than those of the other species (cf. Figs 2 and 6 with Fig. 1). In *P. clavata* (see below) this arm is markedly longer than any observed in *Galtonia*.

Pseudogaltonia clavata: $2n=2x=18$.

This morphologically distinct genus occurs in Namibia and Namaqualand. Its chromosomes are acrocentric to telocentric (Figs 3 and 5), and it has the karyotype formula $10L+8S_V$. The longest pair has a very much longer short arm than any of the *Galtonia* chromosomes. Also, unlike *Galtonia* where the terminal satellite occurs on one of the intermediate pairs, in *Pseudogaltonia* it is borne on the second longest pair of the complement (B in Fig. 3); in this plant it is slightly heteromorphic. Among the eight short chromosomes, one pair is longer than the rest, but less sharply different in size. The karyotype of *Pseudogaltonia* is thus bimodal.

Figs 6–8. Somatic metaphases from colchicine-pretreated root tips.
6: *Galtonia viridiflora* (*Hilliard & Burtt* 16181), $2n=16$, SAT-chromosomes homomorphic.
7: *G. princeps* (*Hilliard & Burtt* 16349), $2n=16$, satellites minute; inset shows over-contracted SAT-chromosomes, one satellite with slight extension.
8: *G. candicans* (RBGE 19694472), $2n=16$, SAT-chromosomes slightly heteromorphic. Photographed under phase contrast.
Scale bars = 10μm; bar in Fig. 6 applies also to Figs 7 and 8. Arrows indicate SAT-chromosomes.

Figs 9–10. Meiotic metaphases.
9: *Galtonia princeps* (*Hilliard & Burtt* 16349), $n=8$, one large bivalent showing heterochromatic constriction in each homologue, giving false impression of median centromere. Two small bivalents often faintly stained.
10: *G. candicans* (RBGE 19694472), $n=8$.
Scale bars = 10 μm; bar in Fig. 9 applies also to Fig. 10.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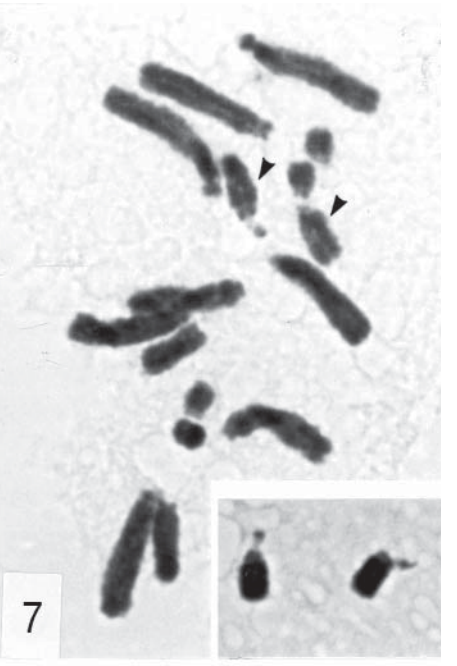
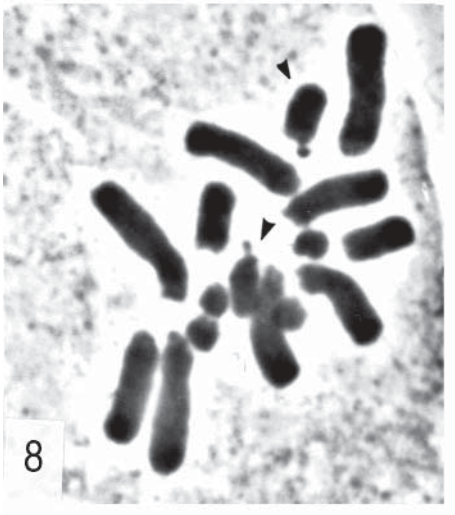

7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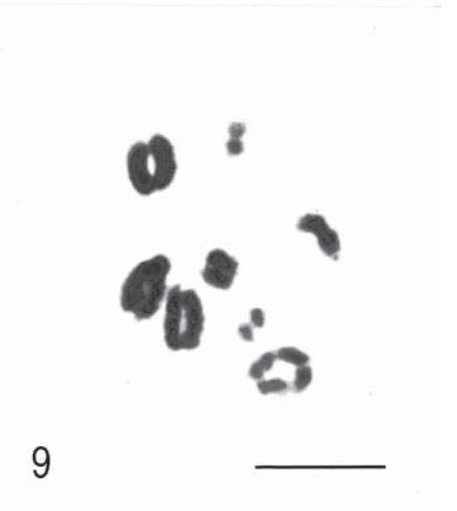
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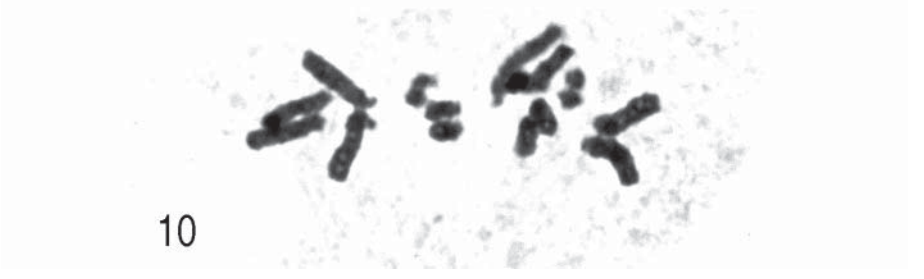
10

Discussion

Galtonia

In a recent generic treatment of the *Hyacinthaceae* (Speta, 1998) *Galtonia* is placed in subfamily *Ornithogaloideae* Speta, with *Albuca* L., *Pseudogaltonia*, *Dipcadi* Medik., *Ornithogalum* L. and a few other genera. In some large genera such as *Ornithogalum* (Cullen & Ratter, 1967) a wide range of karyotypes is known, including bimodal ones. By way of contrast, karyotype uniformity is characteristic of *Albuca* (Jong, 1991). The possibility that *Galtonia* might show a variety of karyotypes has to be considered. The karyotype of *G. regalis* is distinctly trimodal, and is very similar to those of the other species of *Galtonia* re-examined. This broadly conforms to the pattern first described for *G. candicans* by Digby (1910) who, like many early cytologists, favoured this plant for its large chromosomes primarily for studying chromosome behaviour at mitosis and meiosis, and referred to its four very small chromosomes as 'microchromosomes'. Subsequently Newton (1924) provided much fuller karyological details for this species and for *G. princeps*, both being notably trimodal, with $2n = 16$. Sato (1942), in his cytological survey of the *Liliaceae* (sensu Hutchinson, 1934), also presented a karyotype formula for *G. candicans* consistent with these earlier observations. These are in marked contrast to those presented by de Wet (1957) for *G. princeps* and *G. viridiflora*. Of special interest is *G. viridiflora*, a species that has often been confused with *G. regalis* (Hilliard & Burtt, 1988). While the chromosome number recorded for *G. viridiflora* by de Wet (1957) was also $2n = 16$, his idiogram shows a gradation in size, with all the chromosomes having median to submedian centromeres, a size distribution typical of a symmetrical karyotype. He illustrated a similar karyotype for *G. princeps*. These results differ significantly from those obtained in the present study, as well as from those of other authors. As noted in Table 1, except for *G. candicans*, material from more than one locality was examined for each species, and we detected no deviation from the basic *Galtonia* karyological configuration. As Digby (1910), Newton (1924) and de Wet (1957) all based their observations on microtome sections, it seems unlikely that de Wet's very different results were due to artefacts produced through sectioning, and they are difficult to explain. Recent molecular evidence (plastid *trn*L-F DNA sequences) suggests that the genus is polyphyletic (Pfosser & Speta, 1999), *Galtonia candicans* being grouped with *Stellaroides* and *Albuca*, while *G. viridiflora*, *G. princeps* and *Zahariadia* form a different group. *Galtonia regalis* was not included in this survey. The present study clearly demonstrates, however, that all four *Galtonia* species share a common karyotypic pattern.

Pseudogaltonia

The chromosome number of *P. clavata*, $2n = 18$, agrees with that reported by Speta (1985) for this species (as *Lindneria clavata* (Mast.) Speta). Its karyotype is distinctly bimodal, and differs from *Galtonia* in several other obvious respects already noted

above. Thus *P. clavata* is clearly cytologically distinct. Speta (1985) also commented on the large size of the chromosomes compared with *Galtonia* and other members of the *Hyacinthoideae*, but it is not possible to confirm this without further study. Again, our observations differ from those of de Wet (1957), who reported $n = 12$ for this species. The molecular data of Pfosser & Speta (1999) place *Pseudogaltonia* next to *Dipcadi* rather than *Galtonia*.

Bimodal karyotypes seem quite common among African monocotyledons; well-known examples in the *Asphodelaceae* (sensu Smith & Van Wyk, 1998) include *Aloë* L., *Gasteria* Duval and *Haworthia* Duval (Brandham, 1983). They may characterize whole genera, as noted above, or virtually a whole family, as in *Agavaceae*. In other groups, they may occur with varying frequency as part of the pattern of karyotypic variation, e.g. in the cytologically highly variable genus *Lapeirousia* Pourr. (*Iridaceae*: *Ixiodeae*) (Goldblatt, 1990) and in *Ornithogalum* (*Hyacinthaceae*) (Cullen & Ratter, 1967; Stedje, 1989). Extreme bimodality is shown in many species of *Lapeirousia*, with a single pair of very long chromosomes and varying numbers of very small ones. This form of bimodality bears a close resemblance to that observed by the second author (K.J.) in *Cyanixia socotrana* (Hook.f.) Goldblatt & J.C. Manning (*Babiana socotrana* Hook.f.); see Goldblatt *et al.*, p. 517 of this issue. The karyotype of *Galtonia* is unusual in being trimodal, a condition that seems closely related to the bimodal one. For convenience, we combine the two, for the rest of the discussion, as 'polymodal'. Polymodal karyotypes are otherwise of restricted occurrence, and relatively rare amongst dicotyledons (Greilhuber, 1995). Among pteridophytes, they are known for certain in only two African ferns, *Lomariopsis rosii* Holttum and *L. hederacea* Alston, and possibly in one species of *Hymenophyllum* L. (Roy & Manton, 1966). They seem to be more widespread in the animal kingdom, being characteristic of whole major groups such as birds, and common in reptiles.

The origins and adaptive significance of polymodal karyotypes

Chromosomes without a distinct short arm or where one arm is represented by a pointed end or by tiny, often faintly stained, dot-like structures, are here interpreted in *Galtonia* as being telocentric. As White (1973) points out, it is often extremely difficult to distinguish between acrocentrics whose second arm is minute and true telocentrics. Whether chromosomes with truly terminal centromeres actually occur has been the subject of considerable debate (White, 1973). Telocentric chromosomes are thought to arise through fission across the centromeric regions of metacentric or submetacentric chromosomes (Jones, 1978), although it is far from clear how such a mechanism operates. In any case it is doubtful if centric fission (or fusion) alone accounts for the origin of all polymodal karyotypes. Such karyotypes may have been derived, in different plant groups, through a variety of routes, including unequal chromosome translocation, deletion, or hybridization between species with widely divergent chromosome size. For detailed reviews, see Stedje (1989) and Greilhuber (1995).

As to their possible adaptive significance, there appears to be a high frequency of karyotype polymodality, particularly bimodality, in monocotyledons of arid habitats, as exemplified by *Aloe*, *Haworthia* and the *Agavaceae*. *Hosta* is however an exception, as the species are typically of mesic habitats (Stebbins, 1971). Except for *Galtonia viridiflora*, which favours drier areas, other *Galtonia* species occur in damp or wet areas (Hilliard & Burtt, 1988). The association between polymodal karyotypes and aridity is therefore far from straightforward. Perhaps their adaptive significance may be sought in the nature of the karyotype itself, the distinct chromosome size-groups representing subsets of the genome with different recombination potential, i.e. differences in the tightness of linkages of adaptive gene complexes – in Stebbins' terminology, 'adaptive linked gene clusters'. Such a hypothesis has also been mooted by Bruyns & Vosa (1987) and Vosa & Bennett (1990). Bimodality or trimodality may represent just one of a number of alternatives favoured by selection in parcelling genetic material in plants of certain habitats and growth habits. This should be considered in relation to other properties such as chromosome shape, the breeding system and kinetics of chromosome behaviour.

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