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A revised cytotaxonomy of the genus *Tulbaghia* (Alliaceae)

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In memoriam Dr. L. Codd, eminent South African Botanist and a very dear friend.

Abstract — A revision of *Tulbaghia* (Alliaceae) has been carried out. The genus includes twentyone species and one variety. On the basis of the different karyotypes, the genus can be subdivided into seven distinct Groups. Some species have poly-ploid forms but no true polyploid species has been found so far. A number of species possess heterochromatic segments which may be either mostly distally or proximally located. The heterochromatic segments of *Tulbaghia* are cold sensitive and specific fluorochrome staining shows that they are composed mainly of highly repetitive sequences of Guanine-Cytidine nucleotides. The possible evolutionary role of heterochromatin as well as that of the B-chromosomes, present in some species, is briefly discussed. The illustrations include micrographs of the mitotic chromosomes as well as colour photographs of the inflorescence of all the species. The typical habitat of two of the species is also illustrated in colour.

Key words: B-chromosomes, constitutive heterochromatin, cytotaxonomy, karyotype groups, nucleolar organizers, *Tulbaghia*.

INTRODUCTION

Because of its validity, especially regarding the early history of the genus, it has been decided to publish the original introduction by VOSA (1975), in a corrected and appropriately up-dated version.

The genus *Tulbaghia* was created by Linnaeus (*Mant. Pi. p. 148, 1771*) and based on material sent to Europe in 1769 by C. Rijk van Tulbagh, then Governor of The Cape Province. Linnaeus, in fact, used the name *Tulbagia*, which was corrected into *Tulbaghia* by P.D. Giseke (*Prael. Ord. Nat. PL 274, 1792*). The first species to be described, and the basis of the genus, is *Tulbaghia capensis*. It is illustrated in Jacquin (*Pl. Hort. Bot. Vindob., 2: 52, pi. 115, 1772-1773*) and, as *Tulbaghia alliacea*, in the *Bot. Mag. pi. 806 (1805)*. The specimen illustrated in *PL Hort. Vindob.* seems to correspond

to one of the four specimens of *Tulbaghia* present in the Linnaean Herbarium (n° 411.1). Two more species of *Tulbaghia* were described ten years later by Linnaeus filius in the *Suppl. Plant.*, of 1781 (p. 193-194). The first description refers to a new species, *Tulbaghia attiacea* (n° 411.2 of the Linnaean Herbarium — *nectarium ori tubi impositum, sexdentatum, obsoletius, obtusum, crassus, longitudine limbi*). The second description refers to a purple flowered plant with a three-lobed corona (n° 411.4, *Linn. Herb. — differt a T. alliacea nectario triphylo, statura minore*). It gives the name *T. cepacea*, but includes Linnaeus's *T. capensis* as a synonym and refers also to the *PL Hort. Vindob.* illustration. This synonymy, and the name *alliacea* given to the illustration of *T. capensis* in the *Bot. Mag.* (pi. 806, 1805), together with the annotation by J.E. Smith on the *T. capensis* type specimen (411.1) and his note on *T. alliacea* in *Rees Cyclop Roem. etSchult. 7: 993 (1819)*, have been responsible for the confusion in the early nomenclature of the genus.

A little known revision of the genus *Tulbaghia* was published by J.E.L. Ave-Lallemant

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(*Bull. Cl. Phys. Math. Acad. St. Petersb.*, 3: 204, 1844). This author noticed the confused taxonomy and, in an attempt to correct it, accepted *T. alliacea* Linn. fil., renamed *T. capensis* as *T. pulchella* and considered *T. alliacea*, forma a Drège, and *T. ludwigiana* Harvey (as defined in *Kunth Enum.*, 4: 483, 1833) as synonyms of the newly created species *T. cernua* (see notes on the status of this taxon in VOSA, 1980).

Further, he made *T. violacea* Harvey (see discussion on the status of this taxon in VOSA 1980), a synonym of *T. cepacea* Linn. fil. (as re-defined by J.E. Smith in *Rees Cyclop. Roem. et Schult. Syst.*, 7: 993, 1819).

Baker (*Jour. Linn. Soc.*, XI: 369-372, 1871), recognized a total of seven species but, in his account, did not mention the work of Avé-Lallemant, thus continuing the earlier confusion in the nomenclature of *Tulbaghia*. UPHOF (1943), in his review of the genus, lists eighteen species, but leaves the nomenclatural problems unresolved.

Most *Tulbaghia* species possess a strong alliaceous smell which is very persistent and its is still present in herbarium specimen found in the Linnaean Herbarium which were collected more than 200 years ago. The alliaceous smell and relative flavour have given most of the species of *Tulbaghia* the popular name of "wild garlic" (Africans: Wilde Knoklook or Wilde Knoffel).

Enzyme studies have indicated that in *Tulbaghia* and in *Allium* the biochemical mechanism, and therefore the genetic endowment responsible for the odour production, is the same (JACOBSEN *et al.* 1968). The general morphology of *Tulbaghia* (including embryo-sac formation, etc.), apart from some details of floral structure, is also very much like to that of *Allium* and of some related genera. Thus, *Tulbaghia* may be considered to be the Southern African analogue of the Euroasian and American Alliaceae.

Some economic and medicinal use is made of several species of the genus. The KwaZulus use the green parts and the flowers of cultivated *T. violacea*, which they call "icinzini", as vegetable and the rhizome as an emetic and a love potion. The leaf is also used for flavouring meat and vegetable dishes. Other uses by the KwaZulus includes the planting of *T. violacea* around their huts to "ward off snakes". *T. acutiloba* is used by the Southern Sotho for food and, as an infusion, as a chest and stomach medicine. Some other species of *Tulbaghia* are used by the Xhosas of the Transkei and Ciskei: *T. violacea* is

generally used as food. Other uses of *T. violacea* by the Xhosa are: its roots and leaves are used to make a kind of tea, the crushed leaves are rubbed on the head to relieve sinus headache and, as an infusion of the whole plant, for the treatment of rheumatism and of paralysis, to reduce body temperature in case of high fever and as a strong purgative. Apropos of the use of *T. violacea* as food by the Xhosa, I recall an episode during one plant collecting trip along the course of the Buffalo river, near East London, together with the late Miss M. Courtney-Latimer, the late Dr. G.G. Smith and Mr. Kenneth Burras of Oxford. In some spots where in a previous trip we had found several clumps of *T. violacea* there were only holes, obviously made by digging sticks, and some partly burned leaves and rhizomes of the plant. Walking further along the bed of the river, we met with a group of Xhosa, men and women, who were cooking, on a little fire, the unwashed plants of *T. violacea* and eating them with obvious relish.

The strongest smelling species of the genus are said to have good antihelmintic properties and to be somewhat effective in curing pulmonary tuberculosis. The Southern Sothos use *T. leucantha*, together with other plants, to prepare special decoctions to "rid the body of snakes" and the leaf is sometimes used as an additive to pipe tobacco. The early European settlers in the Cape used the rhizome of *T. alliacea* and *T. capensis* to make decoctions said to be efficacious in case of febrile conditions.

The present revision and the previous account by VOSA (1975) as well as his other studies (1979, 1980, 1981, 1982, 1983), on this genus, have been based on living material collected in the field during several trips to South Africa and cultivated and observed over many years. Of course, adequate reference has been made to as many as possible herbarium specimens, to validate the names of the species as already described and to check on the localities of collection in order to establish the geographical range and to plan further collecting trips. This approach, together with the thorough evaluation of the all important cytogenetic findings, make it possible to have the best notion of what constitute a good species.

In our opinion, to work on the principle that: "the optimum classification seems to result from the time-honoured method of grouping

herbarium specimens by overall similarity into a number of heaps and then searching the literature for names to apply to the heaps" (BURBIDGE 1978), may be not the best way of trying to deal with complex taxonomic problems. The sentence: "time-honoured method" is probably symptomatic of the approach in tackling such problems, which seems to be still somewhat prevalent in taxonomic studies conducted in herbaria.

The species insufficiently known are indicated in Appendix I and a taxonomic key is provided in Appendix II.

MATERIALS AND METHODS

The material used in this study consists in living plants and on the relative exsiccata. The living material, for the most part, has been collected by the author during several trips to Southern Africa and cultivated in clay pots in John Innes-type potting compost, with the addition of extra grit, in a cool-greenhouse. Exsiccata have been examined in Botanical Institutions both in South Africa and in Europe namely: SAM, NBG, BOL, STE, GRA, NU, NH, J, PRE, BM, LINN, K, G.

For the cytological preparations, generally, actively growing root-tips and, in some cases, young ovules collected in the field, were pretreated in an aqueous solution of 0.05% colchicine for 3-4 h, at the same temperature of the growing plants. All the cytological material was fixed in 1:3 acetic-alcohol for 5-6 h or overnight. Normal Feulgen squashes were prepared and made permanent by mounting in Euparal. The method suggested by VOSA (1973b), was used for C-banding.

For the fluorescence preparations hydrolysis was reduced to about 10" and the material was squashed in 45% acetic acid and then mounted on coated cover-slips. These were stained in 0.5% Quinacrine dissolved in absolute alcohol, for 5' at room temperature, washed in absolute alcohol and immediately observed with a fluorescence apparatus (Zeiss Ultraphot with a B12 exciter-filter and a n° 50 barrier-filter). Micrographs were taken on Kodak Microfile-type film for the Feulgen and for the C-banded preparations and on Kodak 400 ASA B/W-film for the Quinacrine-stained slides. To establish and/or confirm the position of the nucleolar organizers on the relative chromosomes, I have used the one-step colloidal-silver method suggested by HOWELL and BLACK (1980).

In the indications related to the geographical range and in the localization of the specimens, for the sake of easier comparison with existing data, in most

cases, I have thought expedient to use the former names for the South African Provincial subdivisions.

RESULTS AND DISCUSSION

As seen on herbarium specimens and in the field, most species of *Tulbaghia* show some morphological variation in flower size, in the presence or absence of the leaves, and of their size, at the time of anthesis. This variability is due to the genotype but, at least in part, is also due to ecological factors. One of these factors is that a number of species, growing in the summer-rain areas, are found in pastures which are burnt regularly each spring, before the onset of the rainy season. The majority of the species, in these areas, flower shortly after the start of the rain, but in flower size, flower stem and leaf length and, to a certain extent, morphology, they differ somewhat from plants of the very same species found near, but in places where the fire cannot reach them, and which usually flower later. It has been found that flower size, and the above ground morphology, change gradually after the first burst of flowering. Thus, field observations and herbarium specimens, collected at different times during the growing season, may be not adequate for the exact recognition of the species. In order to obviate this, and for defining valid characters for determination, it has been found necessary to keep many forms of the same species under the same growing conditions for a few seasons.

Because of their morphological characters, karyotype and geographical range, it is likely that *T. violacea* and *T. cominsii* represent the most primitive species of the genus. In both species the corona is scarcely developed and is formed by only three distinct processes, placed opposite the inner perianth-segments, and both whorls of anthers are attached well inside to perianth-tube. Further, in these two species, the perianth-segments, the coronal lobes and the tube are highly coloured or white but in any case very showy. In contrast, most other species have a scarcely lobed, annular and a usually fleshy, crenate corona which is often the only pigmented part of the flower. In such species, the perianth-segments are very much reduced in size, green and often strongly reflexed. There seem to be a gradual progression towards species in which only the corona tends to be promi-

nently coloured. Intermediate types include *T. coddii* and *T. natalemis* where the perianth segments are pigmented but in contrasting colours with the corona. Some species such as *T. galpinii* and *T. rhodesica* represent special cases. *T. galpinii* is a tiny species which resembles a diminutive *T. capensis* with a deeply cut, but not very fleshy corona, very thin flaccid leaves and a different karyotype which places it in the *T. natalensis* group (Group 5). *T. galpinii* is endemic of a very restricted area of the Eastern Cape and all cultivated collections seem to be self-fertile.

Tulbaghia rhodesica is a tropical species. It has a karyotype similar to that of *T. cameroni*, which comes from the same region, but, in contrast with his latter species, has brightly colored flowers with broad perianth segments and a very short, deeply lobed corona of the same colour. It is difficult to define the affinities of *T. rhodesica* which probably represents a very ancient type well adapted to tropical light forest conditions.

Tulbaghia simmleri may represent an extreme evolutionary type. It possesses some peculiar characters such as its flower morphology with somewhat fleshy perianth segments and the comparatively small chromosomes (VosA 1975). Its breeding behaviour in crosses with other species is interesting showing rather scarce affinity. In fact, although a number of seeds in produced in most reciprocal crosses and these germinate well, the resulting plantlets seem to have a defective root system and fail to grow (VOSA 1996c).

Field observations have shown that population structure, in different species, presents some interesting features. In optimal conditions, all the species with highly coloured or white flower, such a *T. violacea*, *T. cominsii*, *T. natalensis* and *T. coddii*, occur often in dense populations especially along water courses or in vleis or, as in the case of *T. simmleri*, in light but somewhat humid mountain forest. All the species with inconspicuously coloured flowers such as *T. acutiloba*, *T. cernua*, *T. alliacea*, *T. capensis*, etc. occur mostly in very small clumps or, more often, as single plants at quite a distance from one another. This situation may probably reflect a kind of strict interaction between flower colour and eventual pollinators.

Taxonomic treatment

1. *Tulbaghia capensis* Linnaeus, Mant. 2:148,223 (1771); Jacq. Hort. Vindob. 2: 52, PL 115 (1772)

1773); WIUd., Sp. Pl. 2:33 (1779) Enum. Hort. Berol. 349 (1809); Baker, J. Linn. Soc. Bot. (London) 11:370 (1871), Fl. Cap. 6: 406 (1897); Uphof, *Herbertia*, 10: 45 (1943); Vos, Ann. Bot. 34: 66-68 (1975); Burbidge, Notes R. hot. GdsEdinb. 36: 84 (1978).

TYPE—411.1 (Linn!).

SYNONYMS—*Tulbaghiapulchella* Ave-Lall. in Bull. Cl. Phys. Math. Acad. Petersb. 3: 204 (1844), *nom. illegit.*

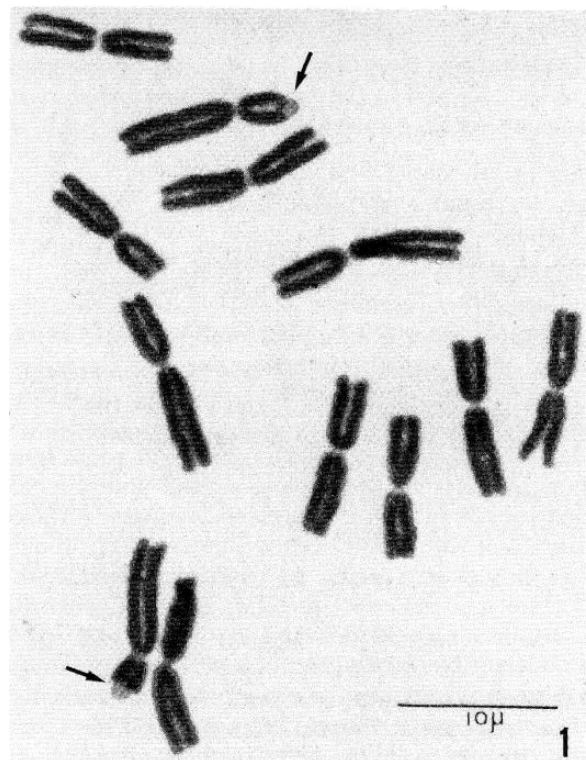
Tulbaghia alliacea auct. non L. f., Sims, Curtis's Bot. Mag. 21: t. 806 (1805).

ICONOGRAPHY—Jacquin in Pl. Hort. Bot. Vindob. 2: 52, PL 115 (1772-1773); Curtis's Bot. Mag. 21: t. 806, 1805; (VosA 1975, fig. 3, Plate I, fig. 3); Plate IA.

CHROMOSOME NUMBERS — $2n=2x=12$; $2n=4x=24$; $2n=6x=36$ (karyotype C, group 1, fig. 22b; fig. 1).

DISTRIBUTION — Endemic to the South Western Cape. Diploids and tetraploids are found only in the eastern part of the range.

EXSICCATA — Diploids: CAPE. - 3421 (Riversdale): 1.5 km E of Heidelberg, Vos, 294/14 (OXF).



Figs. 1-21 — Mitotic metaphases in *Tulbaghia*: in all micrographs, the positions of the nucleolar organizing regions are indicated by arrows. Fig. 1 — *Tulbaghia capensis* (2x), karyotype C.

Tetraploids: CAPE. - 3421 (Riversdale): just W of Heidelberg, *Vosa* 680 (OXF). - 3320 (Montagu) 11 km W of Drew, *Vosa* 2459 (OXF).

Hexaploids: CAPE. - 3318 (Cape Town): Waylands Farm, Darling, *Vosa* 188/2 (OXF); Schwartzvlei Farm, Darling, *Vosa* 189/3, 190/4 (OXF). - 3319 (Worcester): Karoo Garden on rocky hillside, *Vosa* 232/6 (OXF); 8 km S of Villiersdorp, *Vosa* 143/10 (OXF).

Other exsiccata: CAPE. - 3318 (Cape Town): Mamre Hills, Malmesbury, *Compton* 17271 (NBG), *Baker* 1643 (NBG). - 3420 (Bredasdorp), *Lewis* 57187 (NBG); *Axelson* 263, Tinie Versfeld Reserve, Darling (NBG); Slangkop, Darling, *Rycroft* 1778 (NBG).

This taxon is the type species of the genus. It is confined to the winter rain region of South Africa and is distinguished from all others in the genus by its deeply lobed and usually very fleshy corona-lobes.

2. *Tulbaghia alliacea* L. f. in Suppl. PL: 183 (1781); Ave-Lallemand, Bull. Cl. Phys. Math. Acad. Petersb. 3: 201 (1844); Baker J. Linn. Soc. Bot. London, 11: 371 (1871), Flora Capensis, 6: 405 (1897); Uphof, Herbertia, 10: 48 (1943); Marloth, Fl. Pl. S. Africa, 4: pi. 27 (1915); *Vosa*, Ann. Bot. (Rome), 34: 70-71 (1975); Burbidge, Notes R. bot. Gds. Edinb. 36: 94-85 (1978).

TYPE—411.2 (Linn).

SYNONYMS — *Tulbaghia narcissilorn* Salisb. *sensu* Podr. Stirp. 219 (1796); *Tulbaghia inodora* Gaertner, *sensu* De Fruct. et Sem. Pl. 1: 57 (1833); *Tulbaghia brachystemma* Kunth, *sensu* Enum. Pi. 4: 483 (1833)..

ICONOGRAPHY — (*Vosa* 1975, fig. 4, Plate II, fig. 3); Plate IB.

CHROMOSOME NUMBERS — $2n=2x=12$; $2n=6x=36$ (karyotype C, fig. 2).

DISTRIBUTION — This species, one of the oldest established in the genus, is found only in a rather restricted area of the winter rainfall region of South Africa. It is very variable in size. A population with $2n=6x=36$ (hexaploid) is found in the middle of Cape Town, in Rondebosch Common. *Tulbaghia alliacea* is very distinct from all other species of the genus in its morphology and distribution which partly shares with *T. capensis*.

EXSICCATA — Diploids: CAPE. - 3318 (Cape Town): dry slopes above Camp's Bay, *Vosa* 61 (OXF); moist sandy meadow, among large stones, Botanical Reserve, Stellenbosch, *Vosa* 242/9 (OXF); - 3418 (Simonstown): Cape Flats, in fine sandy soil, Vow 48 (OXF).

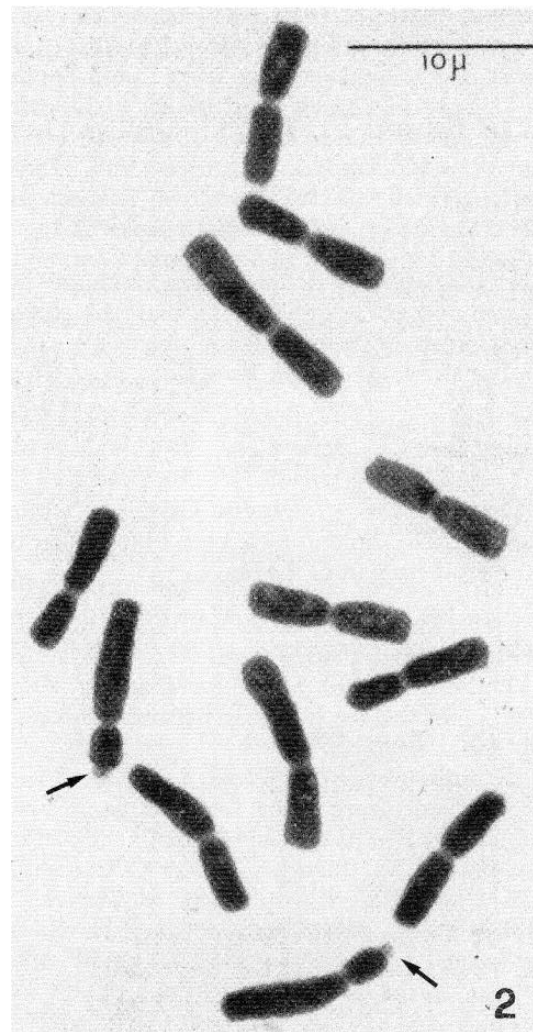


Fig. 2 — *Tulbaghia alliacea* (2x), karyotype C.

Hexaploids: CAPE. - 3318 (Cape Town): Rondebosch Common (Cape Town) in wet peaty soil on low lying ground, *Vosa* 244/11.

Other exsiccata: CAPE. - 3218 (Clanwilliam): slopes along the river Kloof, Olifants Rivier Mountains, *Esterhuysen* 15303 (BOL); - 3318 (Cape Town): Rondebosch Common, *Leigh ton* 1619 (NBG); Stellenbosch, *Boucher* 145 (STE); - 3418 (Simonstown): Slangkop, *Pond* 1497 (BOL); 3419 (Caledon): steep bank above rocks, Riviersonderend Mts. near Greyton, *Esterhuysen* 20754 (BOL).

3. *Tulbaghia cernua* Ave-Lallemand, Bull. Class Phys. Math. Acad. St. Petersb. 3: 202-203 (1844), Ind. Sem. h. Petr. 9: 25 (1844), Linnaea, 18: 222 (1844); *Vosa*, Ann. Bot. (Rome), 34: 75-77 (1975); *Vosa*, J.S. Afr. Bot. 47: 57-61 (1981).

TYPE — Ave-Lallemand 73.6 (LE!).

SYNONYMS — *Tulbaghia alliacea* var. *affinis* Baker, *sensu* Link Enum. alt. 1: 310 (1821); *Tulbaghia alliacea* forma *a* Drege *sensu* Kunth Enum. 4: 483 (1843); *Tulbaghia ludwigiana* Harv. forma *macrior*, *sensu* Kunth. Enum. 4: 483 (1843); *Tulbaghia campanulata* N.E. Br. in Kew Bull. 175: 136 (1901); type: CAPE. - Queenstown Division: mts. near Queenstown, Galpin 1660 (K, holo!).

ICONOGRAPHY — Batten & Bokelmann in "Wild Flowers of the Eastern Cape", p. 10, pi. 6, fig. 7 (1996); Vosa, 1975, fig. 3, Plate I fig. 3; Vosa in J.S. Afr. Bot. 47: 57-61 (1981); Plate 1C.

CHROMOSOME NUMBERS — $2n=2x=12$; $2n=4x=24$ (karyotype A, fig. 3).

DISTRIBUTION — Eastern Cape to Northern Transvaal. The diploids have been found so far only in the southern part of the range.

EXSICCATA — Diploids: NATAL. - 3030 (Port Shepstone): High Flats, Vosa 413/32 (OXF); CAPE.- 3129 (Port St. John): 3.5 km S of Flagstaff Vosa 14 (OXF); - 3130 (Port Edward): between sand dunes, Vow 416/33 (OXF).

Tetraploids: TRANSVAAL. - 3229 (Pieters-burg): Haenetsburg, near Old German Mission, Vosa 58 (OXF). KWAZULU-NATAL. - 2931 (Stan-ger): Groenberg (Inanda), Vosa 406/31 (OXF); -2929 (Underberg): Estcourt, Van der Merwe 2544 (PRE); CAPE. - 3326 (Grahamstown): Haye's Railway Sidings, Vosa 392/28 (OXF); 1.5 km NE of East London, on the side of the road to Gonubie Park, Vosa 306/16 (OXF).

Other exsiccata: CAPE. - 3227 (Stutterheim): King Williams Town, Dyer 254 (PRE); - 3425 (Port Elizabeth): near the town, Eayliss 1567 (K).

VERNACULAR NAMES — Southern Sotho: *Moe-tela*. Xhosa: *Ivimba Mpunzi*. KwaZulu: *Si'kwa*.

Tulbaghia cernua is a variable species and the two cytological forms overlap especially in the size of the flowers and of the leaves. Its main characteristic is the urceolate or barrel-shaped fleshy corona, the lanceolate-obtuse perianth segments and the large rhizomatous base of the bulb. It can be distinguished easily from *T. acutiloba* (with which it shares the character of the corona) by the very different leaves (very much narrower and tapering in *T. acutiloba*), by the larger corm and by the general shape of the flowers which are smaller, narrower and elongated in *T. acutiloba*.

T. cernua has been usually confused with *T. alliacea* and indeed many herbarium collections bear this name. However, it is very distinct and *T. alliacea* is found only in the winter rainfall region of the Cape Province. Besides distribution, the differences be-

tween *T. alliacea* and *T. cernua* include important details of morphology and of karyotype. An illustration agreeing with *T. cernua* appears under the name of *T. alliacea* in: "Wild Flowers of the Eastern Cape Province" by Batten and Bokelmann, p. 10, Pl. 67, fig. 7 (1966). No indication is given about the location of the original plant except that the species is known to occur throughout the Cape.



Fig. 3 — *Tulbaghia cernua* (2x), karyotype A.

4. *Tulbaghia ludwigiana* Harv. Bot. Mag. 64: t. 3547 (1837); Dietr. Synops. 2: 1090 (1840); *non* Kunth Enum. 4: 482 (1843); Ave-Lallemant, Bull. Cl. Phys. Math. Acad. Petersb. 3: 203 (1844); Uphof, *Herbertia*, 10: 46 (1943); Schnizlein, *Icon. gr.* 1: t. 55 (1949); Vosa, *Ann. Bot. (Rome)*, 34: 75-77 (1975); Burbidge, *Notes R. bot. Gds. Edinb.* 36: 86-88 (1978).

TYPE — Harvey in Bot. Mag. 64: t. 3547 (1837): iconotype!

The species has been described and illustrated from cultivated material collected by Mr. Zeir (Zeyhr?) from the border of "Kafferland" and not known to have been preserved as herbarium specimen. The beautiful illustration in Bot. Mag. 64 (1837) has been selected as *iconotype*.



Fig. 4 — *Tulbaghia ludwigiana* (2x), karyotype A.

ICONOGRAPHY— (Harvey, 1837, Bot. Mag. 64: t. 3547; Vosa, 1975, fig. 6, Plate IV, fig. 3); Plate ID.

CHROMOSOME NUMBERS — $2n=2x=12$ (karyotype A, fig. 4).

DISTRIBUTION— Eastern Cape Province.

EXSICCATA — CAPE. - 3327 (Peddie): in grassy fields at edges of *Euphorbia* scrub, south bank near the mouth of the Great Fish River, Vosa 398/29 (OXF), Vosa 2171 (OXF); - 3326 (Grahamstown): W of Eraser's Camp, Barker 6993 (NBG).

This species is closely allied to *T. cernua* but it is easily distinguished by the very broad, lorate leaves which have a more or less distichous arrangement and lie flat on the ground.

5. *Tulbaghia dtegeana* Kunth in Enum. Pl. 4: 483 (1843); Ave-Lall., Bull., Cl. Phys. Math. Acad. Petersb. 3: 203 (1844); Baker, J. Linn. Soc. Bot. (London) 11: 371 (1871) and El. Cap. 6: 405 (1897); Uphof, Herbertia, 10: 46 (1943); Vosa in Ann. Bot. (Rome), 34: 77-79 (1975); Burbidge, Notes R. bot Gds. Edinb. 36: 88-89 (1978).

TYPE — CAPE. - 3018 (Kamiesberg): near Lilyfontein and Ezelfontein, Drege 2658 (BM).

ICONOGRAPHY — (Vosa, 1975, fig. 7, Plate V, fig. 3); Plate IE.

CHROMOSOME NUMBERS — $2n=2x=12$ (karyotype A, group 2, fig. 22b; fig. 5).

DISTRIBUTION — Southern and Western Cape Province.

EXSICCATA — CAPE. - 3118 (Vanrhynsdorp): bottom of Vanrhynsdorp Pass, Vosa 62 (OXF); - 3319 (Worcester): Lemoenspoort, Vosa 1971 (OXF); - 3320 (Towsrivier) Hardy 4228 (NBG); - 2917 (Springbook): Spektakel, Barker 1912 (NBG); Springbook, Barker 6443 (NBG); - 3017 (Hondeklipbaai): Komaggas Mts., Hall 900 (NBG); - 3119 (Calvinia): Botterkloof, Compton 9642 (NBG); - 3219 (Wupperthal): near Wupperthal, Hall s.n. (NBG); Cap. B. Spei, Drege 1575 (K).

A very distinct species found around Wupperthal and Worcester northwards to Springbook. It is easily distinguished from all other species by the very short and fleshy corona and by the perianth segments all inserted at the same level at the base of the corona.

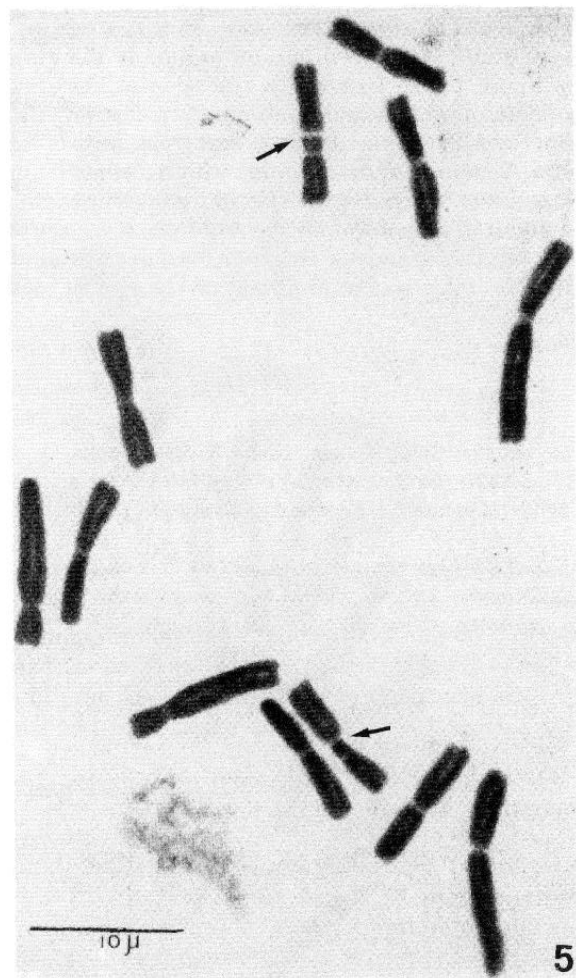


Fig. 5 — *Tulbaghia dregeana* (2x), karyotype A.

6. *Tulbaghia tenuior* Krause & Dinter, Bot Jahrb. 45: 1411 (1910); Uphof, *Herbertia*, 10: 50 (1943); Vosa, *Ann. Bot. (Rome)* 34: 80-82 (1975); Burbidge, *Notes R. bot. Gds: Edinb.* 36: 91-92 (1978).

TYPE — NABIBIA. - 2018 (Grootfontein): near Grootfontein, Dinter 790 (MI).

SYNONYMS — *Tulbaghia karasbergensis* Glover, *Ann. Bot. Herb.* 1: 104 (1915), type: H.H.W. Pearson 8192 (BOLD).

ICONOGRAPHY — (Vosa, 1975, fig. 8, Plate VI, fig. 3); Plate IF.

CHROMOSOME NUMBERS — $2n=2x=12$ (karyotype A, fig. 6).

DISTRIBUTION — North Western Cape Province and Nabibia.

EXSICCATA — NABIBIA. - 1918 (Grootfontein): in dry vlei at Amrib, *Schoenfelder* S454, 955 (PRE); 2120 (Rietfontein): Rietfontein, *Vosa* 136 (OXF); 2217 (Windhoek): Windhoek, *W. Giess* 1598 (PRE). CAPE. - 2919 (Pofadder): 3.5 km NE of Pofadder, *Acocks* 21797 (PRE); 2911 (Prieska): Prieska, *Bryant* 576 (K).

Tulbaghia tenuior Krause & Dinter is a very distinct species proper of the dry and rocky areas of the NW Cape and of Nabibia. It is distinguished by its starry flowers with very long and pointed perianth segments and by its short, fleshy corona. It is more or less deciduous and not very long lived in cultivation. In the wild, it flowers between December and March.



Fig. 7 — *Tulbaghia nutans* (2x), karyotype A.

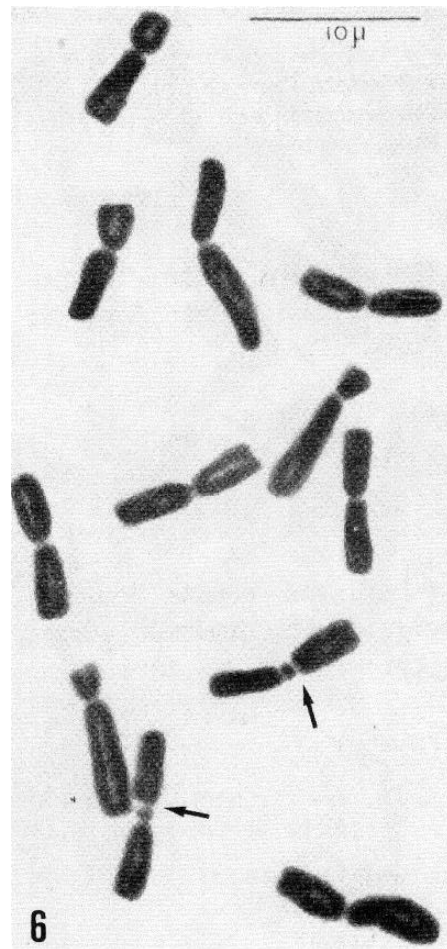


Fig. 6 — *Tulbaghia tenuior* (2x), karyotype A.

7. *Tulbaghia nutans* Vosa, *Ann. Bot. (Rome)*, 34: 82-84 (1975).

TYPE — TRANSVAAL. - 2330 (Tzaneen): Haenetzburg, C. Thompson Farm, in dry sandy field recently burnt, flowering 8/10/1969, *Vosa* 536/55 (OXF); Isotype G.

ICONOGRAPHY — (Vosa, 1975, fig. 9, Plate VII, fig. 3); Plate IIA.

CHROMOSOME NUMBERS — $2n=2x, 4x$ (karyotype A, fig. 7).

DISTRIBUTION — Eastern Cape Province and Transvaal.

EXSICCATA — TRANSVAAL. - 2330 (Tzaneen): Haenetzburg, in grassy field by the road to Dindinie, *Vosa* 538/60 (OXF). CAPE. - 3326 (Grahamstown): in *Euphorbia* scrub in sandy soil, between Cradock and Vaalkrause Track, *Vosa* 1536 (OXF); Hounslow Farm, on the road to Adelaide, *Vosa*

2188; Fishriversrand at the crossroad to Adelaide, Vow 2197.

The original description of this species relates to a small population found in the Northern Transvaal. Further collections near the type locality, and in the Kruger National Park, have established the existence of small populations and of scattered plants in which a tetraploid form predominates. The species is found also in the Eastern Cape but here the plants seem to be exclusively diploid. Thus, the ploidy situation and the geographical range of *Tulbaghia nutans* appear to be similar to that of the more widespread *Tulbaghia cernua* Ave-Lall. which, in the same way, has diploid and tetraploid forms and is found from the Eastern Cape to the Transvaal.

8. *Tulbaghia macrocarpa* Vosa, Ann. Bot. (Rome), 34: 84-87 (1975).

TYPE — ZIMBABWE. - 1731 (Harare): amongst rocks, in an underdeveloped part of the Botanic Garden, Harare, Vosa 132 (OXF), isotype G.

ICONOGRAPHY — (Vosa, 1975, fig. 10, Plate VII, fig. 3); Plate HE.

CHROMOSOME NUMBERS — $2n=2x=12$ (karyotype AA, fig. 8).

DISTRIBUTION — Zimbabwe.

EXSICCATA — ZIMBABWE. - 1731 (Harare): in the Botanic Garden, Harare, *H.M. Biegel*2859.



Fig. 8 — *Tulbaghia macrocarpa* (2x), karyotype AA.



Fig. 9 — *Tulbaghia transvaalensis* (2x), karyotype AA.

This species represents one of the *Tulbaghia* types which are usually labelled "alliacea" in most herbarium collection. However, it is very distinct and, besides its northern tropical distribution, it presents several discriminating characters such as the very large ovary, which develops in a long capsule (hence the specific epithet), and the rather fleshy, laterally expanded corona.

9. *Tulbaghia transvaalensis* Vosa in Ann. Bot. (Rome), 35: 87-90 (1975).

TYPE — TRANSVAAL. - 2330 (Tzaneen): on dry, stony hillside, Gordon McNeil Farm, Unkumani, Dindinnie (Ofcolaco), Vosa 486/49 (OXF), isotype G.

ICONOGRAPHY — (Vosa, 1975, fig. 11, Plate IX, fig. 3); Plate IIC.

CHROMOSOME NUMBERS — $2n=2x=12$ (karyotype AA, fig. 9).,-

DISTRIBUTION — North Eastern Transvaal.

EXSICCATA — TRANSVAAL. - 2330 (Tzaneen): Unkumani, G. Mac Neil Farm, Dindinnie, *Vosa* 4867 29 (OXF); grassy slopes S of Unkumani, *Vosa* 1644; about 2 km SW of Unkumani, in recently burnt field, *Vosa* 1645 (OXF).

Tulbaghia transvaalensis is a very distinct species found so far only in hilly country in the N.E. Transvaal. For a long time it has been confused with *T. alliacea* from which it differs very much in its morphology and distribution. Its karyotype and certain morphological characters place *T. transvaalensis* in the group of *T. macrocarpa* Vosa.



Fig. 10 — *Tulbaghia acutiloba* (2x), karyotype AB.

10. *Tulbaghia acutiloba* Harv., Thes. Cap. 2:51, t. 180 (1854); Baker, J.Linn. Soc. Bot. (London), 11: 371 (1871); Baker, Fl. Cap. 6: 404 (1897); Phillips, Ann. S. Afr. Museum 16: 300 (1917); Uphof in Herbertia, 10:46 (1943); De Wild. Sel. Hort. Thes. 3:120 (1902); Vosa, Ann. Bot. (Rome), 34: 90-92 (1975); Burbidge, Notes R.bot. Gds. Edinb. 36: 96 (1978).

SYNTYPES — EASTERN CAPE. - 3126 Queenstown): *Cooper* 463 (K); 3325 (Somerset East) *Boschberg*, *Macowan* 1582 (K).

ICONOGRAPHY — (Vosa, 1975, Plate X, fig. 3) Plate IID.

CHROMOSOME NUMBERS — $2n=2x=12$ (karyotype AB, fig. 22a, group 4; fig. 10).

DISTRIBUTION — Eastern Cape Province northward to the Transvaal.

EXSICCATA — TRANSVAAL. - 2528 (Pretoria) in recently burnt vlei, Delmas Road, 6 km S of Pretoria, *Vosa* 431/36 (OXF). NATAL. - 2930 Pietermaritzburg): Chelmsford Park, *Vosa* 347/21 (OXF); 2931 (Stanger): Groenberg (Inanda), in short grass at the top of the hill, *Vosa* 405/30 (OXF). CAPE. - 3126 (Queenstown), by the Dam, in short grass among rocks, *Vosa* 373/24 (OXF).

A very small, inconspicuous species which flowers soon after the first spring rain, often in burnt fields. It is found, usually, as widely scattered single plants.

VERNACULAR NAMES — Southern Sotho: *Motsuntsunyane*.

11. *Tulbaghia simmleri* Beauv., Bull. Herb. Boissier, 8:988 (1908).

TYPE — Shilouvane, (Transvaal), legit H.A. Junod, ex hortus G; specimen and drawings on two sheets prepared by G. Beauverd (G, holo!).

SYNONYMS — *Tulbaghia pulchella* Barnes, S. Afr. Card. 20: 185 (1930), non Ave-Lall.; *Tulbaghia daviesii*, C.H. Grey in Hardy Bulbs, 2: 572 (1938) nom. nov. for *Tulbaghia pulchella* Barnes; *Tulbaghia fragrans* Verdoorn in Fl. PL S. Afr. 11: t. 438 (1931); R.A. Dyer in Herbertia, 6: 8 (1939); Uphof, Herbertia, 10 (1943). Type: E. Transvaal, Pilgrim's Rest (2430 - DB) Dientje Farm, just N. of Bourke's Luck Pot-holes, Celliers, 8894 (PRE, holo!); Vosa, Ann. Bot. (Rome) 34: 92-94 (1975); Vosa, J.S. Afr. Bot., 46: 109-114 (1980).

ICONOGRAPHY — Beauverd, 1908 - Bull. Herb. Boissier, 8: 988, fig. 2; Barnes (l.c.) fig. A (as *T. pulchella*); C.H. Grey (l.c.) as *T. daviesii*; Verdoorn (l.c.) fig. 438 (as *T. fragrans*); C. Letty in "Wild Flowers of the Transvaal", pl. 10, fig. 3 (1962) as *T. fra-*

grans; Vosa, 1975 - Ann. Bot. (Rome), 34: 91, pi. XI, fig. 3, p. 93, fig. 13 (1975), as *T. fragrans*; Plate HE.

CHROMOSOME NUMBERS — $2n=2x=12$ (karyotype A, fig. 11).

EXSICCATA — TRANSVAAL. - 2330 (Tzaneen): Letaba, *Codd* 9455 (PRE); - 2430 (Pilgrim's Rest): The Berg, *Vosa* 466/43 (OXF); Graskop, *Vosa* 4687 45 (OXF); Ofcolaco, Cyprus Farm in light moist forest, *Vosa* 530/53 (OXF); near Ohrigstad, among rocks by a stream, *Vosa* 530/53 (OXF); Bourke's Luck Potholes, Graskop, *Vosa* 542/56 (OXF).

The misinterpretation of the drawings by G. Beauverd (attached to the type specimen of *T. simmleri* (see VOSA 1980), by BURBIDGE (1978), has been the origin of the assigning of this epithet to *T. violacea* Harv.

Tulbaghia simmleri is a very decorative and fairly hardy species widely cultivated, usually under the name of *T. fragrans* or *T. pulchella*, in parks and gardens in tropical and sub-tropical countries and in cool greenhouses in temperate regions. It is endemic of a rather small area of the Transvaal, in the northern Drakensberg. It is found as isolated plants on rocky ledges and in fairly thick colonies in light

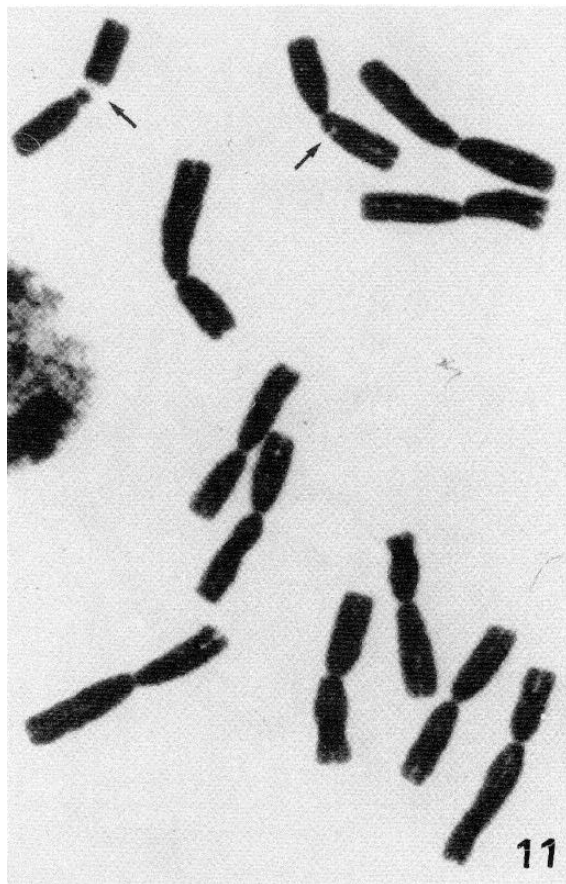


Fig. 11 — *Tulbaghia simmleri* (2x), karyotype A.

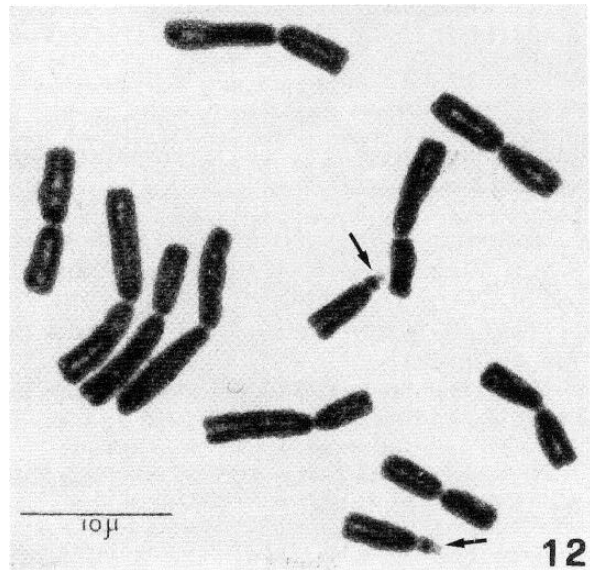


Fig. 12 — *Tulbaghia galpinii* (2x), karyotype D.

tropical forest, together with *Clivia miniata* Regel and epiphytic orchids (mostly *Polystachia* sp.) and ferns, at moderate altitude.

12. *Tulbaghia galpinii* Schl, J. Bot. 34: 383 (1894); Uphof, *Herbertia*, 10: 47 (1943); Vosa, Ann. Bot. (Rome), 34: 94-96 (1975); Burbidge, Notes R. bot. Gds. Edinb. 36: 98-100 (1978).

TYPE — CAPE. - 3126 (Queestown): Andriesberg, *Golpin* 2179 (PRE, isotype!).

ICONOGRAPHY — (Vosa, 1975, fig. 14, Plate XII, fig. 3); Plate IIP.

CHROMOSOME NUMBERS — $2n=2x=12$ (karyotype D, fig. 12).

DISTRIBUTION — Eastern Cape.

EXSICCATA — CAPE. - 3225 (Somerset East): near Cradock, *Vosa* 60 (OXF); Bergquagga Park, *Vosa* 66; 34 km S of Somerset East, *Vosa* 67 (OXF); 48 km N of Cradock, *barker* 7065 (NBG); Bergquagga Park, on Bankberg, *Liebenberg* 7127 (PRE); 43 km S of Somerset East, *Acocks* 16741 (PRE).

A very small species resembling a diminutive *T. acutiloba* in habit but with a scarcely fleshy, deeply lobed corona and known only from a fairly small area of the Eastern Cape. It inhabits dry, rocky country in grassland or in light scrub often associated with dwarf euphorbias.

The three collections cultivated in Oxford (from the Cradock Road, about 11 km from Grahamstown, the Bergquagga Park and from near Somerset East) are all self-fertile but, under cultivation, usually very short lived.

13. *Tulbaghia leucantha* Baker, Flora Capensis, 6:404 (1897); Uphof, *Herbertia*, 10: 47 (1943); Vosa, *Ann. Bot. (Rome)*, 34: 96-99 (1975).

SYNTYPES — NATAL. - Near the river Tugela, Medley Wood 4408 (K!). CAPE. - Zuurberg (Griqualand East), MacOwen 1208 (K!).

SYNONYMS — *Tulbaghia dieterlenii* Phillips, *Ann. S. Afr. Museum* 16: 300 (1917), type: Leribe (Lesotho), *Dieterlen* 361 (BM).

Tulbaghia friesii Suesseng, *Trans. Rhodes Sci Ass.* 43: 76 (1957).

Tulbaghia rhodesica Weimark, *Bot. Not.* 90: 169 (1937) *nom. illeg.*

ICONOGRAPHY— (Vosa, 1975, fig. 15, Plate XIII fig. 3); Plate IIIB.

CHROMOSOME NUMBERS— $2n=2x-12$; $2n=4x=24$ (karyotype D, fig. 13).

DISTRIBUTION— The diploid forms occur from the NE Cape, Lesotho to the NTransvaal while the tetraploids occur from NTransvaal to Swaziland and Zimbabwe. In the Transvaal, from around Warmbad and Pietersburg and the Kruger Park, there seems to be an overlap between the two forms.

EXSICCATA — Diploids: TRANSVAAL. - 2430 (Pilgrim's Rest): Blyde's River Canyon at 'One Mile Walk', in short turf among large rocks Vosa 54/1 (OXF); - 2528 (Pretoria): among rocks near Warmbad, *De Wet* 3799 (PRE); in acid, peaty vlei near the roadside at Delmas, Vosa 430/35 (OXF); Between Kestell and Bethlehem by the Eland's Bridge Vosa 1704 (OXF); on rocks in shallow soil by the road from Maseru to Ladibrand, Vosa 1711 (OXF).

Tetraploids: ZIMBABWE. - 1731 (Harare): Groombridge, *H.M. Eiegel* 2860 (SRGH); TRANSVAAL. - 2431 (Acornhoek): in dry sandy soil in open woodland, 10 km N of Skukuza, Vosa 449/38 (OXF).

Other exsiccata: TRANSVAAL. - 2528 (Pretoria): Delmas Road, *Codd* 2182 (PRE); 10 km W of Hammanskraal, *Leach* 10659 (PRE). SWAZILAND. - 2531 (Mbabane): near Bulunga Poort, Manzini, *Compton* 31754 (NBG). ORANGE FREE STATE. - 2828 (Bethlehem): Hoogland, *Liebenberg* 7291 (PRE). CAPE. - 3028 (Matatiele): Mt. Fletcher, *Killick & Marais* 2076 (PRE). NATAL. - 3029 (Zuurberg): *MacOwen & Bolus* (1208) (K); *Medley Wood* 1200 (K).

VERNACULAR NAMES— Southern Sotho: *leta la phofu*.

Tulbaghia leucantha is found widespread from the N E Cape to N Transvaal, Swaziland and Zimba-

bwe. It is very variable even within the same population in the size of the flowers, in the colour of the corona and in the leaves which can vary from very thin and grass-like to 5-8 mm broad. Overall, the proportion of thin-leaved plants, in a given population, seems to increase with altitude. The tetraploid forms are much less variable than the diploids but on the whole they have slightly larger flowers. In any case, most of the other characters in both forms, overlap in such a way that it is not possible to distinguish them with certainty in the field, or in herbarium specimens.

The morphological variability of *Tulbaghia leucantha* over its considerable range, has resulted in the description of new species, mainly based on herbarium specimens, by various authors. However, all the forms of the species have a very uniform karyotype and are interfertile. In any case, the epithet *T. leucantha*, used by Baker in 1896, has priority over *T. dieterlenii* Phillips (1917) and over *T. friesii* Suesseng (1957).

The name *T. rhodesica* Weimark (1937), cited as a synonym of *T. leucantha*, is illegitimate because it has been already used for a very different species (*T. rhodesica* R.E. Fries, 1916).



Fig. 13 — *Tulbaghia leucantha* (2x), karyotype D. Note the small satellite intercalary to one of the nucleolar organizer thread (double arrow).

14. *Tulbaghia natalensis* Baker, Card. Chron. 3, 9: 668 (1891); Baker, Fl. Cap. 6: 405 (1897), Natal Plants, 1: t. 29 (1899); Uphof, Herbertia, 10: 49 (1943), Fl. Pl. S. Africa, 25: 979 (1945); Vosa, Ann. Bot. 34: 99-101 (1975); Burbidge, Notes R. bot. Gds. Edinb. 36: 89 (1978).

TYPE — NATAL. - 2529 (Underberg): in swamps, near Moorivier, Medley-Wood 4045 (NH!).

ICONOGRAPHY — (Vosa, 1975, fig. 16, Plate XIV, fig. 3); Plate IIIA.

CHROMOSOME NUMBERS — $2n=2x=12$ (karyotype D, fig. 14).

DISTRIBUTION — KwaZulu-Natal.

EXSICCATA — NATAL. - 2929 (Underberg): Thabamhlope, Estcourt, in acid-peaty pasture, Vosa 421/34 (OXF); 28 km S of Nottingham Road, Codd 10582 (PRE); 8 km N W of Nottingham Road, Van der Merwe 10581 (PRE); Impendhale, W. Marais 934 (PRE); Moorivier, Stainbank 3845 (NH); Giant's Castle, Edwards 2174 (NU); Thabamhlope, Estcourt, Van der Merwe 2585 (PRE).

A rather attractive species with showy white flowers, found in vleis and in marshy habitats. It is endemic of Natal and it is almost hardy and easy to cultivate in acid compost.



Fig. 14 — *Tulbaghia natalensis* (2x), karyotype D.



Fig. 15 — *Tulbaghia verdoorniae* (2x), karyotype D.

15. *Tulbaghia verdoorniae* Vosa & Burbidge, Ann. Bot. (Rome), 34: 101-104 (1975).

TYPE — TRANSKEL. - 3228 (Willowvale): between Mpozolo and Mendu in wet soil, 27-01-1966, R. Wood 161, NU 36321 (holo!).

The name *Tulbaghia carnososa*, published by R.B. BURBIDGE (1978), may be considered a synonym of this species.

ICONOGRAPHY — (Vosa, 1975, fig. 17, Plate XV, fig. 3); Plate IIIC.

CHROMOSOME NUMBERS — $2n=2x=12$ (karyotype D, fig. 15).

DISTRIBUTION — Eastern Cape, Transkei.

EXSICCATA — CAPE. - 3228 (Butterworth): in a recently burnt vlei, near the railway at Mpuluswa, 15 km NE of Butterworth (-AA), 07-10-1977, Vosa 1599 (OXF); on a tussocky, rocky hillside, in pockets of wet soil, near the side of the road near Idutywa (-AB), 07-10-1977, Vosa 1601 (OXF).

This species has been cultivated for many years in Botanic Gardens of Kew, Oxford and Edinburgh and it appears in the respective herbaria as either *T. capensis* or *T. alliacea*. Vosa, in his two cytological

papers (1966a,b), misapplied the name *T. dregeana* to this species which has been known under this epithet until 1975.

Two further collections of *Tulbaghia verdoorniae* have been made in October 1977 by Vosa (1980), not very far from the original 1966 collection of R. Wood (161, NH 36321), which now represents the type.

The species has been named in honour of the renowned South African Botanist, Miss I.C. Verdoorn. Following the current nomenclatural rules in the case of a female person, it has been found proper to amend the name *verdoornia*, as in the original description, into *verdorniae*.

16. *Tulbaghia coddii* Vosa & Burbidge, Ann. Bot. (Rome), 34: 101-106 (1975).

TYPE — TRANSVAAL. - 2430 (Pilgrim's Rest): Graskop, 1400 m. L.E. Codd 6746 (PRE).

The name *T. poetica*, published by R.B. BURBIDGE (1978), may be considered a synonym of this species.

ICONOGRAPHY — (Vosa, 1975, fig. 18, Plate XVI, fig. 3); Plate HID.

CHROMOSOME NUMBERS — $2n=2x=12$ (karyotype D, fig. 16).

DISTRIBUTION — Endemic to the Northern Transvaal.

EXSICCATA — TRANSVAAL. - 2430 (Pilgrim's Rest): in a small bog just above Lisbon's Falls, Vosa 496/52 (OXF); very near God's Window, Vosa 5317 54 (OXF); in short humid turf by the road side 4.5 km from Graskop towards God's Window, Vosa 464/41 (OXF); near Lisbon's Falls, Graskop, Brent 134 (E); marshy ground near Pilgrim's Rest, Davidson 68 (E).

A very attractive small species related to *Tulbaghia natalensis*. It has bright green, very thin leaves and pink to white flowers with a yellow-green corona and a sweet smell reminiscent of that of *Narcissus tazetta*. It grows in bogs or in wet turf in acid conditions, sometimes associated with species *otDrosera*.

17. *Tulbaghia montana* Vosa, Ann. Bot. (Rome) 35:106-109(1975).

TYPE — NATAL. - 2929 (Underberg): S.E. ridge of Giant's Castle, Vosa 70 (OXF), isotype G.

ICONOGRAPHY — (Vosa, 1975, fig. 19, Plate XVII, fig. 3); Plate III E.

CHROMOSOME NUMBERS — $2n=2x=12$ (karyotype E, group 6, fig. 22b; fig. 17).

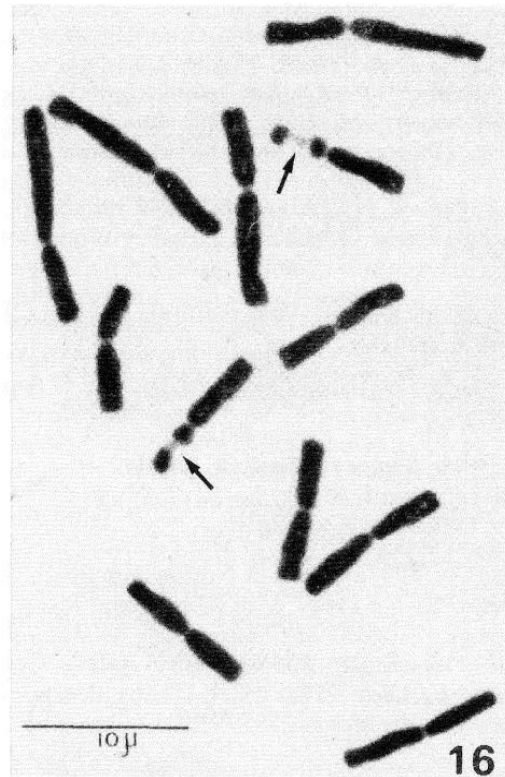


Fig. 16 — *Tulbaghia coddii* (2x), karyotype D.

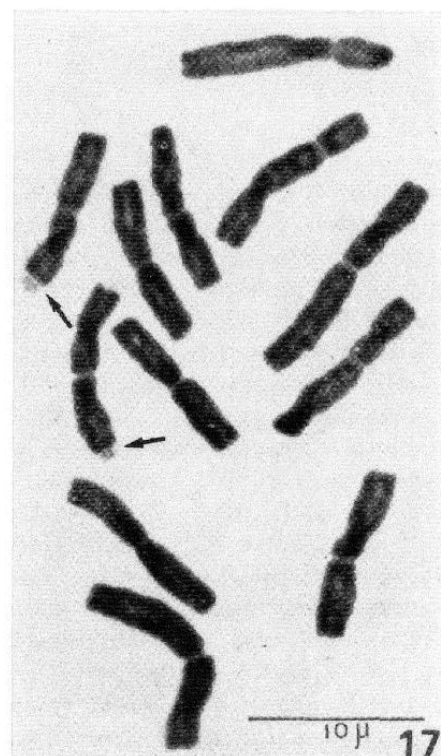


Fig. 17 — *Tulbaghia montana* (2x), karyotype E. ($\times 2000$).

DISTRIBUTION— This small high mountain species is apparently confined to the South Eastern slopes of the Natal Drakensberg. It is fairly hardy and very distinct from the other species of the genus especially on account of its dark-green leaves which have glaucous undersides, a green midrib and inward rolled edges. However, it may be confused with *T. acutiloba* Harv., especially in scarcely annotated and badly dried herbarium specimens.

EXSICCATA — NATAL. - 2929 (Underberg): Drakensberg, on the south eastern ridge of Giant's Castle, growing in short grass in rather humid black soil at the foot of large rocks, *Vosa* 70 (OXF), *Burt* 5687 (E); without a precise locality but still on the south eastern Drakensberg, *Buchanan* 3899 (E); 3 km N of Rama's Gate, *Bayliss* 7831, 7781 (GRA).

18. *Tulbaghia cametoni* Baker, Jour. Bot. 16: 321 (1878); Uphof, *Herbertia*, 10: 48 (1943); *Vosa*, Ann. Bot. (Rome), 34: 11041 (1975).

TYPE — Tanzania, shores of Lake Tanganika, Cameron 2175 (K!).

ICONOGRAPHY — (*Vosa*, 1975, fig. 20, Plate XVIII, fig. 3); Plate IIIE.

CHROMOSOME NUMBERS — $2n=2x=12$ (karyotype AF, fig. 18).

EXSICCATA — ZAMBIA. - 1024 (Mwinilunga distr.): *Richards* 16885 (K); 1426 (Mumbwa distr.): Mumbwa, *Maculay* 982 (K); - 1428 (Chilanga distr.): Mt. Makulo, *Vosa* 59 (OXF); - 1626 (Choma distr.): near the road from Choma to Itulo, *Vosa* 68 (OXF).

Tulbaghia cametoni Bak. is one of the tropical species of the genus and is very variable, with some plants resembling the tetraploid forms of *Tulbaghia leucantha*. Examination of the various herbarium specimens, does not allow a clear view of the characteristics of this species and more field work is necessary to understand its geographical distribution.

19. *Tulbaghia rhodesica* R.E. Fries, Wiss. Ergebn. Schwed. Rhodesia-Kongo Exped. (1911/ 1912) 1: 227-228 (1916), non *Tulbaghia rhodesica* Weimark, Bot. Not. 169 (1937); *Vosa*, Ann. Bot. (Rome) 34: 111-113 (1975); Burbidge, Notes R. hot. Gds. Edinb. 36:97(1978).

TYPE — Zambia. - 828 (Kawambwa distr.): Kalungwisi River, just S of Katwe, R.E. Fries 1911 (LD).

ICONOGRAPHY — (Fl. PL S. Africa, 35: t. 1383; *Vosa*, 1975, fig. 21, p.111); Plate IVA.

CHROMOSOME NUMBERS — $2n=2x=12$ (karyotype AF, fig. 19).

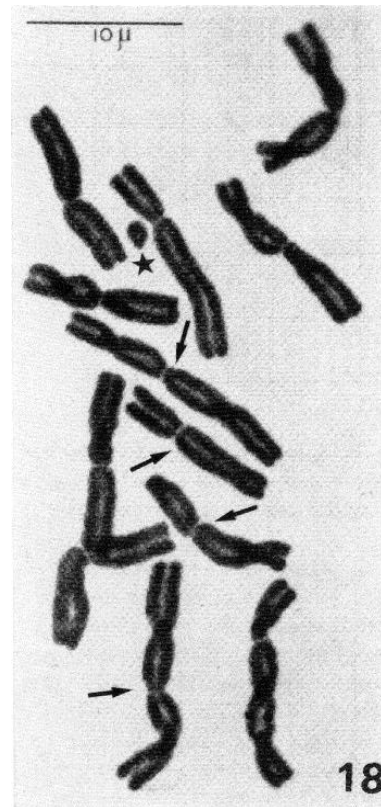


Fig. 18 — *Tulbaghia cametoni* (2x), karyotype AF. Note the telocentric B-chromosome (star).

DISTRIBUTION— Zambia, Southern Tanzania.

EXSICCATA — ZAMBIA. - 830 (Mporokoso distr.): in open bushland in dry sandy soil, near Mporokoso, *Vosa* 74 (OXF); Mporokoso, *Richards* 13717 (K); Chilongwelo, *Richards* 2196 (K).

Tulbaghia rhodesica is a very beautiful species, found in Zambia and in S. Tanzania. In the colour of

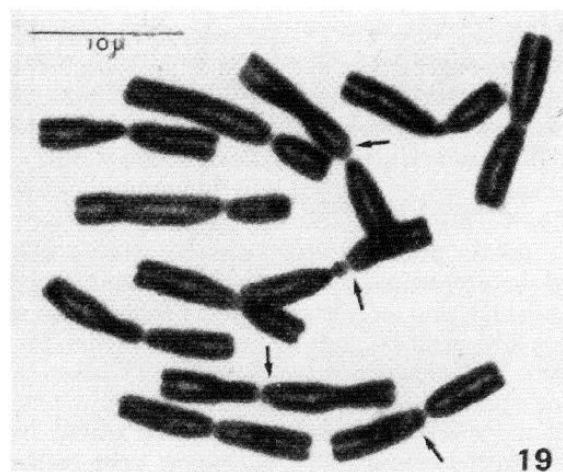


Fig. 19 — *Tulbaghia rhodesica* (2x), karyotype AF.

its flowers it resembles *T. violacea* but cytologically it belongs to the *T. cameroni* group. It is a very desirable species from the horticultural point of view but it is deciduous and has proved to be somewhat difficult to cultivate, growing very slowly and flowering erratically.

20. *Tulbaghia violacea* Harvey in Bot. Mag., 64: t. 3555 (1837); Vosa, Ann. Bot. (Rome), 34: 113-117 (1975) as *Tulbaghia cepacea* L.f.; Vosa, Jl. S. Afr. Bot., 46: 109-114(1980).

TYPE — Described and illustrated from cultivated material in the Ludwigsburg Garden, Cape Town, by Harvey in Bot. Mag. 64, t. 3555, 1837 (iconotype!).

SYNONYMS— *T. cepacea* L.f. in Suppl. PL 194 (1781) *quoad descr. excl. syn., nom. illeg. type: 411/4* (LINN); *Omentaria cepacea* Salisb. Gen. PL Fragm. 87 (1866).

ICONOGRAPHY — (Harvey *l.e.*, Batten & Bokelmann in "Wild Flowers of the Eastern Cape", p. 10, pi. 6, fig. 6, 1966; Vosa, 1975, fig. 22, Plate XX: figs. 3, 4, 5, 22 and 23, incl. var. as *T. cepacea* L.f.); Plate IVB.

For the legitimacy of the name *Tulbaghia violacea* Harvey, see VOSA (1980).

CHROMOSOME NUMBERS— $2n=2x=12$ (karyo-type A, fig. 20).

DISTRIBUTION— From the Transkei to the SW Cape near Port Elizabeth.

EXSICCATA — CAPE. - 3227 (Stutterheim): Mt. Coke, near King William's Town, *Compton* 144/45 (NBG); - 3228 (Butterworth): at the mouth of the river Kei, *Compton* 17674 (NBG); - 3224 (Steytlerville): in rocky scrubland by the river Gantoos at Hankey, *Vosa* 371/23; 3323 (Willowmore): Zuurberge Poort, *Barker* 7132 (NBG); - 3326 (Grahamstown): in bed of dry stream among rocks in the Bloukrans, *Vosa* 354/22, 376/26 (OXF); - 3327 (Peddie): amongst stones in the bed of the river Buffalo, near East London, *Vosa* 308/17 (OXF); - 3424 (Humansdorp): Babeljouw River, *Compton* 24041 (NBG); near Humansdorp, *Britten* 6513 (GRA).

VERNACULAR NAMES— KwaZulu: *Icinzini*.

All the populations of *Tulbaghia violacea*, object of the present study, show a kind of uninterrupted variability and include a number of forms which reasonably might be given the rank of varieties. However, field experience and careful observations during a number of flowering seasons, all over the range of the species and also on cultivated plants, have shown that considerable differences exist even between plants of the same population. Such differences include, besides the dimension of the plants,

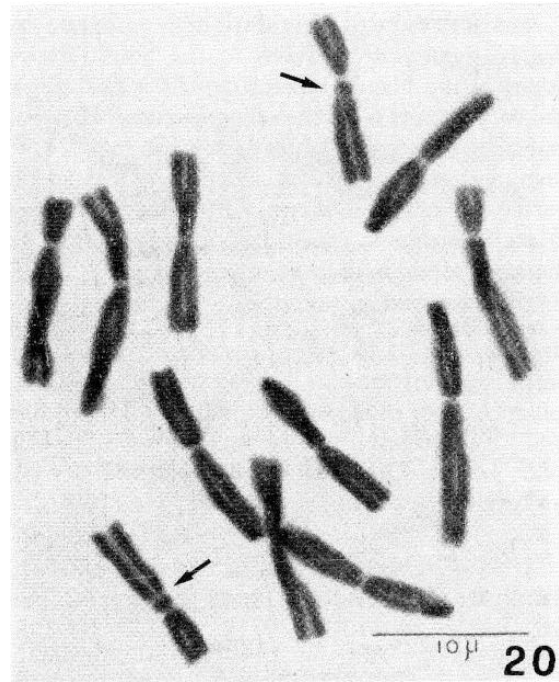


Fig. 20 — *Tulbaghia violacea* (2x), karyotype A.

also the size of the flowers and the length and shape of the lobes of the corona. In a previous account by VOSA (1975), one each of the most common forms from two fairly large populations, located 200 km apart, have been described. A perusal of the descriptions shows indeed that the two forms differ, but only in some small details. Herbarium specimens, perforce limited in number, do not represent the intrinsic variability of *Tulbaghia violacea* populations and cannot be taken as the basis for the creation of the taxonomic rank of varieties. The exception is the establishment of the var. *maritima* by VOSA (1975). This variety is quite distinct morphologically from the typical species and exists in fairly small but very homogeneous populations with a rather restricted habitat near the sea.

20a. *Tulbaghia violacea* Harvey var. *maritima* Vosa, Ann. Bot. (Rome) 34: 113-117 (1975).

TYPE — CAPE. - 3325 (Port Elizabeth): Gantoos River Mouth, *Vosa*, 290/12 (OXF) isotype G.

ICONOGRAPHY — (Vosa 1975, fig. 23, Plate XX, fig. 5, Plate IV, fig. 20a, as *T. cepacea* var. *maritima*); Plate IVC.

CHROMOSOME NUMBERS— $2n=2x=12$ (karyotype A).

EXSICCATA — CAPE. - 3224 (Humansdorp): near the Krom River mouth, *Vosa* 63 (OXF); - 3323

(Willowmore): Twee River mouth in sandy soil, *Vosa* 65 (OXF).

This variety of *T. violacea* Harv. has been found, so far, only near the sea-shore hence the epithet *maritima*. It differs from the type species by its broader, shiny, dark-green leaves without a prominent central vein. It has somewhat flat flowers with very small coronal lobes. All the collections are very similar to one another and self-fertile.

21. *Tulbaghia cominsii* Vosa, Jl. S. Afr. Bot. 45: 127-132 (1979).

TYPE — CAPE. - 3227 (Stutterheim): in kommit-tee soil on rocky ground, often associated with *Nerine filifolia* Baker, near Tamaha, 17 km from King William's Town (-BD), 28-9-57, D. Comins 1718 (RU 10586).

ICONOGRAPHY — (Vosa, 1979, fig. 3, 4); Plate IVD.

CHROMOSOME NUMBERS — $2n=2x=12$ (karyo-type AA, fig. 21).

DISTRIBUTION — Found so far only around the type locality.

EXSICCATA — *Vosa* 1568, 28-10-77 (OXF); *Vosa* 1781, 12-11-77 (OXF), on both sides of the road from King William's Town near Tamaha.

This attractive little species is related to *T. violacea* Harv. but differs in its very thin, glaucous leaves, white or very rarely pinkish flowers with a pink or purplish perianth tube and a different karyotype. The glaucous colour of the leaves is very characteristic and is due to the stomatal pores, which appears as tiny, white streaks under low magnification.

The chromosome complement of *T. cominsii* is very interesting: with its four nucleolar chromosomes of type A, it resembles that of *T. transvaalensis* Vosa and *T. macrocarpa* Vosa, two taxa quite different from the present species whose morphological affinities lie with *T. violacea*. This situation, which parallels that of *T. rhodesica* Fries and *T. cameroni* Bak. (see Vosa, 1975, p. 52), may be an indication of a two-track evolution in which the karyotype and the phenotype seem to evolve independently and, in this case, along established pathways.

The cytology of *Tulbaghia*

All the species of *Tulbaghia* so far studied have a fairly uniform anatomy and embryology. The chief characters of taxonomic value are the morphology of the flowers but vegetative features and geographical distribution have their importance in the differentiation of the species.

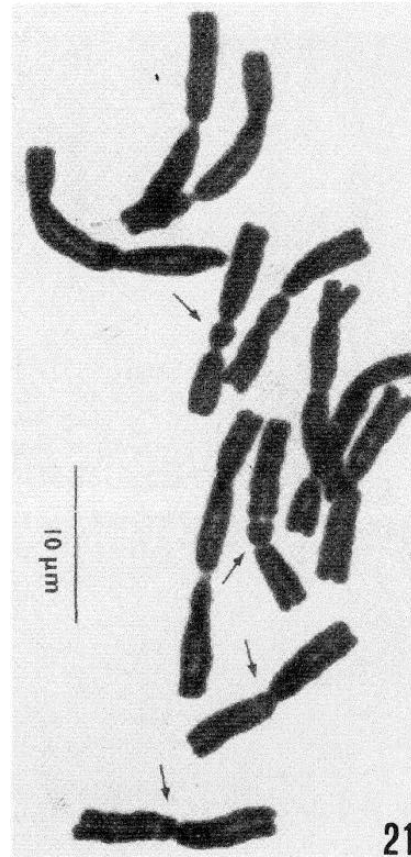


Fig. 21 — *Tulbaghia cominsii* (2x), karyotype AA.

One typical characteristic of the genus is the uniformity of the basic chromosome number which is $x=6$ for all the species. A few taxa have polyploid forms but not true polyploid species has been found as yet. Telocentric B-chromosome of various sizes have been found in four species (Table 2).

The chromosome complement of *Tulbaghia* is composed of sub-median chromosomes which are among the largest in the plant kingdom: the length of the haploid complement vary from 56.5 to 94.3 μm (Table 1, Figs. 22a and b).

The karyotypes differ mainly in the type or combinations of types of nucleolar chromosomes and on this basis the genus may be subdivided into seven group of species (Table 1). Another character of the chromosome complement of some species of *Tulbaghia* is the presence of cold sensitive heterochromatic segments (H-segments). Fluorochrome staining has established that the H-segments of *Tulbaghia* are composed of DNA containing highly repetitive sequences of Guanine-Cytidine (GC) nucleotides (see Figs. 23 and 24).

A

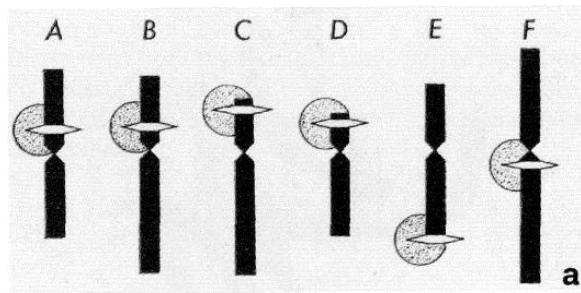


Fig. 22a — Diagrammatic representation of the six nucleolar chromosome types (N.O.R.'s) in *Tulbaghia* drawn according to their relative size.

Type A: occurs in 13 species and is a medium sized chromosome with a submedian centromere and with the N.O.R. located in an intercalary position.

Type B: occurs, in combination with type A, only in one species (*T. acutiloba* Harv.) and is the second longest of the complement: the N.O.R. is located in the short arm in an intercalary position.

Type C: occurs in two species (*T. capensis* L. and *T. alliacca* L. f.) and is a subterminal chromosome and the second longest of the karyotype. The N.O.R. is located distally on the short arm. Type D: occurs in five species and is usually the shortest of the complement with a subterminal centromere. The N.O.R. is located terminally on the short arm and often carries an heterochromatic "satellite" of various sizes.

Type E: occurs in one species (*T. montana* Vosa) and is a medium sized chromosome with a submedian centromere. The N.O.R. is located terminally on its long arm. Type F: occurs, in combination with type A, in two species (*T. rhodesica* Fries and *T. cameroni* Baker) and is the longest of the complement with a submedian centromere: the N.O.R. is located in an intercalary position very near the centromere.

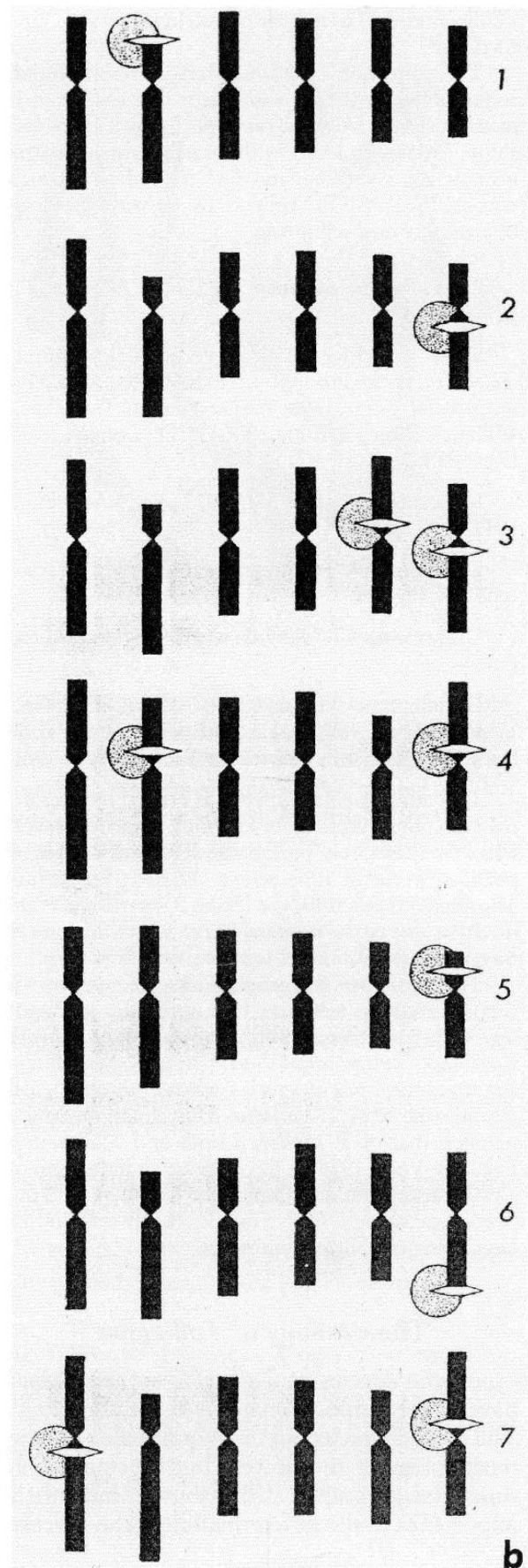


Fig. 22b — Diagrammatic representation of the haploid karyotypes of *Tulbaghia*. One species for each karyotype is illustrated and drawn in accordance with its relative size). Group 1: *T. capensis* L. (karyotype C); Group 2: *T. dregeana* Kunth (karyotype A); Group 3: *T. transvaalensis* Vosa (karyotype AA); Group 4: *T. acutiloba* Harv. (karyotype AB); Group 5: *T. coddii* Vosa & Burbidge (karyotype D); Group 6: *T. montana* Vosa (karyotype E); Group 7: *T. rhodesica* Fries (karyotype AF).



Plate I. (a) *T. capensis* L. (x2). (b) *T. alliacea* L. f. (x2). (c) *T. cernua* Ave-Lall. (x2). (d) *T. ludwigiana* Harvey (x2). (e) *T. dregeana* Kunth (x2). (f) *T. tenuior* Krause & Dinter (x2).

Description of the karyotypes (Table 1)

Group A (six species) - The karyotype consists of five submedian chromosomes one of which carries the nucleolar attachment in a proximal position on the long arm and one almost subterminal chromosome which is the second largest of the complement. In a very few

plants in certain populations, both in the diploid form of *T. cernua* and in *T. ludwigiana*, the short arm of this latter chromosome varies in length, sometimes reaching the size of the shorter arm of the second largest chromosome of the Group D karyotype. However, in all such cases the additional chromosome segment is completely heterochromatic.

Group AA (three species) - The karyotype is overall similar to that of group A but there are two nucleolar chromosomes of type A.

Group AB (one species) - The karyotype consists of six submedian chromosomes. The second largest carries the nucleolar attachment in a proximal position on its short arm (nucleolar chromosome type B). There is another nucleolar chromosome of type A.

Group AF (two species) - The karyotype is overall similar to that of group A, but the longest of the complement carries a nucleolar attachment in a very proximal position on its long arm (nucleolar chromosome type F). There is another nucleolar chromosome of type A.

Group C (two species) - The karyotype resembles that of the species of group A, but the nucleolar attachment is carried distally on the short arm of the second largest chromosome.

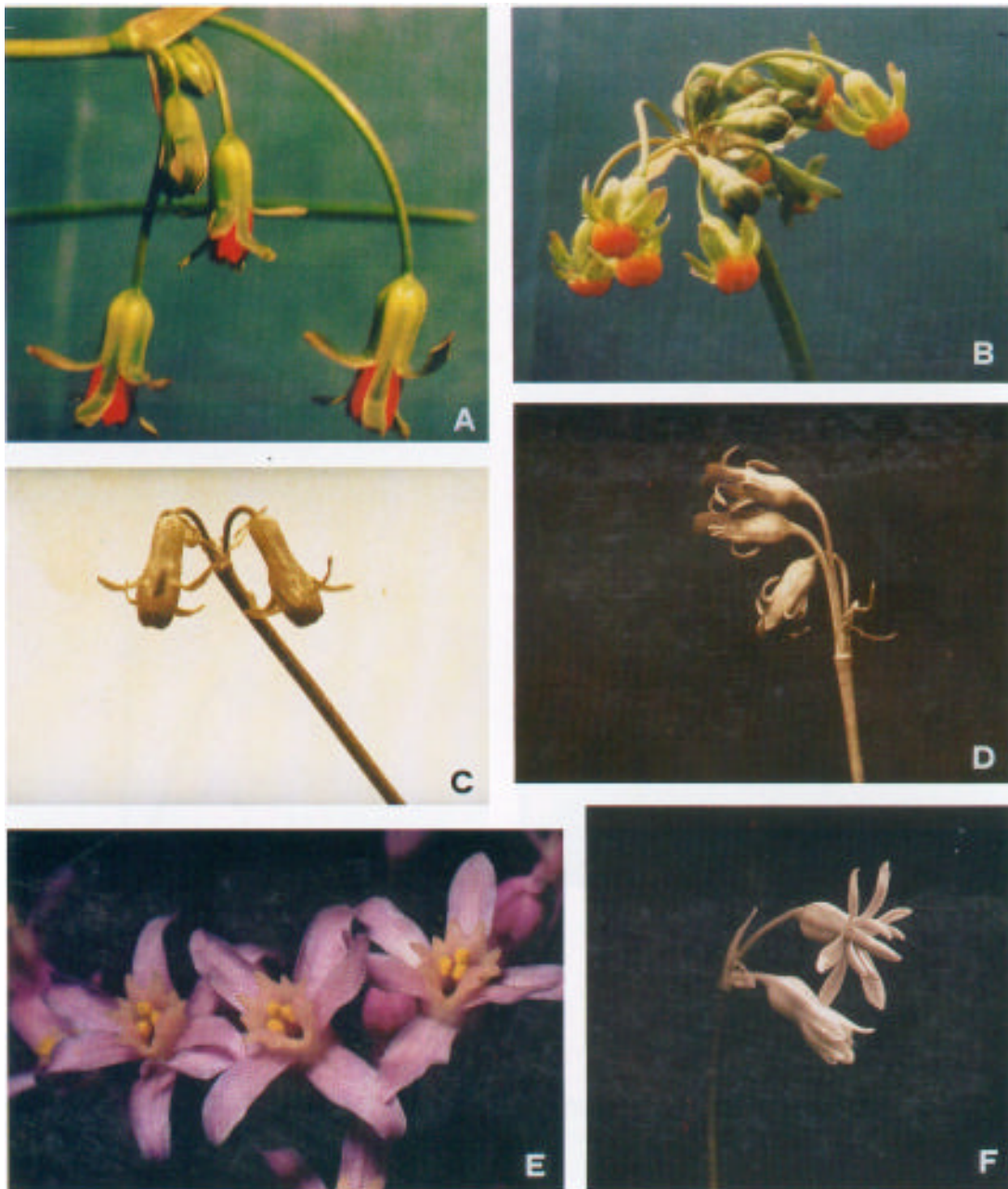


Plate II. (a) *T. nutans* Vosa (x3). (b) *T. macrocarpa* Vosa (x2). (c) *T. transvaalensis* Vosa (x2). (d) *T. acutiloba* Harvey (x2). (e) *T. simmleri* Beauverd (x4). (f) *T. galpinii* Schlechter (x2).



Plate III. (a) *T. natalensis* Baker (x3). (b) *T. leucantha* Baker (x2). (c) *T. verdoorniae* Vosa & Burbidge (x2). (d) *T. coddii* Vosa &

Group D (five species) - The karyotype consists of five sub median chromosomes and one subterminal chromosome, usually the shortest of the complement, which carries the nucleolar organizer on its short arm. The "satellite" distal to the nucleolar attachment is variable in size and in some cases may have almost the size of

the arm of nucleolar chromosome type A. However, in all these cases, the extra chromosome segment is heterochromatic.

Group E (one species) - The karyotype is similar to that of the species of group A, but the nucleolar attachment is carried on the long arm of a submedian chromosome.

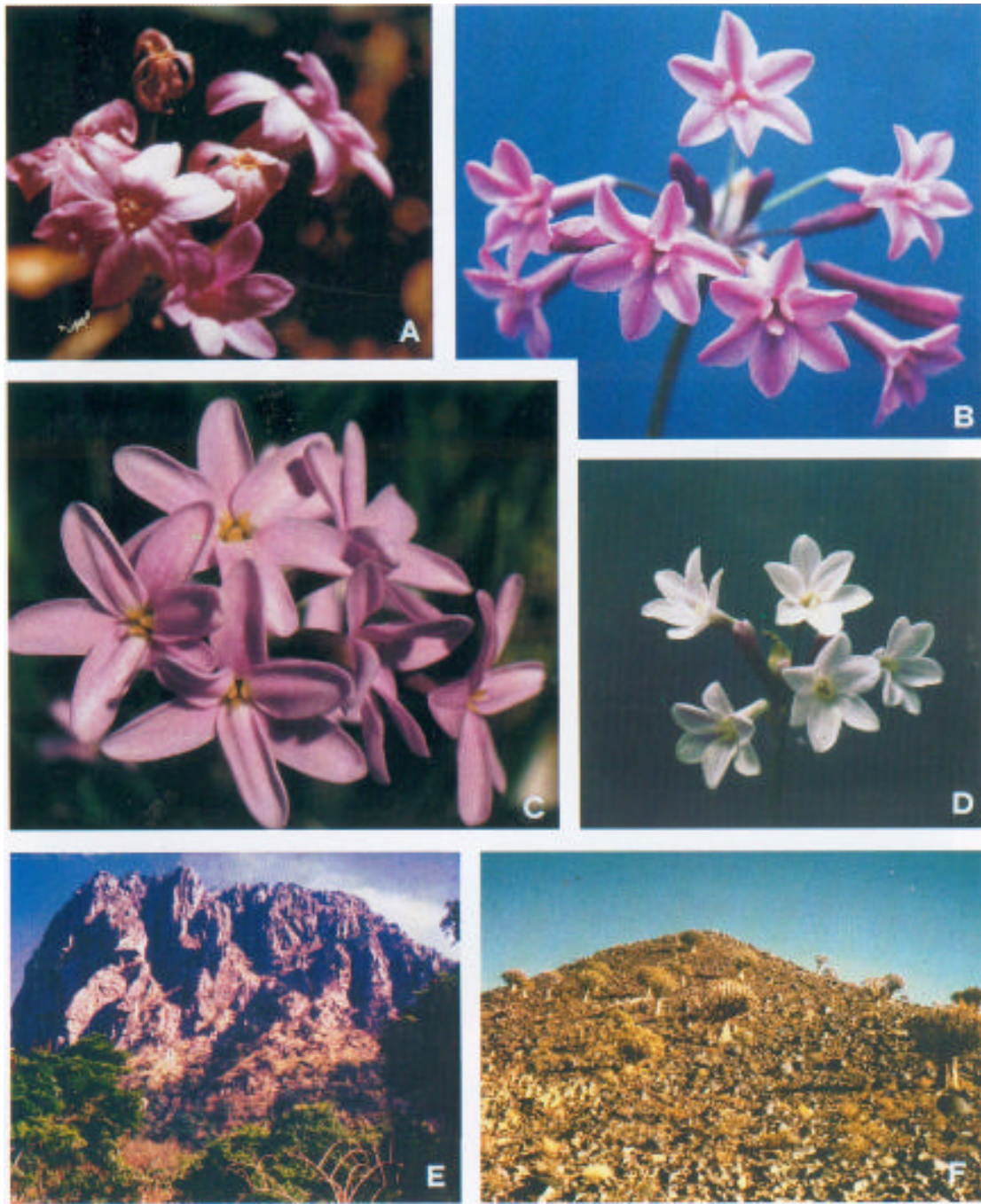


Plate IV. (a) *T. rhodesica* Fries (x2). (b) *T. violacea* Harvey (x2). (c) *T. violacea* Harvey var. *maritima* Vosa (x4). (d) *T. cominsii* Vosa (x2). (e) The craggy hill of 'Unkomaninear Ofcolaco (Northern Drakensberg): from the top to the SW the habitat of *T. transvaalensis* Vosa. (f) Nabibia, small rocky *inselberg* about 75 km N of the Orange River with a population of *Aloe dichotoma* L. f: the typical habitat of *T. tenuior* Krause & Dinter.

TABLE 1 — Karyotype groups, ploidy level and length (μm) of the haploid chromosome complement in *Tulbaghia* (measurements taken on at least five mitotic metaphase cells in each species)

Species	Group	ploidy level (x)	length (μm)
3. <i>cernua</i>	A	6 (2x,4x)	89.3 (dipl.), 93.5 (tetrapl.)
4. <i>ludwigiana</i>		6 (2x)	89.0
5. <i>dregeana</i>		6 (2x)	66.8
6. <i>tenuior</i>		6 (2x)	65.2
7. <i>nutans</i>		6 (2x)	66.3
11. <i>simpleri</i> *		6 (2x)	56.5
20. <i>violacea</i> **		6 (2x)	67.2
20a. <i>violacea</i> var. <i>maritima</i> **		6 (2x)	67.5
8. <i>macrocarpa</i>	AA	6 (2x)	66.4
9. <i>transvaalensis</i>		6 (2x)	66.7
21. <i>cominsii</i> ***		6 (2x)	68.2
10. <i>acutiloba</i>	AB	6 (2x)	79.5
18. <i>cameroni</i>	AF	6 (2x)	94.3
19. <i>rhodesica</i>		6 (2x)	93.4
1. <i>capensis</i>	C	6 (2x,4x,6x)	68.7
2. <i>alliacea</i>		6 (2x,4x,6x)	68.4
12. <i>galpinii</i> ****	D	6 (2x)	64.2
13. <i>leucantha</i>		6 (2x,4x)	66.1
14. <i>natalensis</i>		6 (2x)	66.7
15. <i>verdoorniae</i>		6 (2x)	62.9
16. <i>coddii</i>		6 (2x)	69.8
17. <i>montana</i>	E	6 (2x)	63.7

The number preceding the species name refers to the taxonomic sequence. The number in bold lettering denote values above or below the average haploid length of most of the species.

* This species differs from the others in its group by some of its morphological features and by its much smaller chromosomes.

** In some taxonomic accounts, these two species are sometimes included into the subgenus *Omentaria* because of their much reduced corona, which consists only of three distinct processes placed opposite the inner perianth segments. The subgenus *Omentaria* is not recognized in the present study.

*** This species is very similar phenotypically to *Tulbaghia violacea* Harvey. However, its karyotype, with two nucleolar chromosome of type A, places it together with *Tulbaghia macrocarpa* Vosa and *Tulbaghia transvaalensis* Vosa which have a very different phenotype and distribution.

**** This species has a scarcely fleshy corona composed of six distinctly lanceolate processes and in this character differs from the other species of its karyotype group which have an entire, annular and more or less crenulate corona.

The problem of the number of nucleolar organizers in *Tulbaghia*

The number of nucleolar organizers in *Tulbaghia* vary from two to four and are of five types (fig. 22a). They differ in number and in combinations according to and characterizing the species (fig. 22b).

Observation of silver-stained interphase nuclei in several species has shown that the amount of nucleolar material is very much equivalent whether there are two organizers or four. Thus, it seems that there has been an increase in the number of organizing sites with a proportional decrease in their nucleolar material and in its synthesizing activity. Silver-staining has also confirmed, in *Tulbaghia*, the intrinsic heteromorphism of the nucleolar organizers,

and of their expression in the interphase nucleoli, which seems to be the rule in most organisms and based on a kind of dominance on the line of that demonstrated by NAVASHIN (1934) in hybrids between species of *Crepis*.

The significance of the doubling of the nucleolar organizing sites must be found in the fine tuning of the interaction between the genome *vis-a-vis* the meiotic process and therefore on the inheritance and expression of certain adaptive features. The situation in *T. violacea* and *T. cominsii*, which share a very similar phenotype but with two organizers in the former and four in the latter, is rather interesting and demonstrates very well how little we know as yet on the very specialized biology and especially on the evolutionary meaning of such differences.

Constitutive heterochromatin in *Tulbaghia*

Constitutive heterochromatin can be defined as somewhat dispensable, non-transcribing, usually highly repetitive DNA sequences, preserved by selection and located on the chromosomes as inheritable, inconvertible segments. It differs from facultative heterochromatin which is thought to be the consequence of a cytological situation in which a certain amount of normally coding DNA is temporarily and reversibly repressed by a special molecular mechanism. An example of facultative heterochromatin are the X-chromosomes in female mammals, one of which becomes inactive and heterochromatic and appears, as it were constitutive heterochromatin, as a chromocentre in the interphase nuclei (i.e. the Barr-body of female humans).

Constitutive heterochromatic segments (H-segments) are present in several species of *Tulbaghia* (Table 2 and see VOSA, 1970, 1975). The H-segments number, size and position on the chromosomes is variable between and, to a certain extent, also within species. Such segments are sensitive to cold treatment and present reduced fluorescence when stained with certain fluorochromes, in the same way as those found in *Paris*, *Trillium* and *Cestrum* (DARLINGTON

and LA COUR 1938; DYER 1963; VOSA 1966, 1970, 1973; FILION and VOSA 1980). Experiments have shown that, in *Tulbaghia*, they consist mainly of highly repetitive sequences of DNA composed, for the most part, of Guanine-Cytidine nucleotides (PACHMAN and RIEGLER 1972; WEISBLUM and de HASETH 1972).

In some species of *Tulbaghia*, such as *T. cernua* and *T. ludwigiana*, the total amount of heterochromatin, as a proportion of the length of the chromosome complement, has been found in a few plants to be as much as 25 %.

In respect to the presence and to the localization of the H-segments, the species of *Tulbaghia* may be subdivided into three groups. The first group, which includes 10 species, the segments are generally very small and almost exclusively localized either side of the nucleolar organizers. The second group includes 6 species where the H-segments are relatively large and are located almost always in distal position (fig. 23). This situation is found also in most of the American species of *Trillium* (DARLINGTON and SHAW 1959). In the third group, which includes 5 species, the H-segments are found mostly in intercalary position (fig. 24) as in *Fritillaria*, *Trillium kamschaticum*, *Trillium erectum* and *Cestrum* (DYER 1963). The variation in the presence, absence and size of the H-segments in *Tulbaghia*, follows a very similar pattern in different species within each group, with

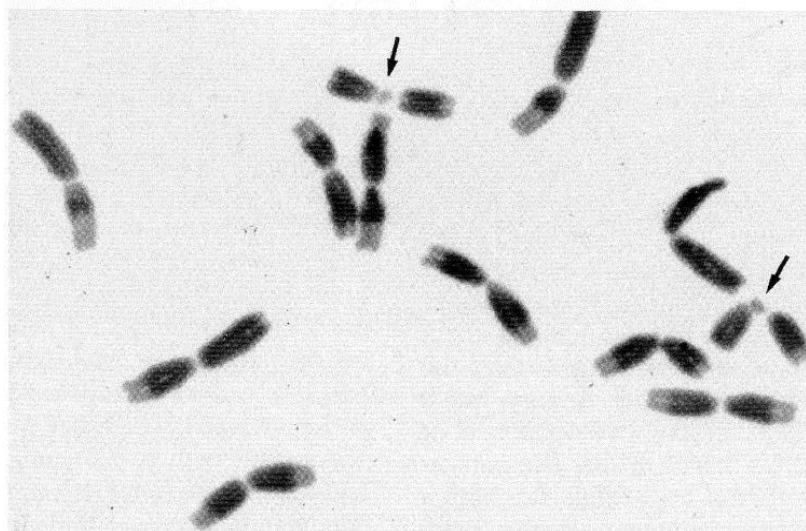


Fig. 23 — Mitotic metaphase in *Tulbaghia cernua*, after 36 h at 3-4 °C, stained in Feulgen (x 1500). Note the lightly stained distally located H-segments. The small segments, intercalary between the centromere and the N.O.'s, are also heterochromatic and lightly stained (arrowed).

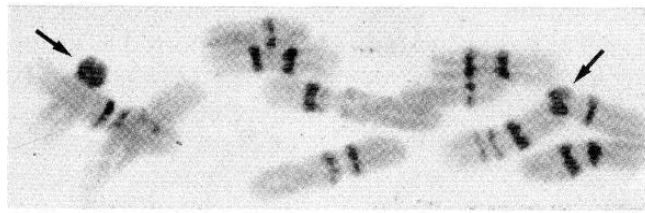


Fig. 24 — C-banded mitotic metaphase in *Tulbaghia leucantha* (x 1500). Note the deeply stained intercalary H-segments. The chromosome portions, distal to the N.O.R.'s, are also heterochromatic and deeply stained (arrowed).

an evident polymorphism which is almost exactly parallel for each chromosome type. This situation is very much the same as that found in *Trillium* and in *Paris* by DARLINGTON and SHAW (1959). In *Trillium*, in fact, the five basic chromosomes correspond in size and morphology throughout the American species, notwithstanding the position of the H-segments. In *Tulbaghia*, however, at least in the group with distal localization, the basic chromosome complement is variable according to the species.

In our genus, the two main types of H-segments localization are distinct and only occasionally we have found intermediate types. In particular, in *Tulbaghia leucantha*, one of the species with proximally localized H-segments, a few plants in some populations have distally located segments of this type adjacent to the nu-

cleolar attachment. The heterochromatin position on the chromosomes does not affect the localization of chiasmata which are almost exclusively proximal to the centromere in all the species. As regards the H-segments found in *Trillium*, *Fritillaria* and in a few other genera, the general situation seems to suggest a clear evolutionary trend from an intercalary towards a distal localization (DARLINGTON and SHAW 1959). In *Tulbaghia*, the almost complete absence of intermediate types probably shows that the proximal localization of the H-segments may be of a more recent origin than the alternative, and that their establishment could be rather apart in time. The two situations are evidently adaptive in their function and in a state of finely balanced polymorphism within their respective interbreeding populations. This problem has been extensively and masterly treated by FORD (1957). As regards *Tulbaghia*, a relatively small survey of heterochromatin polymorphism in two populations of *T. leucantha* (12 and 17 plants, respectively), has shown that the degree of chromosomal heterozygosity is quite high. Nevertheless, the same chromosome types have been found to be present in the same proportion in both samples, thus demonstrating that they belong to a single interbreeding population (VOSA 1973a).

Function and significance of constitutive heterochromatin

In *Tulbaghia*, as well as in many other genera of plants and animals, the presence of heterochromatin raises the question of its role in the framework of the genetic system. The function of heterochromatin seems to be overall non-specific and quantitative rather than qualitative. A few studies have demonstrated the quantita-

TABLE 2 — Heterochromatin and B-chromosomes in *Tulbaghia*

Species	Heterochromatin		B-chromosomes	
	Proximal	Distal	Number	Size
<i>cernua</i> (diploid)	—	+ (a)	2-3	L
<i>ludwigiana</i>	—	+ (a)	2-4	L
<i>simmleri</i>	—	+ (a)	—	—
<i>alliacea</i> (diploid)	—	+ (a)	—	—
<i>capensis</i> (diploid)	—	+ (a)	—	—
<i>leucantha</i> (diploid)	+	+ (b)	2-10	S
<i>leucantha</i> (tetraploid)	+	+ (b)	—	—
<i>coddii</i>	+	+ (b)	—	—
<i>cameronii</i>	—	—	1-4	L
<i>macrocarpa</i>	—	+ (a)	—	—
<i>acutiloba</i>	—	+ (a)	—	—

(a) Heterochromatic segments located proximally only adjacent to the nucleolar organizers (see text).

(b) Heterochromatic segments located distally only adjacent to the nucleolar organizers (see text).

tive function of heterochromatin. In *Allium pulchellum*, VOSA (1976, 1996) has shown that the differences in the amount of heterochromatin, between altitudinally separated populations, indicate a probable adaptive role. In *Ornithogalum* (VOSA 1997), the differences in the amount of heterochromatin are not only indicative of an adaptive role to extreme environmental conditions but, according to quantity, they have a strong influence in the sequence and duration of the life cycle.

The role of heterochromatin in the control of the life cycle has been studied by NAGL (1974a,b) and by NAGL and EHRENDORFER (1973). In the Anthemidae, NAGL (1974a,b) in his study of three perennial species, three annual species with high DNA content and two annual species with low DNA content, has found that the amount of heterochromatin per genome was directly related to a reduction in cell cycle time in the annual species with high DNA content. Now, because heterochromatin generally replicates much faster than euchromatin (BOSTOCK *et al.* 1972), its amount per genome may represent a regulating agent affecting the duration of the cell cycle and, therefore, of the speed of development.

VOSA and STERGIANOU (1990), report some interesting results in their study of the genus *Pleione* (Orchidaceae), where there exist terrestrial as well as epiphytic species, all with the same chromosome number and equivalent DNA amount. Cytological data show that the terrestrial species generally possess asymmetric karyotypes and relatively small amounts of interstitial and centromeric heterochromatin whereas the epiphytic species have symmetric karyotypes and comparatively large amounts of mainly distally located heterochromatin. Thus, as in Anthemidae (NAGL 1974a,b) and in *Ornithogalum* (VOSA 1997), the larger amount of heterochromatin may provide a kind of compensating factor which allows a quicker growth in the epiphytic species, which are known to complete their annual growing period in a rather shorter time than the terrestrial. Further, the differences in karyotype morphology and in the relative position of the H-segments in the two types of *Pleione*, may have an effect on meiosis and on crossing-over, with consequences in their respective heredity of gene sequences. In fact, a correlation between crossing-over and the presence of heterochromatin,

and of its position on the chromosomes, has been reported in plants (RHOADES 1978) and in animals (MIKLOS and NANKIWELL 1976).

In conclusion, constitutive heterochromatin owes its great evolutionary importance to its contribution to an overall increase in variation, which is probably not related to any decisive threshold but that controls both heredity and development.

B-chromosomes in *Tulbaghia*

By definition B-chromosomes are smaller in size than those of the A-complement. They are somewhat unstable at mitosis and at meiosis and therefore variable in number between plants of the same populations. In general, B-chromosomes do not have any specific phenotypic consequence on the individual organism carrying them and seem to have quantitative rather than qualitative effects. Thus, they have been shown to increase the speed of germination in *Allium porrum* (VOSA 1966b), may have a role in adaptation to ecological situation in *Listera ovata* (VOSA 1983) or may affect meiotic recombination in this latter species (VOSA and BARLOW 1972) and in *Puschkinia libanotica* (BARLOW and VOSA 1970). The induced change in recombination, by creating new gene assemblages, may lead to speciation in the long term (DARLINGTON 1971). On the whole, the considerable amount of research has shown that B-chromosomes may be considered, with good reason, as the active basis of quantitative variation. In *Tulbaghia*, so far, only three species have been found to possess telocentric B-chromosomes (Table 2). In *T. cernua*, *T. ludwigiana* and *T. cameronii* (fig. 18), they are relatively large (3-4 micra in length) whilst in *T. leucantha* they are very small (1-2 micra in length). No population analysis regarding occurrence and breeding behaviour of B-chromosomes have been undertaken as yet in *Tulbaghia*. It is interesting that B-chromosomes are absent in the polyploid forms of *T. cernua* and *T. leucantha*, indeed a similar situation as that found in most plant species where, in general, their frequency has been found to be much less in polyploids than in diploids.

CONCLUSIONS

The cytotaxonomic review of *Tulbaghia* has shown that the genus is fairly uniform with relatively small differences between the species. These differences relate chiefly to the size and type of the corona and to certain other morphological characters.

However, the genus, as a whole, possesses large and well differentiated chromosomes which allow precise studies to be made on their structure. In particular, apart from specific differences in the size of the karyotypes and of the existence of heterochromatic segments, the type and number of the nucleolar chromosomes are data of great importance in the definition of the species and to subdivide the genus into groups of taxa which, with some exception, are composed of closely related species.

In any case, for the recognition of the geographical limits of many species of *Tulbaghia*, more extensive field collecting trips are necessary.

Regarding South Africa, this applies particularly to the territories north of the rivers Vaal and Orange.

A survey of the geographical distribution of the species of *Tulbaghia*, has shown that an apparent centre of speciation may be located in the Eastern Cape, where most of the species are found. The basis of this hypothesis may be not really valid because of the vegetation changes brought about by the climatic deterioration made worse, with every probability, also by human activities.

These two factors seem to have been in action for at least the last 500-600 years. In particular, in quite recent times, the above mentioned climatic changes, together with instances of poor farm management and overgrazing, have been responsible for the advance south-eastwards of desert-like conditions over a rather large area. This occurrence, which in some places amounts to about 250 km in width, according to ACOCKS (1953), has reduced drastically the habitat available for many plant species, especially in the north-west, leading in many instances to their disappearance. In the case of *Tulbaghia*, the net result has been an apparent "crowding" of the extant species in the east with a few somewhat specialized "relics", such as *Tulbaghia tenuior* and, in part, *Tulbaghia dregeana*, still able to survive in the west.

Very few collections of *Tulbaghia* have been made north of the river Limpopo and, with a few exceptions, little is known about the tropical species of the genus.

APPENDIX I

Species insufficiently known

Tulbaghia aequinoctialis Welwitsch, Baker in *Trans. Linn. Soc. ser. II*, 1: 146 (1878). Apparently found near Pungo Adongo in Angola. The type is at K (A.M. Reis 43-3754). I have seen two other specimens (*Dinter* 2140 and 2280, BM!) but, in the absence of new evidence, I consider the existing material not sufficient for an accurate appraisal of the epithet.

Tulbaghia affinis Link in *Enum. Pl. Berol.* p. 310. Described as a plant from the Cape of Good Hope but without a precise locality.

Tulbaghia australis Link in *Steud. Nom. Bot.* 1: 857 (1821). It must be considered *nomen nudum* as no description is given and the name has been deleted from the second edition.

Tulbaghia bragae Engler in *Pflanzenw. Ost-Afrika*, 141 (1895). Described from Braga near Beira (Mozambique).

Tulbaghia calcarea Engler and Krause in *Engl. Bot. Jarb.* 45: 142 (1910). Described from around Grootfontein in Nabibia. On the basis of the criteria used in the present work, the existence of only two specimens in M (*Dinter* 761 and 761a) is considered not sufficient to warrant its inclusion in the list of good species.

Tulbaghia hockii de Wildemann in *Feddes Rep.* 11: 546 (1913). This entity has been described as from Upper Katanga (Elizabethville, Congo) but no specimens are indicated.

Tulbaghia hypoxidea Smith in *Rees Cycl.* 36 (1819). The description is apparently based on a plant that flowered in the greenhouses of Messrs. Lees & Kennedy of Hammersmith, London, who received it from Holland. A drawing of the plant was made by a Mr. Soverby but it is said to have been mislaid.

Tulbaghia luebbertiana Engler and Krause in *Engl. Bot. Jahrb.* 45: 145 (1910). Described from Nabibia but the type specimen seen, *Luebbert* 44 (M!), is out of flower.

Tulbaghia karasbergensis Glover in *Ann. Bolus Herb.* 1: 104 (1915). Although he has seen no material, Merxmueller, in *Prod. Fl. Sudwestafrika* of 1969, considers it a good species.

Tulbaghia monantha Engl. & Gilg. in *Warb. Kunene-Zambesi Exp.* 192 (1903). The species has been described as from Cabindere in Angola. The only specimen seen, *Baum* 351 (M!), in my opinion, cannot be taken as the basis of a distinct species.

Tulbaghia pauciflora Baker in *Bot. Jahrb. Syst.* (1892). Described as from the Cape but no specimen is indicated.

APPENDIX II

Taxonomy key to the genus Tulbaghia

1. Corona lobes 3, free to base.....**20. violacea** et var.; **21. cominsii**
1. Corona lobes 6, free or united at base
 2. Corona lobes less than 1/4 as long as perianth segments
 3. Perianth segments and corona purplish-mauve, rarely white; corona not fleshy, lobes free; perianth segments oblong-lanceolate.....**19. rhodesica**
 3. Perianth greenish, lobes long, very narrowly deltate; corona yellow or brownish, fleshy, very shallowly lobed **6. tenuior**
 2. Corona at least 1/3 as long as perianth segments, usually more than 1/2 as long
 4. Corona lobes free almost to base
 - perianth glaucous-green; corona fleshy, brown or brownish-green.....**1. capensis**
 5. Leaves filiform, 1 mm wide, umbel (1) 2 (4) flowered; perianth pale green; corona pale green, not fleshy **12. galpinii**
 4. Corona lobes united for at least half of their length
 6. Corona lobed to 1/3, lobes acute
 7. Leaves more than 1 cm wide; perianth pink or mauve rarely white; corona of the same colour**11. simmlerii**
 7. Leaves up to 7 mm wide; flowers greenish-white; corona brownish-green or yellow
 8. Leaves shiny above, mat beneath, with a prominent midrib on the underside; perianth segments with inrolled margins, usually reflexed, inner and outer whorl more or less of the same length**17. montana**
 8. Leaves mat and glaucous on both surfaces, without a prominent midrib, perianth segments white or pinkish, more or less spatulate usually not reflexed, inner whorl shorter than the outer**14. natalensis**
 6. Corona lobed to less than 1/3, lobes rounded and fleshy
 9. Corona much wider than long
 10. Leaves more than 18 mm wide; outer and inner perianth segments inserted at more or less the same level
 11. Leaves keeled beneath, style much shorter than the long ovary.....**8. macrocarpa**
 11. Leaves not keeled beneath; style more or less as long as the ovary**5. dregeana**
 9. Corona at least as long as broad
 12. Corona with very indistinct lobes
 13. Leaves up to 4-5 mm wide, folded and V-shaped in section; perianth segments markedly reflexed.....**10. acutiloba**
 13. Leaves 6-10 mm wide, more or less flat and only slightly keeled, perianth segments not very markedly reflexed.....**9. transvaalensis**
 12. Corona with distinct lobes
 14. Corona much shorter than the spatulate perianth segments, leaves filiform.....**16. coddii**
 14. Corona more or less equalling the usually acute perianth segments; leaves filiform only in some forms of *leucantha*
 15. Longest pedicels more than 5 cm long; inner perianth segments fused to the corona for most of their length.....**7. nutans**
 15. Longest pedicels less than 2.5 cm long; inner perianth segment fused to the corona for less than half their length
 16. Inner and outer perianth segments arising from the base of the corona.....**2. alliacea**
 16. Inner perianth segments fused to the corona for up to half its length
 17. Perianth segments less than 1/3 as long as broad
 18. Perianth segments flat, apex acute**3. cernua**
 18. Perianth segments with incurved margins, apex obtuse or spatulate.....**15. verdorniae**
 17. Perianth segments at least 4 times as long as broad
 19. Perianth tube much longer than corona, leaves 9-10 mm wide**18. cameroni**
 19. Perianth tube shorter than corona, leaves 1-6 mm wide.....**13. leucantha**

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