CHROMOSOME NUMBERS IN THE GENUS MUSCARI MILL.

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ABSTRACT. Chromosome counts are given for twenty species of *Muscari*, of which seven are reported for the first time. Generic and subgeneric limits are discussed in the light of new information, and a classification for the genus proposed. One new subgenus is described, *M.* subgen. *Pseudomuscari* and one new combination made, *M. eburnea* (Eig & Feinbrun) Stuart.

INTRODUCTION

The present work is part of a more general study of the genus *Muscari* Mill. (Liliaceae-Scilloideae), and was largely based on the extensive collection of living material, both of wild and cultivated origin, assembled by Dr P. H. Davis and grown at the Royal Botanic Garden, Edinburgh.

The taxonomic results of the work are to be presented shortly in another paper, but a very brief account of the suggested classification will be included here. As detailed studies of a number of characters used for species delimitation led me to adopt a much broader species concept than has been customary, the result is that a number of well-known names have been relegated to synonymy. These will be discussed later. At present, the provisional list contains some thirty species, of which three were recently described by Davis & Stuart (1966), and a key published by the author (Stuart, 1965). The species have been grouped within four subgenera, and *Muscari* has been broadly defined for the present, as follows.

Leaves 1 to many per bulb, not provided with elevated veins. Raceme dense or lax, often with sterile flowers at apex. Pedicels of fertile flowers usually horizontal or nodding, those of the sterile flowers horizontal to ascending; pedicels sometimes obsolescent. Perianth of fertile flowers globose to cylindrical, blue, violet, brownish, yellowish or whitish, colour scarcely changing during flowering; generally contracted at the mouth with short teeth, but if campanulate then flowers blue or violet; perianth abscissing round the base as the capsule expands. Capsule with sharply angled valves. Seeds 2 per loculus, black and often shiny, usually minutely wrinkled, always without a waxy bloom.

A synopsis of classification is given below which includes the major synonyms.

SYNOPSIS OF CLASSIFICATION

Genus Muscari Mill.

Subgenus *Muscari*

M. moschatum Willd. (Syn.: *Hyacinthus muscari* L., *Muscarimia muscari* Los.–Los., *Muscari racemosum* Mill. nomen confusum)

M. macrocarpum Sweet (Syn.: *M. moschatum* Willd. var *flavum* Lam., *M. luteum* Tod.)

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Subgenus *Leopoldia* (Parl.) Ascherson & Graebner

M. comosum (L.) Mill. (Syn.: *M. pinardii* Boiss., *M. holzmannii* (Heldr.) Boiss., *M. graecum* (Heldr.) Boiss.)
M. caucasicum (Griseb.) Baker
M. weissii Freyn
M. amoenocomum Rech. fil.
M. cycladicum Davis & Stuart
M. gussonei (Parl.) Tod.
M. tenuiflorum Tausch.
M. longipes Boiss.
M. eburnea (Eig & Feinbrun) Stuart, **comb. nov.** (Syn.: *Leopoldia eburnea* Eig & Feinbrun in Pal. Journ. Bot., J. Ser., iv: 58, 1947).
M. bicolor Boiss.

Subgenus *Botryanthus* (Kunth) Ascherson & Graebner

M. neglectum Guss. (Syn.: *M. racemosum* (L.) Lam. & DC. (non Mill.), *M. atlanticum* Boiss. & Reut., *M. macranthum* Freyn, *M. leucostomum* Woron.)
M. commutatum Boiss.
M. latifolium Kirk
M. armeniacum Baker (Syn.: *M. argaei* Hort., *M. colchicum* Grossh., *M. pyramidatum* Velen., *M. cyaneo-violaceum* Turrill, *M. conicum* Baker, *M. polyanthum* Boiss.)
M. aucheri (Boiss.) Baker (Syn.: *M. lingulatum* Baker, *M. tubergenianum* Hoog)
M. bourgaei Baker
M. microstomum Davis & Stuart
M. botryoides (L.) Mill. (Syn.: *M. heldreichii* Boiss., *M. kerneri* Marches., *M. longifolium* Rigo, *M. transsilvanicum* Schur.)

Subgenus **Pseudomuscari** Stuart, **subgen. nov.** (Syn.: *Muscari* sect. *Pseudomuscari* Los.–Los. in Komarov, Fl. URSS 4: 416 (1935)—nomen, descr. russ.

Radices annuae, haud incrassatae. *Folia* 2–6, angusta. *Flores steriles* pauci vel multi, sessiles vel pedicellati. *Flores fertiles* breviter vel oblonge campanulati, ore haud vel paulo constricti, pallide caerulei vel atrati vel rare brunnescentes, lobis erectis vel recurvis, 1–2 mm longis, tubo concoloris. *Racemum* densum vel laxum. *Capsulae* (ubi cognitae) minus quam 2 cm longae, dehiscentes; semina nigra, nitida, scrobiculata vel laevia.
Typus: *M. pallens* Fischer

M. parviflorum Desf. (Syn.: *M. autumnale* Guss.)
M. pallens Fischer
M. inconstrictum Rech. fil.
M. chalusicum Stuart
M. azureum Fenzl (Syn.: *M. praecox* Siehe)
M. discolor Boiss. & Hausskn.
M. coelestis Fomin
M. turkewiczii (Woron.) Los.–Los.
M. forniculatum Fomin
M. coeruleum Los.–Los.

Material and methods

The plants were all grown in pots in cold frames. Root tips were collected on warm sunny mornings in April and May, and pre-treated for 3–4 hours in paradichlorobenzene. Subsequent fixation was in 3:1 ethanol: acetic acid. Squash preparations were made using the standard Feulgen technique after 10–12 minutes hydrolysis. All counts listed are from root tips; meiosis takes place while the flower spike is still within the bulb. The results are listed below. Edinburgh garden accession numbers are given for each sample, with the collector's name in italics. Discussion of distributions and of the work of previous authors is given under the species; identifications for some of the earlier counts, however, should be treated with caution. A more general discussion is to be found at the end of the list. Voucher specimens are kept at the Herbarium of the Royal Botanic Garden, Edinburgh.

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List of chromosome numbers

Subgenus *Muscari*

	2n (root tips)
M. macrocarpum	
X60 2458 *Grant* ann. 1960. Greece: Samos	18
X60 2638 *Hodgkin* Hort.	18
M. moschatum	
Hort.	18

Subgenus *Leopoldia*

M. comosum	
149/51 Brussels Hort.	1
394/56 *Davis* 25458. Turkey: d. Muğla; Fethiye	1
394/56 *Davis* 26116b. Turkey: d. Mersin; Gülnar	1
283/57 Cluj Hort.	1
X59 3038 *Moggi*. Italy: Firenze, Tavarnuzze	1
X60 2381 *Levrantiades*, comm. Davis 1. Greece: d. Kassandra; Valta	1
X60 2530 *Papageorgiou*. Greece: d. Athens; Psychico	1
X60 2534 *Papageorgiou*. Greece: Hymettus	1
LE60 2930 Leningrad Hort.	1
LD60 3345 *Runemark* 4. Greece: Cyclades; Anaphi	1
LD60 3355 *Runemark* 14. Greece: Ikaria	1
X61 1838 *Agnew*. Iraq: Hatra-Jezira	18
X62 2657 *Furse* 2545. Iran: Demavend	1
X62 2658 *Furse* 2731. Iran: Elburz mtns.	1
LD63 717 *Runemark*. Greece: Samos; Kerki	1
Hort. (forma monstrosum)	1

M. caucasicum

542/57 *Davis* 29528. Turkey: d. Kars; Sarikamiş . . . 18
ER/59 3627 Erevan Hort. 18
LE60 2933 Leningrad Hort. 18
X60 2988 *Synge & Furse* 740. Iran; SE Kuh-i-Sahand . . 18
X60 2989 *Synge & Furse* 839. Iran; Kuh-i-Sahand . . . 18

M. weissii

LD60 3343 *Runemark* 2. Greece; Dodecanese; Tria Nisi . . 18, 36
LD60 3347 *Runemark* 6. Greece: Cyclades; Mikonos . . 18
LD60 3356 *Runemark* 15. Greece: Cyclades; Naxos . . 18
LD60 3357 *Runemark* 16. Greece: Cyclades; Naxos . . 18
LD60 3359 *Runemark* 18. Greece: Cyclades; Makronisi . . 36
LD60 3352 *Runemark* 11. Greece: Dodecanese; Syrina . . 36
X62 3152 *Gathorne-Hardy* 147. Greece: Rhodes, Salakos . 36
LD60 3342 *Runemark* 3. Greece: Cyclades: Anaphi, Vigla . 36
LD60 3356 *Runemark* 15. Greece: Cyclades; Naxos . . 36

M. weissii is the only species in Subgen. *Leopoldia* so far known to contain both diploid and tetraploid cytodemes. The tetraploid and diploid are morphologically indistinguishable, the tetraploid plant being of more frequent occurrence and more widely distributed. It is known to be generally distributed throughout the Cyclades and Dodecanese, whereas the diploid is apparently restricted to the central Cyclades. The species is also found on Crete, and at one location on the south coast of Turkey.

M. cycladicum

LD60 3351 *Runemark* 10. Greece; Cyclades; Kardistina . . 54
LD60 3360 *Runemark* 19. Greece; Cyclades; Naxos, NE of town 54

This newly counted species is the only hexaploid so far recorded in the subgenus, and the only example in the genus of polyploidy being associated with distinct morphological differences. It is restricted to the Cyclades and Dodecanese.

M. amoenocomum

292/50 *Davis*. Greece: Crete, between Theriso and Katsiveli . 18

M. tenuiflorum

232/57 Copenhagen Hort. 18
X60 2764 Copenhagen Hort. 18
X60 3011 *Stainton & Henderson* 5212. Turkey: Sivas; Pinarbaşi 18
X60 3013 *Stainton & Henderson* 5280. Turkey: Sivas; Bey Dağ . 18
X60 3014 *Stainton & Henderson* 8441. Turkey: Gümüşane . 18
X60 3015 *Stainton & Henderson* 5269. Turkey: Gümüşane . 18
X62 2314 *Dudley, D.* 34812. Turkey: Gürün 18

A species widely distributed in eastern Europe and the east Mediterranean. Previous counts, also of 2n = 18, have been for European material.

M. longipes

X60 2710 *Synge & Furse* 755. Iran: Kurdistan . . . 18

Subgen. *Botryanthus*

M. neglectum var. *neglectum*

X61 1403 *Mermoud.* Switzerland: nr. Geneva . . . 36
X61 2416 *Sell.* England: between Eriswell and Lakenheath . 36
X59 2825 Madrid Hort. 45
X59 2028 *Moggi.* Italy: Firenze, Tavarnuzze 45
X60 2532 *Papageorgiou*, comm. Davis 4. Greece: Athens, Psychico 45
X51 1464 Köln Hort. 54
X59 2459 *Rechinger.* Austria: Burgenland: nr. Neusiedler Lake 54
X59 2460 *Rechinger.* Lower Austria: Braunsberg . . . 54
TK59 3325 Tashkent Hort. 54
M6/59 3590 Moscow Hort. 54
V59 3857 *Ehrendorfer.* Austria: Perchtoldsdorf . . . 54
X60 2381 *Levrantiades*, comm. Davis 3. Greece: Kassandra, Valta 54
LO60 2744 Copenhagen Hort. 54
LE60 2940 *Artushenko.* Azerbaijan: Baku; Mardakyan . . 54
K60 3273 Kew. Cyprus: Lefkara 54
X61 1842 *Agnew*, comm. Davis 3. Iraq: nr. Belad Sinjar . . 54

M. neglectum var. *pulchellum*

394/56 *Davis* 25738. Turkey: Antalya; Korkuteli . . . 18
394/56 *Davis* 25782. Turkey: Antalya; Akseki . . . 18
X59 3138 *O. Polunin* 24. Antilebanon: Mt. Hermon . . 18
X59 3876 *Davis* 33354. Crimea: Yaila 72
X60 2379 *Levrantiades* 1. Greece: Methoni . . . 18, 36, 54
X60 2382 *Levrantiades* 1. Greece: Mt. Vermion, Veria . . 18
X60 3020 *Stainton & Henderson* 5162. Turkey: Sivas; Pinarbaşi 18
X61 1840 *Agnew*, comm. Davis 1. Iraq: Hatra Jezira . . 18
X61 4348 *Gathorne-Hardy* 7. Greece: Cyclades; Keos . . 18
X61 4544 *O. Polunin* 12. Greece: Euboea; Steni . . . 18

In this species chromosome number has little constant effect on the appearance of the plant. Diploid plants from Greece and the Orient are often small (scapes generally shorter than 10 cm), and with more or less dense racemes; bulbils are not produced. The various polyploid levels, with a very wide geographical range, may produce plants which are indistinguishable from the diploids, but generally have scapes longer than 15 cm, and very dense racemes; bulbils are frequently produced. The octoploid, a single gathering collected in the Crimea, is the highest polyploid so far known in the genus. Short-scaped, it has narrowly oblanceolate leaves which are unusual for the species. No triploids have been found.

M. commutatum

LD60 3346 *Runemark* 54. Greece: Astipalia 18
LD63 719 *Runemark* 220.3X. Greece: Cyclades; Naxos, nr. Mitria 18
LD63 720 *Runemark* 1036.3X. Greece: Cyclades; Naxos, Oros Zeus 18

LD63 725 *Runemark* 346.1X. Greece: Cyclades; Amorgos, Ag. Elias 18
LD63 728 *Runemark* 245.1X. Greece: Cyclades; Skinousa, S of Naxos 18
LD63 729 *Runemark* 193.4X. Greece: Cyclades; Naxos, nr. Apollona 18

Although no polyploids were found, pentaploids have been reported by Delaunay (1915, 1926).

M. latifolium
80/48 Hort. 18

M. armeniacum var. *armeniacum*
542/57 *Davis* 29467. Turkey: Kars; Sarikamiş . . . 18
X60 *Levrantiades*, Greece: SE Thessalonika; Mt. Diotades . 18
X60 3215 *Khan, Prance, & Ratcliffe* 825. Turkey: Ankara; Kizilcahaman 18
X62 3126 *Davis* 39375. Turkey: Kastamonu; Küre . . . 18
X59 3870. Georgia: Tiflis 36
VA60 955 *Vilmorin-Andrieux* Hort. 36
X60 1712 *A. Dimitrieva*, comm. Davis. Caucasus: Batumi; Selenji Mtns. 36
K60 3275 Kew 4785. Hort. 36

M. armeniacum var. *szovitsianum*
542/57 *Davis* 26257. Turkey: Izmit; Gebze 18
X60 3012 *Stainton & Henderson*. Turkey: Gümüşane, Kelkit . 18
LE60 2938 Moscow Hort. Caucausus: Abchasia 18
X62 2316 *Dudley*, D. 34779. Turkey: Bursa 18
X62 3124 *Davis* 39373. Turkey: Kastamonu; Ilgaz Dağ . . 18
X62 3131 *Davis* 39380. Turkey: Zonguldak; Karadere . . 18
542/57 Davis 26239. Turkey: Istanbul; Heybeli Ada . . 18
X61/1252 *Curtis* 122. Turkey: Aktaş 18

M. armeniacum has been divided into two varieties, var. *szovitsianum* with purplish-blue flowers, and var. *armeniacum* with sky-blue flowers. The former is generally diploid, the latter generally tetraploid. Tetraploid plants frequently produce bulbils in large numbers, a character not seen in the diploid. Much cultivated material is tetraploid, but because of great variability in flower colour is often difficult to assign to either variety. In the wild the diploid is most common, the natural tetraploid only occupying the eastern edge of the species range.

M. aucheri
135/51 Hort. 36
303/51 Hort. 36
K60 3272 Kew 3948 Hort. 36
394/56 *Davis* 26135. Turkey: Adana; Bürücek to Pozanti . . 36
342/57 *Davis* 26291. Turkey: Maraş; Göksun to Çardak . . 18

M. bourgaei
360/56 *H. E. Moore* 7248. Turkey: Ulu Dağ 18

M. microstomum
X60 3016 *Stainton & Henderson* 5156. Turkey: Sivas; Pinarbaşi 18

M. botryoides
482/33 *Balls* 365. Hort. 36
X59 2454 Trieste Hort. 18

M. pallens
LE59 4225 *Artushenko* 13. Caucasus; Krasnodazsk . . . 18
LE60 2941 *Artushenko*. Caucasus: Gizeldron, above Ordzhonikidze 18
X59 3866. Georgia: Kasbek 18

M. inconstrictum
X58 2665 *O. Polunin* 5044. Iraq: Kurdistan; Sefin Dağ, Shaqlawa 18
X61 1836 *Agnew*. Iraq: S of Zakho 18
X61 1837 *Agnew*. Iraq: Dohuk 18

M. azureum
14/57 München Hort. 18
X60 662 Cluj Hort. 18

General discussion

All members of the genus *Muscari* examined in the present work, and also those given in the excellent list of Garbari (1968), have a basic number of 9. Published numbers for the related genus *Bellevalia* (Feinbrun 1938–40) indicate a basic number of 4. Two erstwhile species of *Muscari*, *M. paradoxum* and *M. pycnanthum*, gave counts of n = 4 and n = 4 and 8 respectively and their chromosome morphology is indistinguishable from other species of *Bellevalia*. This has confirmed that they are better placed in that genus, with which they agree in characters of the flower and seed, and where names already exist. Information about chromosome numbers in the genus *Hyacinthella* is scanty. Feinbrun (1961) reports one with n = 12 (*H. nervosa*) and two species with n = 9 (*H. heldreichii* and *H. lineata* var. *glabrescens*). These last two are on morphological grounds clearly species of *Hyacinthella*, not *Muscari*. Dr I. Robertson (private communication) has found two species with n = 8, so that three basic numbers are known in *Hyacinthella*.

The four groups which I propose should be ranked as subgenera show a number of karyotypic differences.

The subgenus *Muscari*, as Garbari (1968) has shown (although he treats it as genus *Muscarimia**), has large and isobrachial chromosomes all of a more or less similar size. No polyploidy has yet been found.

Subgenus *Leopoldia* has two pairs of large, strongly heterobrachial chromosomes (the A and B pairs), clearly differentiated from three pairs of medium-sized chromosomes (the C set), which may show slight differences. There remain four pairs of small chromosomes (the D set). This notation follows Delaunay (1926). Satellites may be found on either the short (*M.*

* Miller (1768), when creating the genus *Muscari*, refers to the illustration in Tournefort's *Inst. Rei Herb.* t. 180 (1719). This only shows the flowers, which seem almost certainly to belong to *M. moschatum*. A further discussion has been given by Turrill (1950).

comosum) or the long arm of the A pair (*M. weissii*, *M. tenuiflorum*, which also has a satellite on the short arm of one of the C set). *Polyploidy* is uncommon, being known only in *M. weissii* (2n = 18, 36) and *M. cycladicum* (2n = 54). Both are members of the yellow-toothed series of *Leopoldia* which includes *M. amoenocomum*, so far known only as a diploid. All the species are Aegean endemics (Cyclades & Crete).

In subgenus *Botryanthus* the differences between the A, B, C and D sets are less marked (as Garbari has pointed out). There are two exceptions. *M. latifolium* and *M. bourgaei* have karotypes similar to those of subgenus *Leopoldia*, but morphologically are clearly members of subgenus *Botryanthus*. Satellites are generally to be found on the short arm (*M. armeniacum*, *M. aucheri*, *M. commutatum*), or rarely on the long arm (*M. latifolium*) of the B pair. I have found polyploidy in eight of the species examined.

Subgenus *Pseudomuscari*, although less well known than the other subgenera, seems to be variable. *M. pallens* shows a considerable difference in size between the A/B and the C/D sets. *M. inconstrictum* and *M. azureum* show rather little. *M. pallens* has a satellite on the long arm of the A pair. *M. inconstrictum* has a satellite on the short arm of the B pair. Tetraploids have been reported for *M. pallens* and *M. parviflorum*.

There are, therefore, a number of karyological differences between the groups I am ranking as subgenera (as well as clear general morphological differences), but also a number of cases where the distinctions break down. On the other hand, *Muscari* sensu lato is strongly differentiated from *Bellevalia* by karyological as well as general morphological characters and from some species of *Hyacinthella* by chromosome number, and from all of them by general morphological characters. Thus it seems reasonable to keep *Muscari* as a rather broadly defined genus, and to rank the four major groups within it as subgenera.

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