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Leopoldia neumannii sp. nov. (Asparagaceae, Scilloideae): a new species of *Muscari* sensu lato from Greece

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Abstract: *Leopoldia neumannii*, a new species from Greece (regions of Ipeiros and Peloponnisos) is described and compared with other species of the genus. Aspects regarding the taxonomic classification of the *Leopoldia* group are discussed in light of an unresolved taxonomic situation within the *Muscari* sensu lato group.

Key words: Asparagaceae, Greece, *Leopoldia*, *Muscari*, new species, taxonomy

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Introduction

Muscari Mill. sensu lato (s.l.) is a genus of Asparagaceae (Scilloideae, Asparagales; APG IV 2016) with about 70 species distributed in Europe, the Mediterranean and W Asia (Garbari & Greuter 1970; Speta 1998; Govaerts 2016). While the centre of diversity is situated in Turkey with 36 documented *Muscari* s.l. species (Yıldırım 2016), ten *Muscari* sensu stricto (s.str.) and six *Leopoldia* Parl. species are recognized for Greece (Dimopoulos & al. 2013). During the last decades, several new species have been described (e.g. Ruiz Rejón & al. 1985; Eker & Koyuncu 2008; Jafari & Maassoumi 2011; Jafari 2012, 2015; Yıldırım 2016), while the taxonomic situation within *Muscari* s.l. is still enigmatic and of ongoing debate. Contrasting taxonomic concepts have been applied in recent publications (e.g. Dimopoulos & al. 2013; Jafari 2015; Yıldırım 2016). At present, the widely accepted classification of the Kew World Checklist (Govaerts 2016) splits *Muscari* s.l. into three genera (*Muscari*

s.str., *Leopoldia* and *Pseudomuscari* Garbari & Greuter), although the basis for this classification remains unclear.

During the last centuries, several taxonomic concepts of *Muscari* s.l. have been proposed (for reviews see Bentzer 1973; Speta 1982, 1998). One of the more recent proposals was made by Garbari & Greuter (1970), who divided the group into four genera. Those authors, as well as recognizing *Muscari* s.str., raised *M.* subg. *Leopoldia* (Parl.) Peterm. and *M.* subg. *Muscarimia* Kostel. ex Los. to generic rank and described *Pseudomuscari* as a new genus based on karyological evidence, although they included only a handful of species. In addition, morphological characters such as the prominent bluish to violet sterile flowers as well as the more or less zygomorphic fertile flowers with apophyses on the shoulders were used to separate *Leopoldia* from the other genera (Garbari & Greuter 1970). However, beside those results as a major argument for a multi-generic treatment, Garbari & Greuter (1970) argued that *Muscari* s.l. would be comparable to the Linnaean sense of the genus *Hyacinthus* L.,

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which is nowadays widely accepted as split into several genera (e.g. *Bellevallia* Lapeyr., *Brimeura* Salisb., *Hyacinthella* Schur, etc.).

In contrast, Speta (1982, 1989, 1998) and other authors (cf. Davis & Stuart 1980, 1984) favoured treating the group as a single genus (*Muscari* s.l.), accepting four subgenera: *M.* subg. *Muscari*, *M.* subg. *Leopoldia*, *M.* subg. *Moscharia* (Baker) Chouard (\equiv *M.* subg. *Muscarimia*) and *M.* subg. *Pseudomuscari* (Losinsk.) D. C. Stuart. Speta (1982, 1989) favoured the “one genus concept”, with a view on several morphological characters shared among all species, e.g. the degree of fusion of the tepals, the alternate arrangement of the anthers, a uniform placentation, as well as the occurrence of sterile flowers. Furthermore, Karlén (1984) found conflicting results in his work on the karyotypes of different *Muscari* species from Greece, compared to Garbari & Greuter (1970), which Speta (1989) interpreted as further evidence for his one genus concept. Some years earlier, Davis & Stuart (1980) stated in their *Flora europaea* treatment of *Muscari* that “the differences between the subgenera are considered to be of a lower order of importance than those that separate *Muscari* s.l. from *Bellevallia* and *Hyacinthella*”.

However, since the late 1980s no further taxonomic treatments of the genus have been proposed. Speta (1982) discussed the typification of the genus *Muscari* s.l. and also presented a typification of the four subgenera, but his concept was not applied by others, possibly because he published in German. While other genera, such as the closely related genus *Hyacinthoides* Heist. ex Fabr., have been solved based on molecular phylogenetic methods (e.g. Grundmann & al. 2010), only the systematic position of the genus *Muscari* within *Asparagaceae* has been assessed so far by a handful of weakly supported phylogenies (cf. Pfosser & Speta 1999; Pfosser & al. 2003).

Nevertheless, according to Govaerts (2016), 14 *Leopoldia* species are accepted, although at least seven more species currently treated in *Muscari* should be considered as belonging to *Leopoldia* (Böhnert unpubl.). Until a full taxonomic and systematic revision can be presented (ongoing own work), we apply the classification of *Asparagaceae* according to Govaerts (2016).

Material and methods

Assessment of the new species was made based on fresh and herbarium material taken from cultivated plants propagated vegetatively from plants collected by M. Neumann at the holotype locality in August 2003 (permit: 608/12.05.2003) and the paratype locality in November 2011. Line drawings were made following the digital drawing technique protocol by Coleman (2003). For scanning electron microscope (SEM) images, pollen material was mounted on aluminium stubs and sputter-coated with palladium (SCD 040, Balzers, Liechtenstein). Samples were observed in a Stereoscan 200 SEM

(Cambridge, U.K.). Plant material for comparative morphological analyses was taken from the living collection of Bonn Botanic Gardens between 2014 and 2016, as follows: *Leopoldia caucasica* (Griseb.) Losinsk. from Georgia (GE-0-BONN-22660), 13 May 2015, T. Böhnert 408 (BONN001671!); *L. comosa* (L.) Parl. from Greece (GR-0-BONN-20087), 24 Apr 2015, T. Böhnert 403 (BONN001672!); and *L. tenuiflora* (Tausch) Heldr. from Georgia (GE-0-BONN-32107), 22 May 2015, T. Böhnert 409 (BONN001673!). In addition, measurements from different Flora treatments (Chernyakovskaya & al. 1935; Bentzer 1973; Davis & Stuart 1980, 1984) were used to supplement our own measurements, shown in Table 1.

Results and Discussion

Leopoldia neumannii Böhnert & Lobin, **sp. nov.** – Fig. 1, 2.

Holotype: [originally collected from Greece, administrative region Ipeiros (Epirus), regional unit Ioannina, municipality Zagori, Monodendri, Vikos Gorge, steep cliff N of monastery of Agia Paraskevi, 39°53'N, 20°45'E, 1140 m, Aug 2003, M. Neumann]; cultivated at Bonn Botanic Gardens (GR-0-BONN-28534), 22 May 2015, T. Böhnert 389 (B; isotype: BONN001674).

Diagnosis — *Leopoldia neumannii* is distinguished from all other *Muscari* (s.l., including *Leopoldia*) species in its overall size of more than 50 cm tall. It differs from other *Leopoldia* species in its remarkably larger inflorescence as well as in its bulb size. It differs from *L. comosa* (the morphologically closest species) in having bulbs nearly twice as large and in forming many bulbils, whereas *L. comosa* never forms bulbils. In *L. neumannii* the hanging leaves are longer and the hooded apex is always wilted before reaching maturity, whereas in *L. comosa* the more erect leaves are shorter and usually do not wilt at the apex. In *L. neumannii* the fertile flowers are cylindric and cream-brown, whereas in *L. comosa* they are rather bell-shaped and comparatively darker brown on the perigon tube. In *L. neumannii* the pedicels are shorter and slightly hanging, forming a cylindric raceme, whereas in *L. comosa* the longer pedicels of the lower sterile flowers form a pseudo-umbellate termination of the raceme.

Description — *Herbs* geophytic. *Bulbs* ovoid to subglobose, 45–50 × 41–52 mm, always with many bulbils; *tunics* bright brownish cream. *Leaves* 5–7, hanging, flaccid, linear, attenuate, flat, not channelled, 30–62 cm × 9–17 mm, margin entire, apex with pointed hood (only visible on young leaves, leaf tips wilt before reaching maturity). *Scape* solitary, rounded in cross-section, 30–57 cm long (45–85 cm long including inflorescence), not distinctly elongating in fruit. *Raceme* consistently cylindric, 15–28 cm long; *axis* dark green at base, vio-

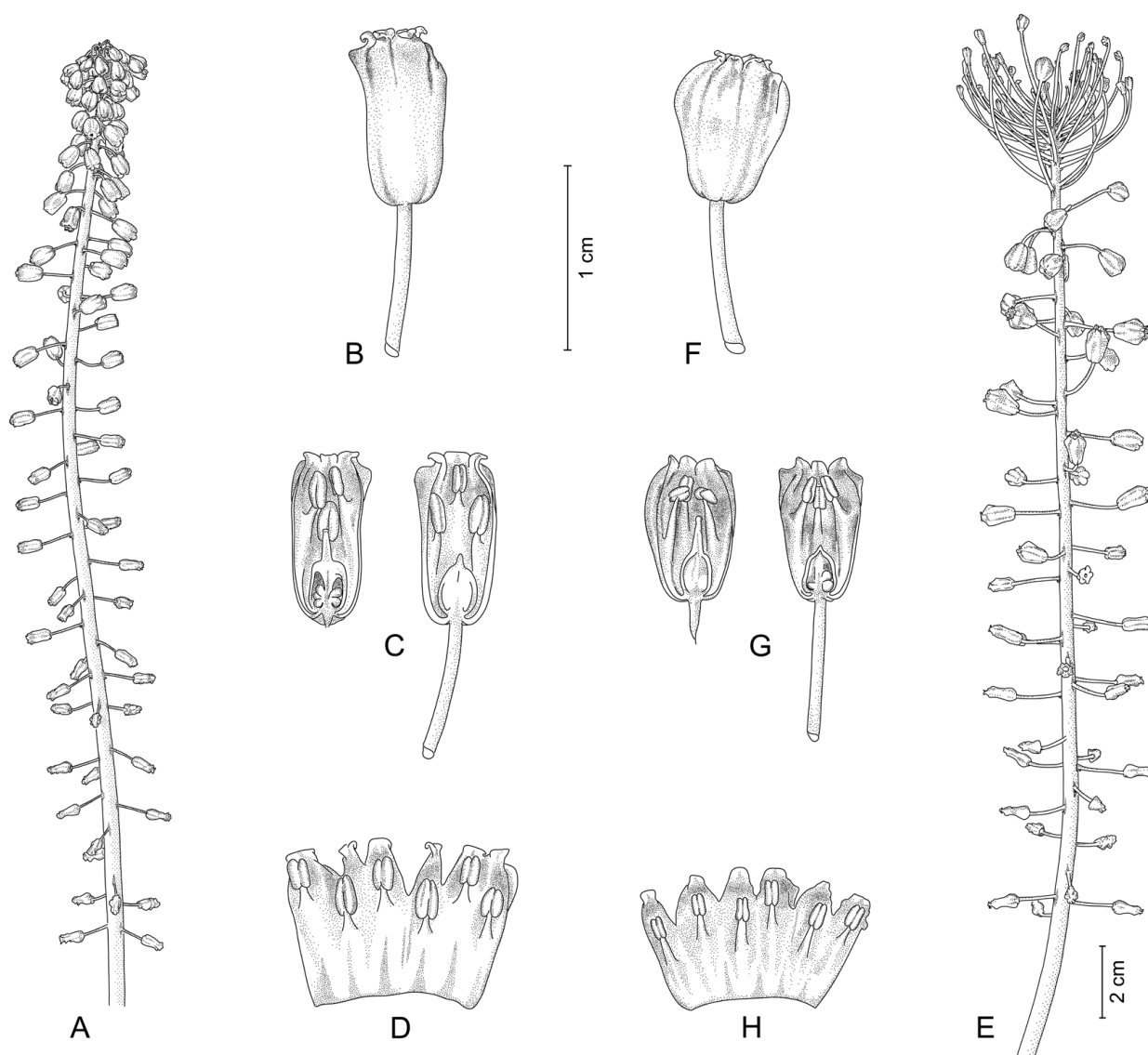


Fig. 1. Digital line drawings of *Leopoldia neumannii* (A–D) in comparison with *L. comosa* (E–H). – A, E: inflorescences; B, F: fertile flowers; C, G: fertile flowers, longitudinal sections; D, H: stamen positions within opened fertile flowers. – Scale bars: A, E = 2 cm; B–D, F–H = 1 cm. – Drawn by T. Böhnert: A–D from type material; E–H from cultivated material collected in Greece (GR-0-BONN-20087).

let at apex. *Fertile flowers* (40–)55–65; *bract* greenish white, minute, c. 1 mm long, membranous; *pedicel* patent at anthesis, (4–)7–9 mm long, not distinctly elongating in fruit; *perigon tube* tricolored, cream-green at base, creamish brown at shoulders, cylindric, (5–)7–9 × (3–)4–5 mm, with minute, bright yellow lobes; *stamens* alternate; *filaments* adnate along basal 1/3 of perigon tube, free portion of filaments 2–2.5 mm long; *ovary* c. 3 × 2–2.2 mm; *style* conic, c. 3 mm long. *Sterile flowers* (15–)25–30, slightly hanging, upper flowers strongly reduced; *bract* minute, longer than those of fertile flowers; *pedicel* bluish violet, 2–10 mm long, shorter at apex of raceme; *perigon tube* violet, cylindric in larger flowers, globose in smaller ones, 4–7 × 1–4 mm. *Fruit* a capsule, dehiscent by 3 valves. *Seeds* black, globose, 2–2.5 mm in diam., surface rugulose. *Pollen* 29–32 × 21–22 µm, monosulcate, sculpturing foveolate-reticulate.

Phenology — The new species flowers in May and fruits in June and July.

Distribution and ecology — *Leopoldia neumannii* is documented so far only from two localities, both in Greece: the Vikos Gorge in Ipeiros (the holotype locality) and Mt Lirkio in Peloponnisos (the paratype locality). The species occurs above 1000 m altitude at both localities. In the Vikos Gorge it grows on ledges of steep cliffs with small depressions forming pot-like structures where sediments and to a minor degree humus accumulate.

Conservation status — We categorize the new species as Data Deficient (DD) according to IUCN criteria (IUCN 2012). Further studies are needed for a more accurate classification.

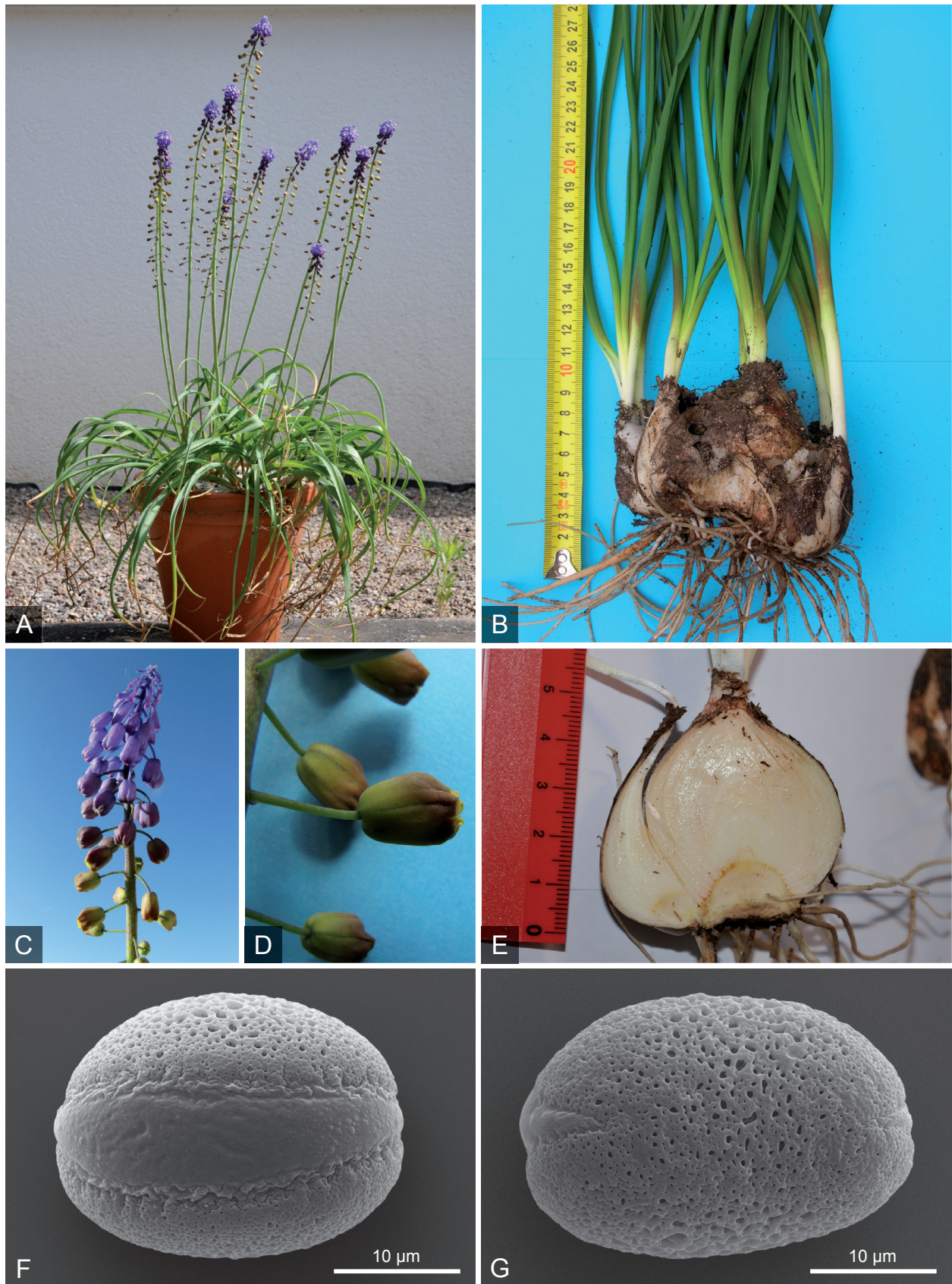


Fig. 2. Additional diagnostic characters of *Leopoldia neumannii*. – A: clump of individuals in cultivation; B: bulb with several bulbils; C: upper section of inflorescence with violet sterile flowers; D: close-up of fertile flowers; E: longitudinal section of mid-size bulb with bulbil; F, G: pollen grains. – Photographs: A, E by T. Böhnert; B–D by M. Neumann; F, G by J. Jeiter.

Table 1. Comparison between the diagnostic characters of *Leopoldia neumannii* and those of the morphologically related species *L. comosa* (GR-0-BONN-20087), *L. caucasica* (GE-0-BONN-22660) and *L. tenuiflora* (GE-0-BONN-32107). – Abbreviations: f.f. = fertile flowers; s.f. = sterile flowers.

Characters	<i>Leopoldia neumannii</i>	<i>Leopoldia comosa</i>	<i>Leopoldia caucasica</i>	<i>Leopoldia tenuiflora</i>
Bulb shape	ovoid to subglobose	globose-ovoid	pear-shaped	pear-shaped
Bulb size	45–50 × 41–52 mm	15–35 × 20–25 mm	20–25 × 15–20 mm	15–20 × 30(–40) mm
Number of bulbils	many	0 (or 1)	0	0
Number of leaves	5–7	3–5	2–4	3 or 4(–7)
Leaf size	30–62 cm × 9–17 mm	36–39 cm × (5–)8–15 mm	18–22 cm × 5–12 mm	15–19(–40) cm × (4–)7–8(–20) mm
Scape length	30–57 cm	(10–)20–50(–100) cm	18–20 cm	10–20(–60) cm
Raceme length	15–28 cm	(5–)10–15(–25) cm	7–10 cm	6–30 cm
Number of fertile flowers	(40–)55–65	(10–)25–50(–100)	(14–)20–40	30–60(–150)
Pedical length (f.f.)	(4–)7–9 mm	(4–)8–11(–20) mm	2–4 mm	1–10(–20) mm
Perigon tube colour (f.f.)	green-yellowish at base, creamish brown at shoulder, minute lobes yellow	green-yellowish at base, dark brown at shoulder, minute lobes white	cream-greenish, only shoulders reddish brown, lobes yellow	cream-white, minute lobes dark
Perigon tube shape (f.f.)	cylindric	bell-shaped	cylindric, shoulders sharply angled	cylindric
Number of sterile flowers	(15–)25–30	10–50	11–15	18–23
Arrangement of sterile flowers	slightly hanging	ascending, forming a pseudo-umbellate termination of raceme	ascending, forming a pseudo-umbellate termination of raceme, but smaller than in <i>Leopoldia comosa</i>	horizontal and slightly ascending
Pedical colour (s.f.)	bluish violet	bluish violet	dark bluish violet	blue to dark blue
Pedical length (s.f.)	2–10 mm	>30 mm on lower flowers, becoming shorter toward apex of raceme	1–2 mm	(2–)5–16 mm

Eponymy — *Leopoldia neumannii* is named in honour of its original collector, Michael Neumann, horticulturist responsible for the geophyte collection at the Bonn Botanic Gardens.

Remarks — Individuals of the new species cultivated outside of a pot can reach significantly larger bulb sizes, up to 70 × 75 mm, and single individuals with bulbs more than 100 mm in diameter have been observed. Larger bulb size appears always to be correlated with the formation of many bulbils.

Leopoldia neumannii differs in many characters compared to the morphologically closest species, *L. caucasica*, *L. comosa* and *L. tenuiflora*. Whereas bulbs of *L. neumannii* can reach sizes of nearly 50 mm long or more and produce many bulbils per growing season, the other species always have smaller bulbs and no or almost no bulbils. Furthermore, the scape is on average about twice as long as that of *L. comosa* and even longer compared with the other two species (although in some Greek populations of *L. comosa* plants with scapes up to 100 cm long have been documented; cf. Bentzer 1973). A common character in *Leopoldia* is the extended and ascending pedicels of the sterile flowers forming a pseudo-umbellate termination of the raceme, which is not the case in *L. neumannii* and only to a minor degree in *L. tenuiflora*. Differences between the four species were also found in pollen size. The pollen of *L. neumannii* appears >10 µm shorter compared to the measurements for *L. caucasica*, *L. comosa* and *L. tenuiflora* by Pehlivan & Özler (2003). However, only two pollen grains were measured for the new species, so this result might not be representative. Further morphological differences between *L. neumannii* and the morphologically related species are summarized in Table 1.

At the Vikos Gorge locality, plants of *Leopoldia comosa* have not been found on the cliffs, but occur on the ground in open forest at altitudes below 1000 m, where *L. neumannii* is always absent (M. Neumann pers. com.). An additional collection of *L. neumannii* from above 1000 m on Mt Lirkio in NE Peloponnisos (see below) indicates a wider distribution of the new species at a similar altitude to the Vikos Gorge locality. According to observations by the collector (M. Neumann pers. comm.), *L. neumannii* seems to replace *L. comosa* at altitudes above 1000 m, where the latter is always absent, indicating allopatric speciation. It can be assumed that, due to some superficial similarities between *L. comosa* and *L. neumannii*, the new species has been hitherto overlooked as distinct. Nevertheless, further field observations and herbarium studies are needed to understand the distribution patterns and conservation status as well as the systematic situation in this group and in *Muscari* s.l. in general.

Additional specimen seen (paratype) — [Originally collected from Greece, administrative region Peloponnisos, regional unit Arkardia, municipality Tripoli, municipal unit Mantinea, Mt Lirkio, above monastery of

Agios Nikolaos near Pikernis, 37°40'15"N, 22°24'36"E, 1130 m, Nov 2011, *M. Neumann*]; cultivated at Bonn Botanic Gardens (GR-0-BONN-39279), 22 May 2017, *T. Böhnert 461* (BONN).

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References

- APG IV 2016: An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. – Bot. J. Linn. Soc. **181**: 1–20.
- Bentzer B. 1973: Taxonomy, variation and evolution in representatives of *Leopoldia* Parl. (*Liliaceae*) in the southern and central Aegean. – Bot. Notiser **126**: 69–132.
- Chernyakovskaya F. G., Fedchenko B. A., Goncharov N. F., Gorshkova S. F., Grossgeim S. S., Ilin M. M., Knorring O. E., Komarov V. L., Krasheninnikov I. M., Krishtofovich A. N., Kuzeneva O. I., Lozina-Lozinskaya A. S., Nevskii S. A. and Vvedenskii A. I. 1935: Genus 281. *Leopoldia* Parl. – Pp. 314–316 in: Komarov V. L. (ed.), Flora of the U.S.S.R. **IV**. *Liliiflorae* and *Microspermae*. [Translated from Russian]. – Jerusalem: Israel Program for Scientific Translations.
- Coleman C. O. 2003: “Digital inking”: how to make perfect line drawings on computers. – Organisms Diversity Evol. **3**: 303–304.
- Davis P. H. & Stuart D. C. 1980: *Muscari* Mill. – Pp. 46–49 in: Tutin T. G., Heywood V. H., Burges N. A., Moore D. M., Valentine D. H., Walters S. M. & Webb D. A. (ed.), Flora europaea **5**. – Cambridge: Cambridge University Press.
- Davis P. H. & Stuart D. C. 1984: *Muscari* Mill. – Pp. 245–263 in: Davis P. H. (ed.), Flora of Turkey and the East Aegean Islands **8**. – Edinburgh: Edinburgh University Press.
- Dimopoulos P., Raus Th., Bergmeier E., Constantinidis Th., Iatrou G., Kokkini S., Strid A. & Tzanoudakis D. 2013: Vascular plants of Greece. An annotated checklist. – Athens: Hellenic Botanical Society; Berlin: Bo-

- tanic Garden and Botanical Museum, Berlin-Dahlem. – Englera **31**.
- Eker İ. & Koyuncu M. 2008: *Muscari babachii* sp. nov. (*Hyacinthaceae*) from south Anatolia. – Nordic J. Bot. **26**: 49–52.
- Garbari F. & Greuter W. 1970: On the taxonomy and typification of *Muscari* Miller (*Liliaceae*) and allied genera, and on the typification of generic names. – Taxon **19**: 329–335.
- Govaerts R. 2016: World checklist of *Asparagaceae*. Facilitated by the Royal Botanic Gardens, Kew. – Published at <http://apps.kew.org/wcsp/> [accessed 9 Aug 2016].
- Grundmann M., Rumsey F. J., Ansell S. W., Russell S. J., Darwin S. C., Vogel J. C., Spencer M., Squirrel J., Hollingsworth P. M., Ortiz S. & Schneider H. 2010: Phylogeny and taxonomy of the bluebell genus *Hyacinthoides*, *Asparagaceae* [*Hyacinthaceae*]. – Taxon **59**: 68–82.
- IUCN 2012: IUCN Red List categories and criteria: version 3.1, ed. 2. – Gland & Cambridge: IUCN. – Published at <http://www.iucnredlist.org/technical-documents/red-list-documents>
- Jafari A. 2012: A new species of *Leopoldia* (*Asparagaceae Scilloideae* formerly *Hyacinthaceae*) from Iran. – Feddes Repert. **123**: 291–294.
- Jafari A. 2015: A new species of *Leopoldia* (*Asparagaceae*) from Iran. – Phytotaxa **43**: 61–64.
- Jafari A. & Maassoumi A. A. 2011: Synopsis of *Leopoldia*, *Muscari* and *Pseudomuscari* (*Hyacinthaceae*) in Iran, with *Leopoldia ghouschtchiensis* sp. nova. – Ann. Bot. Fenn. **48**: 396–400.
- Karlén T. 1984: *Muscari pulchellum* (*Liliaceae*) and associated taxa in Greece and W Turkey. – Willdenowia **14**: 89–118.
- Pehlivan S. & Özler H. 2003: Pollen morphology of some species of *Muscari* Miller (*Liliaceae-Hyacinthaceae*) from Turkey. – Flora, Morphol. Distrib. Funct. Ecol. Pl. **198**: 200–210.
- Pfosser M. & Speta F. 1999: Phylogenetics of *Hyacinthaceae* based on plastid DNA sequences. – Ann. Missouri Bot. Gard. **86**: 852–875.
- Pfosser M., Wetschnig W., Ungar S. & Prenner G. 2003: Phylogenetic relationships among genera of *Massonieae* (*Hyacinthaceae*) inferred from plastid DNA and seed morphology. – J. Pl. Res. **116**: 115–132.
- Ruiz Rejón M., Pascual L., Ruiz Rejón C., Valdés B. & Oliver J. L. 1985: A new species of *Muscari* subgenus *Leopoldia* from the Iberian Peninsula. – Biochem. Syst. Ecol. **13**: 239–250.
- Speta F. 1982: Über die Abgrenzung und Gliederung der Gattung *Muscari*, und über ihre Beziehungen zu anderen Vertretern der *Hyacinthaceae*. – Bot. Jahrb. Syst. **103**: 247–291.
- Speta F. 1989: *Muscari* (subg. *Leopoldia*) *mirum* Speta, spec. nova, im Kreise seiner nächsten Verwandten. – Phytion (Horn) **29**: 105–117.
- Speta F. 1998: *Hyacinthaceae*. – Pp. 261–285 in: Kubitzki K. (ed.), The families and genera of vascular plants **III**. – Berlin, Heidelberg: Springer.
- Yıldırım H. 2016: *Muscari elmasii* sp. nova (*Asparagaceae*). A new species from western Anatolia, Turkey. – Turkish J. Bot. **40**: 380–387.

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