



Article

An Updated Taxonomic Appraisal of *Narcissus* (Amaryllidaceae) in the Maltese Islands

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Abstract: A previous study of *Narcissus* species on the Maltese Islands had suggested the existence of a natural hybridogenous species. A fresh study on *Narcissus* in Malta was conducted in 2021 and 2023 with the primary aim of studying the previously reported populations of intermediate forms and to update the taxonomy of *Narcissus* in Malta. Four main taxa of native species were identified: N. deficiens, two distinct morphotypes of N. tazetta, and a new hybrid species. The species identified as N. deficiens replaces records of N. serotinus and N. obsoletus. One of the two morphotypes ("autumn-flowering") is now combined as subsp. aequilimbus (previously described from Maltese material as *Hermione aequilimba*) and the other one ("spring-flowering") corresponds to subsp. tazetta. The new hybrid is derived from N. deficiens and N. tazetta and is named N. briffae. This hybrid was previously incorrectly reported as N. elegans. Detailed morphometric analysis and ecological data justify these new taxonomic appraisals. A dichotomous identification key for eight *Narcissus* taxa (including non-native ones) is provided to facilitate the identification of the occurring and doubtful species recorded on the Maltese Islands.

Keywords: *Narcissus deficiens; Narcissus tazetta; Narcissus aequilimba;* hybrid species; flora of Malta; Mediterranean region



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1. Introduction

Narcissus is a monocot genus that has weak interspecific hybridisation barriers, and that consequently has numerous hybrids described [1], including several natural ones [2]. A few examples described from the Mediterranean region in the last 20 years, mainly by Spanish authors, include $N. \times$ *alleniae* Donnison-Morgan [3], $N. \times$ *perangustus* Fern.Casas [4], $N. \times$ *alentejanus* Fern.Casas and $N. \times$ *perezlarae* Font Quer [5], $N. \times$ *egabrensis* J.López-Tirado, $N. \times$ *repulloi* J.López-Tirado and $N. \times$ *trianoi* J.López-Tirado [6], and $N. \times$ *hispalensis* J.López-Tirado [7], amongst others. A comprehensive list of *Narcissus* hybrids can be found in [2].

The insularity and small size of the Maltese archipelago, its comparatively rich flora of some 800 native species and the high density of pollinators make these islands an ideal geographic niche for processes of plant hybridisation. In the last decade, several hybridogenous species have been reported from Malta, including *Ophrys melitensis* \times *tenthredinifera* [8], *Romulea columnae* \times *variicolor* [9], *Allium commutatum* \times *polyanthum* [10], and *Bolboschoenus glaucus* \times *maritimus* [11]. A natural hybridogenous species of *Narcissus* from the Maltese Islands was already anticipated in a preliminary study of the *Narcissus* [12], where two main taxa with various stages of intermediate morphotypes were identified, leading the authors to postulate a range of morphological transitions from *N. serotinus* L. at one end of the spectrum flowering in October and *N. tazetta* L. at the other end reaching its flowering peak in February–March. Within this range of morphotypes, a distinct wild daffodil has been identified and, according to the available keys used for that study [13,14], this daffodil species morphologically matched best with *N. elegans* Spach, owing to its narrow caniculate

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leaves formed during anthesis, scapes with 3–6 flowers, and tufted habitat. Introgression and hybridisation might be the explanation for these plants, as their morphology seems to be intermediate between the putative parent species [12]. No formal description of a new hybrid or declaration of an already described hybrid was reported [12].

A study on *Narcissus* occurring in the Maltese Islands is much needed, primarily to investigate those intermediate morphotypes [12], for possible undescribed hybrids, and to update the taxonomy of *Narcissus* spp. This is necessary since various works on Mediterranean *Narcissus* during recent years [3,5,15–18] have presented new concepts and drastic changes in the taxonomy and species delimitation of several wild daffodils in the region.

2. Materials and Method

A total of 29 populations were studied, each representing a different sample collection at least 50 m apart. These were labelled and were labelled NRC01 to NRC29 (Table 1). For each population, at least 15 individuals were examined. Selected samples were either a number of individuals scattered within a population, as in "N. serotinus", or individuals within a tuft or cluster of plants for species such N. tazetta s.l. In any case, at least fifteen scapes were examined per population, either as individuals, or from a single tuft, or, in widespread populations, three scapes from at least five different tufts.

Morphological characters selected to compare and demarcate species were those traditionally used by various authors to discriminate between *Narcissus* species [2,13–15,19], as shown in Table 2. Character states were recorded between October 2021 and December 2023 for known populations of "*N. serotinus*", "*N. elegans*", *N. tazetta* s.l., and assumed intermediates, some of which were reported in [12]. Species demarcation was, however, measured with a new approach based on recent studies and knowledge, as discussed below.

Bulbs were not examined in order not to harm the plants and because they are not particularly diagnostic except in N. gr. bulbocodium. Whole plants were only collected for typification and subsequently deposited in an herbarium. Photographs were taken both in situ and on dissected flower parts in the laboratory. When necessary, these structures (e.g., small coronae, anthers) were observed through a stereomicroscope equipped with a calibrated micrometer (SM-4TZ-144A, AmScope, Irvine, CA, USA). Palynological analysis was carried out on fresh material as it may provide new data for the genus and give an important indication of sterility (hybridisation). Pollen from different anthers of the same flower was admixed on a droplet of 1% cotton blue solution (to increase contrast) on a microscope slide, covered with a 32×22 mm coverslip and pressed gently with the thumb. The slide was mounted and observed using a compound microscope (Axiolab 5, Carl-Zeiss, Oberkochen, Germany), and pollen viability, shape, and size were determined.

A leaf sample was taken and dried in silica gel at 30 °C for possible cytological or molecular investigations. The habitat and dominant vegetation present near the studied populations were also recorded.

Numerical data, namely, measurements or flower counts, were presented in a very simplified format of \overline{x} (minimum–maximum), hence the average followed by the range. Extreme or exceptional measurements are further indicated in parenthesis prior to or behind the minimum or maximum value.

A more meticulous analysis using more material was carried out on intermediate/introgressed morphotypes that did not match described species, and that therefore represent potential new hybrids or taxa. Further remarks on how some specific character states were observed, measured, obtained, or reported are given below.

Habitat: a general label the dominant vegetation structure and landscape in the vicinity of the studied plants.

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Table 1. Locations of examined populations, including altitude, coordinates and attributed morphotype code.

Sample Code	Examination Date	Island	Locality	Toponym (Valley Name)	Altitude (m)	Geographic Coordinates	Morphotype
NRC01	29 October 2022	Gozo	Qala	Ħondoq ir-Rummien			Narc-A
NRC02	29 October 2022	Gozo	Qala	Hondoq ir-Rummien	-		Narc-A
NRC03	29 October 2022	Gozo	Qala	Hondoq ir-Rummien	-		Narc-A
NRC04	29 October 2022	Gozo	Qala	Hondoq ir-Rummien	45–55	36°1′45.50″–47.88″ N 14°19′12.04″–13.70″ E	Narc-A
NRC05	29 October 2022	Gozo	Qala	Ħondoq ir-Rummien	-		Narc-A
NRC06	29 October 2022	Gozo	Qala	Hondoq ir-Rummien			Narc-B
NRC07	29 October 2022	Gozo	Qala	Hondoq ir-Rummien	-		Narc-B
NRC08	4 November 2022	Malta	Dingli	Dingli Cliffs (Radar station)	240	35°51′9.36″ N 14°23′5.75″ E	Narc-A
NRC09	4 November 2022	Malta	Mellieħa	Qortin tal-Mistra	35	35°57′16.76″ N 14°23′21.31″ E	Narc-A
NRC10	5 November 2022	Gozo	Qala	Ħondoq ir-Rummien	70	36°1′55.10″ N 14°19′39.08″ E	Narc-A
NRC11	12 November 2022	Gozo	Sannat	Ta' Ċenċ	135	36°1′18.87″ N 14°15′16.99″ E	Narc-A
NRC12	12 November 2022	Gozo	Munxar	Il-Fekruna	60	36°1′57.64″ N 14°13′45.18″ E	Narc-B
NRC13	12 November 2022	Gozo	Xagħra	Tal-Pergla	80	36°4′1.55″ N 14°16′12.76″ E	Narc-A
NRC14	14 November 2022	Gozo	Sannat	Ta' Ċenċ (il-gruwa)	75	36°1′14.77″ N 14°15′43.50″ E	Narc-C1
NRC15	15 November 2022	Malta	Mellieħa	Selmun area	25	35°57′49.33″ N 14°23′51.66″ E	Narc-B
NRC16	16 November 2022	Gozo	Sannat	Wied Mġarr ix-Xini	FO FF	36°1′28.24–28.41″ N	Narc-C1
NRC17	16 November 2022	Gozo	Sannat	Wied Mġarr ix-Xini	- 50–55	14°15′45.43–45.95″ E	Narc-C1
NRC18	16 November 2022	Malta	Mellieħa	Selmun area	40	35°57′33.50″ N 14°23′43.16″ E	Narc-B
NRC19	25 November 2022	Gozo	Munxar	Wied il-Munxar			Narc-C1
NRC20	25 November 2022	Gozo	Munxar	Wied il-Munxar	40-60	36°1′52.20–52.84″ N 14°13′56.46–57.49″ E	
NRC21	25 November 2022	Gozo	Munxar	Wied il-Munxar	-	11 13 30.10 37.17 E	Narc-C1
NRC22	11 January 2023	Malta	Siġġiewi	Verdala	220	35°51′38.48″ N 14°23′54.45″ E	Narc-C2
NRC23	4 February 2023	Malta	Mellieħa	Selmun-Mistra area	30	35°57′41.89″ N 14°23′38.26″ E	Narc-C2
NRC24	5 February 2023	Gozo	Qala	Tal-Muxi area	100	36°2′20.69″ N 14°19′31.68″ E	Narc-C2
NRC25	18 February 2023	Malta	Dingli	Tar-Rehba area	230	35°51′23.48″ N 14°23′3.20″ E	Narc-C2
NRC26	28 February 2023	Gozo	Rabat	Gelmus Hill	80	36°2′50.13″ N 14°14′7.40″ E	Narc-C2
NRC27	12 December 2023	Malta	Mellieħa	Selmun-Mistra area	40	35°57′39.70″ N 14°23′38.37″ E	Narc-B
NRC28	29 December 2023	Malta	Żurrieq	Wied Babu	60	35°49′23.56″ N 14°27′33.47″ E	Narc-C1
NRC29	29 December 2023	Malta	Mosta	Wied il-Għasel	40	35°55′5.87″ N 14°25′38.37″ E	Narc-C1

Flowering period: Month, and period within month, subdivided into three month-periods as "beg." (1–10 days), "mid." (11–20 days), and "end" (21–30/31 days) of the month. Flowering dates recorded during autumn 2023 were later than expected as the first consistent rains of that season started approximately 6–8 weeks later than the climatic norm.

Plant (scape) height: Length from the ground to the tip of the scape below the pedicels. The inflorescence not included due to variable orientation affecting the observed height.

Habit: plants growing as isolated individuals, in small open clumps, in dense tufts, etc. Leaf formation at anthesis: presence of leaves when mature flowers are present and an approximate ratio of leaf length to scape length.

Width: Maximum width (usually at the lower third of the leaf length), given as a range and average if more than one leaf was present. Length is not diagnostic and was not taken into account; however, its proportion with the length of the flowering scape was recorded.

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Table 2. Comparison of examined characters of *Narcissus* morphotypes occurring in the Maltese Islands.

Character	Narc-A	Narc-B	Narc-C1	Narc-C2
Habitat	Exposed rocky ground, steppe, low garigue	Steppe, low garigue, rocky valley banks	Rocky ground at valley sides or escarpments, especially rocky banks and ledges	Abandoned clayey fields or clay slopes, gardens, derelict agricultural areas
Habit	Solitary, rarely in small gregarious groups	Dense tufts of (10–)25–50(–70) plants closely packed to each other	Singular or isolated small groups of 4–10 plants, often close to each other and merging to form larger clusters of plants.	Dense tufts of (10–)25–50(–80) plants are closely packed to each other. Very rarely seen as singular individuals.
Flowering time	Autumnal (September– November)	Autumnal (October–November) but later from Narc-A	Autumnal (November–December) much earlier from Narc-C2	January–March
Plant length	15 (10–30) cm	25 (22–35) cm	40 (20–70) cm	50 (30–120) cm
Presence of leaves with flowers	Absent	Present, about half the length of the scape	Present, reaching the same length of the scape	Present, reaching the same length of the scape
Leaves per plant	1–2	1(-2)	3–4	(3–)4
Basal sheath	Indistinct	Pale green with longitudinal parallel bright green veins.	Pale green with longitudinal parallel bright green veins.	Pale green with longitudinal parallel bright green veins.
Basal sheath length	N/a	5–12 mm long, 1 layer exposed above ground level	15–35 mm or even up to 100 cm in shaded locations, 3–4 layers exposed above ground level	10–30 mm 2–3(–4) layers exposed above ground level
Leaf length	5–18 cm	15–28 cm	20–40 cm, subequal to the scapes. Can get longer when plants are growing within bushes due to etiolation	30–40 cm, shorter than the scapes
Leaf width	1 mm	2–5 mm	7–14(–19) mm	10–25 mm
Leaf cross-section	Terete	Crescent with rounded ends, fleshy	Canaliculate to flattened V-shaped, thin and not fleshy	Canaliculate to flattened V-shaped, thin and not fleshy
Flowers per scape	1-2(-4)	(2-)3-5(-6)	(3-)4-7(-8)	(4-)6-10(-12)
Length of longest pedicels	Up to 15 mm	Up to 42 mm	Up to 68 mm	Up to 58 mm
Length of perianth tube	14 (12–17)	15 (14–16)	16–24 mm	17–19 mm
Flower diameter	17–35 mm	22–35 mm	18–30 mm	24–36 mm
Tepal colour	Pure white	Whitish-cream	Whitish-cream	Whitish-cream
Length lower tepals	12.5 (8.0–16.0) mm	10.5 (9.5–12.5) mm	13.4 (11.5–15.0) mm	16.0 (14.0–17.5) mm
Width lower tepals	5.0 (4.0–6.5) mm	5.5 (5.0–6.5) mm	10 (8.5–11.0) mm	11.5 (9.5–13.5) mm
Length upper tepals	11.0 (7.0–13.5) mm	9.5 (8.5–11.0) mm	Subequal to lower tepals	Subequal to lower tepals
Width upper tepals	4.0 (3.0–5.0) mm	5.0 (4.5–6.5) mm	Subequal to lower tepals	Subequal to lower tepals

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Table 2. Cont.

Character	Narc-A	Narc-B	Narc-C1	Narc-C2
Tepal imbrication	Usually free, but sometimes marginally imbricated at the base	Free to slightly imbricated from the basal third, then free	Imbricated from the basal half, free above	Imbricated from the basal half, free above
Diameter of corona	2.2 (1.8–3.0)	5.0 (3.5–6.5)	9.0 (7.0–11.5) mm	11.0 (9.0–13.5)
Height of corona 1.5 (0.8–2.2)		2.0 (1.6–2.5)	5.0 (3.7–7.0) mm	6.0 (5.0–7.5)
Corona colour	Greenish yellow to yellow and golden yellow sometimes deeper hues to amber (but not orange or reddish)	Golden yellow	Bright lemon-yellow	Bright lemon-yellow
Corona outline shape	Subdeltate, trigonous, or rarely almost circular	Circular to subtrigonous, rarely triangular-like	Circular occasionally trigonous or with three shallow lobes (esp. in examples with shallow coronae)	Circular or subcircular, seldom showing any signs of trigonometry
Corona margin	Subentire to crenated, occasionally shallowly lobed	Entire with three equidistant pleats	Subentire, crenated or rarely 3-lobed	Subentire
Corona lateral profile	Parallel sides (cup-shaped) sometimes slightly converging at the upper part (urn-shaped)	Parallel or more frequently divergent from the base (bowl-shaped)	Parallel or divergent from the base, comparatively deep (bowl-shaped) or shallow (saucer-shaped)	Mostly parallel or slightly divergent and deep.
Corona wall	Variable, notched, clefted or deeply incised to the bottom from (1–)3 equidistant locations forming 3 distinct flaps	Usually pinched (pleated) at the top from 3 locations, or rarely with 1(–3) clefts or full incisions.	Mostly entire but sometimes with 1–3 pleats at the top, rarely with 1(–2) clefts or partial incisions	Entire, sometimes with 1–3 pleats or a pinched area at the top
Tepal length/corona diameter ratio	5–6	2–2.5	≈1.3	≈1.4
Viable seeds	Yes	No or very few	Yes	Yes
Viability pollen	Yes (≈95% viable)	≈10% viable	Yes (≈92% viable)	Yes (≈80% viable)
Pollen shape Broadly ellipsoid with one compressed side		Dimorphic, broadly ellipsoid and sub-spherical	Broadly ellipsoid with one compressed side	Broadly ellipsoid with one compressed side
Average pollen size	42.5 × 32.0	Broadly elliptic pollen $38.0 \times 29.5 \ \mu m$; Subspherical pollen ca. $52.0 \times 45.5 \ \mu m$	40.2 × 31.1	47.7 × 35.6
Lipid texture on pollen testa	Scanty, small, about 3–5 µm wide	Prominent, sometimes as large semispherical warts, up to 5.9 μm wide	Prominent, numerous sometimes as large semispherical warts, up to 7.2 μm wide	Prominent, sometimes as large semispherical warts, up to 6.7 μm wide

Leaf cross-section: the mature leaf (when present) was dissected along its midpoint, and its cross-section was observed.

Cross-section of scape: observed at the upper half of the scape.

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Pedicel length: Length from its attachment with the scape (base of pedicel) up to the base of the flower (apex of pedicel). The pedicels elongate with age, and hence this character has limited diagnostic value.

Flower tube: Length from the top of the ovary to its base or insertion of the lower whorl of tepals. The ovary is distinct by always being darker than the perianth tube. The shape (lateral view) of the tube was also observed, especially where it widens, and whether it was gently tapering or widening abruptly,

Tepal size: Maximum length and width of the upper and lower whorl was measured. For scapes with three or more flowers, an average was taken on three flowers per scape. The mucro was not included in the length of the tepals.

Corona colour: greenish-yellow, bright yellow (lemon-like), golden yellow, amber (orange hue).

Corona general shape: a lateral view of the corona was observed to assess which of the following shapes it possessed: parallel sides (cup-shaped), divergent sides from the base (bowl-shaped), convex sides (urn-shaped), or very shallow and divergent sides (saucer-shaped).

Corona outline shape: Observation of the outline shape observed from the frontal (top) view. Details of the margin (entire, subentire, crenulate, crenate, and lobed) were also observed. If lobed or somewhat discontinuous, a further detailed description is provided as indicated below.

Corona wall: examination of incisions or lobes in the corona wall and rim was carried out, generally using the following categories: pleated or pinched (irregular projection), notched (minute cut), cleft (and the degree of split down the corona wall), or completely incised to the base, hence forming a free segment or lobe

Corona size: given as the diameter of the longest width, either if this is the rim in divergent coronas or the walls in urn-shaped forms, followed by the height from the rim to the basal attachment with the underlying tepal.

Fruit 'sterility': Indicated by the presence of fruit and the presence of fertile (hard) seeds within the fruit. Failure of seed production in at least 80% of the sample size (15 plants) was considered a sign of "sterility". This threshold was established arbitrarily but was deliberately high so as to account for the relatively small (in statistical terms) sample size.

The following palynological characters were studied:

Pollen viability: Pollen was viewed at a magnification of $\times 100$, and its viability estimated by a simple proportion of viable turgid grains and non-viable ones. Shrunken, deformed, or empty pollen grains were assumed to be dysfunctional and inviable. This assumption was based on the authors' past experience and was considered reasonable. This was repeated for five individual plants within a population to confirm viability, hence ensuring that sterility was not due to a localised disorder of a single aberrant plant. An approximate percentage of viable pollen was then estimated.

Pollen shape: Only the general shape of the pollen grains was described. It was beyond the scope of this study to give a rigorous description of pollen morphology.

Pollen size: The mean size and range of the pollen grains was given after measuring the longest width and breadth of 30 pollen grains using a calibrated ocular micrometer and using Pixemetre V5.10 to extrapolate the statistical measurements. The ratio of the length to the width is denoted as the $\bf Q$ ratio.

Morphological analysis: Morphological traits of the *Narcissus* specimens were analysed to determine variations among four morphs: NRC-A, NRC-B, NRC-C1, and NRC-C2. Non-metric multidimensional scaling (nMDS) was performed using Euclidean distance to visualise morphological differentiation. Missing values in the dataset were imputed with the mean of the corresponding trait. The nMDS plots were generated using the seaborn and matplotlib libraries in Python 3.11.8.

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3. Results

The morphological results in this study are consistent with those reported in an earlier study [12] but are interpreted using a recently updated taxonomic approach (see Introduction). After examining all populations and samples, three distinct morphotypes were recognised, here referred to as Narc-A, Narc-B, and Narc-C. The latter was further and marginally demarcated into two slightly different entities, primarily based on differences in their phenology, habit, habitat, and some morphological traits. These were labelled as Narc-C1 and Narc-C2. The morphological features of these *Narcissus* morphotypes are provided in a detailed account below, tabulated and compared in Tables 2 and 3, illustrated in Figures 1–5, while their taxonomic interpretation is analysed below.

Table 3. Comparison of selected characters between $N. \times briffae$ and its parents N. deficiens and N. tazetta indicating which characters of the hybrid have an affinity to either parent (yellow for N. deficiens and blue for N. tazetta), which are intermediate (green), and which are unique (grey) due to its hybridogenous nature (e.g., sterility).

Character	N. deficiens	N. imes briffae	N. tazetta (subsp. aequilimbus)	Character Affinity
Habitat	Exposed rocky ground, steppe, low garigue	Steppe, low garigue, rocky valley banks	Rocky ground at valley sides or escarpments, especially rocky banks and ledges	Closer to N. deficiens
Habit	Solitary, rarely in small gregarious groups	Dense tufts of (10–)25–50(–70) plants closely packed to each other	Singular or isolated small groups of 4–10 plants, often close to each other and merging to form larger clusters of plants	N. tazetta
Flowering time	Autumnal (September–November)	Autumnal (October–November)	Autumnal (November–December)	Intermediate
Average plant length	15 cm	25 cm	40 cm	Intermediate
Presence of leaves with flowers	Absent	Present, about half length of the scape	Present, reaching same length of the scape	N. tazetta
No. of leaves/plant	1–2	1(-2)	3–4	N. deficiens
Basal sheath	Indistinct or very short (above ground level)	Pale green with longitudinal parallel bright green veins.	Pale green with longitudinal parallel bright green veins.	N. tazetta
Basal sheath length	Nil—2 mm	5–12 mm long, 1 layer exposed above ground level	15–35 mm or even up to 100 cm in shaded locations, 3(–4) layers exposed above ground level	N. tazetta (reduced)
Leaf length	5–18 cm	15–28 cm	20–40 cm (can get longer when plants are growing within bushes due to etiolation)	Intermediate
Leaf width	1 mm	2–5 mm	7–19 mm	Intermediate
Leaf cross-section	Terete	Crescent with rounded ends, fleshy	Canaliculate to flattened V-shaped, thin and not fleshy	Considered as an Intermediate form between terete and flattened V-shaped
No of flowers/scape	1-2(-4)	2–5(–6)	(3-)4-7(-8)	Intermediate or reduced <i>N. tazetta</i>
Length of longest pedicels	Up to 15 mm	Up to 42 mm	Up to 68 mm	Intermediate
Tepal imbrication	Sometimes, usually free tepals	Imbricated from the basal third, then free	Imbricated from the basal half, isolated above	N. tazetta
Diameter of corona	2.2 (1.8–3.0)	5.0 (3.5–6.5)	9.0 (7.0–11.5) mm	Intermediate
Height of corona	1.5 (0.8–2.2)	2.0 (1.6–2.5)	5.0 (3.7–7.0) mm	N. deficiens
Corona outline shape	Subdeltate, trigonous, or rarely almost circular	Circular to subtrigonous, rarely triangular-like	Circular occasionally trigonous or with three shallow lobes (esp. in examples with shallow coronae)	Intermediate or both parents

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Table 3. Cont.

Character N. deficiens		N. imes briffae	N. tazetta (subsp. aequilimbus)	Character Affinity
Corona lateral profile	Parallel sides (cup-shaped), sometimes slightly converging at the upper part (urn-shaped)	Parallel or more frequently divergent from the base (bowl-shaped)	Parallel or divergent from the base, comparatively deep (bowl-shaped) or shallow (saucer-shaped)	Both parents
Corona wall	Variable, notched, cleft or deeply incised to the bottom from (1–)3 equidistant locations forming 3 distinct flaps	Usually pinched (pleated) at the top from 3 locations, or rarely with 1(–3) clefts or full incisions.	Mostly entire but sometimes with 1–3 pleats at the top, rarely with 1(–2) clefts or partial incisions	Somewhat intermediate (pleats can be assigned as halfway between incised and entire
Tepal length/corona diameter	5–6	2–2.5	≈1.4	Intermediate
Viable seeds	Yes	No or negligible	Yes	Hybrid character
Pollen abundance on the anthers	Copious	Scanty	Copious	Hybrid character
Pollen viability	Yes (≈95% viable)	≈10% viable	Yes (≈90% viable)	Hybrid character
Pollen shape	Broadly ellipsoid with one compressed side	Dimorphic, broadly ellipsoid and sub-spherical	Broadly ellipsoid with one compressed side	Unique character possibly due to pollen dysfunction/sterility
Average pollen size	42.5 × 32.0	Broadly elliptic pollen 38.0 \times 29.5 μ m; Subspherical pollen ca. 52.0 \times 45.5 μ m	40.2 × 31.1	Both parents
Warts on pollen testa	Scanty, small, about 3–5 μm wide	Prominent, sometimes hemispherical up to 5.9 µm wide	Prominent, numerous hemispherical and large, up to 7.2 μm wide	N. tazetta

3.1. Morphotype Narc-A (Figure 1)

This is an early-flowering *Narcissus*, traditionally referred to as *N. serotinus*, which flowers soon after the first substantial autumn rains, typically blooming as early as late September but also as late as the start of December (as was the case in autumn 2023, when the first substantial precipitation took place at the end of November 2023). These are small plants with one to (rarely) few flowers, with the leaves appearing almost always after anthesis and fruiting.

Material examined: NRC01-NRC05, NRC10: Hondoq ir-Rummien (Qala, Gozo), 29 October 2022, 5 November 2022; NRC08: Dingli Cliffs, (Dingli, Malta), 4 November 2022; NRC09: Qortin tal-Mistra, (Mellieħa, Malta), 4 November 2022; NRC11: Ta' Ċenċ, (Sannat, Gozo), 12 November 2022; NRC12: il-Fekruna area (Munxar, Gozo), 12 November 2022; NRC13: il-Pergla (Xaghra, Gozo) 12 November 2023; these samples shared the same habitat, which were low garigues or steppes on coralline limestone bedrock and with (at the time of anthesis) few potential competitors.

Typical accompanying vegetation include the following species: *Allium polyanthum* Schult. and Schult.f., *Arisarum vulgare* O.Targ.Tozz., *Asphodelus ramosus* L., *Brachypodium hybridum* Catalán, Joch.Müll., Hasterok and G.Jenkins, *Bromus fasciculatus* C.Presl, *Bromus madritensis* L., *Chiliadenus bocconei* Brullo, *Erica multiflora* L., *Ferula melitensis* Brullo, C.Brullo, Cambria, Giusso, Salmeri and Bacch., *Galactites tomentosus* Moench., *Hyparrhenia hirta* (L.) Stapf., *Leontodon autumnalis* L. (*Scorzoneroides autumnalis* (L.) Moench), *Muscari parviflorum* Desf., *Plantago lagopus* L., *Prospero* cf. *autumnale* (L.) Speta, *Ranunculus bullatus* L., and *Drimia pancration* (Steinh.) J.C. Manning and Goldblatt.

Description: **Habit**, solitary, sometimes in pairs, rarely more. **Leaves**, absent during anthesis, formed after fruiting, linear, erect and ached, up to 10 cm long. **Scape**, terete, 14 ((5–20)(–30)) cm long (flower excluded), 1.0–2.0 mm diameter. **Basal sheath** indistinct, when occasionally emerging above ground, not more than 3 mm high, hyaline with very faint veins. **Bract**, membranous, frail, lanceolate, beige, 22 ((18–25(–34)) \times 6 (5–7) mm. **Flowers** 1, occasionally 2–3 (Figure 1b), very rarely more, 17–35 mm in diameter (remarkably variable in size, Figure 1a), pure white, with a very light flushing of pale green or yellow adjacent to the corona, delicately fragrant. **Pedicel(s)**, 5–15 mm long. **Perianth tube**, 14 (12–17) mm

long, tubular with a linear outline, gently diverging below the corolla, yellowish green (Figure 1c). **Tepals**, free or less often touching to slightly imbricated at the basal region; **lower tepals**, $12.5 (8.0-16.0(-19.0)) \times 5.0 (4.0-6.5(-8.0))$ mm, tip cuspidate (0.5-2.0 mm long); **upper tepals**, $11.0 (7.0-13.5(-18.0) \times 4.0 (3.0-5.0(-6.5))$ mm, tip acute to blunt, rarely shortly mucronate. **Corona**, (Figure 1d,e) $2.2 (1.8-3.0) \times 1.5 (0.8-2.2)$ mm, bright yellow to greenish yellow, mostly subtrigonous to subcircular, vertically incised to the base or partly so at three equidistant locations (occasionally with only one or two incisions), incisions either reaching the base forming three separated flaps, partially incised halfway the corona or only clefted (notched) minutely at the top, yet forming three distinct flaps or lobes; edge irregularly subentire, shallowly crenulate or notched, sometimes bifid giving the allusion of six lobes. **Anthers**, of upper stamens pale yellow 1.0 (0.8-1.2) mm long; those of lower stamens 1.4 (1.2-1.7) mm long and covered with more pollen but not abundantly so. **Fruit**, a cylindrical, broadly rugose capsule opening from the apex into three valves, 8-22 mm long. **Seeds**, numerous, black, polished, pip-shaped with irregular edges, 1-2 mm long.

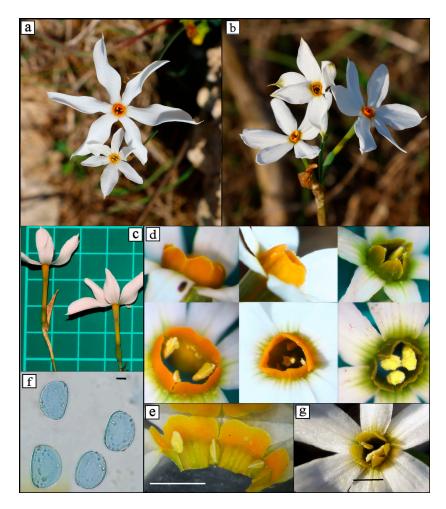


Figure 1. *Narcissus deficiens* Herb. from the Maltese Islands: (a) flowers from two individuals, very variable in size, generally 1–2 per scape; (b) rare occasions of 3-flowered example; (c) linear floral tube that expands slightly below the tepals (grid = 1×1 cm; (d,e) variation of the corona—yellowish green to golden yellow to amber; terete to trigonous outline with subentire to fully incised wall forming three segments, each being emarginate, notched to clefted (scale bar 1 mm); (f) pollen grains at $\times 100$ magnification (scale bar = $10 \mu m$) with an average size of $43 \times 32 \mu m$ (stained in cotton blue); (g) corona with a circular outline and six fully incised, free segments characteristic of *N. serotinus* (scale bar 2 mm).

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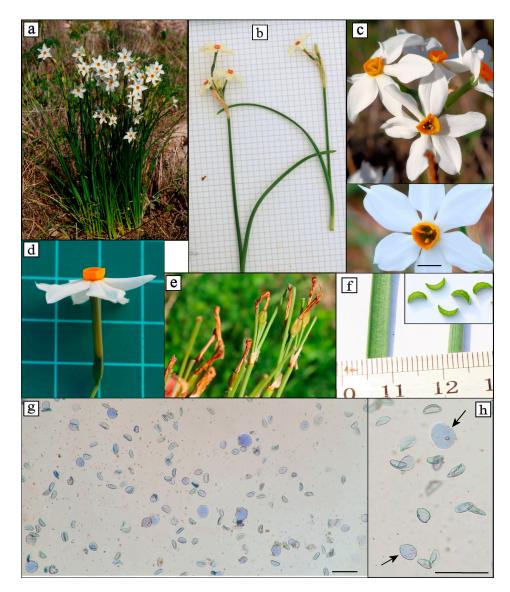


Figure 2. *Narcissus* × *briffae* Mifsud nothosp. nov. from the Maltese Islands: (a) habit in small dense tufts of about 40 plants; (b) individual plants with one narrow leaf (ca. 5 mm wide) and 3–5 flowers (grid = 5×5 mm); (c) detail of flower with slightly imbricated tepals and a shallow corona with a subtrigonous to subterete outline having three pleats or pinched-like folds (scale bar in (c) = 5 mm); (d) lateral view of the corolla showing shallow corona and dimensions (grid = 10×10 mm); (e) scapes with fallen or shrivelled seedless fruit due to sterility of the hybrid; (f) narrow leaves with fleshy crescent cross-section (ruler scale = 1 mm/div); (g) pollen grains at ×100 magnification (g) and × 400 magnification (h) (scale bar = 100 μm) mostly shrivelled or empty, with few turgid grains of two different sizes, the small ones ((h) bottom arrow) measuring on average $38 \times 29 \text{ μm}$ and the larger ones ((h) top arrow) measuring $52 \times 40 \text{ μm}$ and stain stronger in cotton blue.

Pollen, (Figure 1f) copious on the anthers, >90% fertile (very few deflated pollen grains observed), turgid and looking viable. Grains broadly ellipsoid, compressed or flattened at one side. NRC01: 42.1 (38.0–45.9) × 31.9 (30.8–33.2) μm; Q = 1.39 (1.3–1.4) (n = 31). NRC02: 43.7 (41.2–45.2) × 32.7 (30.5–34.9) μm; Q = 1.34 (1.3–1.4) (n = 31). NRC05: 42.2 (40.5–44.2) × 31.6 (30.5–32.4) μm; Q = 1.35 (1.3–1.4) (n = 31). NRC12: 42.0 (39.1–43.9) × 31.1 (28.5–33.1) μm; Q = 1.40 (1.3–1.5) (n = 29). Testa featuring some small bump-like rounded projections about 3–5 μm wide.

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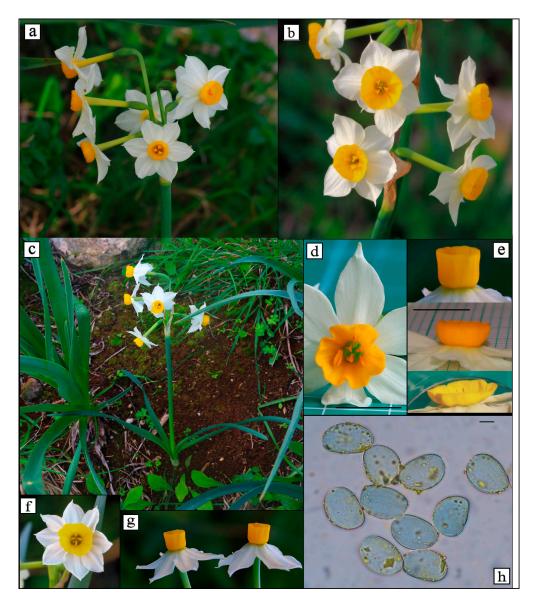


Figure 3. *Narcissus tazetta* L. subsp. *aequilimbus* (Herb.) Mifsud from the Maltese Islands: (a) inflorescence usually made of 5–7 flowers; (b) closeup of flowers showing corona and imbricated tepals; (c) individual plant in its natural habitat with four leaves ((c) 12 mm wide); (d,e) variation in the corona from lemon to gold yellow, cup-shaped ((e) top), bowl-shaped ((e) middle), or saucer-shaped ((e) bottom) with a circular or (three-) shallow-lobed outline usually unsegmented and without clefts or incisions (scale 10 mm); (f) very rare example of tetramerous corolla with 8 tepals; (g) flowers with deflexed petals; (h) pollen grains at ×100 magnification (scale bar = 10 μm) with an average size of 40×31 μm and numerous yellow warts (stained in cotton blue).

3.2. *Morphotype Narc-B (Figure 2)*

Rather early-flowering plants, typically flowering from mid-October (more or less 3–4 weeks after anthesis of morphotype Narc-A) characterised by forming small tufts of few to 70 small plants each with 2–5 flowers per scape and narrow leaves present during anthesis. In the year 2023, flowering was delayed to the beginning of December due to the absence of substantial rain in most of the autumn—the first significant precipitation occurred during the last week of November.



Figure 4. (a) Field comparison of *Narcissus* × *briffae* Mifsud (left) and *N. tazetta* subsp. *aequilimbus* (Herb.) Mifsud (right) growing together (Qortin tal-Magun, Nadur, Gozo, 14 November 2009): (b) habit and habitat of *N. tazetta* subsp. *aequilimbus* scattered as individuals or small groups (rarely well-formed tufts) along shrubby vegetation on rocky shelves and banks (plateaux overlooking Wied Mġarr ix-Xini, Ta' Ċenċ, Sannat, Gozo, locus of the neotype, 8 January 2024).

Material examined: NRC06, NRC07: limits of Ħondoq ir-Rummien (Qala, Gozo), 29 October 2022; NRC12, NRC18: Il-Fekruna area (Munxar, Gozo), 12 November 2022; NRC15, Rdum il-Bies, limits of Selmun area, (Mellieħa, Malta), 15 November 2022, 12 December 2023; NRC27: il-Ħarrieq limits of Selmun area, (Mellieħa, Malta), 12 December 2023. These sampled specimens shared a common habitat represented by a low and sloped or banked garrigue of coralline limestone, located close to cliffs, rocky escarpments, or valley sides, and often accompanied by xeric grasses and steppic flora, indicative of some disturbance or degradation.

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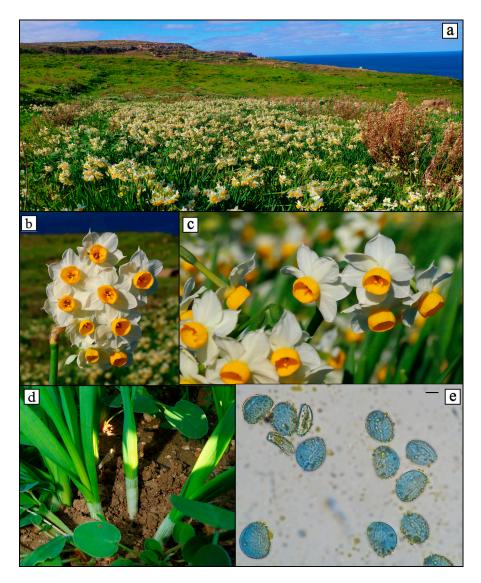


Figure 5. *Narcissus tazetta* subsp. *tazetta* L. from the Maltese Islands: (a) habitat, typically steppe and abandoned fields on clay slopes or clayey soil; (b) inflorescence with 9 flowers; (c) detail of flower with imbricated broadly ovate tepals and golden yellow corona with a circular outline, subentire margin and unlobed or undivided wall; (d) stocky plants with well-developed sheath (3 layers) enveloping 4 wide leaves (typically 15–20 mm wide) and a central scape; (e) pollen grains at $\times 100$ magnification (scale bar = $10 \mu m$) with an average size of $47 \times 38 \mu m$ covered with numerous yellow warts (stained in cotton blue).

Typical accompanying vegetation includes the following species: *Asperula aristata* subsp. scabra Nyman, *Arisarum vulgare* O.Targ.Tozz, *Asparagus aphyllus* L., *Asphodelus ramosus* L., *Bituminaria bituminosa* (L.) C.H.Stirt., *Brachypodium hybridum* Catalán, Joch.Müll., Hasterok and G.Jenkins, *Bromus fasciculatus* C.Presl, *Bromus madritensis* L., *Chiliadenus bocconei* Brullo, *Erica multiflora* L., *Euphorbia dendroides* L., *Ferula melitensis* Brullo, C.Brullo, Cambria, Giusso, Salmeri and Bacch., *Galactites tomentosus* Moench., *Hyparrhenia hirta* (L.) Stapf, *Periploca angustifolia* Labill., *Prasium majus* L., *Ranunculus bullatus* L., *Teucrium fruticans* L., *Thymbra capitata* (L.) Cav., *Drimia pancration* (Steinh.) J.C.Manning and Goldblatt.

Description: **Habit**, dense tufts of (10–)25–70 plants (Figure 2a). **Leaves**, present during anthesis, usually one per plant/bulb (Figure 2b), rarely two, variably long but usually about half the scape's length, narrow and not twisted, 2–5 mm wide, cross-section crescent with rounded ends, moderately succulent or fleshy (Figure 2f). **Basal sheath**, present, about 5–12 mm above ground level, single-layer, semi-membranous, pale green

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with 10-16 distinct longitudinal bright green veins, margin smooth. Scape, terete, 25 (22–35) cm long (excluding flowers), ca. 3 mm in diameter. Bract, membranous, frail, lanceolate, beige, 24 (28–45) \times 8 (7–10) mm. Flowers, 2–4(–6) per scape (Figure 2c), 22-35 mm in diameter, whitish-cream, slightly more colourful adjacent to the corona, very fragrant. Pedicels, of variable length, the longest 30-42 mm long at anthesis (longer in fruit). **Perianth tube**, 15 (14–16) mm long, tubular (Figure 2d), sometimes with an irregular (angled) outline, narrow and widening slightly below the tepals, sometimes slightly ribbed above, fading to slightly light green at the base and contrasting with the dark green ovary below. Tepals, imbricated up to their basal third, very rarely free or slightly touching each other; lower tepals, $10.5 (9.5-12.5(-15.0)) \times 5.5 (5.0-6.5(-8.5))$ mm, tip obtuse and distinctly cuspidate (1.5–3 mm long); **upper tepals**, 9.5 (8.5–11.0(–13.0)) \times 5.0 (4.5–6.5) mm, tip acute mucronate (ca. 0.5 mm long) rarely blunt and without an appendage. Corona, 5.0 $(3.5-6.5) \times 2.0$ (1.6-2.4) mm, butter to golden yellow, seldom with a hint of green in young flowers, shallow bowl-shaped with somewhat divergent profile, margin always irregular, outline shape subcircular to subtrigonous occasionally subdeltate (in very young flowers), wall continuous and often with three (sometimes two or one), small, equidistant pleats or minute notches, rarely with one vertical shallow cleft (incision) reaching down not more than half the corona's height; edge subentire to crenulate. Anthers of upper stamens bright yellow, 1.0–3.0 mm long often smooth without copious pollen; those of the lower stamens 3.0-4.0 mm long with little pollen cover. Bulbs dark brown, often tightly grouped together in three to five clumps. Fruit capsules undeveloped and fall prematurely (Figure 2e). Seeds seldomly formed, mostly shrivelled. Plants are sterile.

Pollen (Figure 2g,h) scant or not seen on the anthers, mostly sterile, shrivelled or empty (less than 25 μm wide), only about 5–15% with a normal turgid shape. Viable pollen grains dimorphic, one form having a broadly ellipsoid ovate shape with one side laterally compressed and the other form are markedly larger with a subspherical, potato-like shape, and stain stronger in cotton blue. Measurements of the small and large forms as follows: NRC06: small form—42.0 (34.4–46.5) × 32.9 (26.3–38.1) μm; L/W ratio 1.3 (1.2–1.4) (n = 21); large form—57.7 (52.2–70.4) × 50.3 (43.2–57.0) μm; L/W ratio 1.15 (1.1–1.2) (n = 13). NRC07: small form—39.9 (35.6–43.1) × 28.1 (24.6–33.7) μm; L/W ratio 1.3 (1.2–1.4) (n = 17); large form—51.3 (48.5–55.5) × 40.3 (37.4–45.8) μm; L/W ratio 1.2 (1.1–1.3) (n = 15); NRC15: small form—38.5 (35.6–40.4) × 30.7 (28.7–33.6) μm; L/W ratio 1.19 (1.1–1.3) (n = 17); large form—49.4 (43.4–58.2) × 41.4 (37.4–57.4) μm; L/W ratio 1.19 (1.1–1.3) (n = 13). Yellow, bump-shaped or hemispherical lipid projections, up to 6.0 μm wide observed on the testa of the small-type pollen grains but often absent on the larger type.

3.3. Morphotype Narc-C (Figures 3–5)

This morphotype has a longer flowering period, starting from November up to March, forming plants grouped in small (5–12 plants) to crowded tufts (up to 80 plants) with 4–9 flowers per scape and well-developed leaves before and during anthesis. The morphology of the flowers is not very variable, with minor differences in sizes and flower numbers, but because of apparent divergences in phenology, habitat, and habit, this group can be further divided into the early-flowering "autumnal" rock-dwelling morphotype Narc-C1, and the later winter–spring morphotype Narc-C2 growing more profusely in comparatively open areas such as abandoned fields, clay slopes and open ground with deep, usually clayey soil.

3.4. Morphotype Narc-C2 (Figure 5)

Material examined: NRC22: limits of Verdala close to Buskett Woodland (Siġġiewi, Malta), 11 January 2023; NRC23: Selmun area (Mellieħa, Malta), 4 February 2023; NRC24: Il-Muxi area, (Qala, Gozo), 5 February 2023; NRC25: Tar-Rehba area (Dingli, Malta), 23 February; NRC26: l-Għolja tal-Gelmus, (Rabat, Gozo), 28 February 2023. These plants grew on clayey soil, namely, open abandoned fields, except for NRC22, which was found in a habitat with stony loam soil in shaded patches of an open woodland area.

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Typical accompanying vegetation includes the following species: *Asparagus aphyllus* L., *Avena barbata* Brot., *Avena sterilis* L., *Bituminaria bituminosa* (L.) C. H.Stirt., *Cynara cardunculus* L., *Dittrichia viscosa* (L.) Greuter, *Foeniculum vulgare* Mill., *Galactites tomentosa* Moench., *Hordeum leporinum* Link., *Medicago polymorpha* L., *Oxalis pes-caprae* L., and *Drimia pancration* (Steinh.) J.C.Manning and Goldblatt.

Description: **Habit**, in tufts of (20–)30–80 ca. plants, mostly crowded with bulbs closely packed (Figure 5a). Leaves present before and during anthesis, 3-4 per plant (bulb), almost of equal length and a few cm shorter than the flowering scape, strap-shaped, twisted by one revolution, (18-)25-40 cm \times (8-)15-21 mm wide, glaucous green, cross-section gently canaliculate, thin (not fleshy) with acute to obtuse ends, margin smooth. Basal sheath up to 52 mm above ground level, 2–3 concentric layers exposed above ground level (1-2 below ground level), semi-membranous, pale green, uppermost sheath with >15 distinct longitudinal, parallel, bright-green veins, margin smooth (Figure 5d). Scape terete and slightly compressed laterally (broadly ellipse in cross-section) (20–)27–55 cm long, ca. 6-7 mm diameter, minutely ribbed longitudinally. Bract membranous, frail, lanceolate, beige, $30-45 \times 10-16$ mm. Flowers, 6-10(-12) per scape (Figure 5a), rarely less in unmature plants; 24–36 mm in diameter, whitish-cream, very fragrant. Pedicels of variable length, the longest 45–58 mm long at anthesis (longer in fruit). **Bracteoles**, four usually present, linear, 25–35 mm long \times 1 mm wide, unequal in length, pale green, very thin and hyaline. Perianth tube, 17-19 mm long, subtrigonous, slightly expanding gradually towards the perianth, light green throughout. Tepals broadly ovate/lanceolate, imbricated up to the basal half of the tepal length, sometimes slightly more; lower tepals $16.0 (14.0-17.5) \times 11.5$ (9.5–13.5), broadly ovate (widest part below the centre); tip subacute and mucronate (1 mm long), white and often with a pale green midrib; upper tepals subequal in size and shape to the upper, but with a reduced mucro. Corona, $11.0 (9.0-13.5) \times 5.0-7.0$ mm, yolk-yellow, cup-shaped (sides straight) to bowl-shaped (sides slightly convex sides), shallow with a slightly irregular or smooth circular margin, sometimes with 1(-2) shallow and tiny notches or angular pleats; edge entire to subentire to shallowly undulate (Figure 5c). Stamens, in two rows attached to the corolla by short filaments, one attached at the base of the corona, the other about 5 mm below at the neck of the tube. Anthers, subequal length, 3.5–5.5 mm long; moderately abundant in pollen, included but occasionally slightly exerting the corona. **Seeds**, fertile and numerous, black, pip-shaped, about 3 mm wide

Pollen, (Figure 5e) copious, about 80% fertile (some deflated pollen observed), turgid, and looking viable. Grains broadly ellipsoid, compressed or flattened on one side. NRC24: 47.7 (45.2–50.7) \times 35.6 (33.1–38.8) µm; L: W ratio 1.3 [1.2–1.4] (n = 33). NRC25: Lipid projections large, hemispherical or cushion-shaped, up to 6.7 µm across, numerous, and prominent.

3.5. Morphotype Narc-C1 (Figures 3 and 4)

Material examined: NRC14: Ta' Čenċ (Sannat, Gozo), 14 November 2022; NRC16, NRC17: Wied Mġarr ix-Xini (Sannat, Gozo), 16 November 2022; NRC19, NRC20, NRC21: Wied tal-Munxar, (Munxar, Gozo), 25 November 2022; NRC28: Wied Babu, (Żurrieq, Malta), 29 December 2023; NRC29: Wied il-Għasel, (Mosta, Malta), 29 December 2023. These specimens were found specifically on rocky valley banks, close to the valley bed (up to 50 m above), but seldom at the valley bed, even if it is not inundated. Hence, this morphotype shows a rupestral preference, often growing in loamy soil present in deep pockets within karstic rock and rocky shelves of valley sides. Interestingly, they seem to prefer a semi-shaded, moist, south-facing side and seldom occur on the south-facing valley sides exposed to sun.

Typical accompanying vegetation includes the following species (those underlined are the most abundant): Arisarum vulgare O.Targ.Tozz.; Asphodelus ramosus L.; Erica multiflora L.; Euphorbia dendroides L.; Galium murale M.Bieb.; Geranium dissectum L.; Geranium molle L.; Hypericum aegyptium Blanco; Oxalis pes-caprae L.; Prasium majus L.; Rhamnus oleoides L.; Rubus ulmifolius J.Presl and C.Presl.; Teucrium flavum L.; Teucrium fruticans L.; Drimia pancration (Steinh.) J.C.Manning and Goldblatt; Bryophytes.

Description: Habit, isolated plants, small groups of 4–10 plants (Figure 4b) or, rarely, loose tufts of groups of plants close to each other merging together, occasionally a cluster of 15-25 plants. Leaves present before anthesis, (3-)4 per plant slightly shorter to longer than the scape, strap-shaped, twisted by not more than one revolution, 20–35 (–60) cm \times 7–14(–19) mm wide, can grow much longer and surpass the inflorescence when occurring beside higher shrubby vegetation; cross-section canaliculate to flattened V-shaped, thin, not fleshy, with subacute to obtuse ends, margin smooth, glaucous, non-bluish green with a hint of yellowish hue. **Basal sheath**, 15–35(–100) mm above ground level, 2–3 concentric layers (1–2 more below ground, total of 4), semi-membranous, pale green with >15 distinct longitudinal, parallel, bright-green veins, margin smooth. Scape, terete and slightly compressed laterally (broadly ellipse in cross-section) above, 20-45 (-70) cm long, 5-7 mm diameter, minutely ribbed longitudinally. **Bract** membranous, frail, lanceolate, beige, 45 (35–52) \times 9 (10–15) mm. Flowers, (3–)4–7(–8) per scape, 18–30 mm in diameter, whitish-cream, sometimes with a pale green midrib, very fragrant, somewhat nauseating. Pedicels of variable length, the longest 45-68 mm long at anthesis (longer in fruit). Bracteoles, four when present, filiform, 20–40 mm long \times <1 mm wide, unequal in length, pale green or beige, membranous. Tepals broadly ovate/lanceolate, imbricated up to the basal half, sometimes slightly more, tinged in pale yellow at the base, close to the corona, often seen deflexed backwards; lower tepals, $13.4 (11.5-15.0) \times 10 (8.5-11.0)$, broadly elliptical (widest part at the centre) to oblanceolate (widest part slightly above the centre); tip obtuse-rounded and shortly mucronate (1.0 mm long), white often with a pale green midrib; upper tepals, subequal to the lower tepals, same shape but tip truncate to emarginate, without a mucro. Perianth tube, 19 (16–24) mm long, pale to light green throughout, tubular, and expanding slightly below the tepals, trigonous in cross-section at the distal part. Corona very variable, 9.0 (7.0–11.5) \times 5.0 (3.5–7.0) mm, bright lemon to golden yellow, never orangish or amber, cup-shaped (with vertical parallel sides), bowl-shaped (with long diverging sides) to sometimes saucer-shaped (with wide, shallow diverging sides) (Figure 3e), generally rim with a circular outline or rarely three shallow-lobed (Figure 3d) and having a margin the varies from entire and smooth (especially in cup-shaped forms), crenulate or crenated, pleated (especially in saucer-shaped forms), or rarely notched, with angular folds or tiny clefts. Stamens in two rows attached to the corolla by short filaments, one attached at the base of the corona, the other about 5 mm below at the neck of the tube. **Anthers**, subequal length, 4.0–7.5 mm long; covered with abundant pollen, included but occasionally slightly exerting the corona. Seeds, fertile and numerous, black, pip-shaped, about 3-4 mm wide. N.B.: when plants are found within thick vegetation or in very shaded pockets, they etiolate, forming abnormally longer leaves and scapes reach almost 1 m in height.

Pollen (Figure 3h), copious on the anthers, about 85–90% fertile (only very few deflated pollen grains observed), generally turgid and viable. Grains broadly ellipsoid, flattened at one side. NRC14: 39.8 (36.3–42.3) \times 30.7 (29.1–32.2) µm; L/W ratio 1.3 [1.2–1.4] (n = 31). NRC16: 41.5 (39.9–43.7) \times 31.7 (30.8–32.6) µm; L/W ratio 1.3 [1.2–1.4] (n = 37). NRC19: 39.3 (37.6–41.7) \times 31.0 (29.3–32.2) µm; L/W ratio 1.3 (1.2–1.4) (n = 31). Lipid projections numerous, large, hemispherical or cushion-shaped, up to 7.2 µm across.

3.6. Morphological Analysis

The separation between the four morphotypes emerged clearly in the results of the morphological analysis (Figure 6). There is a clear separation between NRC-C1 and NRC-C2 morphs on axis 1 of the nMDS plot, whilst morphs NRC-A and NRC-B were separated on axis 2. The results of the analysis lend support to the field observations by the authors.

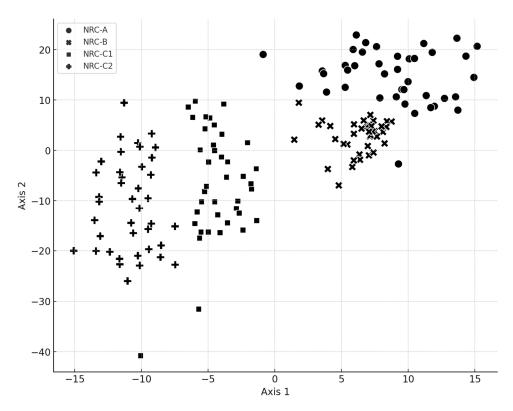


Figure 6. Separation of four morphs based on their morphometry based on non-metric multidimensional scaling (nMDS).

4. Discussion

Morphotype Narc-A represents the early-flowering species first mentioned by Zerapha $\overline{[20]}$, which in the literature has long been referred to as *Narcissus serotinus*. However, the description given in [20] as a multi-flowered spathe with canaliculate leaves does not match perfectly with this species, which usually has one—two flowers and thin subcylindrical leaves. A later flora [21] assumed that this species was N. cupanianus Guss., but Parlatore confirmed a voucher specimen sent to him by Grech Delicata (not the same one that Zerapha described) from Malta as N. serotinus [22], leaving an open question regarding what Zerapha had actually seen (see discussion on morphotype Narc-C, below). N. serotinus was reported to occur in the Maltese Islands repeatedly in subsequent works [12,22-28] until taxonomic questions and inquiries started to emerge sometime later following broad taxonomic studies and monographs on autumnal Narcissus [5,15,16]. This species was also reported differently as N. obsoletus (Haw.) Spach [29], stating that the closely related N. serotinus is confined to the extreme west of the Mediterranean Region. This taxon was also mentioned in another work on the Maltese flora [30].

However, morphotype Narc-A, characterised by a three-cut or segmented corona and linear perianth tube, neither matches *N. serotinus* having a six-cut corona and diverging (expanding) perianth tube nor *N. obsoletus* having an entire, unsegmented, urn-shaped corona [31].

Donnisan-Morgan et al. [3] examined plants—at that time, all referred to as "N. serotinus"—from Spain, Portugal, and Morocco. Their results obtained from flow cytometry revealed that there are two morphotypes of N. serotinus: the sensu stricto with a DNA content of 20 picograms and another one with 50 picograms. The latter showed a few important morphological differences from N. serotinus s. str., namely, in a more linear perianth tube, and, according to the authors, a corona with stronger reddish or orange tones. They described the new species as N. miniatus Donn.-Morg., Koop. and Zonn. and postulated it to have originated from a long-established allotetraploid hybrid between N. obsoletus (or N. elegans) and N. serotinus.

Soon after, Spanish authorities resurrected a forgotten taxon—*N. deficiens* Herb., described by Herbert (1847) from Santa Maura on the Greek Island of Lefkada. For a long time, this taxon was used as a synonym for *N. obsoletus* and neglected by everyone—also by Donnisan-Morgan et al. [3]. This has been described as having a distinct three-flapped (deeply dissected) or three-lobed corona, typically trigonous in outline, which differs from *N. serotinus* having a six-lobed or flapped corona with a subtrigonous to almost circular outline and from *N. obsoletus*, which have an undivided, bowl-shaped corona with a circular in outline (refer to details in [4]). These scholars suggested that *N. deficiens* corresponds with the same *Narcissus* previously described as *N. miniatus*, which is common in Spain. Moreover, Fernández Casas [4] put *N. miniatus* in synonymy with *N. deficiens* but supported its allotetraploid hybrid origin as suggested by Donnisan-Morgan et al. [3] and later by other authors [15].

Some taxonomic disagreements still exist between the different schools of thought on whether *N. miniatus* and *N. deficiens* are different or conspecific. The controversy originates from *N. deficiens* being described and depicted from an aberrant form with a much-reduced corona (hence the epithet "deficiens"). Hence, some suggested that *N. deficiens* should refer specifically to corona-reduced forms, and the "typical forms" with a developed three-parted corona should be treated as *N. miniatus*; while others prefer a more conservative approach and include all forms within a single species and accept *N. deficiens* for being described first. This misperception was settled when specimens from a population of an autumnal daffodil collected from the locus classicus of *N. deficiens* (Alexander's Castle, now known as Agia Mavra Castle in Lefkas, Greece) had variable, well-defined coronae dissected in three parts or three lobes with a trigonous outline (Soc. Med. Comm: Carles Jiménez, *Narcissus* FB group, 27 October 2023), hence supporting further that Herbert's *N. deficiens* should be attributed to a more diverse species rather than restricted to a corona-deficient form as the name implies. This ambiguity may have led many researchers in the past to assume *N. deficiens* to be a daffodil without or only a remnant corona and became neglected.

With regards to the Maltese Islands, the early-flowering Narcissus (morphotype Narc-A) characterised by having no leaves during anthesis and forming one to few flowers with a subtrigonous corona composed of three lobes or flaps should be attributed to *N. deficiens*.

However, *N. serotinus* was recorded from the Maltese Islands precisely from Triq il-Batterija, Marsalforn, Gozo, close to a hillock known as il-Qolla l-Bajda [5]. According to these investigations, their specimen labelled S.MLT genetically corresponded to *Narcissus serotinus*. Surveys carried out by the present author at il-Qolla l-Bajda in 2020 and 2022 did not confirm *N. serotinus*, but only a fragmented population of *N. deficiens. Narcissus serotinus* is distinct in having an inflated (abruptly widening) perianth tube and six distinct and fully incised corona segments. An example found by the author on 30 October 2004 with a corona divided into six distinct free segments (Figure 1g) might be additional evidence of the presence of *N. serotinus* in Malta, but photos showing the lateral view to fully confirm the species were not taken on that occasion. Since *N. serotinus* is regarded as a species restricted to eastern Spain, western Portugal, and northern Morocco [32], then the presence of *N. serotinus* in the Maltese Islands is biogeographically improbable, as it is out of the currently reported natural range. Notwithstanding this, the occurrence of *N. serotinus* in Malta should be considered as tentative, at best, until further studies are conducted.

Morphotype Narc-C (Figures 3–5) represents two forms, of *Narcissus tazetta*. The typical and locally frequent form, morphotype Narc-C2 (Figure 5), flowers between mid-January and March and grows on clay slopes or in clayey soil of abandoned fields or field margins, along pathways, grassland, and sometimes in rocky ground with deep soil. The other form, morphotype Narc-C1 (Figures 3 and 4) flowers from the end of October and occurs on rocky banks, shelves, and ledges in semi-shaded valley sides amongst shrubby, garigue, phrygana, or scrub-type sclerophyllous vegetation.

Narcissus tazetta has been reported since the first modern listing of the Maltese flora [20], and like *N. serotinus*, in all subsequent floras, guidebooks, or accounts of the Maltese flora [12]. The reported flowering time of five to six months is relatively too long for a

single monocot species, as these, including other member species of *Narcissus*, typically have specific and short flowering times. Hence, this raises the question of whether Narc-C1 is distinct from the typical *N. tazetta*. When compared (Table 2), there are no significant morphological differences other than that Narc-C2 is a winter–spring-flowering species that is more robust, has larger leaves, denser and larger tufts, more flowers per scape, and slightly larger and deeper coronas.

Interestingly, the distinction of the autumnal variety of *N. tazetta* had already been identified [33] from Maltese material sent to Herbert by Zerapha. Applying the same arguments above with the early flowering time and habitat, Herbert could not assign it to *N. tazetta* and described the early-flowering Maltese daffodil as *Hermione aequilimba* Herb. [34]. He gave a very detailed account and an excellent illustration (Figure 7), which matches with morphotype Narc-C1. All accounts synonymising *H. aequilimba* with *N. obsoletus* (e.g., [35]) are therefore not correct because this species is noticeably different from *N. obsoletus* and resembles the stockier *N. tazetta*. Similarly, Herbert [34] mentions explicitly that Zerapha made a mistake in assigning this plant to *N. serotinus*: "Zerapha has certainly made an error in referring this African plant [H. aequilimba] to the little 1-flowered (rarely 2-flowered) N. serotinus of Clusius, which grows in Spain, Naples, and Sardinia".

According to Errol Vela (pers. comm. To S. Mifsud, November 2020), similar early-flowering *tazetta* exist in the Middle East and he suggested comparing this with the description of *N. tazetta* subsp. *syriacus* (Boiss. and Gaill.) Boiss. This description of this subspecies was checked from the protologue [36] and it was found that while no reference is made to the early flowering character, the main distinction from *N. tazetta* s. str. seems to be based on differences in the corolla, namely, its narrower tepals: "*Perigonii laciniae oblongae longiores et angustiores magis discretae*..." [36]. This minor difference might not justify the distinction from *N. tazetta* s. str., and, more importantly, does not match with the Maltese "autumnal *N. tazetta*", which have broad tepals and hence cannot be ascribed to subsp. *syriacus* in the sense as described in the protologue. Further specimens should however be examined to understand what *N. tazetta* subsp. *syriacus* really refers to and whether it merits distinction at subspecies level.

Herbert's description from Maltese material ventures into whether to assign the autumn-flowering morphotype of *N. tazetta* (Narc-C1) to *H. aequilimba* (=Narcissus aequilimbus (Herb.) Nyman) based on different chorology, habitat, stature, the number of flowers per scape, and minor differences in the size of some flower parts. In accordance with Herbert's approach, the findings in this study, and the opinions of scholars of this genus (e.g., pers. comm. Errol Vela and Oron Peri), the autumnal *N. tazetta* merits taxonomic distinction from the spring-flowering *N. tazetta*. It must be noted that a bulb that blooms in autumn would not flower again in spring; thus, this situation does not implicate flowering of the same bulb at two different seasons. Notwithstanding that the distinction between the two morphotypes is not pronounced, *N. aequilimbus* is proposed to be ranked at the infraspecific level in line with other infraspecific taxa of *N. tazetta* with slight differences from *N. tazetta* s. str. such as *N. tazetta* subsp. *aureus* (Haw.) Baker, *N. tazetta* subsp. *canariensis* (Burb.) Baker, and *N. tazetta* subsp. *italicus* (Ker Gawl.) Baker.

For taxonomic procedures, *Hermione aequilimba* is further epitypified on collected material from Malta, including entire plants with bulb, where currently the type is only based on a partial illustration (Figure 7) of a plant [34]. It is here combined into a subspecies ranking as follows:

Narcissus tazetta L. subsp. aequilimbus (Herb.) Mifsud comb. nov.

- =Hermione aequilimba Herb. (basionym) in Amaryllidaceae: 404 (1837)
- =Narcissus aequilimbus (Herb.) Nyman in Syll. Fl. Eur.: 365 (1855)

<u>Type</u>—coastal areas in Malta, but locality and exact date (only "flowering in October") are not given; epitype is based on illustration Pl. 48 in the protologue [34].

Epitype—Designated here from Ta' Čenč (ta' fuq il-Gruwa), Sannat, Gozo, Malta. Collected 12 November 2022, leg. S. Mifsud. Deposited at ARG! (collection SM140; Neoisotype SM141).

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<u>Isoepitype</u>—Second epitype is designated here from Hondoq ir-Rummien, Qala, Gozo, Malta. Collected 12 November 2022, leg. S. Mifsud. Deposited at ARG! (collection SM142).



Figure 7. Iconotype of *Hermione aequilimba* Herb. (=*Narcissus tazetta* subsp. *aequilimbus* (Herb.) Mifsud) collected from the Maltese Islands, flowering in October [6].

<u>Diagnosis</u>—Same as *N. tazetta* s. str. but flowers much earlier, about six weeks after the first substantial autumnal rains, typically starting by the end of October to November, plants formed in loose groups, scattered, sometimes singular, very rarely in clusters (Figure 4b) on rocky banks, shelves and ledges of valley sides and mouths over the coast, preferring shaded (hence damper) sides typically in loamy soil besides garigue or scrub shrubby vegetation (Figure 4b). Leaves narrower, mostly between 9–14 mm wide, can reach up to 50 cm in length due to etiolation, somewhat less glaucous and less twisted. Scapes with less flowers, averaging 5–6 per scape. Tepals smaller by 2–3 mm, broadly ovate/lanceolate, creamy-white normally, with pale greenish midribs. Corona variable, cup-shaped (parallel sides) or bowl-shaped (divergent sides) with subentire to crenated rim, diameter smaller,

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on average measuring 9×5 mm. A full description is given in above (see Section 3 Results, morphotype Narc-C1).

Specimens examined were Ta' Čenċ (Sannat, Gozo); Wied Mgarr ix-Xini (Sannat, Gozo); Wied tal-Munxar, (Munxar, Gozo); Wied Babu (Żurrieq, Malta); Wied il-Għasel, (Mosta, Malta). Refer to Table 1 for more details.

The autumnal *N. tazetta* (morphotype Narc-C1) should be referred to subsp. *aequilimbus*, whereas the typical winter/spring flowering form (Narc-C2) should be referred to *N. tazetta* s. str. It is already assumed that this subspecies is not endemic to Malta because similar autumnal forms have been observed in the Eastern Mediterranean Region (pers. comm. Oron Peri, August 2019; Errol Vela, November 2020).

Morphotype Narc-B represents plants that were identified as *N. elegans* for several matching morphological characteristics with that species [12], the most important being the narrow, 3–5 mm wide caniculate leaves present at anthesis, the early flowering in mid-October, and the formation of tufts and the multi-flowering scapes. These plants reported as *N. elegans* were also perceived by the authors to be an intermediate species between *N. serotinus* (=*N. deficiens*) and *N. tazetta*, and the authors further suggested that they may have introgressed with either species to form hybrid swarms.

The present study provided further crucial knowledge on this morphotype by indicating new populations in addition to those reported in [12] and, more importantly, detecting sterility in all examined material with reference to the dysfunctional, unviable pollen (Figure 2h) as well the lack of seed formation in poorly developed and often dropping fruit capsules (Figure 2f). All examined plant populations were largely sterile, leading to two fundamental conclusions: these plants are not *N. elegans*, and they should represent a natural sterile hybrid.

There are only two species that can act as putative parents where their flowering period overlaps: hence *N. deficiens* and *N. tazetta* subsp. *aequilimbus*. Both species are within pollinator reach, for example, at Il-Fekruna/Wied il-Munxar, and at Hondoq ir-Rummien, the parents and preseumed hybrid (morphotypes Narc-B) were in sympatry. Cross-pollination is also feasible because populations of both parents are locally frequent to abundant. The hypothesis that morphotype Narc-B is a natural hybrid between *N. deficiens* and the autumnal *N. tazetta* s.l. is also strongly supported by morphological findings. Some character states of the presumed hybrid resemble one of the parents, some are similar to the other parent and others are considered as intermediate forms of both parents. For example, the moderately fleshy leaf with a crescent cross-section ca. 3–5 mm wide of the presumed hybrid is intermediate between the cylindrical 1 mm leaf of *N. deficiens* and the 7–16 mm flattened leaf of *N. tazetta* s.l. Table 3 provides a detailed comparison of many morphological characters, indicating which has affinity to either parent and which is intermediate. This new hybrid is described as follows:

Narcissus × *briffae* Mifsud, nothosp. nov. (Figure 2)

N. deficiens Herb. × N. tazetta L. subsp. aequilimbus (Herb.) Mifsud

<u>Etymology</u>—Named after Michael Briffa (1926–2019), a student of the Maltese flora and macrofungi for most of his life, leaving behind several important findings and publications enriching the knowledge and conservation of the biodiversity of the Maltese Islands.

<u>Diagnosis</u>—Plants in tufts of about 25–70 plants. Leaves present during anthesis, 3–5 mm wide, crescent with rounded edges in cross-section, fleshy. Basal sheath present, pale green with bright green veins, ca. 10 mm long above ground level. Perianth tube tubular with parallel sides tapering gently, green, but fading considerably at the lower half. Scape up to 30 cm long, 3 mm in diameter, bearing 2–5(–6) flowers. Tepals cream-white, broadly lanceolate or ovate, imbricated up to the lower half, approx. 10×5 mm. Corona bowl-shaped with a subcircular to faintly trigonous outline, with three equidistant small pleats (sometimes shallow clefts) on the rim, lemon to golden yellow, 5×2 mm. Pollen not abundant on anthers, mostly shrivelled and empty, hence unviable. Fruit capsules small, shrunk without seeds or seldom a few. (Refer to the description of morphotype Narc-B in Section 3 Results for a full description).

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Type—MALTA. Qala: Hondoq ir-Rummien, elevation 70 m, 36°1′45.42″ N 14°19′15.47″ E, 7 December 2023, Leg. S. Mifsud (holotype ARG!, collection SM150, isotype ARG!, collection SM151).

Studied material in the Maltese Islands—Selmun-Mistra area (various locations), Mellieħa, Malta! (1 November 2008); Dwejra, San Lawrenz, Gozo (17 October 2009); Qortin tal-Magun, Nadur! (Gozo, 14 November 2009) (Figure 4a); Limits of Wied is-Simar, Qala, Gozo (14 November 2010); Ta' Ċenċ, Sannat, Gozo! (16 November 2014); Ħondoq ir-Rummien, Qala, Gozo! (29 October 2022); Il-Fekruna/Wied tal-Munxar, Munxar, Gozo! (3 November 2022). (! Indicates both parents have been seen together within a distance of 100 m; date given is that of the first observation).

Narcissus \times briffae was mistaken for N. elegans in [12], and in historical records [20,21] that reported their "N. elegans" as being frequent in Malta. More recently, the record of N. elegans by H. Spiteri found in the 1980s and cited in the Red Data Book of the Maltese Islands [37] in a similar habitat to N. \times briffae is likely a similar misidentification. Unless typical records of N. elegans are confirmed, it is safe to reject it from the flora of Malta and replace it with N. \times briffae.

5. Conclusions

Narcissus is a very dynamic genus, with fluid taxonomy (especially considering nothotaxa), changes in distribution or species demarcation, and synonymising of taxa are ongoing regularly. Its taxonomy can be subjective sometimes, given the difficulty in assessing member species with simple and affordable molecular techniques such as ITS sequencing. This study reshaped the inventory of Narcissus occurring in the Maltese Islands, now represented at least by four native taxa: N. deficiens (syn. N. miniatus), previously referred as N. serotinus or N. obsoletus; Narcissus \times briffae (N. deficiens \times N. tazetta subsp. aequilimbus) a newly described hybrid replacing N. elegans; and N. tazetta s.l., which comprises of N. tazetta subsp. aequilimbus—previously described from Malta [34] but neglected—and N. tazetta s. str. The intriguing records of N. serotinus from Malta ([5]; Figure 1g) are currently considered as doubtful and probably safe to exclude because this species is assumed to have a restricted distribution in western parts of Spain and adjacent regions in Portugal.

This study advocates authors of Mediterranean flora to revise this genus in their territories since, as resulted in this study, it warrants similar taxonomic updating, with special reference to the autumnal species. Other alien species occurring in Malta include *N. papyraceus* Ker. Gawl. and *N. tazetta* subsp. *italicus* (Ker. Gawl.) Baker, sometimes forming localised naturalised populations [38,39]. This study provides a dichotomous identification key of the *Narcissus* species occurring or previously recorded from the Maltese Islands.

Key to *Narcissus* spp. in the Maltese Islands.

Characters should be based on observing at least five flowers since due to the variability within the species and occasionally the presence of atypical examples which may not key properly, especially with regard to the number of flowers and sizes.

- 1. Scape with 1–2 flowers; leaves ca. 1 mm wide, absent during anthesis. 2
- + Scape with 3 or more flowers; leaves > 2 mm wide present during anthesis. 3
- 2. Perianth tube widens abruptly halfway its length (bottle-shaped); corona always with six isolated segments. *N. serotinus* *
- + Perianth tube tubular with almost parallel sides and widens slightly (barely detectable) at the tip below the tepals; corona mostly with three segments or continuous a single unit with three shallow lobes or subentire. *N. deficiens*
- 3. Corona distinctly lemon to yolk yellow, similar in colour to the anthers; flower tube light green or yellowish-green. 4
- + Corona white, cream or pale yellow, much contrasting with the golden-coloured anthers; flower tube white. 7
- 4. Tepals very narrow, linear-oblong, never imbricated. Corona < 4 mm wide. N. elegans +

- + Tepals broadly ovate, overlapping at the lower half. Corona > 4 mm wide. 5
- 5. Plants with 1–2 leaves; 3–5 flowers per scape; fruit capsules shrivelled, undeveloped and seedless, anthers with little scanty pollen, which is mostly shrivelled or empty when observed under the microscope, dimorphic. *N.* × *briffae*
- + Plants with 3–4 leaves; five or more flowers per scape; fruit capsules barrel-shaped with viable black seeds; anthers covered with copious pollen, turgid, and broadly ellipsoid with a slightly flattened side, all the same shape. *6 (N. tazetta s.l.)*
- 6. First flowers blossoming in October–November, average 4–6 flowers per scape, plants in small groups or singular (seldom forming sizeable tufts). subsp. *aequilimbus*
- + First flowers blossoming in January, average of 8–9 flowers per scape, often forming large, dense tufts of plants. subsp. *tazetta*
- 7. Corona white and the same colour as the tepals. *N. papyraceus* ^
- + Corona cream and dissimilar from the white tepals. *N. tazetta* subsp. *italicus* ^
- * species recorded from Malta, but occurrences are doubtful and require further verification; unlikely to be present in Malta.
- + past misidentifications.
- ^ alien species for the Maltese Islands.

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