Botanical Journal of the Linnean Society, 2008, **158**, 460–469. With 5 figures

A morphometric study of species delimitation in *Sternbergia lutea* (Alliaceae, Amaryllidoideae) and its allies *S. sicula* and *S. greuteriana*

EWAN GAGE[1,2] and PAUL WILKIN[2]* FLS

[1]*Plant Science Laboratories, The University of Reading, Whiteknights, Reading, Berkshire RG6 6AS, UK*
[2]*Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK*

Received 22 October 2007; accepted for publication 13 May 2008

The morphological chararacters used to differentiate the species *Sternbergia lutea* (L.) Ker Gawl. ex Spreng., *Sternbergia sicula* Tineo ex Guss. and *Sternbergia greuteriana* Kamari & R.Artelari were found not to possess discrete or consistently different states during an attempt to produce an electronic multi-access key to the genus. Thus, variation in floral and leaf morphology in the three species was further explored to re-evaluate taxon limits using herbarium specimens and statistical methods, including principal components analysis (PCA) and elliptic Fourier analysis (EFA). This confirmed that variation was continuous between the three species. *Sternbergia sicula* and *S. greuteriana* are sunk into *S. lutea* and a revised description provided. It is suggested that cultivar status is the most appropriate rank for the cultivated forms of the *S. lutea* complex. © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, **158**, 460–469.

ADDITIONAL KEYWORDS: Amaryllidaceae – CITES – conservation status – geographical distribution – Mediterranean – systematics.

INTRODUCTION

Sternbergia L. (Alliaceae, Amaryllidoideae) is a genus of seven (Mathew, 1983) to nine (Govaerts *et al.*, 2007) species of geophytes that are mainly distributed around the Mediterranean basin. Species diversity is highest in the eastern Mediterranean. Some species are valued in horticulture and have become naturalized elsewhere. The genus can readily be differentiated from other Eurasian Amaryllidoideae through possession of a solitary, goblet-shaped flower with an extended perianth tube (Mathew, 1983). Most species produce yellow flowers in the autumn, although in *S. vernalis* (Mill.) Gorer & J.H.Harvey and *S. candida* B.Mathew & T.Baytop anthesis occurs in spring, with the latter possessing a creamy–white perianth.

The majority of species within the genus are defined by discrete morphological characters, although *S. lutea* (L.) Ker Gawl. ex Spreng. is a notable exception. It was first described as *Amaryllis lutea* by Linnaeus (1753), before being reassigned to *Sternbergia* by Sprengel (1825). This was followed by the description of *S. sicula* Tineo ex Guss. in 1845. These two species are similar in their macromorphology, and Webb (1978) suggested that subspecific rank would be more appropriate because of the high level of morphological overlap between them. This led to their treatment as *S. lutea* subsp. *lutea* and *S. lutea* subsp. *sicula* (Tineo) D.A.Webb in *Flora Europaea* (Webb, 1980). However, this treatment has not been universally accepted; *S. sicula* and *S. lutea* were retained as species by Mathew (1984) in *The Flora of Turkey* and by Davis & Mathew in the CITES bulb checklist (Davis *et al.*, 1999). In their paper, in which a third closely related species was described (*S. greuteriana* Kamari & R.Artelari), Kamari & Artelari (1990) assigned specific status to *S. sicula* and separated it from *S. lutea* on the basis of vegetative and

*Corresponding author. E-mail: p.wilkin@kew.org

floral morphological characters. *Sternbergia greuteriana* is an endemic of Crete and the Eastern Aegean Islands and was said by Kamari & Artelari to show a strong similarity to *S. lutea*. *Sternbergia sicula* is distributed throughout the Aegean Islands, Crete, Cyclades, Greece, Italy, Sicily and Turkey. *Sternbergia lutea* has been recorded through the Mediterranean from Spain to Iran and the Caucasus, although this distribution has probably been artificially extended by its horticultural use (Mathew, 1983). A fourth taxon has also been described, *S. minoica* Ravenna. However, this is thought to be a form of *S. sicula* in which the scape fails to develop and thus the ovary remains subterranean, an occurrence which has been observed in several individuals growing in populations near the type locality in Crete.

Different systematists have employed a number of characters to separate the three species. Mathew (1983) and Kamari & Artelari (1990) used leaf width as a key character, with the latter authors also placing importance upon the cross-sectional shape and colour of fresh leaf material. Polunin & Huxley (1965) suggested that *S. sicula* and *S. lutea* could separated on the basis of the presence or absence of glandular cilia on the leaf margins, although Kamari & Artelari (1990) reported that no significant difference could be found in this character between either species or *S. greuteriana*. In his account of *Sternbergia* for *Flora Europaea*, Webb (1980) separated *S. lutea* subsp. *lutea* from subsp. *sicula* through the former having 4 to 15 mm wide leaves and 7 to 15 mm wide perianth segments, with the leaf margins usually being entire or sometimes obscurely crenulated and the latter having 3 to 5 mm wide leaves and 4 to 8 mm wide perianth segments and leaf margins with small but discernible crenulae. Webb also stated that there was a difference in the diploid chromosome number of the two subspecies (see below).

Kamari & Artelari (1990) and Artelari & Kamari (1991) placed strong emphasis on the shape and dimensions of the perianth segments as diagnostic characters. They suggested that the perianth segments of *S. sicula* were acute and oblanceolate and contrasted this with the obtuse and obovate forms found in both *S. lutea* and *S. greuteriana*. *Sternbergia greuteriana* and *S. lutea* were distinguished from each other by leaf and perianth segment dimensions, with *S. lutea* having significantly larger dimensions in each case (for example, they gave leaf width ranges of 2–5(–6) mm in *S. greuteriana* and 7–12 mm in *S. lutea*). They stated that *S. greuteriana* more closely resembles *S. lutea* than *S. sicula* in both morphology and karyology (Kamari & Artelari, 1990). As part of their recent survey of the genus, Pasche & Kerndorff (2002) employed filament length to separate *S. sicula* and *S. greuteriana*, giving ranges of 10–17 mm and 15–32 mm, respectively. However, Kamari & Artelari (1990) reported that although some differences occur in filament length between the three species, intraspecific variation renders it unusable as a diagnostic character. Pasche & Kerndorff (2002) separated *S. lutea* from *S. sicula* on the basis of leaf width and colour and perianth segment dimensions.

When these classifications were evaluated and checked against specimens from K, BM and RNG (see http://sweetgum.nybg.org/ih/ for herbarium acronyms) with the aim of writing an electronic multiaccess key, it was discovered that none of the characters used by previous authors enabled a key to these three species to be produced. This suggested that re-examination of species limits was necessary. Other than the studies cited above, recent taxonomic treatments of *Sternbergia* in, for example, Turkey (Mathew & Baytop, 1984), Spain (Morales & Castillo, 2004), the former USSR (Artjushenko, 1970) and the Aegean Islands (Kamari & Artelari, 1990) have each considered a country in isolation. Even the paper of Artelari & Kamari (1991) did not sample taxa outside Greece. The work of Pasche & Kerndorff (2002) was orientated towards plant material in cultivation. Thus, it appeared that the morphological characters of *S. sicula*, *S. lutea* and *S. greuteriana* had not been evaluated across the full extent of their geographical distributions since Webb (1978) and there has been no attempt to employ modern computational methods to explore variation in a group of species with complex variation patterns.

A number of conflicting chromosome counts have been published for *S. sicula* and *S. lutea*: Moore (1982) cited counts of $2n = 18$ and $2n = 22$ for the two species, respectively, whereas Löve & Löve (1974) listed counts of 12, 16, 18, 20, 22, 24 and 33 for *S. lutea*. Kamari & Artelari (1990) and Artelari & Kamari (1991) suggested a basic chromosome number of $x = 11$, with $2n = 22$ in all three species, although they commented that *S. lutea* can also be found to exhibit a count of $2n = 3x = 33$. As a result of such variability in chromosome number, the extent to which karyological data can be applied as a systematic research tool is limited until carefully gathered, population-level data are available. Molecular systematic methods have been applied to *Sternbergia* in two studies to date. Açik *et al.* (1997) reported that, whereas a number of other members of *Sternbergia* were separable on the basis of random amplified polymorphic DNA–polymerase chain reaction (RAPD-PCR) results, they were unable to separate *S. sicula* and *S. lutea* from each other. Meerow *et al.* (2006) suggested that *S. lutea* and *S. sicula* could not be differentiated, but that *S. colchiciflora* Waldst. & Kit. was a distinct taxon with significant sequence diver-

gence from *S. lutea*, *S. sicula* and *S. greuteriana*. The sequences used in that study are available from GenBank.

The shape and dimensions of perianth segments are among the main characters that have been used in delimiting species in this complex, e.g. by Kamari & Artelari (1990). Although these characters are well preserved in herbarium material, unlike the presence or absence of a glaucous central leaf stripe, all previous studies of perianth segment shape have been qualitative and thus potentially subjective. Therefore, it was considered that an assessment of the variation in these organs carried out on a quantitative basis would be of benefit when attempting a re-evaluation of the existing classification of these three species. The analysis of elliptic Fourier descriptors has been used by a number of authors in the quantitative analysis of organ shape. This method, first employed by Rohlf & Archie (1984), and then by White, Rentice & Verwist (1988) for plants (in research on *Betula*), allows the conversion of an outline into a mathematical expression by converting the coordinate data of the outline into Fourier coefficients. Mathematical techniques can then be applied to these data, such as principal components analysis (PCA), a method that was employed by Yoshioka *et al.* (2004) in their analysis of petal shape variation in *Primula sieboldii* E.Morr. This method was selected because of its sensitivity to shape variation and it is one of the more efficient methods of examining taxonomic groupings within a large sample of individuals, as commented on by White *et al.* (1988). No previous report of the application of this method to herbarium specimens was found, but it was felt important to base the assessment on individuals taken from as broad a geographical and ecological range as possible. It would be preferable to work with living material in order to examine those characters that are not preserved in herbarium material, but the quantity of material that would be required to examine the species complex throughout its large geographical range would be impractical to source from wild populations. Plants from cultivation would be more straightforward to acquire, but are the product of a process of selection for desirable characteristics and thus potentially not representative of the patterns of morphological variation in wild populations. In addition to using elliptic Fourier analysis (EFA), a morphometric study based on linear measurements was also carried out for comparative purposes. The latter method has been more widely used in recent systematic studies (see, e.g., Wilkin, 1998) Therefore, the variation within and between *S. sicula, S. lutea* and *S. greuteriana* was explored through the use of both a series of linear measurements and EFA, the results of each method then being subjected to PCA.

MATERIAL AND METHODS

The material held at BM, K and RNG of *S. sicula, S. lutea* and *S. greuteriana* was examined and specimens in good condition exhibiting all necessary organs were scored (see Appendix). An isotype of *S. sicula* is held at K (*Tineo* s.n.) and a digital image of the holotype of *S. lutea* (LINN 416/1) was examined. All of the specimens held at K of *S. greuteriana* have been determined by the authors of this species and many of them were cited by Kamari & Artelari (1990) and thus are paratypes. For the linear measurement-based analysis, measurements were taken for the following continuous characters: leaf width, leaf length, bulb width, bulb length, perianth tube length, perianth segment length, style length, filament length and spathe length. Additionally, the width of the perianth segment was recorded at a point 3 mm from the apex and at three-quarters, one-half and one-quarter of the length of the perianth segment. These characters are compared with those used in the taxonomic treatments cited in the Introduction (Webb, 1978, 1980; Mathew, 1983; Kamari & Artelari, 1990; Artelari & Kamari, 1991; Pasche & Kerndorff, 2002), leaf width was included in all studies. Fresh leaf cross-sectional shape, the colour of fresh leaves and leaf longitudinal central stripe presence/absence were excluded from our research because they are not available in dried material. However, both the authors' observations of cultivated material and other experts' knowledge of wild plants suggest that, while some plants can be assigned to the extreme character states of dark green or glossy green leaves, longitudinal central stripes present/absent and cross-sectional shapes which are canaliculate or flat, intermediates exist in all three cases. Leaf marginal cilia presence/absence was not found to be of systematic value (see Results below). Among the floral characters, perianth segment length and width and perianth segment shape were used both in these analyses and previous studies. However, multiple width measurements were used here to recover shape objectively rather than through subjective terminology. Spathe length and style length were added in this research to the previously used filament length.

Values were recorded for each character from each individual (some herbarium sheets consist of several plants), including the type specimens and, in cases where multiple leaves or flowers were present on the same individuals, mean values were recorded. This was in order to examine within- and between-population variation as far as it is possible from herbarium specimens. The inner and outer whorls of the perianth were identified in each individual and separate sets of values were recorded for each whorl. This was deemed necessary because of the significant differences present in the shape and dimensions of

perianth segments of the two whorls. The inner whorl tepals are usually narrower and possess a different apex shape than the outer whorl, although the degree of variation can differ. Therefore, data from the two whorls were analysed separately. Values were recorded to an accuracy of 0.1 mm using a Moore & Wright dial caliper. It should be noted, however, that because of the occurrence of hysteranthous leaf development, the age of some of the material used and the incomplete nature of some herbarium specimens, it was not possible to compile a complete data matrix for all the characters listed above. The PCA methods employed required a complete data set for each individual, so those individuals with incomplete data sets had to be removed from the data matrix. In order to preserve as large a sample group as possible, a number of characters which could not be universally scored had to be excluded. The resulting characters that were included in the final linear measurement-based PCA were as follows: perianth segment length, width at 3 mm from the perianth segment apex and at three-quarters, one-half and one-quarter of its length for segments from both the inner and outer whorls and the perianth tube length. These floral variables were chosen as they were present in the greatest proportion of examined material, whilst retaining the greatest number of examined characters. The linear measurements were standardized using the STAND batch command in NTSYS-pc (see below) before any analyses were run to meet assumptions of normality and equality of variance in the PCA.

Despite being excluded from the linear measurement-based PCA, the variation in leaf width was examined through the analysis of frequency distribution of mean leaf width values recorded for each individual, a procedure that was also applied to examine variation in the perianth segment length. Histograms were constructed for the distribution of leaf width and perianth tube length based upon the linear measurements and the resulting plots are given below. This analysis was run in Microsoft Excel [Microsoft Corporation, 1985–2001; version 10.4302.4219) SP-2] and PAST (Hammer, Harper & Ryan, 2001; version 1.62) The standardized linear measurement data were used to generate a correlation matrix upon which the PCA was run.

The specimens for the EFA were digitized using an inverted Epson Expression 10 000XL scanner attached to a Dell Precision 380 Intel Pentium 4® Personal Computer. The images were imported directly into Adobe Photoshop (Adobe Systems Inc., 2001; version 6.0.1) and saved as an RBG colour image (JPEG format). Manual isolation of the perianth segments was carried out before the images were imported into tpsDig (Rohlf, 2006; version 2.1) in order to extract the outline of each perianth segment. Outlines were recorded as a sequence of *xy* coordinates in a TPS file. These in turn were imported in Morpheus *et al.* (Slice, 1998; revision 01-30-98 beta) to carry out the EFA. The analysis was carried out using 35 harmonics and the resulting elliptic Fourier coefficients were saved into a central data matrix. The perianth segments that comprised the inner and outer whorls were separated, because their shapes differ, producing twin data matrices which were subject to separate PCA studies. Unlike the linear measurement-based analysis, each perianth segment was treated as an individual entity, producing multiple data sets for each individual. Invariant characters were removed from the matrix prior to the running of PCA. The elliptic Fourier descriptors were used to generate a variance/covariance matrix upon which a PCA was run for the data relating to both the inner and outer whorls. The resulting eigenvalues were extracted and used to generate principal component axes upon which the original entities were projected. All statistical analyses were carried out in NTSYSpc (Rohlf, 2005; version 2.20d). Large volumes of data were generated by both the linear measurement-based and the EFA-based PCA; these are available on request from the authors.

RESULTS

Examination of material of *S. lutea*, *S. sicula* and *S. greuteriana* showed that leaf margin crenulation was of little systematic value. The majority of specimens of *S. lutea* examined under 25 × magnification showed a similar degree of leaf margin crenulation to that in *S. sicula*. In a few individuals of *S. lutea*, the crenulae varied in size and position.

Two of the characters most heavily weighted by Pasche & Kerndorff (2002), Kamari & Artelari (1990) and Artelari & Kamari (1991) in their classifications of *S. lutea*, *S. sicula* and *S. greuteriana* were leaf width and perianth tube length. The distribution of mean leaf widths among the specimens examined after standardization is given in a histogram presented as Fig. 1. Although the distribution is approximately normal, there is an element of bimodality, with two peaks present at leaf widths of 2 and 6 mm, respectively. However, leaf width variation is not discrete among the three taxa studied. The distribution of perianth tube length is given in a histogram presented as Fig. 2. It is similar to the leaf width data presented in Figure 1 in that it is weakly bimodal. Again, this character does not display discrete variation between the three species. This variation is contrasted with the use of numerical ranges in these characters to define discrete entities in the works cited above. The other linear measurement characters, including perianth segment dimensions, show

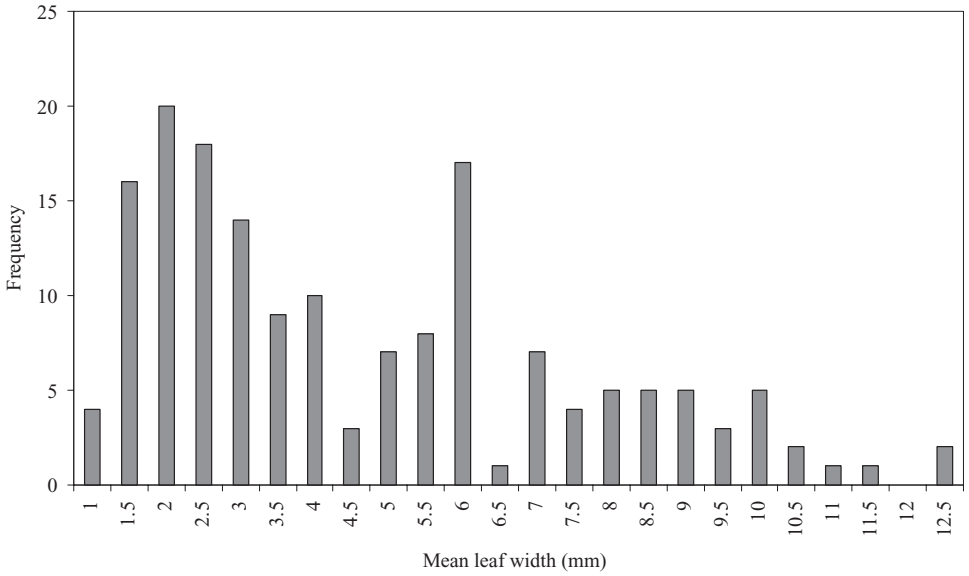

Figure 1. Histogram of mean leaf width values.

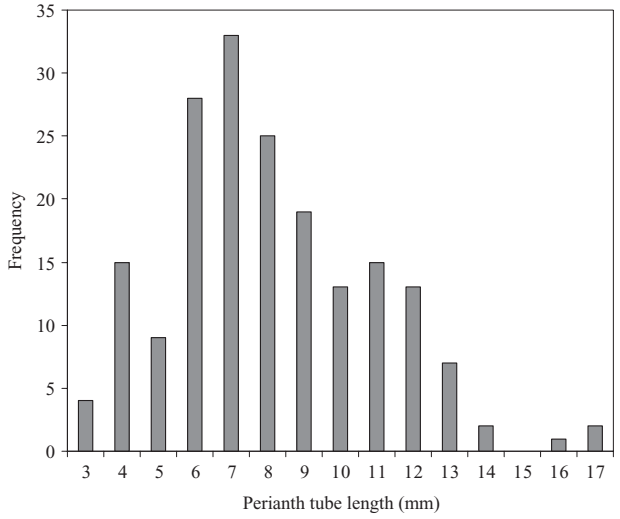

Figure 2. Histogram of perianth tube length values.

similar frequency distributions but are not presented here to save space.

Matrix plots of the PCA products run on the linear measurements are given in Figs 3 and 4 and the corresponding variable loadings and eigenvalues in Tables 1 and 2. The first and second principal components together account for 77% of the variance within the data, and the third principal component accounts for a further 7.8% of the variation (Table 2). Component 1 is mainly variation in size, as in most PCA studies of variation. It can be seen from Figs 3 and 4 that the distributions of the three species in multivariate space are greatly interspersed, although some trends are present within the data. Individuals identified as *S. lutea* and *S. sicula* are highly dispersed across both axes, although some separation is shown on the first principal component axis, with individuals of *S. sicula* being focused towards the lower end and individuals of *S. lutea* towards the higher end. However, there is no indication that they occupy distinct areas of multivariate space. Individuals of *S. greuteriana* demonstrate a broad range of distribution on the second principal component, but occupy a narrow range on the first component. However, the

Table 1. Table of variable loadings on each of the three components for the linear measurement-based principal components analysis (PCA)

	Axis	1	2	3
Inner whorl	3 mm	0.886	0.023	0.069
	3/4L	0.914	–0.125	0.090
	1/2L	0.915	–0.090	0.193
	1/4L	0.825	–0.006	0.322
	Length	0.775	–0.365	–0.443
Outer whorl	3 mm	0.814	0.270	0.017
	3/4L	0.926	0.064	–0.068
	1/2L	0.927	0.062	0.044
	1/4L	0.776	0.227	0.320
	Length	0.789	–0.344	–0.449
	Peri. tube	0.280	0.796	–0.456

3 mm, width of perianth segment 3 mm down from the apex; 3/4L, 1/2L, 1/4L, width of the perianth segment at the three-quarter, half and quarter point of the perianth segment; Length, perianth segment length. Peri. tube, length of perianth tube. The inner and outer whorls have been separated.

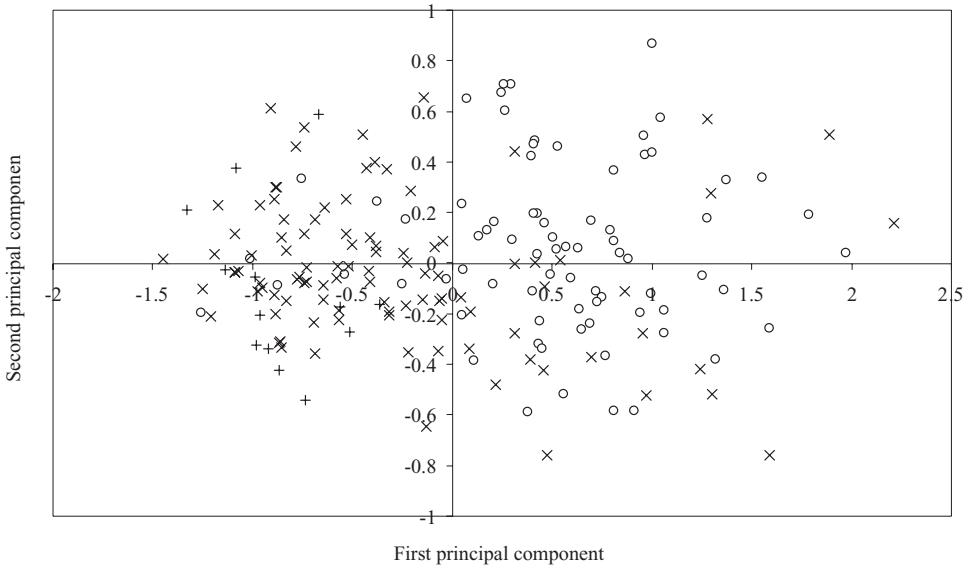

Figure 3. Matrix plot of linear measurement-based principal components analysis (PCA) of the first and second principal components; ○, *Sternbergia lutea*; ×, *S. sicula*; +, *S. greuteriana.*

Table 2. Table of eigenvalues for the first six principal components, with the percentage and cumulative variance for each component

	Eigenvalue	Per cent	Cumulative
1	7.421	67.468	67.468
2	1.043	9.478	76.945
3	0.869	7.899	84.844
4	0.578	5.258	90.103
5	0.496	4.509	94.612
6	0.185	1.682	96.294

distribution of individuals of *S. greuteriana* across both components overlaps almost entirely with the ranges shown by individuals of *S. sicula* and *S. lutea*. It can be seen from Table 1 that all the factor loadings are relatively high (greater than 0.5) on the first component, with the notable exception of perianth tube length. This character is the only one with a high positive loading on the second component, on which perianth segment length (both inner and outer whorl) has a fairly high negative loading. Thus, component 1 is recovering overall perianth segment size and shape, whereas component 2 is mainly based on the ratio of perianth tube length to perianth segment length The majority of loadings on the third component are low, with the exception of the quarter-width values and the segment length of both perianth whorls and the perianth tube length, with the latter three characters receiving strong negative loadings.

The matrix plots of the principal components generated by the PCA run on the data produced by the EFA are given in Fig. 5 for the inner perianth segments. The outer perianth segments gave a similar result; it is not reproduced here to save space. Little structure is present within the data and there is nothing to suggest that three distinct species are present. Therefore, the separation of the three species by Kamari & Artelari (1990) and Artelari & Kamari (1991) on the basis of perianth segment shape is not supported by our data. As in the linear measurement-based PCA, *S. greuteriana* occupies a more restricted area of multivariate space, although it is less pronounced than in Fig. 3. As a result of the high number of variables generated by the EFA of the perianth segments, it has not been possible to reproduce the variable loadings within this article, but they are available from the authors upon request.

DISCUSSION

Patterns of variation and the existing species limits

A wide range of characters has been employed in the division of *S. lutea*, *S. sicula* and *S. greuteriana*, but only leaf width, colour, cross-sectional shape and longitudinal central strip presence/absence, perianth tube length and the size and shape of the perianth segments have been routinely applied in recent studies (Webb, 1978; Mathew, 1983; Kamari & Artelari, 1990; Artelari & Kamari, 1991; Pasche & Kerndorff, 2002). The results of this study suggest that all of these characters fail to show discrete patterns of variation, an idea further supported by the linear measurement-based PCA (Figs 3, 4). It is

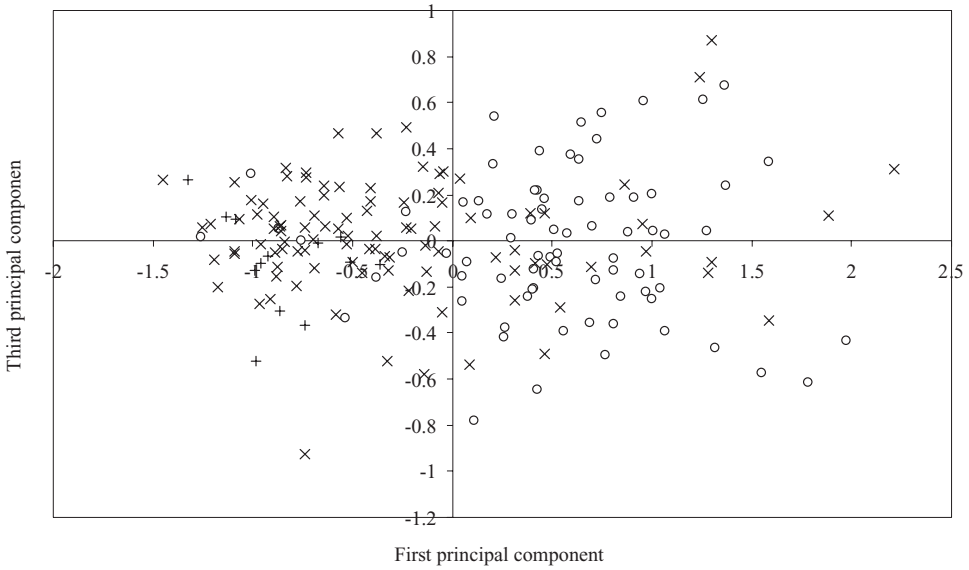

Figure 4. Matrix plot of linear measurement-based principal components analysis (PCA) of the first and third principal components; ○, *Sternbergia lutea*; ×, *S. sicula*; +, *S. greuteriana*.

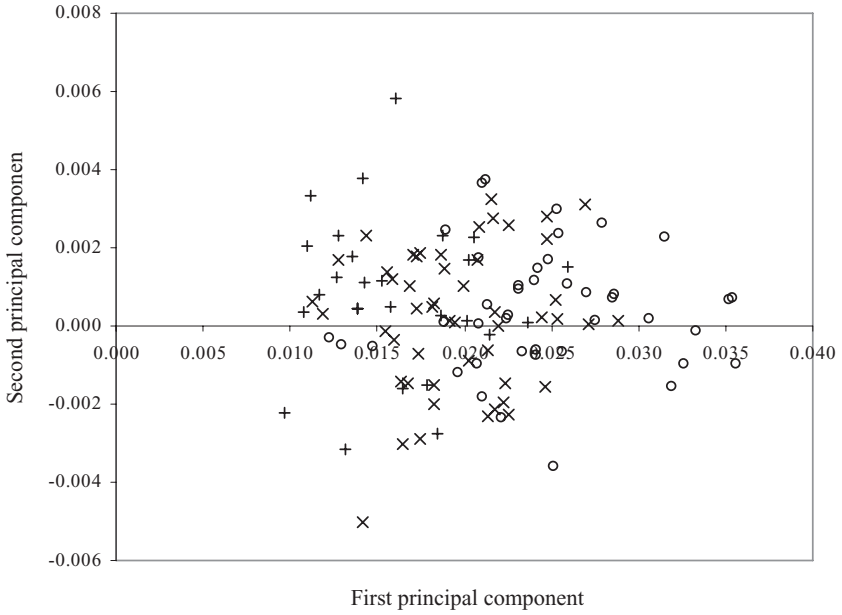

Figure 5. Matrix plot of the first and second principal components of the elliptic Fourier analysis (EFA) data for the inner perianth whorl; ○, *S. lutea*; ×, *S. sicula*; +, *S. greuteriana*.

possible that the frequency peaks of leaf width at 2 and 6 mm in Fig. 1 correspond to the concepts of *S. sicula* and *S. lutea*, respectively, but they are not separate morphological entities.

The relationship between perianth tube length and perianth segment size may act as a means of distinguishing elements of the variation. To explore this variation further, examination of living populations would be beneficial, especially with regard to pollination biology in relation to floral morphology. Studies of molecular marker variation and ploidy level would also be helpful. Leaf anatomical studies to review in particular the cross-sectional shape and the nature of the longitudinal central stripe are also desirable. Very limited data on *S. lutea* are available in Artjushenko (1970). The limited molecular systematic studies to date (Açik *et al.*, 1997; Meerow *et al.*, 2006) have yielded similar results to those presented here, in so

far as none has shown significant divergence between *S. lutea*, *S. sicula* and *S. greuteriana*. Various ploidy states of *S. lutea* have been recorded (e.g. Löve & Löve, 1974; Moore, 1982; Kamari & Artelari, 1990; Artelari & Kamari, 1991). No clear patterns of variation emerge from such studies, but polyploids may be confined to plants attributable to *S. lutea*.

Tepal shape and EFA

Kamari & Artelari (1990) placed particular significance on the shape of the perianth segments as an identification characteristic by separating *S. sicula* from *S. lutea* and *S. greuteriana* on the basis that the former possessed acute, oblanceolate segments compared with obtuse, obovate segments expressed in the latter two. *Sternbergia greuteriana* was separated from *S. lutea* on the basis of leaf width, a conclusion that is not supported by the results of our linear measurement-based studies. Furthermore, the separation of *S. sicula* from *S. lutea* on the basis of linear measurements is not supported by this research, a principle that is strengthened by the EFA-generated data. The quantitative analysis of segment shape, as presented in Fig. 5 for the inner perianth whorl, shows that all the individuals are well dispersed in multivariate space and that the extent of overlap present between them makes separation of any of the three species on the basis of segment shape impossible. The outer whorl variation exhibited the same pattern. It is unfortunate that variation in the perianth tube could not be taken into account in the EFA analysis, although it is possible that this could be effected by the use of living specimens in further such studies.

Taxonomy

This research has highlighted a lack of distinctive characters by which *S. sicula*, *S. lutea* and *S. greuteriana* can be separated. In addition to the floral characters used in this research, Kamari & Artelari (1990) and Artelari & Kamari (1991) suggested that *S. sicula* can be distinguished on the basis of the presence of a central glaucous leaf stripe that is absent from individuals of *S. greuteriana* and *S. lutea* and the shade of green of the leaf. As a result of the degradation of leaf pigmentation during the preservation of herbarium material, these features could not be examined. However, our observations of cultivated plants suggest that the occurrence of a central leaf stripe and leaf colour is continuously variable within populations of these taxa and this renders it ineffective as an identification tool. This is also supported by observations of plants in the field (B. Mathew, pers. comm.).

As a result of the continuous variation shown in leaf width, tube length and perianth segment size and shape, it is not possible to differentiate the three existing species from each other. Therefore, *S. sicula*, *S. greuteriana* and *S. lutea* should be regarded as a single species, *S. lutea* (see below). Webb (1978) placed *S. sicula* as a subspecies of *S. lutea* and separated the two entities on the basis of leaf width, leaf crenulation and perianth segment width. The results of this study do not support this approach. There is no geographical basis to the variation traditionally assigned to *S. lutea* and *S. sicula*. Although it would be desirable to retain the taxonomic concepts of *S. lutea* and *S. sicula* at the rank of variety, especially for the horticultural community, there is no character which permits this to be done. Perhaps cultivar status is most appropriate for horticultural selections.

Description

S. lutea (L.) Ker Gawl. ex Spreng, Syst. Veg. 2:57 (1825) Typus: 'Habitat in Hispania, Italis, Thracia', date unknown, LINN 416.1 (Holo- LINN, digital image!)

Amaryllis lutea L., Sp. Pl. 292 (1753)

Oporanthus luteus (L.), Herb. Appendix [Bot. Reg.] 38 (1821)

S. aurantiaca Dinsm. in Post, Fl. Syria ed. 2, 2:607 (1934) (no specimens cited)

S. sicula Tineo ex Guss. Fl. Sic. Syn. 2:811 (1844-45) Typus: Italy, Sicily, Militello, Val di Noto, 1847, *Tineo* s.n. (Iso- K!)

Oporanthus siculus (Tineo ex Guss.) Parl. Fl. Ital. 3:97 (1858)

S. lutea (L.) Ker Gawl. ssp. *sicula* (Tineo ex Guss) D.A.Webb, Bot. J. Linn. Soc. 76:358 (1978)

S. greuteriana Kamari & R.Artelari, Willdenowia 19:371 (1990) Typus: Greece, Crete, Nomos Lasithiou, Ep. Lasithiou: NW side of Lasithi Plateau, 10.x.1985, *Kamari* 20292 (Holo- UPA, iso- B)

BULB globose to ovoid, (1.2–)2.4–4.6(–5.7) cm in diameter; may be continuous with an extended neck 0–8.6(–10.8) × 0–1.6 cm which partially encloses the sheath; tunic chartaceous, turning dark brown when dry. SHEATH tubular, 1.7–14.6 × 0.2–2.1 cm, tubular, tapering to an abruptly acute apex to one side; membranous in texture. INDUMENTUM of sparse, fine white appressed hairs on both leaf surfaces, otherwise glabrous. LEAVES 4–6(–7), linear to narrowly lanceolate, 0.7–33.3(–39) × (0.7–)1–1.2 cm at flowering, appearing with or just after the flowers, elongating after fertilization; apex acute; margins minutely crenulate with regular or irregular crenulae; upper surface slightly furrowed, underside keeled; surfaces concolorous, bright to dark green, occasionally with a greyish or greenish median stripe when fresh, drying to a dark olive green to brown; leaves chartaceous when dry. INFLORESCENCE a solitary sessile flower;

scape 1(–5), 0.3–20 × 0.1–0.5 cm, held erect at flowering, elongating and curving toward the ground at fruiting; smooth or faintly ridged. SPATHE (0.6–)1–5(–6) cm long, lanceolate, apex acute, occasionally apically divided, attached below and completely enclosing ovary and extending part-way up perianth tube; membranous. OVARY inferior, ovoid to oblongoid–ovoid, 0.4–1.4 × 0.1–0.8 cm at flowering, epidermis smooth or with faint ridges continuous with segment veins when dry. FLOWER wholly deep yellow in colour; erect at flowering; tube 0.2–1.9 × 0.1–0.4 cm, with perianth segments inserted at the apex; segments 6(7) in two separate whorls that may or may not be distinct, where distinct, outer whorl segments broader and apically acute, sometimes inner whorl apically obtuse, outer whorl often cucullate; 1.6–6 × 0.2–2.2 cm. FILAMENTS (0.7–)1.1–5 cm in length, thread-like; didynamous; anthers dorsifixed, dehiscing extrorsely. STYLE 1.6–5.5(–6.5) cm in length, projecting above anthers; stigmatic surface capitate. FRUIT a few-seeded capsule, drying dark brown: dehiscence not observed. SEEDS globose, 2.5–3(–3.5) mm in diameter, normally with a fleshy aril extending from one pole completely or partly to the equator.

Phenology: Flowering between September and November.

Distribution and ecology: Found throughout southern Europe from the South of France to Spain, Italy and Greece and across North Africa east from Morocco extending into Asia as far as the Caucasus and Iran. This range may have been artificially extended by cultivation and introduction. It is found from near sea level to *c.* 1500 m in elevation in stony habitats on limestone or in scrubland in the open where it receives full sun and can be common in cultivated areas.

Conservation status: Given the extremely broad geographical range of this species, its conservation status is likely to be LC (IUCN, 2001).

Specimens examined: see Appendix.

ACKNOWLEDGEMENTS

We would like to thank Brian Mathew, Aaron Davis, Martyn Rix, Gina Douglas of the Linnean Society, Vicky Papworth and John Hunnex of the Natural History Museum Botany Department and Julie Hawkins and Stephen Jury at the University of Reading. Dave Simpson and Simon Mayo made constructive comments on an earlier version of this manuscript and the latter helped extensively with the EFA. We also thank two anonymous referees who strengthened the paper through their comments.

REFERENCES

Artelari R, Kamari G. 1991. The genus *Sternbergia* (*Amaryllidaceae*) in Greece. II. Taxonomy and karyology. *Botanica Chronica* **10:** 239–251.

Artjushenko ZT. 1970. *Amaryllidaceae J. St. Hil. SSSR. Morphology, systematics and uses*. Leningrad: Akademii Nauk SSSR Botanicheskii Instituti V.L. Komarova.

Açik L, Samanci B, Duman H, Ünal F. 1997. Polymorphism and phylogenetic relations among Turkish species in the genus *Sternbergia* (*Amaryllidaceae*) as determined by RAPD-PCR. *Turkish Journal of Botany* **21:** 265–268.

Davis AP, McGough HN, Mathew B, Grey-Wilson C. 1999. *CITES bulb checklist*. Kew: Royal Botanic Gardens.

Govaerts R, Snijman DA, Marcucci R, Silverstone-Sopkin PA, Brullo S. 2007. *World checklist of Alliaceae*. Kew: The Board of Trustees of the Royal Botanic Gardens. Published on the Internet. Available at http://www.kew.org.uk/wcsp/monocots/ (accessed 14 August 2007).

Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: palaeontological Statistics software package for education and data analysis. *Palaeontologia Electronica* **4**. Available at http://palaeo-electronica.org/2001_1/past/issue1_01.htm

IUCN. 2001. *IUCN Red List Categories: Version 3.1. Prepared by the IUCN Species Survival Commission*. Gland, Switzerland & Cambridge: IUCN.

Kamari G, Artelari R. 1990. Karyosystematic study of the genus *Sternbergia* (Amaryllidaceae) in Greece. I. South Aegean Islands. *Willdenowia* **19:** 367–388.

Linnaeus C. 1753. *Species Plantarum* 2. Stockholm.

Löve Á, Löve D. 1974. *Cytotaxonomical atlas of the Slovenian Flora*. Lehre: J. Cramer.

Mathew B. 1983. A review of the genus *Sternbergia*. *The Plantsman* **5:** 1–16.

Mathew B. 1984. *Sternbergia*. In: Davis PH, ed. *Flora of Turkey and the East Aegean islands*, Vol. 8. Edinburgh: Edinburgh University Press, 360–364.

Mathew B, Baytop T. 1984. *The bulbous plants of Turkey*. London: Batsford.

Meerow AW, Francisco-Ortega J, Kuhn DN, Schnell RJ. 2006. Phylogenetic Relationships and Biogeography within the Eurasian Clade of Amaryllidaceae Based on Plastid *ndhF* and nrDNA ITS Sequences: Lineage Sorting in a Reticulate Area? *Systematic Botany* **31:** 42–60.

Moore DM. 1982. *Flora Europaea. Checklist and chromosome index*. Cambridge: Cambridge University Press.

Morales R, Castillo J. 2004. El género *Sternbergia* (Amaryllidaceae) en la Península Ibérica. *Anales del Jardin Botánico de Madrid* **61:** 119–128.

Pasche E, Kerndorff H. 2002. Die Gattung *Sternbergia* Waldst. & Kit. (Asparagales, Amaryllidaceae) im Vergleich, unter besonderer Berücksichtigung der wiederentdeckten *Sternbergia schubertii* Schenk. *Stapfia* **80:** 395–417.

Polunin O, Huxley A. 1965. *Flowers of the Mediterranean*. London: Chatto & Windus.

Rohlf FJ. 2005. *NTSYSpc: numerical taxonomy system ver. 2.20d*. Setauket, NY: Exeter Publishing. Available at http://www.exetersoftware.com/cat/ntsyspc/ntsyspc.html

Rohlf FJ. 2006. TpsDig Version 2.1. Digitising software; Available at http://life.bio.sunysb.edu/morph/

Rohlf FJ, Archie JW. 1984. A comparison of Fourier methods for the description of wing shape in mosquitoes (Diptera: Culicidae). *Systematic Zoology* **33:** 302–317.

Slice D. 1998. MORPHEUS *ET AL.* Software for morphometric research. Available at http://life.bio.sunysb.edu/morph/morpheus

Sprengel K. 1825. *Systema Vegetabilium, Vol. 2*. Göttingen.

Webb DA. 1978. Flora Europaea. Notulae Systematicae. No. 20, Short Note 278. Amaryllidaceae. *Botanical Journal of the Linnean Society* **76:** 358.

Webb DA. 1980. Amaryllidaceae. In: Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH, Walters SM, Webb DA, eds. *Flora Europaea* **5:** 75–84. Cambridge: Cambridge University Press.

White R, Rentice HC, Verwist T. 1988. Automated image acquisition and morphometric description. *Canadian Journal of Botany* **66:** 450–459.

Wilkin P. 1998. A morphometric study of *Dioscorea quartiniana* A. Rich. (Dioscoreaceae). *Kew Bulletin* **54:** 1–18.

Yoshioka Y, Iwata H, Ohsawa R, Ninomiya S. 2004. Analysis of petal shape variation of *Primula sieboldii* by elliptic Fourier descriptors and principal component analysis. *Annals of Botany* **94:** 657–664.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Table of specimens used for analysis.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.