

HYBRIDIZATION BETWEEN *SCILLA NON-SCRIPTA* AND *S. HISPANICA* (LILIACEAE) IN THE NETHERLANDS

J. H. IETSWAART, S. J. M. DE SMET and J. P. M. LUBBERS

Vakgroep Biosystematiek, Biologisch Laboratorium, Vrije Universiteit, De Boelelaan 1087, 1081 HV Amsterdam

SUMMARY

Six *Scilla non-scripta*/*S. hispanica* populations in The Netherlands have been investigated with regard to their morphology, reproduction, chromosomes and ecology.

All six belong to the larger Dutch populations and are situated in the western part of The Netherlands, in man-made woods (*Alno-Padion* vegetations) on former beach planes or beach walls. One population consists of *S. non-scripta*, another mainly of *S. hispanica* specimens. The other four are morphologically intermediate between the two taxa and hybrid swarms. Characters of the hybrids range from *S. hispanica* to *S. non-scripta*, but in general habit they are often more like the latter taxon. Reproduction in the populations is mainly by means of seeds. The chromosome number found in all populations is $2n=16$ ($x=8$), while only some minor differences in shape and size of the chromosomes have been noted between *S. non-scripta* and *S. hispanica*. Finally it will be concluded that the two taxa are conspecific, and they will be given a new status. Basionym, type and synonyms of the two taxa will be given.

1. INTRODUCTION

Scilla non-scripta (Linnaeus) Hoffmannsegg et Link and *S. hispanica* Miller form, together with *S. italica* Linnaeus, a somewhat distinct group within the genus *Scilla* Linnaeus, characterized by coalescent bulb scales (as against free), two (as against none or one) bract(s) and more or less coherent (as against free) perianth segments. On this basis the Flora Europaea (TUTIN et al. 1980) places these species in the genus *Hyacinthoides* Medikus. This is not followed by us because the differences regarding the morphological variation within *Scilla* as a whole are relatively unimportant (see also HEUKELS & VAN DER MEIJDEN 1983). In addition to the taxa mentioned *S. vincentina* Hoffmannsegg et Link and *S. reverchonii* Degen et Hervier also belong to the group, and they are both related to or may even be varieties of *S. italica* (HEYWOOD 1980).

S. vincentina and *S. reverchonii* are found locally in the southern part of the Iberian peninsula, while *S. italica* grows on both sides of the Franco-Italian border (HEYWOOD 1980). *S. hispanica* as well as *S. non-scripta* are atlantic elements in the European flora. The native distribution of *S. hispanica* is confined to the Iberian peninsula and the opposing part of North-Africa, whilst it is naturalized in France, England, Ireland, Italy and Yugoslavia. *S. non-scripta* occurs

Table 1. Characters of *S. hispanica* and *S. non-scripta* from the literature.

	<i>S. hispanica</i>	<i>S. non-scripta</i>
Bulbs	2-4(-7) cm in diameter, purple-blue outside (sometimes greenish)	1-3(-5) cm in diameter, greyish outside (sometimes greenish)
Leaves	4-8 per bulb, 20-50 cm long, 10-35(-40) mm wide	3-6(-9) per bulb, 20-50 cm long, 6-15(-25) mm wide
Scapes	Erect or somewhat curved, up to 50 cm long	Curved towards the apex, up to 50 cm long
Flowers	4-16 per scape, arranged all around the shape or slightly unilateral, with 5-20 mm long pedicels (in fruiting stage up to 40 mm); campanulate, blue (pink or white), not scented	4-16(-20) per scape, unilateral, with 3-10 mm long pedicels (in fruiting stage up to 30 mm); cylindrical-campanulate, violet-blue (pink or white), scented
Perianth segments	Apex more or less bent outwards, c. 12 mm long	Apex recurved, 2-4 mm wide, 15-20 mm long
Stamens	All equal, inserted at the middle of the perianth segments; anthers blue	Unequal, the outer 3 inserted at the middle of the perianth segments, the inner 3 in the lower quarter; anthers cream-coloured
Chromosome number	2n = 16 (24)	2n = 16 (24)

as native in the north-western part of the Iberian peninsula, where it is sympatric with *S. hispanica*, and it is further found in France, England, Ireland, Belgium and locally in The Netherlands and West-Germany. Moreover it is naturalized in Italy and Romania (DUPONT 1962; HEYWOOD 1980; MEUSEL 1965; ROISIN 1969; SCHUMACHER-WALDBRÖL 1939).

In table 1 the characters of *S. hispanica* and *S. non-scripta* are given as they are found in various publications, referring to natural populations as well as cultivated specimens (BLACKMAN & RUTTER 1954; BONNIER & DOUIN 1929; BOOM & RUYS 1950; CLAPHAM et al. 1962; COUTINHO 1939; FIORI 1923; GARCKE et al. 1972; HEGI 1939; HEUKELS & VAN DER MEIJDEN 1983; HEYWOOD 1980; VAN OOSTSTROOM & REICHEL 1964; WILLKOMM & LANGE 1870).

The aim of the present study is to investigate the morphology, chromosome number and shape, and the reproduction of *S. hispanica* and *S. non-scripta* in The Netherlands. The general taxonomic position of *S. non-scripta* and *S. hispanica* will be also considered.

2. METHODS IN GENERAL

These investigations were carried out in 1981. From twenty five *Scilla* populations visited, six have been chosen for comprehensive study (approximate numbers of specimens are given between brackets): Sorghvliet, Den Haag (10^5 - 10^6); Zuidwijk, Wassenaar (10^5 - 10^6); Duivenvoorde, Voorschoten (c. 10^3); Vogelenzangse Bos, Vogelenzang (c. 10^3); Duinvliet, Overveen (10^3 - 10^4); and Wildrijk, Sint Maartenszee (10^5 - 10^6). Within The Netherlands context all these six populations can be classified as large. The populations are all situated in

Table 2. Characters of the six *Scilla* populations. For nearly every character a mean, minimum and maximum value is given. For characters of fruits and seeds see table 4.

	Duivenvoorde	Zuidwijk	Duinvliet	Sorghvliet	Wildrijk	Vogelenzang
Bulb length in mm	24 (20-26)	19 (14-26)	22 (16-26)	25 (13-31)	21 (16-25)	13 (11-17)
Bulb width in mm	23 (18-25)	21 (12-33)	19 (15-27)	24 (13-31)	18 (15-24)	11 (9-15)
Leaf number per plant	5 (3-9)	6 (3-9)	5 (3-8)	6 (3-10)	5 (3-7)	5 (3-7)
Leaf length in cm	28 (20-39)	27 (13-38)	39 (20-44)	31 (19-42)	37 (27-48)	20 (13-26)
Leaf width in mm	17 (11-24)	13 (7-20)	13 (7-20)	15 (7-23)	13 (9-17)	12 (9-17)
Stem number per plant	1 (1-2)	1	1	1 (1-3)	1	1
Stem length in cm	40 (26-51)	38 (20-54)	37 (25-50)	45 (29-58)	40 (28-59)	20 (13-29)
Stem width in mm	5 (3-7)	4 (2-12)	3 (2-5)	4 (2-6)	4 (2-5)	2 (1-3)
Stem apex position (1 is vertical, 2 is 45° inclined etc.; inclined means also flowers more or less unilateral)						
Flower number per stem	1 (1-2)	1 (1-3)	1.5 (1-3)	1.5 (1-3)	1.5 (1-3)	1.5 (1-2)
Bract length of lowest flower in mm	16 (7-16)	9 (2-23)	6 (3-14)	9 (3-18)	7 (4-5)	5 (3-9)
Pediceal length of lowest flower in mm	25 (13-37)	18 (10-25)	16 (11-22)	19 (10-37)	16 (8-27)	17 (10-24)
	20 (8-30)	11 (4-32)	11 (6-20)	16 (5-42)	9 (4-21)	10 (5-18)
Measure of length of tubiform part						
recurring of perianth in mm	10 (6-14)	12 (8-18)	10 (6-14)	11 (7-15)	10 (6-13)	11 (8-14)
perianth length of perianth segments	18 (15-21)	18 (15-23)	16 (9-21)	18 (14-23)	16 (11-21)	16 (11-18)
segment in mm	5 (4-7)	4 (3-8)	4 (3-6)	4 (2-6)	4 (3-5)	4 (2-6)
Width of perianth segments in mm						
Filament of outer stamina	3 (2-4)	2.5 (2-4)	2 (1.5-3.5)	2.5 (2-4.5)	2 (1.5-4)	2.5 (2-3)
length in mm	1/2 (3/10-6/10)	1/2 (3/10-6/10)	1/2 (2/10-6/10)	1/2 (3/10-6/10)	1/2 (2/10-6/10)	1/2 (3/10-6/10)
inserted at (from base)						
Filament of inner stamina	4 (3-5.5)	3.5 (2-5)	3 (2-4)	3.5 (3-6)	3 (2-5)	3 (3-4)
length in mm	1/6 (2/10-3/10)	1/5 (2/10-3/10)	1/4 (1/10-4/10)	1/4 (2/10-4/10)	1/4 (1/10-3/10)	1/5 (1/10-3/10)
inserted at (from base)						
Anther	length in mm (outer and inner equal)					
colour (0 is cream, 1 is blue)	5 (3-6)	4 (3-5)	5 (4-6)	4.5 (3-5)	4 (3-5)	4 (3-4)
	1 (0-1)	0	0	0 (0-1)	0	0
Flower colour (% of respectively blue, light blue, pink, white)	10+80+10+0	93+0+7+0	98+0+0+2	90+8+2+0	80+0+20+0	100+0+0+0
Flower scent	++	+	+	+	+	±

the coastal area of Zuid- and Noord-Holland, in parks and on estates on former beach planes or beach walls (DOING 1962/63). All populations grow in humous sand, five in woods and the population at Duivenvoorde in a grass vegetation surrounded by woods. The latter should be considered to belong to the *Arrhenatherion elatioris* and the other vegetations all to the *Alno-Padion* (according to WESTHOFF & DEN HELD 1975).

From each of these populations forty specimens were randomly selected and the morphological characters studied in situ. In an area of radius 15 cm round each plant the number of seedlings were counted, and then ten specimens were uprooted for morphological study of the underground parts and chromosomes. The remaining thirty were marked for further observations on the production of fruits and seeds.

In addition herbarium specimens of the *Scilla* taxa from natural sites in southern and western Europe have been studied from the herbaria of Leiden and Madrid, as well as type specimens from the British Museum (Natural History, London).

3. RESULTS

3.1. Morphology

In *table 2* the characters measured for the six populations are summarized. All characters (except one) have been put into numerical form for further comparison. In *table 3* the characters are given for ten specimens each of *S. hispanica* and *S. non-scripta* from Spain and France respectively.

From *tables 1-3* the following conclusions can be drawn. The populations of Duivenvoorde and Vogelenzang show the greatest differences. A number of characters overlap slightly or not at all (e.g. bulb size, length and width of stem, position of stem apex, number of flowers per stem, anther colour and flower scent). The Vogelenzang population agrees quite well with *S. non-scripta* as this taxon emerges from *tables 1* and *3*; the greater part of the Duivenvoorde population fits *S. hispanica*. The other four populations are intermediate and may be regarded as hybrid populations. A distance diagram according to WELLS (1980) (*fig. 1*, for which nearly all characters from *tables 2* and *3* have been used) makes this rather plausible. Further it can be concluded that natural forms of *S. hispanica* are smaller and cultivated ones bigger than *S. non-scripta*.

3.2. Reproduction

On the uprooted bulbs some offsets have been observed only in the Vogelenzang population. Bulbets have been found on some dried specimens with damaged bulbs from the Sorghvliet population (see WILSON 1959).

Fertility of the pollen has been studied for one flower of the forty specimens selected from each of the six populations, by staining with lactophenol. The results are given in *fig. 2*, from which it can be concluded that the pollen fertility of the populations Duivenvoorde, Zuidwijk, Duinvliet, Sorghvliet and Wildrijk

Table 3. Characters of Spanish *S. hispanica* and French *S. non-scripta* from ten herbarium specimens of each, from natural sites. For each character is given a mean, minimum and maximum value.

	S. hispanica	S. non-scripta
Leaf length in cm	15 (12-20)	21 (16-29)
Leaf width in mm	8 (5-13)	7 (6-14)
Stem length in cm	22 (14-33)	28 (20-34)
Stem width in mm	3 (2- 4)	2 (1- 3)
Stem apex position (1 is vertical, 2 is 45° inclined etc.; inclined means also flowers more or less unilateral)	1 (2)	2 (1)
Flower number per stem	7 (5-10)	6 (4-12)
Bract length of lowest flower in mm	17 (7-22)	18 (13-24)
Pedicel length of lowest flower in mm	10 (3-21)	7 (2-14)
Measure of length of tubiform part of recurving perianth segments	length of perianth in mm length of perianth segment in mm	9 (6-13) 8 (6-11)
Width of perianth segment in mm	13 (10-14)	16 (11-20)
Filament of outer stamina	length in mm inserted at (from base)	3 (2- 4) 3 (2- 4)
Filament of inner stamina	length in mm inserted at (from base)	2.5 (1.5-3.5) 1/2 (2/10-6/10)
Anther	length in mm (outer and inner equal) colour (0 is cream, 1 is blue)	2 (1.5-3) 1/2 (3/10)-7/10)
	3 (2- 4) 1 (0)	4 (2- 5) 0

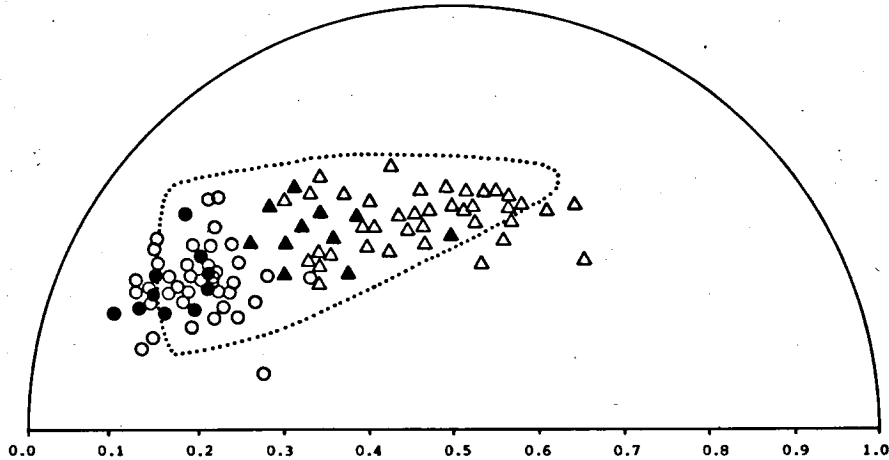


Fig. 1. Distance diagram (after WELLS) for the characters a) of the six Dutch *Scilla* populations (Δ Duijenvoorde, \circ Vogelenzang, the other four Dutch populations together); b) of Spanish *S. hispanica* (\blacktriangle) and French *S. non-scripta* (\bullet). See also tables 2 and 3.

is high (mean 89%–96%), and of the Vogelenzang population considerably lower (mean 76%).

Further, the number of fruits per plant and the number of seeds per fruit as well as per plant have been established. These data are given in *table 4*. From this table it becomes clear that the Duivenvoorde population has the highest production of seeds per fruit as well as per plant and that the Sorghvliet population has the lowest. The other populations, except that of Vogelenzang, show approximately the same values. It is remarkable that the Vogelenzang population did not produce any fruits at all. In *table 4* the number of seedlings, making distinction between one, two and three years old plants are given (see *fig. 3*). In the Vogelenzang population no one year old seedlings were found, but a rather high number of two to three years old plants. In the Duivenvoorde population no one year seedlings could be counted because the (grass) vegetation was cut regularly. Of the other populations, again Sorghvliet shows the lowest value.

Summarizing it can be concluded that, in the populations studied, reproduction mainly takes place by means of seeds.

3.3. Chromosomes

The number, shape and size of the chromosomes have been studied by means of the squashing method. Five plants out of each population were investigated. The root tips were pretreated with a colchicine solution, fixed with Carnoy, macerated, and stained with aceto-orceine.

In all countings the diploid number $2n = 16$ has been established. In *fig. 4* an idiogram is presented, while in *table 5* the data concerning the measurements of the chromosomes are summarized. The particular shape and size of the individual chromosomes will not be discussed here. It is only noticed that satellites do occur in chromosome 4 in both *S. hispanica* and *S. non-scripta* as well as in the hybrids. They are not always found, and sometimes only in one of the two homologue chromosomes.

The differences between the six populations are generally small, but the following are worth mentioning. The *S. non-scripta* population at Vogelenzang has the shortest chromosomes (added length of all eight chromosomes 84.1 μm) and the *S. hispanica* population at Duivenvoorde the longest (added length 91.9 μm). In this character the Duinvliet population (added length 84.1 μm) is like that of Vogelenzang and the Zuidwijk population (added length 91.1 μm) differs only slightly from that of Duivenvoorde. The other two hybrid populations (Sorghvliet and Wildrijk) are intermediate (added length 86.3 respectively 88.2 μm).

Further it should be mentioned that the long arms of the chromosomes 2 and 6 are considerably longer for the Duivenvoorde population than for the Vogelenzang one (11.1 and 7.1 against 9.6 and 6.0 μm). The arm ratio in the Duivenvoorde population for chromosome 2 is higher than for all other populations (4.8 against 3.5–3.8 μm). The same can be asserted for the Duivenvoorde and Vogelenzang populations concerning chromosomes 4 (both 6.5 against

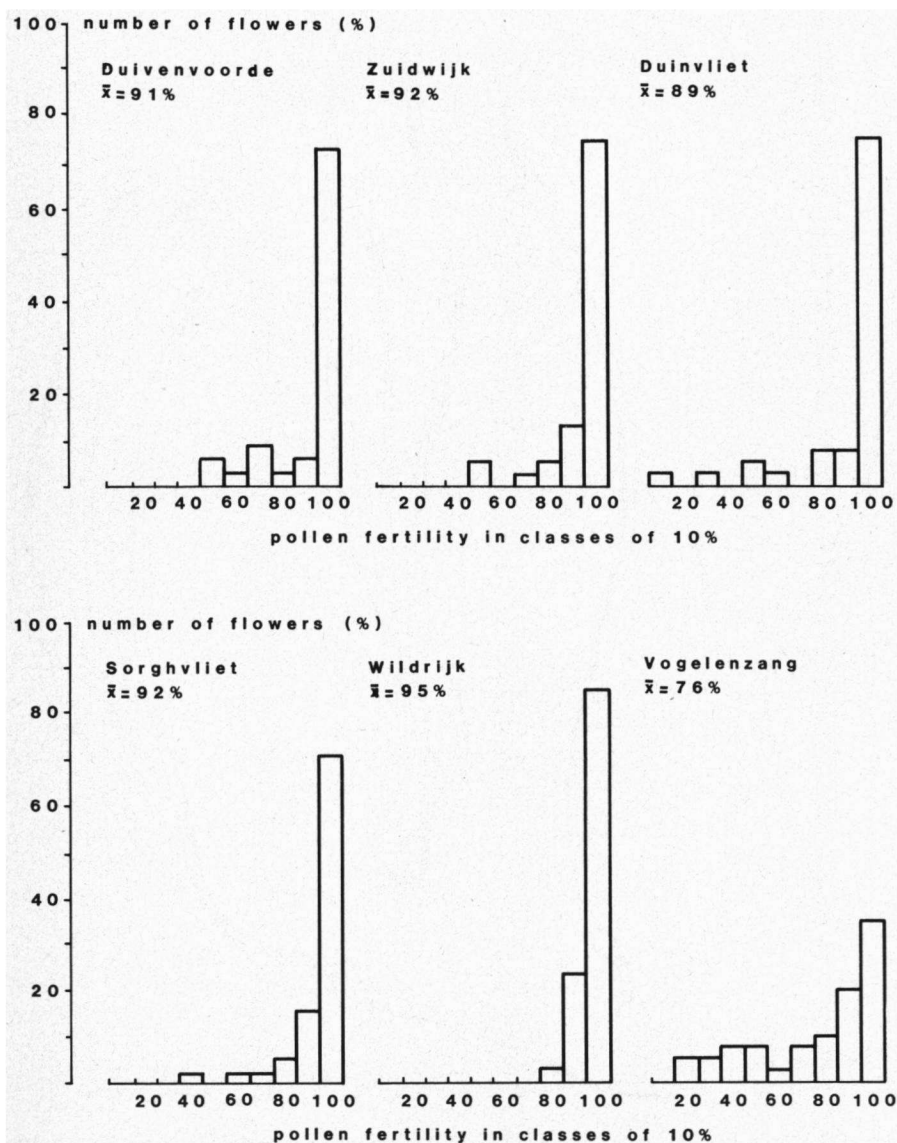


Fig. 2. Pollen fertility for the six *Scilla* populations. For each population also the mean percentage is given.

5.0–5.6 μm). Finally the Vogelenzang population has a higher arm ratio for chromosome 7 compared with all other populations (6.5 against 4.9–5.4 μm).

In conclusion it can be stated that *S. hispanica*, *S. non-scripta* and their hybrids possess the same chromosome number and that the taxa differ only in some minor characters of shape and size of the chromosomes.



Fig. 3. Seedlings of *Scilla* (population Wildrijk). a. one year, b. two years, and c. and d. three years old; d. with contractile root.

4. DISCUSSION

4.1. Morphology and identification

The presence of flower scent in the Duivenvoorde *S. hispanica* population is in contradiction to most of the literature (e.g. HEYWOOD 1980). DE WEVER (1934)

Table 4. Data concerning the sexual reproduction of the six *Scilla* populations. A mean value and a standard deviation are given.

	Duiven- voorde	Zuidwijk	Duinvliet	Sorgh- vliet	Wildrijk	Vogelen- zang
Percentage of ovaries setting seed	37 ± 12	34 ± 20	27 ± 15	14 ± 10	48 ± 29	0
Diameter of ovary in mm	11 ± 1	10 ± 1	9 ± 2	8 ± 2	9 ± 2	—
Number of fruits per plant	6 ± 3	3 ± 2	2 ± 1	1 ± 1	4 ± 3	—
Number of seeds per fruit	10 ± 4	8 ± 4	9 ± 3	6 ± 2	8 ± 5	—
Number of seeds per plant	57 ± 33	21 ± 18	18 ± 15	6 ± 8	26 ± 21	—
Number of one year old seedlings	0	13 ± 12	9 ± 7	2 ± 2	25 ± 16	0
Number of two and three years old seedlings	2 ± 4	3 ± 3	5 ± 6	3 ± 3	5 ± 3	8 ± 5

Table 5. Length of the long and short arm and arm ratio of the eight *Scilla* chromosomes, with standard deviation, averaged for the six populations (see also fig. 4).

Number of chromosomes	Length of long arm in μm	Length of short arm in μm	Arm ratio
1	11.3 ± 0.4	4.4 ± 0.2	2.5 ± 0.1
2	10.0 ± 0.6	2.7 ± 0.2	3.8 ± 0.5
3	10.6 ± 0.7	1.7 ± 0.2	6.4 ± 1.0
4	10.2 ± 0.5	1.8 ± 0.2	5.6 ± 0.7
5	6.2 ± 0.3	5.4 ± 0.2	1.2 ± 0.1
6	6.5 ± 0.4	3.0 ± 0.2	2.2 ± 0.1
7	6.5 ± 0.2	1.2 ± 0.2	5.3 ± 0.5
8	4.1 ± 0.2	2.2 ± 0.1	2.0 ± 0.1

on the other hand, states that there are slight or no differences between *S. hispanica* and *S. non-scripta* which includes the scent. It is questionable whether man selected forms of *S. hispanica* are involved.

Giant forms are known for both *S. hispanica* and *S. non-scripta*. The first are described by DE MOL VAN OUD LOOSDRECHT (1950) from bulb growers stock in Holland and also by TURRILL (1952) from gardens in England. The specimens described by the latter have been examined cytologically by WILSON (1956, 1958), who found they were auto-triploid. She mentioned these forms also for *S. non-scripta* from natural sites in woods near Cambridge. Here sixteen out of thirty giant plants appeared to be triploids.

TURRILL (1952) gives a picture of a hybrid *S. hispanica* × *non-scripta*, which in fact looks like a somewhat smaller example of his *S. hispanica*. This opinion is followed by VAN OOSTSTROOM & REICHGELT (1964). It should be pointed out here that in our opinion the hybrids can possess all grades of characters intermediate between the two parental species. This means that hybrids sometimes have a number of general habit characters more or less in common with *S. non-scripta*:

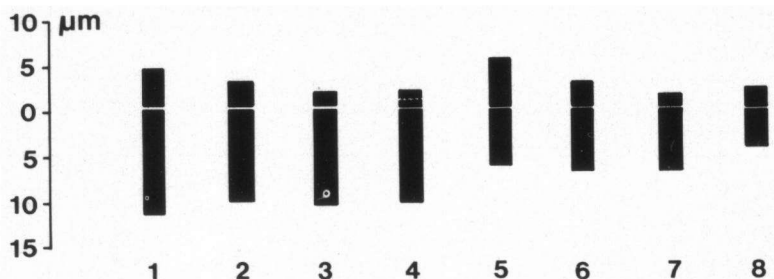


Fig. 4. Idiogram for the six *Scilla* populations (see also table 5). Note the secondary constriction in chromosome 4.

curved scapes, unilaterally arranged flowers and recurved perianth segments. From *S. non-scripta* these specimens differ in being bigger in all parts and in possessing somewhat paler blue, more or less campanulate flowers.

The morphological and other variations mentioned here are partly due to the fact that man has grown, selected and interbred both *S. hispanica* and *S. non-scripta* for many years (BAKER 1872; DE MOL VAN OUD LOOSDRECHT 1950). The *Scilla* forms thus obtained are larger and more vigorous than the natural *S. non-scripta* and *S. hispanica* forms, particularly the latter. Those man-made forms have been set out in semi-natural situations where they naturalized. Moreover in some cases they formed hybrids through introgression with already existing populations of *S. non-scripta*. This often makes it difficult to identify *Scilla* populations in western Europe with either *S. hispanica* or *S. non-scripta*.

Nodding stem tips which cause unilateral inflorescences, recurved perianth segments and cream-coloured anthers are distinctive characters of pure *S. non-scripta* specimens, whilst erect stem tips with multilateral inflorescences, straight perianth segments and blue anthers are characters of pure *S. hispanica* specimens. Flower scent is of doubtful and insertion of stamens of no value for identification.

4.2. *Scilla* in The Netherlands

The situation described above is probably very relevant to The Netherlands. Morphological intermediates, as well as the occurrence of white, pink and also giant forms, are strong indications. Dutch *Scilla* populations most likely originated through naturalizing of planted, selected forms of *S. non-scripta* and *S. hispanica* or hybrids between them. In the case of the latter two taxa hybridization with already existing populations of *S. non-scripta* and introgression of characters has led to the origin of hybrid swarms with characters ranging from those of *S. non-scripta* to those of *S. hispanica*. This is more or less the case in the populations of Duinvliet, Sorghvliet, Wildrijck and Zuidwijk. A detailed study of the origin of *S. hispanica*, *S. non-scripta* and their hybrids in The Netherlands, as well as distribution maps of the three taxa will be published by QUENÉBOTERENBROOD (1984a, 1984b).

4.3. Reproduction

Some authors are of the opinion that vegetative multiplication is the most important way of reproduction in *S. non-scripta*, while some others state that it is unimportant or does not even occur. ELLIOT (1953) believes that vegetative reproduction is not found in *S. non-scripta*, BLACKMAN & RUTTER (1954) however state that it is the most important method of reproduction. On the basis of bulb anatomy CHOUARD (1926, 1930) thinks that vegetative multiplication may happen, while PRIESTLEY & SCOTT (1949) conclude from anatomical diagrams that it seldom occurs. Finally WILSON (1959) observes from counts as well as experiments in some populations in southern England that both vegetative and sexual reproduction take place and that the latter with some 94% of the total reproduction is by far the most important. Our observations in *S. hispanica* and hybrid populations agree with the latter results. The absence of any seed-setting in the Vogelenzang population in 1981 might be due to unfavourable (weather) conditions during the flowering period. BLACKMAN & RUTTER (1954) state that in southern England "seed is set every year". On the germination of seeds the latter authors remark "in some seasons seedlings are abundant but in others they are often difficult to find". On the basis of experiments as well as observations in the field THOMPSON & COX (1978) establish that seeds of *S. non-scripta* germinate optimally at a temperature of 11°C, but only after having passed through a period of high temperature (26–31°C). Under natural conditions this means germination in autumn or in spring.

4.4. Chromosomes

On the whole the various authors who have studied the chromosomes of the *Scilla* taxa in question give a rather uniform picture of their shape. The chromosome shape we found for *S. hispanica*, *S. non-scripta* and hybrids is conformable to this. Some differences, mainly concerning the chromosome size, will be discussed here.

SATO (1935) gives portraits of three *Scilla* taxa. The total length he found for the chromosomes of *S. non-scripta* is 82.5 µm (in our plants 84.1 µm), while the *S. hispanica* chromosomes are 74.5 µm long. This is rather different from the 91.9 µm we found, but his *S. campanulata* (with a total length of 89.5 µm) agrees very well with this figure. The chromosome morphology given by MARGHERITA & MAUGINI (1952) for *S. hispanica* ssp. *campanulatus* agrees generally with ours for *S. hispanica* (population Duivenvoorde), including the secondary constrictions in chromosome 4. The arm sizes they gave are, however, twice or three times shorter than those we found. This is probably due to the use of a different method of treatment. WILSON (1958) says that the shape of the *S. non-scripta* and *S. hispanica* chromosomes is nearly the same, but that the latter are somewhat shorter. Their total length is nearly the same as SATO (1935) gives for *S. hispanica*.

4.5. Taxonomic status of *S. hispanica* and *S. non-scripta*

The two taxa *S. hispanica* and *S. non-scripta* differ in some morphological characters as a consequence of isolation. There are, however, no genetic and physiological barriers between them for exchange of genetic material. Actually, this very often takes place when the two taxa are sympatric (HEYWOOD 1980) or when otherwise growing together, as can be concluded from this study and from SMITH (1975). In these situations hybrids are usually numerous, linking the two parental taxa by forming fertile swarms. This is not surprising in view of their great chromosome similarity. In fact, the two taxa *S. non-scripta* and *S. hispanica* are somewhat different components of the same (bio)species and therefore conspecific. Consequently the following new status is recognised: *S. non-scripta* ssp. *hispanica*; and thus the nominate subspecies is: *S. non-scripta* ssp. *non-scripta*.

5. TAXONOMY

The correct names and authors of the taxa mentioned are given here together with basionyms, types and a number of synonyms. Literature citations are according to STAFLEU & COWAN (1976–1981). They are not repeated under “References”.

Scilla non-scripta (L.) Hoffmanns. et Link ssp. *non-scripta*.

Hyacinthus non-scriptus Linnaeus, Species plantarum: 316 (1753). (Non Hablitz ex Marschall von Bieberstein, Flora taurico-caucasica 1: 283 (1808): *Hyacinthus racemosus* Linnaeus = *Muscari neglectum* Gussone ex Tenore.) *Scilla non-scripta* (Linnaeus) Hoffmannsegg et Link, Ges. Naturf. Fr., Neue Schrift.: 19 (1803). *Endymion non-scriptus* (Linnaeus) Garcke, Flora Deutschland: 322 (1849). *Hyacinthoides non-scripta* (Linnaeus) Chouard ex Rothmaler, Feddes Repert. 53: 14 (1944); Chouard, Bull. Soc. Bot. France 81: 625 (1934).

Type: Linnaeus 438.1 (holo. LINN).

Hyacinthus cernuus Linnaeus, Species plantarum: 317 (1753). *Scilla cernua* (Linnaeus) Salisbury, Prodromus: 242 (1796). *Endymion cernuus* (Linnaeus) Dumortier, Florula belgica: 140 (1827). *Agraphis cernua* (Linnaeus) Reichenbach, Flora germanica 1: 105 (1830).

Scilla festalis Salisbury, Prodromus: 242 (1796).

Scilla nutans Smith, English botany 6: tabula 377 (1797). *Hyacinthus nutans* (Smith) Gray, Natural arrangement 2: 177 (1821). *Endymion nutans* (Smith) Dumortier, Florula belgica: 140 (1827). *Agraphis nutans* (Smith) Link, Handbuch 1: 166 (1829). (Non *Hyacinthella nutans* Wendelbo, Kew Bull. 28(1): 33 (1973): species from Iraq.)

Hyacinthus pratensis Lamarck, Flore française 3: 271 (1778). (Non *Scilla pratensis* of various authors.)

Scilla non-scripta (L.) Hoffmanns. et Link ssp. *hispanica* (Mill.) Ietswaart stat. nov.

- Scilla hispanica* Miller, Gardeners dictionary, ed. 8: no. 8 (1768); Chouard, Bull. Soc. Bot. France 81: 623 (1934). *Hyacinthoides hispanica* (Miller) Rothmaler, Feddes Repert. 53: 14 (1944). (Non *Hyacinthus hispanicus* Lamarck, Encyclopédie méthodique 3: 191 (1789): *Hyacinthus amethystinus* Linnaeus = *Bri-meura amethystina* (Linnaeus) Chouard.) Type: Miller s.n. (holo. BM).
- Hyacinthus amethystinus* Lamarck, Encyclopédie méthodique 3: 190 (1789).
- Hyacinthus campanulatus* Miller, Gardeners dictionary, ed. 8: no. 3 (1768). *Scilla campanulata* Aiton, Hortus kewensis 1: 444 (1789). *Agraphis campanulata* (Miller) Link, Handbuch 1: 166 (1829). *Endymion campanulatus* (Miller) Parlato, Flora italiana 2: 478 (1857).
- Scilla hyacinthoides* Jacquin, Collectanea 1: 61 (1787).
- Scilla jacquini* Gmelin, Systema naturae 1: 552 (1791).
- Scilla patula* Lamarck, Flore françoise 3: 271 (1778). *Hyacinthus patulus* (Lamarck) Desfontaines, Tableau, ed. 1: 26 (1804). *Endymion patulus* (Lamarck) Dumortier, Florula belgica: 140 (1827). *Agraphis patula* (Lamarck) Reichenbach, Flora germanica 1: 10 (1830). *Hyacinthoides patulus* (Lamarck) Rothmaler, Feddes Repert. 53: 14 (1944).
- Hyacinthus spicatus* Moench, Methodus: 632 (1794).

ACKNOWLEDGEMENTS

Prof. Dr. T. W. J. Gadella, Prof. Dr. C. Kalkman and Prof. Dr. M. Vroman are thanked for their critical reading of the manuscript and valuable suggestions. The comprehensive information given by Dr. C. E. Jarvis of the Linnaean Society Typification Project, concerning the Linnean types is gratefully acknowledged, as well as the loan of indispensable specimens from the herbaria of the British Museum (Natural History, London), Leiden and Madrid.

REFERENCES

- BAKER, J. G. (1872). A study of wood hyacinths. *Gardeners Chronicle*: 1038–1039.
- BLACKMAN, G. E. & A. J. RUTTER (1954). *Endymion nonscriptus* (L.) Garcke. *J. Ecol.* 42: 629–638.
- BONNIER, G. & R. DOUIN (1929). *Flore complète de France* etc., vol. 10: 87. Orlhac, Paris.
- BOOM, B. K. & J. D. RUYLS (1950). *Flora der cultuurgewassen*, vol. 2: 338–339. Veenman, Wageningen.
- CHOUARD, P. (1926). Germination et formation des jeunes bulbes de quelques Liliiflores (*Endymion*, *Scilla*, *Narcissus*). *Ann. Sc. Nat. Bot.* 10: 299–352.
- (1930). *Types de développement de l'appareil végétatif chez les Scillées*. Thesis, Paris.
- CLAPHAM, A. R. et al. (1962). *Flora of the British Isles*, ed. 2: 974. University Press, Cambridge.
- COUTINHO, A. X. PEREIRA (1939). *Flora de Portugal*, ed. 2 by R. T. PALHINHA, reprint 1974: 160–161. Cramer, Lehre.
- DOING, H. (1962/63). De buitenplaatsen en bossen langs de binnenduinrand van Noord- en Zuid-Holland. *Natuur en Landschap* 16 (4): 261–281.
- DUPONT, P. (1962). *La Flore Atlantique Européenne*, in *Documents pour les Cartes de Productions Végétales*: 106–107. Faculté des Science, Toulouse.
- ELLIOTT, C. G. (1953). *Variation in chiasma frequency with special reference to the effect of temperature*. Ph. D. thesis, Cambridge.
- FIORI, A. (1923). *Nuova Flora Analitica d'Italia*, vol. 1, reprint 1969: 258–260. Edagricole, Firenze.
- GARCKE, A. et al. (1972). *Illustrierte Flora* etc., ed. 23: 123. Paul Parey, Berlin, Hamburg.
- HEGI, G. (1939). *Illustrierte Flora von Mittel-Europa*, vol 2: 309–313. Hanser, München.

- HEUKELS, H. & R. VAN DER MEIJDEN (1983): *Flora van Nederland*, ed. 20: 431–432. Wolters-Noordhoff, Groningen.
- HEYWOOD, V. H. (1980): Hyacinthoides, in T. G. TUTIN et al. (eds.), *Flora Europaea*, vol. 5: 43–44. Cambridge University Press, Cambridge.
- MARGHERITA, M. E. S. & E. MAUGINI (1952): Osservazioni sul cariogramma di *Endymion hispanicus* (Mill.) Chouard subsp. *campanulatus* Parl. (Liliaceae). *Caryologia* 4(3): 359–366.
- MEUSEL, H. et al. (1965): *Vergleichende Chorologie der Zentral-europäischen Flora*. Fischer, Jena.
- MOL VAN OUD LOOSDRECHT, W. E. DE (1950). A giant *Scilla*. *Gardeners Chronicle* 127: 214.
- OOSTSTROOM, S. J. VAN & TH. J. REICHGELT (1964): *Flora Neerlandica*, vol. 1(6): 128–132. Koninklijke Nederlandse Botanische Vereniging, Amsterdam.
- PRIESTLEY, J. H. & L. I. SCOTT (1949): *Introduction to Botany*, ed. 2. Blackie & Son, London.
- QUENÉ-BOTERENBROOD, A. J. (1984a): Over het voorkomen van *Scilla non-scripta* (L.) Hoffmanns. et Link, *S. hispanica* Mill. en hun hybride in Nederland. *Gorteria* (in preparation).
- (1984b): *Scilla*, In J. MENNEMA, A. J. QUENÉ-BOTERENBROOD & C. L. PLATE (eds.). *Atlas of the Netherlands flora*, vol. 2 (in preparation).
- ROISIN, P. (1969): *Le domaine phytogéographique atlantique d'Europe*: 149–195. Duculot, Gembloux.
- SATO, D. (1935): Analysis of karyotypes in *Scilla* with special reference to the origin of aneuploids. *Bot. Magazine* 4: 298–305.
- SCHUMACHER-WALDBRÖL, A. (1939): Über *Scilla non-scripta* H. et L. in Deutschland. *Feddes Repert.* 47: 180–193.
- SMITH, P. M. (1975): *Endymion*, in C. A. STACE (ed.), *Hybridization and the flora of the British Isles*: 460. Academic Press, London.
- STAFLEU, F. A. & R. S. COWAN (1976–1981): *Taxonomic literature*, vol. 1–3. Bohn, Scheltema & Holkema, Utrecht and Junk, Den Haag.
- THOMPSON, P. A. & S. A. COX (1978): Germination of the bluebell (*Hyacinthoides non-scripta* (L.) Chouard) in relation to its distribution and habitat. *Annales Bot.* 42: 51–62.
- TURRILL, W. B. (1952): *Endymion hispanicus*. *Curtis's Bot. Mag.*: t. 176.
- TUTIN, T. G. et al. (eds.) (1980): see HEYWOOD.
- WELLS, H. (1980): A distance coefficient as a hybridization index. *Taxon* 29(1): 53–65.
- WESTHOFF, V. & A. J. DEN HELD (1975): *Plantengemeenschappen in Nederland*. Thieme, Zutphen.
- WEVER, A. DE (1934): *Scilla non-scripta*. *Natuurh. Maandbl. Limburg* 23: 48–49.
- WILLKOMM, M. & J. LANGE (1870): *Florae Hispanicae*, vol. 1: 213–215. Schweizerbart, Stuttgart.
- WILSON, J. Y. (1956): Polyploidy in bluebells (*Endymion non-scriptus* and *E. hispanicus*). *Nature* 178: 196–197.
- (1958): Cytogenetics of triploid bluebells *Endymion nonscriptus* (L.) Garcke and *E. hispanicus* (Mill.) Chouard. *Cytologia* 23: 435–446.
- (1959): Vegetative reproduction in the bluebell, *Endymion nonscriptus* (L.) Garcke. *New Phytol.* 58: 155–163.