Zeitschrift: Candollea: journal international de botanique systématique =

international journal of systematic botany

Herausgeber: Conservatoire et Jardin botaniques de la Ville de Genève

Band: 37 (1982)

Heft: 1

Artikel: Taxonomy and cytology of the genus Hyacinthella (Liliaceae-

Scilloideae) with special reference to the species in S.W. Asia: Part II

Autor: Persson, Karin / Wendelbo, Per

DOI: https://doi.org/10.5169/seals-880022

Nutzungsbedingungen

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. Mehr erfahren

Conditions d'utilisation

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. En savoir plus

Terms of use

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. Find out more

Download PDF: 21.11.2025

ETH-Bibliothek Zürich, E-Periodica, https://www.e-periodica.ch

Taxonomy and cytology of the genus Hyacinthella (Liliaceae-Scilloideae) with special reference to the species in S.W. Asia. Part II

KARIN PERSSON &
PER WENDELBO

RÉSUMÉ

PERSSON, K. & P. WENDELBO (1982). Taxonomie et cytologie du genre Hyacinthella (Liliacées-Scilloidées) avec traitement détaillé des espèces du S.W. de l'Asie. Partie II. *Candollea* 37: 157-175. En anglais, résumé français.

Seize espèces sont attribuées au genre *Hyacinthella*, quatre dans le S.E. de l'Europe et douze en Asie du S.W. Ces dernières sont traitées plus en détail avec des descriptions complètes et des cartes de distribution. Une clé pour toutes les espèces est ajoutée. Les espèces nouvelles sont: *H. acutiloba* K. Persson & Wendelbo, *H. campanulata* K. Persson & Wendelbo et *H. glabrescens* (Boiss.) K. Persson & Wendelbo. *Scilla atropatana* Grossh. est inclus sous le nom *H. atropatana* (Grossh.) Mordak & Zakharyeva comb. nova. L'épithète *H. dalmatica* (Baker) Chouard est illégitime et le nom correct de l'espèce est *H. pallens* Schur. Le genre se reconnaît bien sur la base d'une série de caractères morphologiques et cytologiques. Les nombres chromosomiques 2n = 16, 18, 20, 22 et 24 ont été dénombrés. On considère que x = 9 est le nombre de base primitif. La morphologie du caryotype est caractéristique et nettement distincte de celle des genres voisins *Muscari*, *Bellevalia*, *Alrawia* et *Hyacinthus*. Certains groupes d'espèces affines sont suggérés sur la base de la morphologie, de la cytologie et de la distribution. L'évolution et la migration du genre à partir d'un centre de dissémination hypothétique situé au sud de l'Anatolie centrale sont discutées.

ABSTRACT

PERSSON, K. & P. WENDELBO (1982). Taxonomy and cytology of the genus Hyacinthella (Liliaceae-Scilloideae) with special reference to the species in S.W. Asia. Part II. *Candollea* 37: 157-175. In English, French abstract.

Sixteen species have been recognized in the genus *Hyacinthella*, four of which are found in S.E. Europe and twelve in S.W. Asia. The latter have been treated more

CODEN: CNDLAR ISSN: 0373-2967 37(1) 157 (1982)

© CONSERVATOIRE ET JARDIN BOTANIQUES DE GENÈVE 1982 in detail with full descriptions and maps of distribution. A key to all species is provided. New species are: $H.\ acutiloba\ K.\ Persson\ \&\ Wendelbo,\ H.\ campanulata\ K.\ Persson\ \&\ Wendelbo,\ and\ H.\ glabrescens\ (Boiss.)\ K.\ Persson\ \&\ Wendelbo.\ Scilla\ atropatana\ Grossh.\ has been included as\ H.\ atropatana\ (Grossh.)\ Mordak\ &\ Zakharyeva,\ comb.\ nova.\ The epithet\ H.\ dalmatica\ (Baker)\ Chouard\ is\ illegitimate\ and\ the\ species\ must\ now\ be\ called\ H.\ pallens\ Schur.\ The\ genus\ is\ well\ characterized\ by\ a\ combination\ of\ morphological\ and\ cytological\ characters.\ The\ chromosome\ numbers\ 2n\ =\ 16,\ 18,\ 20,\ 22\ and\ 24\ have\ been\ recorded.\ x\ =\ 9\ is\ considered\ to\ be\ the\ original\ basic\ number.\ The\ morphology\ of\ the\ karyotype\ is\ characteristic,\ clearly\ distinguished\ from\ the\ related\ genera\ Muscari,\ Bellevalia,\ Alrawia\ and\ Hyacinthus.\ Certain\ species\ affinity\ groups\ are\ suggested\ on\ the\ evidence\ of\ morphology,\ cytology\ and\ distribution.\ Evolution\ and\ migration\ of\ the\ genus\ from\ a\ hypothetical\ centre\ in\ South\ Central\ Anatolia\ are\ discussed.$

Morphological and other characters

Morphological characters considered of high diagnostic value in *Hyacinthella* are:

- 1. Plants small, scape 3.5-20 cm high in flowering stage.
- 2. Leaves 2(-3), or up to 4(-5) when more than one scape present.
- 3. Bracts minute, often appearing as a mere rim.
- 4. Flowers ascending or more rarely patent, never nodding.
- 5. Perianth persistent during development of fruit.
- 6. Capsule small, 3.5-5 mm in diam., depressed globose or rarely broadly pyriform or obovoid-cordate, valves rounded at back, always with a small beak formed by the persistent style, rather thick-walled, coriaceous.
- 7. Seeds black, \pm wrinkled, testa at high magnification reticulate or more rarely with a pattern of low intertwined ridges.

The capsule is the most distinctive character of Hyacinthella (Fig. 1B) and distinguishes it at once from the related genera of Bellevalia, Muscari s.l., Alrawia and Hyacinthus. In all of these genera the capsule is larger. Furthermore, in the two first mentioned genera it is 3-winged, i.e. concave at the back of the valves. Hyacinthus has a \pm globular capsule with rather fleshy walls that shrivel at ripening, much reminding of Scilla species. Alrawia is more similar to Hyacinthella in fruit characters than any of the other genera, but apart from being larger the capsule is ovoid in shape and narrowed at base into a short thick foot.

Seed characters have been somewhat difficult to use partly due to lack of material. However, it seems that there are clear differences between the genera in the pattern of the testa. Most species of *Hyacinthella* have a clearly reticulate testa (Fig. 11C), in *H. nervosa* the reticulate pattern is less distinct due to some kind of outgrowths obscuring the pattern (Fig. 11E), and in *H. persica* and *H. atropatana*, the most advanced species, there is a pattern of low intertwined ridges (Fig. 11D).

Very characteristic of *Bellevalia* are the usually globular seeds that look completely smooth under a hand lense. At higher magnification the testa is minutely foveolate (Fig. 11F), and this seems to be characteristic for species of all groups within the genus. *Muscari* with its wrinkled seeds shows great variation in the pattern of the seed testa and must in this respect be studied much more thoroughly before any conclusion can be drawn. In *Alrawia* is found a kind of double reticulation (Fig. 11G), and finally in *Hyacinthus* the complicated pattern is also very characteristic (Fig. 11H), common to the two sections of the genus.

As regards other characters there is much overlapping between the genera in different combinations. Many species of *Bellevalia* and particularly of *Muscari* are small-sized plants. Several species of *Bellevalia*, especially sect. *Oxyodon*, are 2-leaved and may look a little like *Hyacinthella* species (cp. Wendelbo, 1980). A species like *Muscari* (subgen. *Pseudomuscari*) azureum Fenzl with its 2-3 rather broad leaves and the dense inflorescence of campanulate blue flowers may easily be mistaken for a *Hyacinthella* and was in fact transferred to that genus by Chouard (1931).

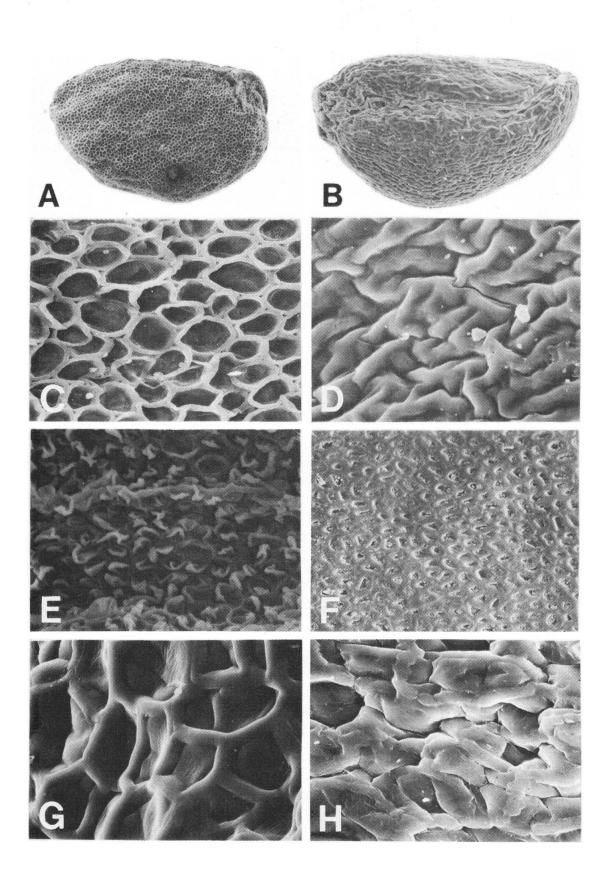
The ascending or more rarely patent perianth of Hyacinthella is characteristic, but in Bellevalia that usually has nodding flowers, at least in some stage of the anthesis, there are small-sized species with upright flowers, e.g. $B.\ decolorans$ Bornm., $B.\ feinbrunae$ Freitag & Wendelbo, $B.\ hyacinthoides$ (Bertol.) K. Persson & Wendelbo, and $B.\ tabriziana$ Turrill. Apart from Muscari subgen. Leopoldia with \pm patent flowers, the other subgenera of Muscari have nodding flowers. In Alrawia the perianth is nodding in both species.

The perianth has overlapping lobes in *Hyacinthella* as in *Bellevalia*, *Alrawia* and *Hyacinthus*, whereas this is not the case in *Muscari* including subgen. *Pseudomuscari*, the long-lobed species of which superficially are so like a *Hyacinthella*.

It is of interest to note that the characteristic oblique crestlike outgrowths found especially on the 3 outer lobes of the perianth of *Alrawia* and most *Bellevalia* species are also seen more or less well-developed in *Hyacinthella* species.

In contrast to the related genera the perianth in *Hyacinthella* is not shred during ripening of the fruit. This must partly be connected with the small size of the capsule.

The filaments that are so characteristic of *Bellevalia*, i.e. somewhat flattened and triangular, often connate at base and attached at the base of the perianth lobes, do not have the same diagnostic value in *Hyacinthella*. In this genus they are threadlike and attached in the perianth tube below the base of the lobes or further down in the tube, even near middle as in *H. siirtensis*. In



many respects the filament characters approach those of *Muscari*, but the filaments are never markedly biseriate as in many species of that genus.

Chemical characters of importance for generic delimitation may be found in the pigments of the perianth. All Hyacinthella species have clear blue or blue-violet (in H. persica sometimes pinkish) hues of different tone and intensity, hardly changing during flower development. The 3 species of Hyacinthus have colours similar to those of Hyacinthella and so have the species of Muscari subgen. Botryanthus and subgen. Pseudomuscari. In the two species of Muscari subgen. Muscari the colours are yellow or bluish and brownish. In Bellevalia there is a wider spectre of hues, characteristically they are often mixed and impure: greenish white, yellow, brown, purple, violet and blue. Often there is a constant change in the colours from bud stage through flowering to wilting when the perianth of most species becomes brownish or livid. The similarity between perianth colours of *Muscari* subgen. Leopoldia and many species of Bellevalia is partly superficial. In Muscari subgen. Leopoldia it is the sterile top flowers that have brighter colours, whereas in the similar-looking Bellevalia species it is the young buds. These characters must be connected with the pollination syndrome, and both groups have achieved the same effect from the colours of the inflorescence in a somewhat different way. Finally, in *Alrawia* the perianth is several-coloured like in many species of Bellevalia, e.g. B. longistyla Wor.

Certain characters have not yet been investigated to such an extent that they can be used with certainty. It has been noticed that in some species of *Hyacinthella*, notably *H. heldreichii*, and in *Alrawia*, the outer but not the outermost bulb tunic is covered with a "powder" consisting of minute needle-shaped particles. When touched the powder gives a soapy, "talkous" feeling. Whether these particles are some kind of exudate from the bulb scales or are connected with the particular soil type in the usual habitat of these plants is not known.

Anatomical features may give a number of additional characters. Feinbrun (1961) showed how the vascular bundles of the leaves of most species of *Hyacinthella* are accompanied by fibre strands that give the characteristic raised nerves of the dried leaves. Sections of perianth tubes indicate that the connate tepals may be fused in different ways in the different genera, and also that the filaments are fused with the tube in different ways. For instance, in *Hyacinthella* the adnate filaments form ridges inside the tube. Nothing is known about the anatomy of seeds, and nothing has been done on the pollen of the different genera.

As so often in *Liliaceae*, also in *Hyacinthella* there are few morphological characters to study and use in taxonomic delimitation. However, capsule characters combined with other morphological characters of less diagnostic value, after all make *Hyacinthella* a fairly uniform and easy to recognize

Fig. 11. — Seeds and seed surfaces. A, C: Hyacinthella micrantha. B, D: H. atropatana. E: H. nervosa. F: Bellevalia tristis. G: Alrawia bellii. H: Hyacinthus transcaspicus. A, B: × 25; C-H: × 185 (SEM photo E. Gilert).

genus. The addition of cytological data to morphological characters are conclusive for the delimitation of the genus.

Cytology

From a karvological point of view it seems difficult to relate Hyacinthella to any other genus of the Scilloideae in Europe and S.W. Asia. The chromosomes are smaller, about 1-5 μ m long with the preparation technique used, and thinner than in most species in other genera. Also the cells in root tips are smaller, and so are pollen grains and stomata (pers. obs. and ÖSTERGREN & al., 1958). In species of Scilla and Muscari s.l. with comparatively small chromosomes, these are generally thicker, and at least one to a few pairs are also longer than in Hyacinthella. Only in some polyploid species, such as Muscari heldreichii Boiss., M. tubergenianum Hoog ex Turrill (both with 2n = 36, Garbari, 1968b), and M. pseudomuscari (Boiss.) Wendelbo (= M. chalusicum Stuart, 2n = 54, pers. obs.), the chromosomes are so small that they can be compared in length and breadth to those of Hyacinthella. Another interesting exception is Scilla litardierei Breistr. (= S. pratensis Waldst. & Kit. non Berg., S. amethystina Vis.) from the coastal areas of Yugoslavia and N. Albania. The chromosomes of this species have been studied by several authors, usually on plants of horticultural origin. Different numbers are given: 2n = 24 (Sharma, 1956), 2n = 26 (Sato, 1942; GIMÉNEZ-MARTÍN, 1959d; SPETA, 1974), and 2n = 28 (Maude, 1940; FINDLEY & McNeill, 1974). Two records of 2n = 28 for spontaneous material exist, viz. LOVKA & al. (1972), and SPETA (1980). Judged from illustrations in some of these works, the karyotype of this species is very similar to that of Hyacinthella both in morphology and size. Thus the chromosomes illustrated are about 1-6 μ m (= Hyacinthella) in SATO (1942), but a little smaller in SPETA (1974) and a little larger in MAUDE (1940). SPETA (1980) discusses the possibility of a closer relationship between S. litardierei and the genus Hyacinthella on the basis partly of this similarity in karyotype, partly of the fact that both have two ovules per locule. The latter character is shared with several other Scilla species, however. We have not studied the karyotype of S. litardierei, but we lean towards the opinion that this species is too diverging in external morphological characters to be considered in the neighbourhood of Hyacinthella if excluded from Scilla s.str. Grossheim (1935) suggested a relationship with S. atropatana (= Hyacinthella a.), but this was rejected by MORDAK (1971), who created a monotypic section within Scilla, sect. Atropatanae, for this species. Later, she and the present authors have come to the conclusion that S. atropatana is really a true Hyacinthella, closely related to H. persica. The similarity in karyotypes between S. litardierei and Hyacinthella is probably only secondary, a case of convergent evolution within the Scilla s.l. lineage and the lineage leading to the present Hyacinthella species.

The pattern of chromosome morphology of *Hyacinthella*, with the largest chromosomes ± subtelocentric to telocentric (Fig. 12), is characteristic also of species in a few other scilloid genera of the area. A similar pattern can be found e.g. in scattered Scilla species (SPETA, 1974; RUIZ REJON, 1978), Puschkinia (Greilhuber & Speta, 1976), Brimeura (Garbari, 1970), and above all, Muscari subgen. Botryanthus, Leopoldia and Pseudomuscari (GARBARI, 1966, 1968b, 1969; BENTZER, 1969, and pers. obs.). Otherwise, the largest chromosomes are generally \pm metacentric: most Scilla groups (BATTAGLIA, 1956, 1959; GIMÉNEZ-MARTÍN, 1959a, b, c; GREILHUBER & SPETA, 1976, 1978, and pers. obs.), Ornithogalum (Cullen & Ratter, 1967; AGAPOVA, 1974), Muscari subgen. Muscari (GARBARI, 1966, and pers. obs.), Bellevalia (Feinbrun, 1938; Persson & Wendelbo, 1979a, b; Bothmer & WENDELBO, 1981), Alrawia (PERSSON & WENDELBO, 1979c), and Hyacinthus (BENTZER & al., 1974; PERSSON & WENDELBO, unpubl.; for further references on these genera see mentioned works). A characteristic feature of morphology, viz. the discontinuity in size between the large subtelocentrics (telocentrics) and the rest of the chromosome set, Hyacinthella has in common with a few Scilla species (e.g. S. messeniaca Boiss., S. litardierei Breistr.), Brimeura, Muscari subgen. Botryanthus (at least some species) and subgen. Leopoldia (most species). As in a few species of the latter subgenus and in Scilla litardierei, the large subtelocentrics (telocentrics) in the whole of the genus Hyacinthella comprise just one pair, however, Thus, in Hyacinthella morphology and size together make up a highly characteristic karyotype, as easily distinguished from that of the vast majority of taxa in the Scilloideae as that of *Bellevalia*.

Within the genus there are only small variations in karyotype, except in number. Four species with 2n = 18 immediately stand out as forming a group of their own, viz. *H. hispida* (Figs. 1C, 12A), *H. heldreichii* (Figs. 1E, 12B), *H. glabrescens* (Figs. 2D, 12C) and *H. campanulata* (Figs. 3D, 12D), all from S. Anatolia. These are the only species within the genus in which the second chromosome has a practically median centromere and is as long as or longer than the long arm of chromosome No. 1. Another shared trait is the mostly satellited subtelocentric chromosome No. 6. Also in other details the respective karyotypes are very similar to each other.

Large metacentric chromosomes are generally, also by the present authors, believed to be a primitive character within this and several other liliaceous groups, though in some cases, e.g. *Hyacinthus orientalis* L. (Bentzer & al., 1974), this type of morphology in one or a few chromosomes of the set for one reason or another has been considered to be secondary in character. However, the basic number in the *H. hispida* group is 9, i.e. the same as in several other scilloid groups, e.g. the *Scilla bifolia* group, the least specialized *Hyacinthus* species, and above all, the whole of the genus *Muscari*, the karyotype of which also seems rather close from a morphological point of view, as discussed above. Thus the presence of large metacentric chromosomes in combination with basic number and, not the least, with characters of external morphology and geographical distribution

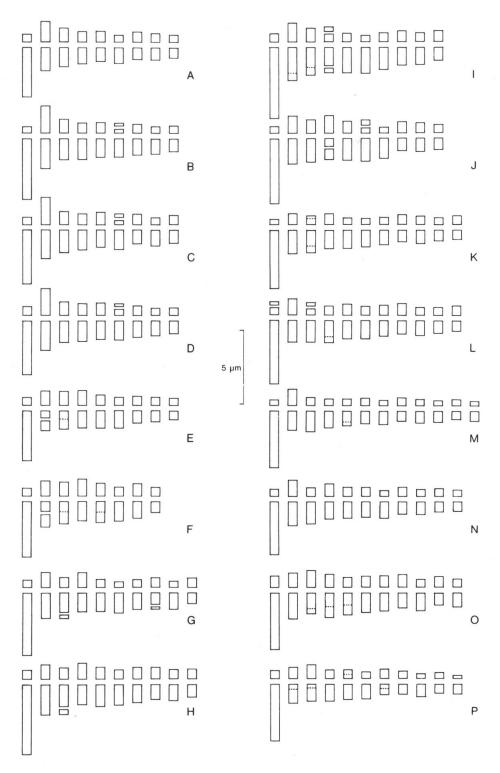


Fig. 12. — Idiograms. A: Hyacinthella hispida. B: H. heldreichii. C: H. glabrescens. D: H. campanulata. E: H. acutiloba. F: H. lineata. G: H. leucophaea. H: H. atchleyi. I: H. pallasiana. J: H. pallens. K: H. millingenii. L: H. siirtensis. M: H. nervosa. N: H. micrantha. O: H. persica. P: H. atropatana. Hatched lines indicate weak secondary constrictions.

(see that chapter) all point towards the primary position of these species within the genus. Higher numbers (x=10, 11 and 12) are obviously derived, and so are smaller (evident especially in some of the species with x=11 and 12) and more asymmetric chromosomes. One possible explanation to the progressive increase in basic number could be the mechanism suggested by Darlington (1937) in his *Crepis* studies, a process involving a system of reciprocal translocations of unegual chromosome segments. It is interesting to note that some of the recorded examples are within liliiflorous groups, e.g. *Fritillaria* (Darlington, 1936), *Allium* (Levan, 1932, 1935) and *Crocus* (Brighton, 1978). A similar process may result in a decrease in number, as proved by Tobgy (1943) in *Crepis*. Another example might be found in the evolution of the only 16-chromosome species in *Hyacinthella*, *H. lineata* (Figs. 5E, 12F), which is obviously very closely related to *H. acutiloba*, 2n=18 (Figs. 4E, 12E).

Translocations and other structural mutations such as inversions may as well be the origin of the transition from symmetry towards asymmetry in Hyacinthella, particularly evident in chromosome No. 2 but there is a tendency towards higher asymmetry overall in species with x=11 and 12. It is indeed very probable that chromosome structural alterations have played a great role during the evolution of the genus, a hypothesis especially supported by the rather unusual variation in basic number in an otherwise well circumscribed group of species, and the fact that the total chromosome material seems to be of much the same length in related cytotypes.

Secondary constrictions seem to be rather common in the genus. Small satellites on the short arm of subtelocentric to submetacentric chromosomes occur in the H. hispida group as mentioned above (No. 6), in H. pallasiana (No. 4, Fig. 12I), H. pallens (No. 6, Fig. 12J), H. millingenii (No. 3, Fig. 12K), H. siirtensis (Nos. 1 and 3, Fig. 12L), and H. atropatana (No. 5, Fig. 12F). H. siirtensis (Fig. 12L) is the only example in the genus with a satellited first chromosome. Secondary constrictions in the long arm of one or more of Nos. 2-7 are particularly distinct (visible in almost all preparations) in the four European species together with the Anatolian H. lineata and H. acutiloba, and usually also in H. persica together with H. atropatana. Judging from chromosome morphology, species within each of these two groups are obviously related inter se, and this is confirmed by external morphology. Evolution within the first-mentioned group has thus, interestingly enough, taken the course of both increase and decrease in chromosome number (from 2n = 18 towards 2n = 20 and 2n = 16, respectively).

H. siirtensis and H. nervosa which are very much alike in gross morphology, have apart from chromosome number (2n = 22 and 24, respectively) fairly similar karyotypes (Fig. 12L, M). In both, the comparatively small chromosome No. 2 has a nearly median centromere, most of the other chromosomes are highly asymmetric, especially in H. nervosa, and secondary constrictions are rare and weak, except in the satellited first and third chromosome of H. siirtensis.

Material and methods

The cytological investigation was carried out on material from the following localities.

- **H. hispida:** Turkey, Içel: between Çamliyayla and main road Pozanti-Tarsus, 550 m, *Renz & Taubenheim* s.n.
- **H. heldreichii:** Turkey, Burdur: S. of Burdur, 1000 m, Runemark & Wendelbo 350. Antalya: 10 km S. of Akseki, 800 m, Runemark & Wendelbo 395; N. of Cevizli, 1250 m, Runemark & Wendelbo 429; above Cevizli, between Akseki and Beysehir, 1200-1250 m, Renz & Taubenheim s.n.; between Murtiçi and Akseki, 900 m, Mathew 9635.
- **H. glabrescens:** Turkey, Adana: Cilician Gates near Pozanti, 1200 m, *Mathew & Tomlinson 4463*.
- **H. campanulata:** Turkey, Konya: W. of Konya, 1100 m, *Runemark & Wendelbo 413*; W. of Konya by the river, limestone cliffs above dam site, 1300 m, *Runemark & Wendelbo 416*.
- H. acutiloba: Turkey, Sivas: between Sivas and Talica, 1600 m, Tobey 1653. Kaiseri: Pinarbasi to Gürün, Ziyaret Tepesi, 2000 m, Coode & Jones 1344.
- **H. lineata:** Turkey, Manisa: Manisa Dağ, 1050 m, *Baytop 44 530.* Denizli: Uschak to Denizli road, between Civril and Baklan, 1000 m, *Baytop, Brickell & Mathew 8245*; Kazikbeli pass Denizli-Kale near Cucurköy village, 800 m, *Baytop, Brickell & Mathew 8273*.
- **H. leucophaea:** Roumania, Dobrogea: Constanta, Itagieni, *Prasil* s.n. USSR, Ucraine: Odessa, Chadjibeysky liman, *Mordak & al.* 1586.
- H. atchleyi: Greece, Viotia: between Halkis and Thive, Horton 1402.
- **H. pallasiana:** USSR, Ucraine: Denatzk, reserve "Kamennii mogili", *Mordak & al. 1368*.
- **H. pallens:** s. loc., Van Tubergen s.n. (commercial plant, as H. dalmatica).
- **H. millingenii:** Cyprus: s. loc., *Mathew* s.n.; 10 km W.S.W. of Larnaka, 100 m, *Wollin* s.n.
- **H. siirtensis:** Turkey, Siirt: pass between Eruh and Sirnak, 5600′ (1700 m), Rix 407.
- **H. nervosa:** Turkey, Gaziantep: Kazikli Köy, between Kilis and Gaziantep, 700 m, *Renz & Taubenheim* s.n. Iraq, Mosul: Jabal Sinjar, 650 m, *Ali al-Rawi* s.n.
- **H. micrantha:** Turkey, Çorum: 29 km from Çorum, *Marais* 1608.

- **H. persica:** Iran, Tehran: Qazvin-Rasht, 13 km S. of Loushan, 700 m, Wendelbo & Masoumi 19 064. Gilan: Qasvin-Rasht, 12 km N.W. of Loushan, 390 m, Wendelbo & Masoumi 19 078.
- H. atropatana: USSR, Armenia: Meghri, near Agarak, Gabrielian s.n.

Root tips were pretreated in a mixture of 0.6% colchicine and 2 mM 8-hydroxyquinoline (1:1) and then squashed and stained in aceto-orcein.

Distribution and phylogeny

The species of *Hyacinthella* show an interesting distributional pattern. In Asia *H. hispida* and *H. glabrescens* are the only partly sympatric species. *Hyacinthella* evidently comprises a series of vicariads. The map of distribution of the species in Anatolia, Syria and Cyprus (Fig. 13) demonstrates this quite clearly.

The highest concentration of species is found in the central part of southern Anatolia. Here the related species of what might be called the hispida-group, H. hispida, H. heldreichii, H. glabrescens and H. campanulata, more or less approach each other geographically or come into closer contact. They are all fairly similar in habit as well as in details of morphology, and they all have the chromosome number 2n = 18 considered to be the original number within the genus, and they also have much the same karyotype.

H. acutiloba of Central Anatolia also with 2n = 18 has a karyotype which differs in morphologic features from that of the previous group. Both in cytological and gross morphological characters the species is close to H. lineata of W. Anatolia with the more derived number 2n = 16.

All the European species, the *leucophaea*-group, consisting of H. *leucophaea*, H. atchleyi, H. pallens and H. pallasiana, have the chromosome number 2n=20 and seem to be related *inter se*. Morphologically and cytologically they show similarities to the two Anatolian species of the *lineata*-group.

In the hot and dry steppic areas of S.E. Anatolia and Syria there are two closely related species, H. nervosa (2n = 24) and H. siirtensis (2n = 22), which are morphologically rather distinct from the species mentioned above. Possibly the Cyprian species H. millingenii (2n = 22) should be referred to this group even if more distantly related.

H. micrantha is morphologically somewhat isolated from the other Turkish species in the lack of fibrous strands in the leaf nerves and in the more urceolate perianth with short triangular lobes. The chromosome number is 2n = 22. It occurs in a comparatively small area in N. Anatolia. Being a pale-flowered, inconspicuous plant which flowers early in the year like other Hyacinthella species, it has perhaps been overlooked in many places. It is even possible that its real area of distribution comes closer to that

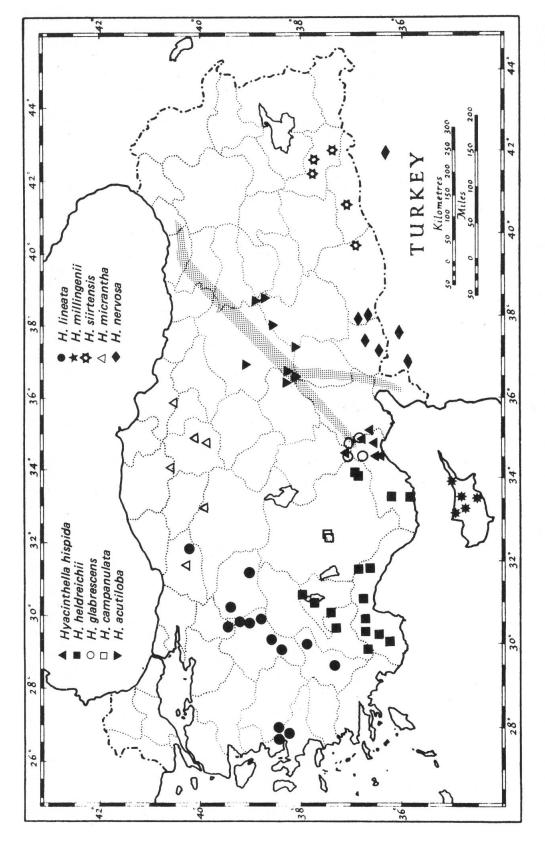


Fig. 13. — Total known distribution of different *Hyacinthella* species. *H. nervosa* has more localities in Syria, Lebanon, Israel and Jordan. Shaded area: the so-called Anatolian Diagonal (after DAVIS, 1971).

of *H. heldreichii* than is apparent from the map of localities observed up till now (Fig. 13). As will be remembered, there are plants with 2n = 22 in Adana, Nigde and Içel which we have interpreted as belonging to a hybrid complex *H. micrantha* \times *heldreichii*. The present distribution of *H. micrantha* may of course also be of a reduced relic nature.

Geographically isolated are H. persica (2n = 22) of N.W. Iran and the Transcaucasian H. atropatana (2n = 22) found in the Soviet Republic of Armenia. Both species have narrow leaves without fibre strands like H. micrantha but with ribs of a different nature. H. atropatana differs from all other species of the genus in the perianth, which is split to the base, and in the lobed capsule. However, its karyotype is quite conclusive, being very similar to that of other Hvacinthella species.

Thus the 16 known species of *Hyacinthella* are scattered with more or less isolated distributional areas over a large part of S.W. Asia and S.E. Europe. They are all plants with few-seeded capsules on upright, short scapes. As ballists, their capacity for dispersal over long distances must be very limited compared to e.g. tall *Eremurus* species with long scapes and partly winged seeds, which must have spread rapidly over large areas when changes in climate or ecology made conditions favourable (Wendelbo, 1964). The present pattern of distribution is probably rather of a relic nature. It is quite feasible that geographical isolation has been an important factor in the evolution of the genus beside structural chromosomal changes.

Even though nothing is really known about compatibility between different species, a tentative division into groups of related species can be made. It is postulated that the *hispida*-group (2n = 18) contains the more primitive species. As they are concentrated in the central part of S. Anatolia, this could be considered the centre of origin for the genus (Fig. 15). From the general pattern of distribution it is not too difficult to accept that the other groups have spread out from this area.

The *lineata*-group probably had its origin in the *hispida*-group (or the ancestors of this group) and spread into West and Central Anatolia, where H. *lineata* (2n = 16) and H. *acutiloba* (2n = 18) respectively are the present day species. This group again might have given rise to a taxon with 2n = 20 chromosomes that migrated into S.E. Europe and there evolved into the species of the *leucophaea*-group.

During the evolution of the genus a branch with 2n = 22 might have split off from the original 2n = 18 group at an early stage, and then split again into three separate branches leading to the present species or species groups, viz. *H. micrantha* in the north, *H. atropatana* and *H. persica* in the north-east, and the *H. nervosa*-group in the south-east. Alternatively, these groups which are morphologically distinctly differentiated from each other, may have originated separately from the primitive group, i.e. the chromosome number 2n = 22 may have arisen more than one (Fig. 15).

Davis (1971) draws the attention to an important feature of Anatolian phytogeography, viz., the remarkable floral break through the middle of Inner Anatolia. A high number of species either do not occur west of this

line, which Davis calls the Anatolian Diagonal (cp. Fig. 13), or have only scattered stations west of it. Similarly, there are many species not occurring east of the Diagonal. Physical and climatic differences do not seem adequate to explain such a major floral break at specific and generic rank. According to Davis, the phenomenon probably stems from Anatolia's Tertiary history.

As is apparent from the maps of distribution (Figs. 13, 14), the *Hyacinthella hispida*-group, *H. micrantha* and the *H. lineata*-group with the exception of a number of *H. acutiloba* localities, all occur only west of the Anatolian Diagonal, while the two most diverging groups, the *nervosa*-group and the *persica*-group are restricted to areas east of the Diagonal. Following the trains of thought of Davis one might postulate that the genus *Hyacinthella* originated south-west of the Diagonal during the Miocene, when most of this part of Anatolia was a region of islands, separated from the north by the Tethys. Eastern Anatolia had not yet risen from the sea. As the land rose after the Miocene-Pliocene transition, a north-ward migration took place and the genus then spread further into S.E. Europe and in the north towards Caucasus and N.W. Iran. During Pliocene as Mesopotamia rose from the sea,

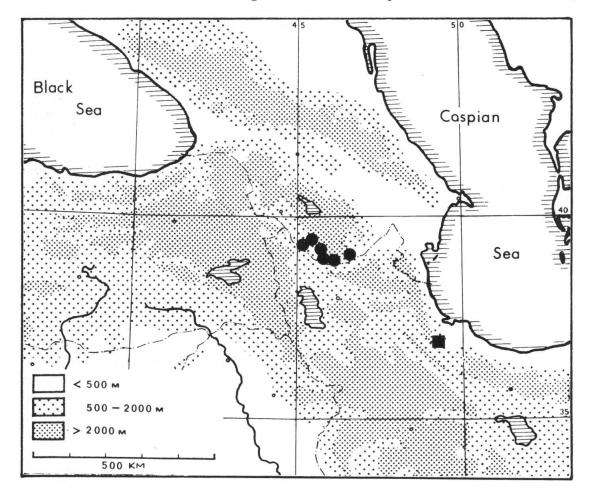
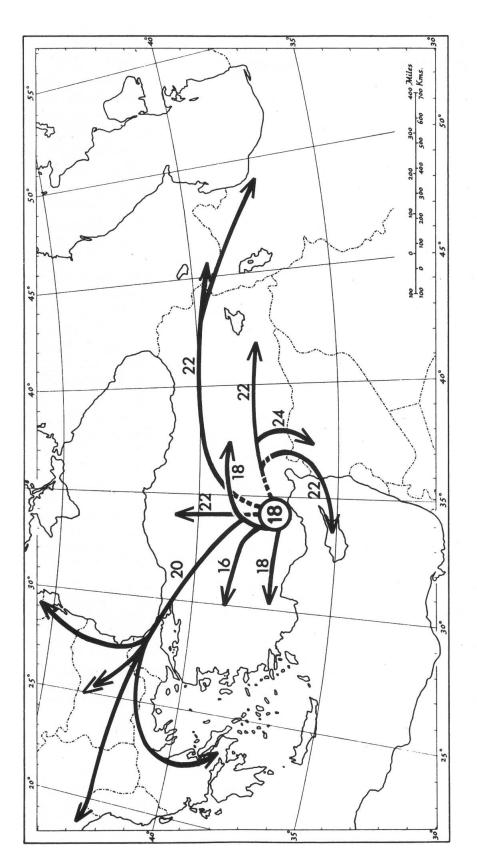


Fig. 14. – Total known distribution of Hyacinthella atropatana (dots) and H. persica (square).



to be derivatives from the 2n = 18 lineage also leading to H. acutiloba. 2n = 22 may have originated once or several times and is now represented by H. milingenii in Cyprus and H. siirtensis in S.E. Turkey. Closely related to the latter is H. nervosa (2n = 24) in the Middle East. Fig. 15. — Evolution within the genus Hyacinthella. Large circle represents hypothetical centre of origin. 2n = 18 is believed to have been the ancestral chromosome number from which all other cytotypes have evolved. It is still represented by the H. hispida group in S. Turkey and by H acutiloba in E. Central Anatolia. H. lineata with 2n=16 in W. Anatolia and the H. leucophaea group with 2n=20 in S. E. Europe are believed

the *nervosa*-branch migrated into this area. Changes in climate during the Pleistocene have certainly influenced the distributional patterns. Thus the genus, which was earlier probably more widely and evenly distributed, must have split up into the now apparent disjunct pattern of distribution. Particularly *H. atropatana* and *H. persica* have evidently isolated relic areas.

Even if such a discussion is very theoretical, certain views on the origin of Hyacinthella may be raised. We have postulated that the genus originated in the area which now forms the central southern part of Anatolia. It is difficult to point out any genus that is closely related to Hyacinthella, but one may well be Muscari. Other genera undoubtedly but more distantly related are Bellevalia and Alrawia and perhaps also Hyacinthus. Whether certain groups of Scilla may come into the picture is still unclear. It is of great interest to note that both Bellevalia and Muscari are clearly connected with Hyacinthella geographically. Feinbrun (1940) pointed out that Bellevalia trifoliata (Ten.) Kth. probably is the most primitive species of the genus and in this we can agree. It is found in S.W. and S. Anatolia. *Muscari* subgen. *Muscari* is W. and S. Anatolian, subgen. Leopoldia is concentrated in the E. Mediterranean, and subgen. Botryanthus has its centre in Anatolia. Alrawia, found in N. Iraq and W. Iran, may well be a somewhat later development from a common stock of the genera mentioned. Hyacinthus orientalis L. is mainly a N.E. Mediterranean species (WENDELBO, 1980), but the two other species of the genus, found in N.E. Iran and Turkmenistan, are considered more primitive (Bentzer & al., 1974), so the history of this genus is probably quite a different one.

ACKNOLEDGEMENTS

The present study has been supported by grants from the Swedish Natural Science Research Council.

Living bulbs were kindly sent us by Dr. A. al-Rawi, Baghdad; Professor T. Baytop, Istanbul; Dr. E. Gabrielian, Erevan; Mr. B. Mathew, Kew; Dr. E. V. Mordak, Leningrad; Dr. J. Renz, Basel and Mr. H. Wollin, Göteborg.

Material from the following herbaria has been studied: B, E, G, GB, GOET, H, JE, K, LE, LD and M. In addition the herbaria of Professors A. & T. Baytop, Istanbul; Dr. A. Huber-Morath, Basel; Professor M. Koyuncu, Ankara; Dr. H. Peşmen, Ankara and Dr. F. Sorger, Wien have been studied. Dr. B. Peterson, Göteborg has arranged most of the loans.

Dr. H. Burdet, Genève and Dr. I. Kukkonen, Helsinki have been of great help in solving certain bibliographical problems.

Mrs. V. Aldén made the cytological preparations, Mrs. E. Gilert prepared the SEM photographs, and Mr. H. Zetterlund has been responsible for the cultivation of the bulbs.

For all valuable assistance we thank the persons mentioned above and the Directors and Curators of the listed institutes.

REFERENCES

- AGAPOVA, N. D. (1974). Comparative karyological characteristics of three species of the genus Ornithogalum L. (in Russian). *Bot. Zhurn.* 59(3): 406-414.
- BAKER, J. G. (1871). A revision of the genera and species of herbaceous capsular gamophyllous Liliaceae. J. Linn. Soc. Bot. 11: 349-436.

- BAKER, J. G. (1874). On new and little-known capsular gamophyllous Liliaceae. J. Bot., N.S. 3: 3-8.
- BARANOVA, M. V. (1965). Giatsint (sistematika, sorta, morfogenez, kultura). Moskva, Leningrad.
- (1979). Hyacinthella Schur. In: A. FEDOROV (ed.), Flora Partis Europaeae URSS 4: 252-253.
 Leningrad.
- BATTAGLIA, E. (1956). Filogenesi del cariotipo nel genere Scilla. V. Scilla lilio-hyacinthus L. *Caryologia* 9(1): 19-37.
- (1959). Il cariotipo di Scilla hyacinthoides L. (Liliaceae). Caryologia 11(3): 261-272.
- BELJANINA, N. B. & G. M. PROSKURJAKOVA (1978). K sistematike turkmenskikh giatsintov. Nauchnye doklady byshei shkoly biologicheskie nauki 1978 (1): 98-107.
- BENTZER, B. (1969). Chromosome morphology in Aegean populations of Leopoldia Parl. (Liliaceae). *Bot. Not.* 122: 457-480.
- R. VON BOTHMER & P. WENDELBO (1974). Cytology and morphology of the genus Hyacinthus L. s.str. (Liliaceae). Bot. Not. 127: 297-301.
- BOISSIER, E. (1882-1884). Flora orientalis 5. Genevae et Basiliae.
- BOTHMER, R. VON & P. WENDELBO (1981). Cytological and morphological variation in Bellevalia (Liliaceae). *Nord. J. Bot.* 1: 4-11.
- BRIGHTON, C. A. (1978). Telocentric chromosomes in Corsican Crocus L. (Iridaceae). *Pl. Syst. Evol.* 129: 299-314.
- BUVAT, R. (1945). La structure du noyau quiescent de quelques Liliacées et son intérêt en systématique. Compt. Rend. Soc. Biol. (Paris) 139: 291-294.
- CHOUARD, P. (1930-1931). Révision de quelques genres et sous-genres de Liliacées bulbeuses d'après le développement de l'appareil végétatif (Scilla, Endymion, Hyacinthus). *Bull. Mus. Hist. Nat. Paris, Sér. 2,* 2: 698-706; 3: 176-180.
- (1931b). Types de développement de l'appareil végétatif chez les Scillées. Ann. Sci. Nat. Bot., Sér. 10, 13: 131-323.
- CULLEN, J. & J. A. RATTER (1967). Taxonomic and cytological notes on Turkish Ornithogalum. Notes Roy. Bot. Gard. Edinburgh 27(3): 293-339.
- DARLINGTON, C. D. (1936). The external mechanics of the chromosomes. *Proc. Roy. Soc., Ser. B, Biol. Sci.* 121: 264-319.
- (1937). Recent advances in cytology. Second ed. Blakiston, Philadelphia. 671 pp.
- DAVIS, P. H. (1971). Distribution patterns in Anatolia with particular reference to endemism. *In:* DAVIS, P. H., P. C. HARPER & I. C. HEDGE (eds.), *Plant life of South-West Asia*. Edinburgh.
- EDMONDSON, J. R. & H. W. LACK (1977). The Turkish and Caucasian collections of C. Koch I: Turkey. *Notes Roy. Bot. Gard. Edinburgh* 35: 321-344.
- FEINBRUN, N. (1938-1940). A monographic study on the genus Bellevalia Lapeyr. (Caryology, taxonomy, geography). *Palest. J. Bot., Jer. Ser.*, 1: 42-54, 131-142, 336-409.
- (1961). Revision of the genus Hyacinthella Schur. Bull. Res. Counc. Israel 10D: 324-347.
- FINDLEY, J. N. & J. MCNEILL, J. (1974). IOPB chromosome number reports XLV (ed. Á Löve). Taxon 23: 620-621.
- GARBARI, F. (1966). Contributo allo studio citologico dei Muscari Italiani. *Caryologia* 19(4): 419-428.
- (1968a). Il genere Muscari (Liliaceae): Contributo alla revisione citotassonomica. Giorn. Bot. Ital. 102: 87-105.
- (1968b). Iconografia cromosomica di alcune Liliaceae. Atti Soc. Tosc. Sci. Nat. Pisa Mem., Ser. B, 75: 163-178.

- GARBARI, F. (1969). Nuove osservazioni citologiche sui generi Muscari e Leopoldia. *Giorn. Bot. Ital.* 103: 1-9.
- (1970). Il genere Brimeura Salisb. (Liliaceae). Atti Soc. Tosc. Sci. Nat. Pisa Mem., Ser. B, 77: 12-36.
- GIMÉNEZ-MARTÍN, G. (1959a). Estudio cariológico en especies de Scilla. I. S. tubergeniana Hoog, S. sibirica L., S. amoena L., S. roseni Koch y S. bithynica Boiss. *Phyton (Argentina)* 12: 121-129.
- (1959b). Cariologia de Scilla. II. Phyton (Argentina) 13: 145-152.
- (1959c). Cariologia de Scilla. III. Phyton (Argentina) 13: 153-162.
- (1959d). Numero cromosomico en especies de Scilla. Gen. Iber. 11: 97.
- GREILHUBER, J. & F. SPETA (1976). C-banded karyotypes in the Scilla hohenackeri group, S. persica, and Puschkinia (Liliaceae). *Pl. Syst. Evol.* 126: 149-188.
- & F. SPETA (1978). Quantitative analyses of C-banded karyotypes, and systematics in the cultivated species of the Scilla siberica group (Liliaceae). Pl. Syst. Evol. 129: 63-109.
- GROSSHEIM, A. A. (1935). Scilla atropatana Grossh. sp. nova (Sect. Prospero Baker). *In:* KOMAROV, V. L. (ed.), *Flora URSS* 4: 740-743. Moskva, Leningrad.
- HOLMBOE, J. (1914). Studies on the vegetation of Cyprus. Bergens Mus. Skrifter, Ny raekke: 1(2).
- KRAUSE, K. (1930). Liliaceae. *In:* ENGLER, A. (ed.), *Die natürlichen Pflanzenfamilien*. 2. Aufl., 15a: 227-386.
- LEVAN, A. (1932). Cytological studies in Allium, II. Chromosome morphological contributions. *Hereditas* 16: 257-294.
- (1935). Cytological studies in Allium, VI. The chromosome morphology of some diploid species of Allium. Hereditas 20: 289-330.
- LOVKA, M., F. SUŠNIK, Á. LÖVE & D. LÖVE (1972). IOPB chromosome number reports XXXVI (ed. Á. Löve). *Taxon* 21: 337-339.
- LOZINA-LOZINSKAYA, A. S. (1935). Bellevalia to Muscari. *In:* KOMAROV, V. L. (ed.), *Flora USSR* 4: 395-422.
- MARSCHALL VON BIEBERSTEIN, F. A. (1819). Flora taurico-caucasica 3. Charkov.
- MAUDE, P. F. (1940). Chromosome numbers in some British plants. New Phytol. 38: 17-32.
- MORDAK, E. V. (1971). Scilla of the Soviet Union. II. Taxonomy and geography (in Russian). *Bot. Zhurn.* 56: 1444-1458.
- ÖSTERGREN, G., R. MORRIS & T. WAKONIG (1958). A study in Hyacinthus on chromosome size and breakability by X-rays. *Hereditas* 44: 1-18.
- PERSSON, K. & P. WENDELBO (1979a). Bellevalia hyacinthoides, a new name for Strangweja spicata (Liliaceae). *Bot. Not.* 132: 65-70.
- & P. WENDELBO (1979b). The taxonomic position of Bellevalia tabriziana (Liliaceae). Bot. Not. 132: 197-200.
- & P. WENDELBO (1979c). Alrawia, a new genus of Liliaceae-Scilloideae. Bot. Not. 132: 201-206.
- & P. WENDELBO (1979d). The artificial hybrid Hyacinthus orientalis × transcaspicus. Bot. Not. 132: 207-209.
- POPOVA, M. T. (1972). IOPB chromosome number reports XXXV (ed. Á. Löve). *Taxon* 21: 164-165.
- POST, G.-E. & E. AUTRAN (1899). Plantae Postianae, Fasc. IX. Bull. Herb. Boissier 7: 146-161.
- REICHENBACH, H. G. L. (1826). Iconographia botanica, seu plantae criticae 4. Lipsiae.

- RUBTSOVA, N. J. (1972). Opredelitel' vysshikh rastenii Kryma. Leningrad.
- RUIZ REJON, M. (1978). Estudios cariologicos en especies españolas del Orden Liliales III. Familia Liliaceae. *Anal. Inst. Bot. Cavanilles* 34(2): 733-759.
- SATÔ, D. (1942). Karyotype alteration and phylogeny in Liliaceae and allied families. *Jap. J. Bot.* 12: 57-161.
- SHARMA, A. K. (1956). A new concept of a means of speciation in plants. Caryologia 9: 93-130.
- SCHUR, F. (1856). Zur Flora von Siebenbürgen. Österr. Bot. Wochenbl. 6(29): 225-229, (30): 235-238.
- SPETA, F. (1974). Scilla messeniaca Boiss. (Liliaceae) und ihre verwandtschaftlichen Beziehungen. *Ann. Mus. Goulandris* 2: 59-67.
- (1975). Vier neue Scilla-Arten aus dem Bereich der "Flora iranica". Linzer Biol. Beitr. 7: 249-256.
- (1980). Die Frühjahrsblühenden Scilla-Arten des östlichen Mittelmeerraumes. Naturk. Jahrb. Stadt Linz 25: 19-198.
- STEVEN, C. (1857). Verzeichnis der auf taurischer Halbinsel wildwachsenden Pflanzen. *Bull. Soc. Imp. Nat. Moscou* 30(3): 65-160.
- TOBGY, H. A. (1943). A cytological study of Crepis fuliginosa, C. neglecta, and their F₁-hybrid, and its bearing on the mechanism of phylogenetic reduction in chromosome number. *J. Genetics* 45: 67-111.
- VISIANI, R. DE (1842). Flora dalmatica 1. Lipsiae.
- WENDELBO, P. (1964). On the genus Eremurus (Liliaceae) in South-West Asia. Arb. Univ. Bergen, Mat.-Nat. Ser. 1964(5): 1-45.
- (1973). Contributions to the Flora of Irap, XII. New species and new combinations in the Liliaceae. Kew Bull. 28: 29-35.
- (1980). Notes on Hyacinthus and Bellevalia (Liliaceae) in Turkey and Iran. Notes Roy. Bot. Gard. Edinburgh 38: 423-434.

Address of the authors: Department of plant geography, University of Göteborg, Carl Skottsbergs Gata 22, S-413 19 Göteborg, Sweden.