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

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RÉSUMÉ

PERSSON, K. & P. WENDELBO (1982). Taxonomie et cytologie du genre *Hyacinthella* (Liliacées-Scilloïdées) 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

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 *Arawia* 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).

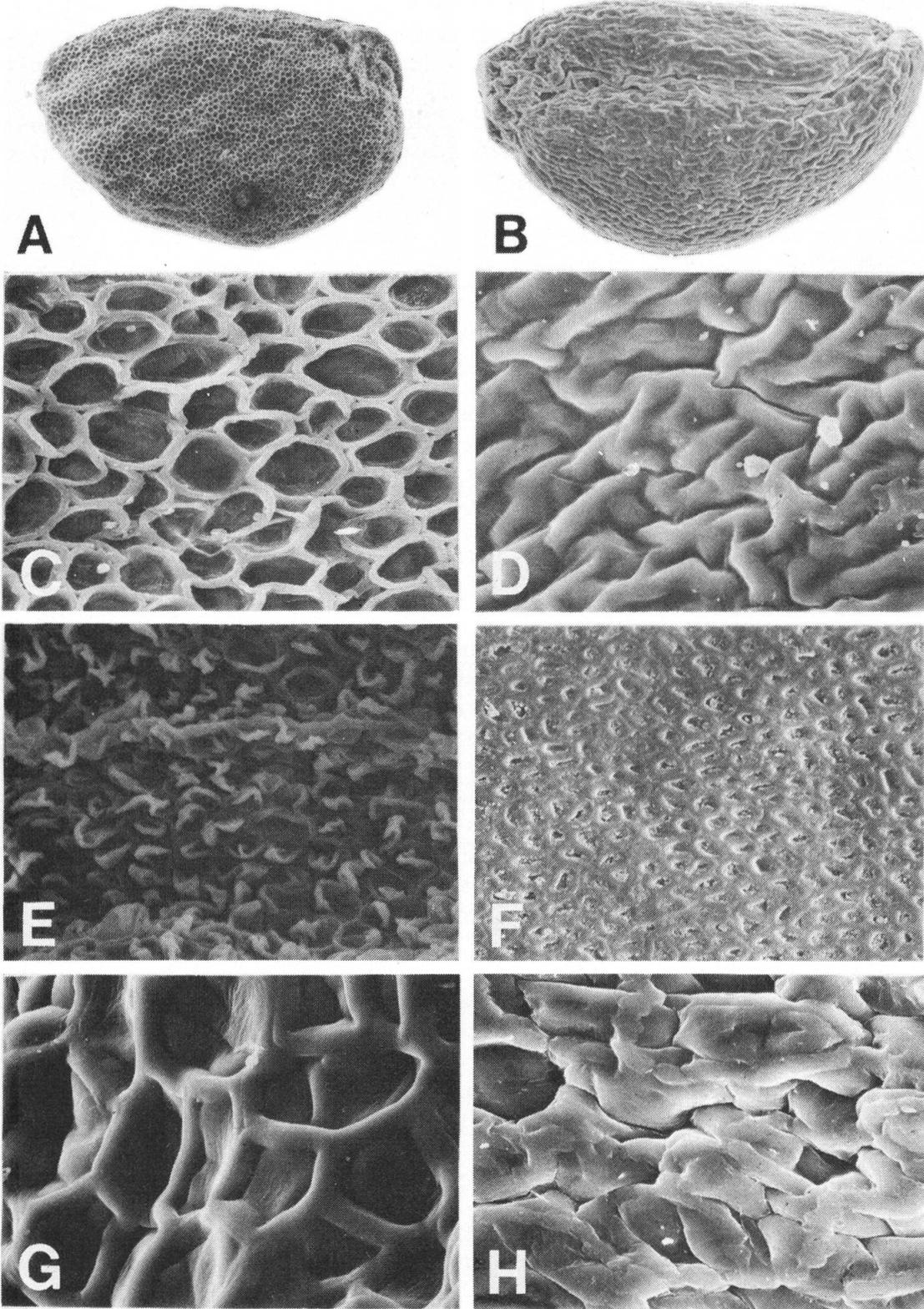
The ascending or more rarely patent perianth of *Hyacinthella* is characteristic, but in *Bellevalia* that usually has nodding flowers, at least in some stage of the anthesis, there are small-sized species with upright flowers, e.g. *B. decolorans* Bornm., *B. feinbrunae* Freitag & Wendelbo, *B. hyacinthoides* (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 *Arawia* the perianth is nodding in both species.

The perianth has overlapping lobes in *Hyacinthella* as in *Bellevalia*, *Arawia* 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 *Arawia* 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:** $\times 25$; **C-H:** $\times 185$ (SEM photo E. Gilert).

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

Cytology

From a karyological 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 μm 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), $2n = 26$ (SATŌ, 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 μm (= *Hyacinthella*) in SATŌ (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 \pm 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

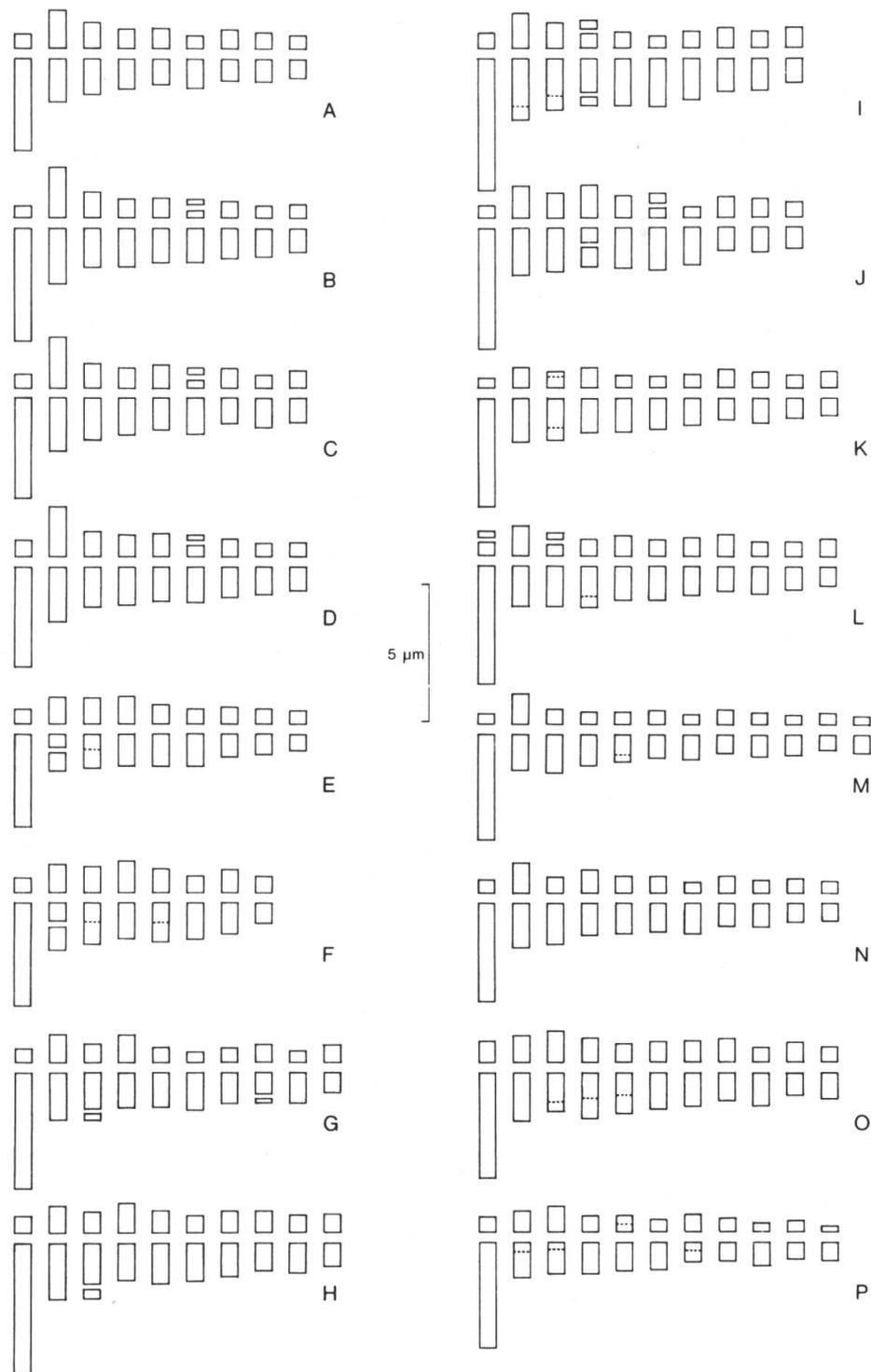


Fig. 12. — Idiograms. **A:** *Hyacinthella hispida*. **B:** *H. heldreichii*. **C:** *H. glabrescens*. **D:** *H. campanulata*. **E:** *H. acutiloba*. **F:** *H. lineata*. **G:** *H. leucophaea*. **H:** *H. atchleyi*. **I:** *H. pallasiana*. **J:** *H. pallens*. **K:** *H. millingenii*. **L:** *H. siirtensis*. **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 unequal 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, İçel: 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 Murtıçı 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, Ukraine: Odessa, Chadjibeysky liman, *Mordak & al.* 1586.
- H. atchleyi:** Greece, Viotia: between Halkis and Thive, *Horton* 1402.
- H. pallasiana:** USSR, Ukraine: 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

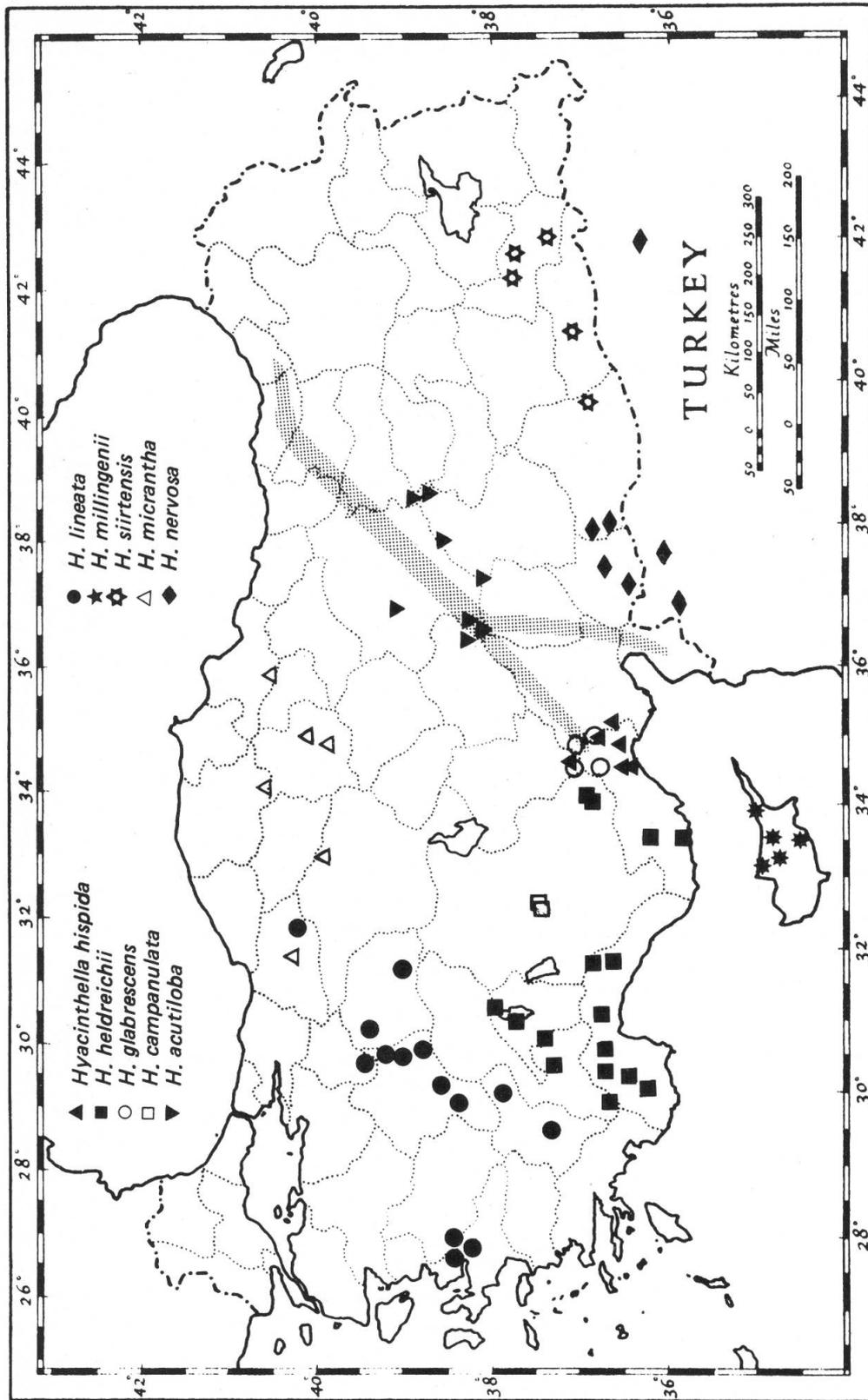


Fig. 13. — Total known distribution of different *Hyacinthella* species. *H. nervosa* has more localities in Syria, Lebanon, Israel and Jordan. Shaded area: the so-called Anatolian Diagonal (after DAVIS, 1971).

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 *Hyacinthella* 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 *hispidia*-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 *hispidia*-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,

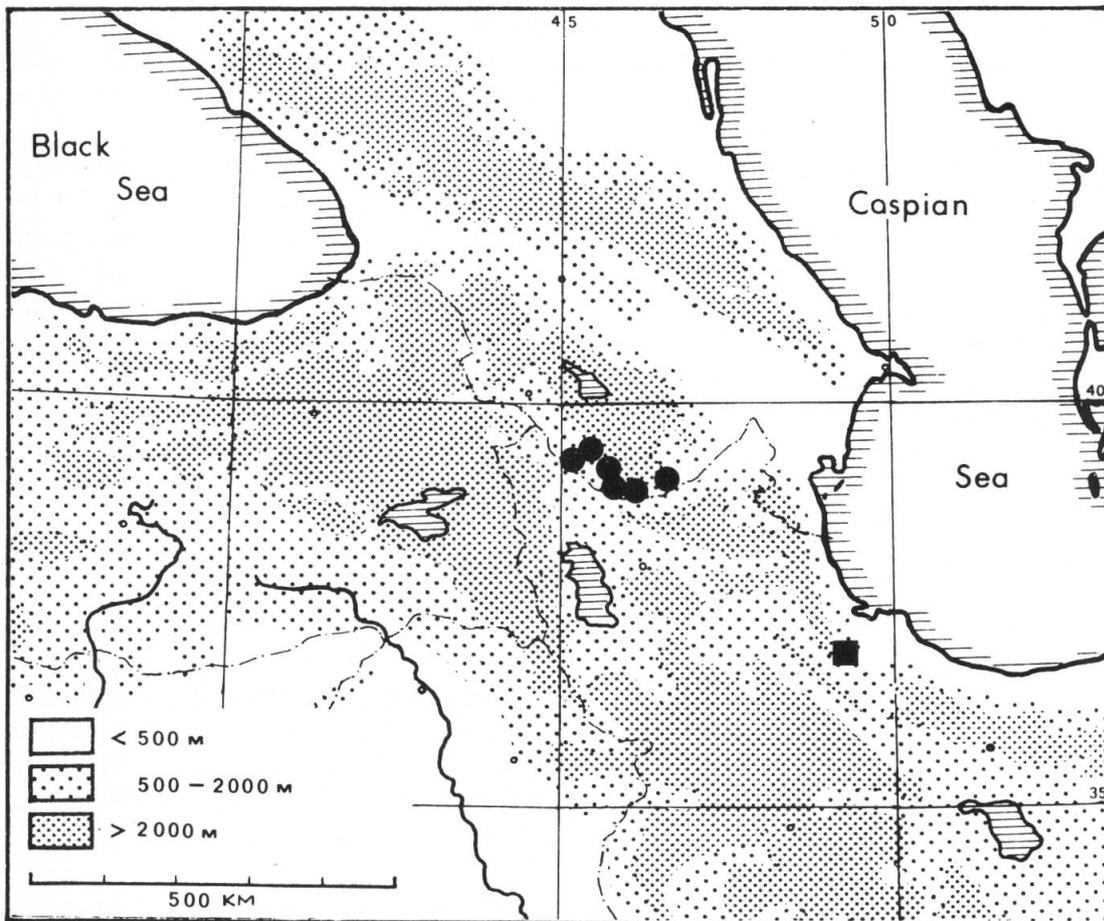


Fig. 14. — Total known distribution of *Hyacinthella atropatana* (dots) and *H. persica* (square).

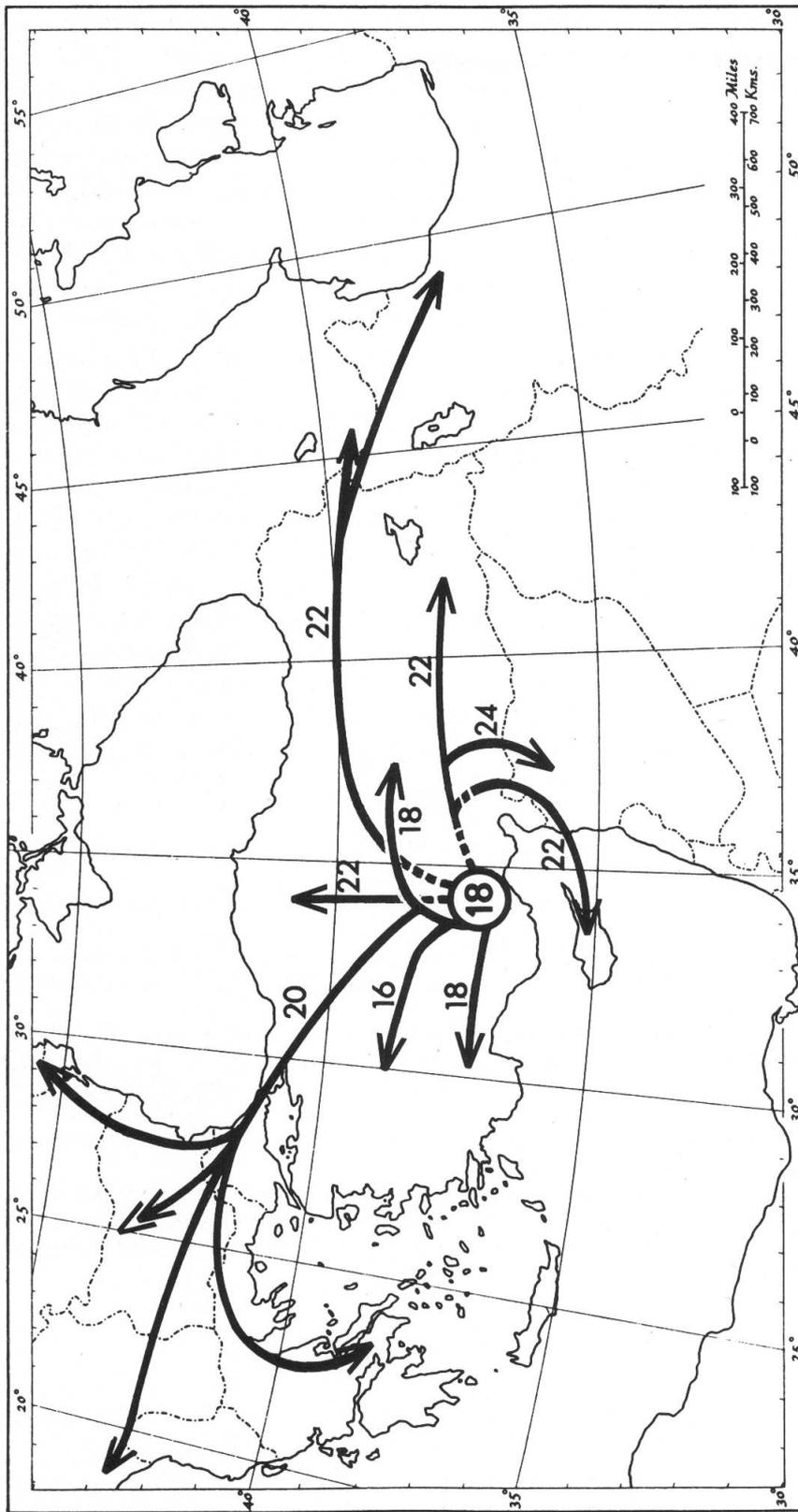


Fig. 15. — Evolution within the genus *Hyacinthella*. Large circle represents hypothetical centre of origin. $2n = 18$ is believed to have been the ancestral chromosome number from which all other cytotypes have evolved. It is still represented by the *H. hispida* group in S. Turkey and by *H. acutiloba* 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 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. micrantha* in N. Turkey, the *H. persica* group in Armenia and Iran (Gilan), *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.

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.

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