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Taxonomic problems in Mediterranean *Allium*, and relationships with non-Mediterranean *Allium* groups

Abstract

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The Mediterranean region is one of the centres of diversity of the genus *Allium*. Representatives of 4 out of 6 subgenera occur here, reflecting the rather heterogeneous evolutionary history of *Allium* in the Mediterranean area. Some are representatives of the basic stock of the genus, belonging e.g. to *A.* subg. *Rhizirideum* (mainly distributed in continental temperate Eurasia, and with rather unspecialized features) and subg. *Amerallium* (with the subendemic *A.* sect. *Molium* and some other small, derived species groups, adapted by their growth rhythm to the Mediterranean climate with its prolonged dry season). The majority of species belong to *A.* subg. *Allium*, whose evolution and radiation can be correlated to the development of vast arid regions, open for colonization, after the shrinking of the Tethys sea in the so-called Old Mediterranean region. The few Mediterranean species of *A.* subg. *Melanocrommyum* represent eastern immigrations from the Irano-Turanian province.

Introduction

The Mediterranean region is one of the centres of species diversity of the genus *Allium*. As computed from recent floras and taxonomic papers, 165 species occur in this area, i.e., almost ⅓ of the world total of *Allium* species. In terms of taxonomy, the Mediterranean species are a very heterogeneous assemblage: with the exception of two small, mainly E Asian subgenera, they represent all important subgenera of the genus, and reflect their geographic and phylogenetic diversity.

The subgenera

Table 1 is an overview of the absolute and relative importance of the subgenera of *Allium* occurring in the Mediterranean area, in terms of numbers of species present and of percent values of the world total for each subgenus.

Table 1. Subgenera of *Allium* in the Mediterranean area.

Allium	species n°	of approx. world total species n° per subg. or genus	of total Mediterranean species n°
subg. *Rhizirideum*	11	7 %	6.7 %
subg. *Amerallium*	27	22 %*	16.4 %
subg. *Melanocrommyum*	17	15 %	10.3 %
subg. *Allium*	110	40 %	66.7 %
Total	165	25 %	100.0 %

* > 70 % of Old World species of the subgenus.

Each of the four subgenera will be shortly characterized. The first two belong to the basic stock of the genus, whereas the two last represent derived groups with several obvious specializations.

Allium subg. *Rhizirideum*. – This is one of the largest groups of the genus. It is mainly a temperate Eurasian group, and the Eurasian steppe belt and adjacent mountain ranges in Middle and Central Asia are its centres of diversity. It is poorly represented in the Mediterranean countries, where it is mainly found in the northern submediterranean zone and in some mountainous districts.

Allium subg. *Rhizirideum* is extremely variable both morphologically and ecologically. Many of its species are only moderately xero-mesophytic, or may even grow in mesic habitats like moist meadows, mountain grasslands, or the herb layer of forests. This is also true for the Mediterranean representatives. The subgenus is further subdivided into 15 sections, based upon marked differentiations in many characters of the reproductive as well as vegetative sphere. Even the feature characterizing the subgenus as a whole, the presence of a rhizome, is subject to distinct variations. In the Mediterranean flora only 5 sections occur, each with a single or few species, of which only one (*A. horvatii* Lovrić) is a true (sub)mediterranean endemic. In general terms, this subgenus, in our area, appears in the form of mere outposts of taxa with a more northern and continental distribution. The lack of distinct specializations in most sections of the subgenus, and the occurrence of ancestral character states (perennial rhizomes with long-lived roots, the formation of functionally undifferentiated leaves and of several shoot generations per year, a simple and sometimes completely smooth testa structure, simple septal nectaries, bi-ovulate ovary locules, symmetrical karyotypes with the primary basic number $x = 8$, and the lack of a dormancy period within the growth cycle; see Hanelt & al. 1992) characterize *A.* subg. *Rhizirideum* as a basic group within the genus, one from which the evolution of the more derived groups may have started.

Allium subg. *Amerallium*. – The species in this group are less numerous than in *A.* subg. *Rhizirideum*, but they exhibit a very wide and disjunctive distribution. With a few exceptions, all American *Allium* taxa belong to subg. *Amerallium*. In the Old World, and apart from 1 or 2 species from the Himalayas and perhaps W China, this subgenus is concentrated in the Mediterranean region, with some extensions into the adjacent Near East (Caucasus, N Iran), Ethiopia, Portugal, and W to Central Europe. Some of the

Table 2. Sections of *Allium* subg. *Amerallium* in the Mediterranean area.

Allium	species n°	of approx. world total species n°
sect. *Molium*	21	70 %
sect. *Briseis*	2	67 %
sect. *Chamaeprason*	1	100 %
sect. *Rhynchocarpum*	1	100 %
sect. *Narkissoprason*	1	33 %
sect. *Arctoprason*	1	100 %

monospecific sections of *A.* subg. *Amerallium* (Table 2) are Mediterranean endemics, and the relatively large and important *A.* sect. *Molium* can be described as a Mediterranean subendemic.

With respect to its morphology and ecology, *Allium* subg. *Amerallium,* too, is very heterogeneous. This is also true for its Mediterranean members. Just compare:

- *Allium ursinum* L., of the monospecific *A.* sect. *Arctoprason* (moist broad-leaved forests; outstanding leaf morphology and development, deviating bulb morphology);
- *Allium paradoxum* (M. Bieb.) G. Don, of the oligospecific *A.* sect. *Briseis* (ecologically similar, but with a deviating basic chromosome number, seeds with an elaiosome, and leaves without petioles);
- *Allium narcissiflorum* Vill., of the oligospecific *A.* sect. *Narkissoprason* (grassy alpine slopes; rhizomatous plants with very large flowers and large seeds); and
- *Allium subhirsutum* L., of *A.* sect. *Molium* (dry slopes, open pine forests, garigues; with a typical *Allium*-like appearance).

In spite of their diverse character expressions, these species have important features in common, such as the primary basic chromosome number $x = 7$, and a special type of leaf anatomy (vessel arrangement in one row, subepidermal laticifers; see Fritsch 1988). The monophyletic status of the subgenus is confirmed by strong serological affinities, even between widely differing taxa (see Hanelt & al. 1992). Within *A.* subg. *Amerallium* there are distinct adaptive trends to aridity, both among the American and the Old World taxa. The complex formed of *A.* sect. *Molium,* sect. *Chamaeprason* and sect. *Rhynchocarpum,* with a seasonal growth rhythm reflecting Mediterranean climatic conditions (summer dormancy, late autumn or winter-spring growth cycle) and with formation of true bulbs with specialized storage scale leaves for survival during the dry season, nicely illustrates this trend. Many of the characters that indicate the basic position of *A.* subg. *Amerallium* within the genus, which have their parallel in *A.* subg. *Rhizirideum,* are found only in the American members of the subgenus. The Mediterranean members are obviously relatively derived, by analogy to groups in other subgenera that have likewise developed in adaptation to an arid climatic regime.

Allium subg. *Melanocrommyum.* – This subgenus is somewhat smaller than *A.* subg. *Amerallium.* Within the Mediterranean region, its distribution is limited to the east, mainly to Turkey and to the Mediterranean portions of Syria, Lebanon, and Israel. A few

species also occur in the central and western parts of S Europe. The main distribution of the subgenus is in the Irano-Turanian floristic region, especially the Turkestanic province. In some areas, its species make up for approximately 50 % of the total number of indigenous *Allium* species, and species diversity in this subgenus is the best justification for considering Middle Asia as the main centre of speciation of the genus.

The subgenus consists of strongly xerophilous and heliophilous plants, and completely lacks adaptations to more mesic environmental conditions such as can often be observed in the two first-named subgenera. These plants are components of dry steppes, semi-deserts or even deserts, arid mountain slopes, scrub and sometimes open, park-like dry woodland in the Central Asian mountain ranges. The severe climatic conditions (dry summer, cold winter) are reflected by an ephemeroid growth cycle, typical for most species of the subgenus. It is characterized by a long summer-and-winter dormancy and a short active phase from spring to early summer (Pistrick 1992).

Although rather variable in some features of vegetative parts, inflorescences, flowers and capsules, *Allium* subg. *Melanocrommyum* is a monophyletic group with several distinct synapomorphic character states: an increased number of ovules per locule, large seed size, subterranean leaf sheaths, basal and mostly broad leaves, a special seedling type with epigeal germination and an extremely long upper cotyledon portion, specialized testa structures, a deviating anatomy of septal nectaries (Druselmann 1992, Fritsch 1992, Kruse 1992b), and a special seed storage protein with a molecular weight of 65,000-70,000, not yet found in any other group of *Allium* (Maass 1992). *A.* subg. *Melanocrommyum* possesses true bulbs with one or two specialized storage cataphylls, often of a considerable size, which enable the plants to survive during a long dormancy period.

Obviously, *Allium* subg. *Melanocrommyum* represents a derived but very old branch of the genus. Its most pronounced serological affinities proved to be with some rather primitive groups of *A.* subg. *Rhizirideum* (sect. *Anguinum*, sect. *Butomissa*) and of *A.* subg. *Amerallium*, much less than with *A.* subg. *Allium* and with the more advanced sections of the other subgenera (Hanelt & al. 1992). The Mediterranean members of the subgenus seem to be a group of rather recent immigrants from its Near and Middle Eastern centre of development.

Allium subg. *Allium*. – This is the largest subgenus, comprising almost 40 % of the total species number of the genus, and it is likewise the most numerous group in the Mediterranean flora (Table 1). It occurs in all Mediterranean countries, but the species number clinally decreases westward (Greece, 40 species; Spain, 23 species; Stearn 1981, Pastor & Valdés 1983). Although widely distributed from temperate Europe to NW China and Japan, *A.* subg. *Allium* is a typical "Old Mediterranean" element in the sense of Russian phytogeographers (Popov 1983), with diversity centres in the Mediterranean and the Irano-Turanian regions (Hanelt & al. 1992). Ecologically it is restricted to various types of open, dry habitats with little competition by other plants; it seldom inhabits open woodland.

Allium subg. *Allium* is very difficult to circumscribe morphologically. Like *A.* subg. *Melanocrommyum*, it belongs to the $x = 8$ branch of the genus and can best be characterized by the lack of salient features such as rhizomes, multi-ovulate ovary locules, subter-

ranean sheaths, unusual germination patterns, leaf petioles, seed appendages, ovary crests, etc. True bulbs with one or a few storage cataphylls enable the plants to survive unfavourable seasons, such as the Mediterranean summer, in a state of dormancy. A prolonged mid-summer to winter dormancy apparently characterizes some species from Near or Middle Eastern countries (Pistrick 1992), whereas winter-green taxa like *A. porrum* L. and its relatives reflect the mild and rainy Mediterranean winter season.

The subgenus is a rather heterogeneous group and can be divided into several sections, all except a small Inner Asian one occurring in the Mediterranean area. They are listed in Table 3. Numerical taxonomic studies (Hanelt & al. 1992, and unpublished data) indicate that *Allium* subg. *Allium* may be an artificial assemblage, its members appearing as different branches in the dendrograms, clearly distinguished by their similarity levels. *A.* sect. *Scorodon,* sect. *Brevispatha,* and sect. *Codonoprasum* obviously form a coherent group within which the sectional limits are sometimes difficult to draw; e.g., some Turkish species are transitional between *A.* sect. *Codonoprasum* and sect. *Scorodon* (Kollmann 1984), and for several species it is questionable whether they belong to *A.* sect. *Scorodon* or sect. *Brevispatha.*

Allium sect. *Scorodon* is itself rather heterogeneous with respect to characters such as testa sculpturation, leaf sequence (Kruse 1992a, b), growth cycle (Pistrick 1992), and ovary anatomy (Fritsch 1992). Presently, the section can hardly be defined in a positive manner and is in need of further investigation. It is a mainly an Irano-Turanian group, agreeing with *A.* subg. *Melanocrommyum* in its distribution. Only one fifth of its species occur in the Mediterranean area. Here, especially in the Eastern part, *A.* sect. *Brevispatha* – an offspring of this section in which it was formerly included – is relatively more important.

In general terms, *Allium* sect. *Codonoprasum* with its characteristic unequal and long-caudate spathe leaves is much more homogeneous. It is a typically Mediterranean group, which with many of its species extends from the E Mediterranean into the Caucasus.

As is well illustrated by numerical dendrograms (Hanelt & al. 1992 and unpubl. data), *Allium* sect. *Allium,* with its distinctly dimorphic stamens, stands apart from the other sections and is well delimited. It is the largest and most widely distributed group of the subgenus (B. Mathew 1996). It extends from N and W Europe to W Asia, but is centred on the Mediterranean, Oriental and Caucasian floristic (sub)regions (Hanelt & al. 1992),

Table 3. Sections of *Allium* subg. *Allium* in the Mediterranean area.

Allium	species n°	of approx. world total in section	of total Mediterranean species n° in subgenus	of total Mediterranean species n° in *Allium*
sect. *Codonoprason*	37	62 %	33.6 %	22.4 %
sect. *Scorodon*	19	20 %	17.3 %	11.5 %
sect. *Brevispatha*	13	90 %	11.8 %	7.9 %
sect. *Allium*	41	33 %	37.3 %	24.8 %
Total	110		100.0 %	66.7 %

with many characteristic Mediterranean species (*A. ampeloprasum* L., *A. commutatum* Guss., *A. amethystinum* Tausch, *A. sphaerocephalon* L., *A. guttatum* Stev., etc.).

Available data indicate that *Allium* subg. *Allium* is a derived and actively evolving group; its rapid diversification probably took place subsequent to the desiccation of the Tethys and aridification of S Europe, when vast land areas opened up for colonization. This view is confirmed by the lack of clear-cut limits between the sections and, especially, species, which are often difficult to determine because many transitions occur (particularly in *A.* sect. *Codonoprasum* and sect. *Allium*); by the widespread occurrence of polyploids, including intraspecific polyploid series and odd polyploids; by the frequent formation of bulbils instead of flowers, and concomitant loss of seed fertility; by the tendency to anthropochory and colonization of man-made habitats (true weeds, in *Allium,* are only found in this subgenus); and by several apomorphic character states of the androecium, spathe, testa structure, etc.

Molecular data

At the Gatersleben Institute a research programme has been established, to use molecular markers for the study of taxonomic and phylogenetic problems. Within this programme, Dr. G. Linne von Berg has analysed cpDNA restriction patterns of various *Allium* species, revealed by the restriction enzyme Ban I. Preliminary results support the above assumptions; definite conclusions, however, can only be drawn after careful mapping of the restriction fragments. So far, the patterns confirm the coherence of all analysed taxa of *Allium,* with *Nothoscordum* used as outgroup. The heterogeneous nature of *A.* subg. *Amerallium* is borne out by a dendrogram based upon restriction fragments data: one species group *(A. ursinum, A. subhirsutum)* stands rather isolated, the other is associated with different branches representing species of *A.* subg. *Rhizirideum.* Among this second group there are some N American species and *A. moly* L. from the Mediterranean, all of which have identical restriction patterns. This strongly favours the hypothesis of a common ancestry of European and American taxa of *A.* subg. *Amerallium* and of a basic positions of this subgenus within *Allium. A.* subg. *Rhizirideum* is similarly heterogeneous, which mirrors its diversity in morphological and other respects. *A.* subg. *Allium* appears in the dendrogram as a separate branch, with some relations to *A.* subg. *Rhizirideum* and subg. *Melanocrommyum.* It proved to be extremely uniform, exhibiting almost identical restriction patterns even for phenotypically rather different subgroups. These data confirm the monophyletic nature of this derived, apparently rather recently but strongly diversified subgenus (Linne von Berg 1996).

References

Druselmann, S. 1992: Vergleichende Untersuchungen an Vertretern der *Alliaceae* Agardh. 1. Morphologie der Keimpflanzen der Gattung *Allium* I. – Flora **186:** 37-52.

Fritsch, R. 1988: Anatomische Untersuchungen an der Blattspreite bei *Allium* L. *(Alliaceae)* I. Arten mit einer einfachen Leitbündelreihe. – Flora **181:** 83-100.

– 1992: Septal nectaries in the genus *Allium* – shape, position and excretory canals. – Pp. 77-85 in: Hanelt, P., Hammer, K. & Knüpffer, H. (ed.), The genus *Allium* – taxonomic problems and genetic resources. – Gatersleben.

Hanelt, P., Schultze-Motel, J., Fritsch, R., Kruse, J., Maass, H. I., Ohle, H. & Pistrick, K. 1992: Infrageneric grouping of *Allium* – the Gatersleben approach. – Pp. 107-123 in: Hanelt, P., Hammer, K. & Knüpffer, H. (ed.), The genus *Allium* – taxonomic problems and genetic resources. – Gatersleben.

Kollmann, F. 1984: 11. *Allium* L. – Pp. 98-211 in: Davis, P. H. (ed.), Flora of Turkey and the East Aegean islands, **8.** – Edinburgh.

Kruse, J. 1992a: Growth form characters and their variation in *Allium* L. – Pp. 173-179 in: Hanelt, P., Hammer, K. & Knüpffer, H. (ed.), The genus *Allium* – taxonomic problems and genetic resources. – Gatersleben.

– 1992b: Variability of testa sculptures in the genus *Allium* L. – Pp. 181-182 in: Hanelt, P., Hammer, K. & Knüpffer, H. (ed.), The genus *Allium* – taxonomic problems and genetic resources. – Gatersleben.

Linne von Berg, G., Samoylov, A., Klaas, M. & Hanelt, P. 1996: Chloroplast DNA restriction analysis and the infrageneric grouping of *Allium (Alliaceae).* – Pl. Syst. Evol. (in press).

Maass, H. I. 1992: Electrophoretic study of storage proteins in the genus *Allium* L. – Pp. 183-189 in: Hanelt, P., Hammer, K. & Knüpffer, H. (ed.), The genus *Allium* – taxonomic problems and genetic resources. – Gatersleben.

Mathew, B. 1996: A review of *Allium* section *Allium.* – Kew.

Pastor, J. & Valdés, B. 1983: Revisión del género *Allium (Liliaceae)* en la península Ibérica e Islas Baleares. – Sevilla.

Pistrick, K. 1992: Phenological variability in the genus *Allium* L. – Pp. 243-249 in: Hanelt, P., Hammer, K. & Knüpffer, H. (ed.), The genus *Allium* – taxonomic problems and genetic resources. – Gatersleben.

Popov, M. G. 1983: Osnovy florogenetiki. – Pp. 132-237 in: Popov, M. G., Izbrannye trudy, **1.** – Kiev.

Stearn, W. T. 1981: The genus *Allium* in the Balkan Peninsula. – Bot. Jahrb. Syst. **102:** 201-213.

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