1 Evolution, Domestication and Taxonomy

R.M. Fritsch[1] and N. Friesen[2]

[1]*Institut für Pflanzengenetik und Kulturpflanzenforschung,
D-06466 Gatersleben, Germany;* [2]*Botanischer Garten der Universität, D-49076
Osnabrück, Germany*

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1. The Genus *Allium* L.

1.1 General characteristics

The taxonomic position of *Allium* and related genera has long been a matter of controversy. In early classifications of the angiosperms (Melchior, 1964), they were placed in the *Liliaceae*. Later, they were more often included in the *Amaryllidaceae*, on the basis of inflorescence structure. Recently, molecular data have favoured a

division into a larger number of small mono-phyletic families. In the most recent and competent taxonomic treatment of the monocotyledons, *Allium* and its close rela-tives were recognized as a distinct family, the *Alliaceae*, close to the *Amaryllidaceae*. The fol-lowing hierarchy has been adopted (Takhtajan, 1997):

1. Class *Liliopsida*.
2. Subclass *Liliidae*.
3. Superorder *Liliianae*.
4. Order *Amaryllidales*.
5. Family *Alliaceae*.
6. Subfamily *Allioideae*.
7. Tribe *Allieae*.
8. Genus *Allium*.

However, other classifications still have their proponents and are still used in some litera-ture.

There is more agreement about the delimitation of the genus *Allium* itself. It is a large genus of perennial, mostly bulbous plants sharing as characteristics:

- Underground storage organs: bulbs, rhi-zomes or swollen roots.
- Bulbs: often on rhizomes; true bulbs (one or two extremely thickened prophylls) or false bulbs (thickened basal sheaths plus thickened prophylls (bladeless 'true scales')); several tunics, membranous, fibrous or coriaceous; annual or peren-nial roots.
- Rhizomes: condensed or elongated; rarely runner-like; with very diverse branching patterns.
- Leaves: basally arranged, frequently cov-ering the flower scape and thus appear-ing cauline.
- Bracts: two to several, often fused into an involucre ('spathe').
- Inflorescence: fasciculate to often umbel- or head-like, (one-) few- to many-flowered, loose to dense.
- Flowers: pedicelled, actinomorphic, hypogynous, trimerous.
- Tepals: in two slightly differentiated whorls, free.
- Stamens: in two whorls, sometimes basally connected, the inner ones often widened and/or toothed.

- Ovary: trilocular, three septal nectaries of various shape, two or more curved (campylotropous) ovules per locule, sometimes diverse apical appendages (crests and horns); developing into a loculicidal capsule dehiscing along the midrib of the carpels.
- Style: single, with slender, capitate or, more rarely, trilobate stigma.
- Seeds: angular to globular, black (epider-mal layer contains phytomelan), orna-mentation of the cells extremely variable.
- Chemical characters: reserve compounds consist of sugars, mainly fructans, and no starch; enzymatic decomposition prod-ucts of several cysteine sulphoxides (see Randle and Lancaster, Chapter 14, and Keusgen, Chapter 15, this volume) cause the species- and group-specific (though sometimes missing) characteristic odour.
- Karyology: predominant basic chromo-some numbers $x = 8$ and $x = 7$ with polyploids in both series; chromosome morphology and banding pattern differ-ent between taxonomic groups.

Shape, size, colour and texture of rhi-zomes, bulbs, roots, leaves (e.g. flat, chan-nelled, terete or fistulose, sheath/lamina ratio), scapes, spathes, inflorescences, tepals (mostly white or rose to violet, rarely blue or yellow), stamens, ovaries and seeds may vary considerably and in very different manners. The same is true for the anatomy, cross-sections and internal structure of all the listed plant parts.

Basal bulblets and bulbils (topsets) are important in vegetative propagation. As far as known, most *Allium* species are alloga-mous. Spontaneous interspecific hybridiza-tion is not as rare as formerly believed, but strong crossing barriers exist in some groups, even between morphologically simi-lar species.

1.2 Distribution, ecology and domestication

The genus *Allium* is widely distributed over the holarctic region from the dry subtropics to the boreal zone (Fig. 1.1). One or two
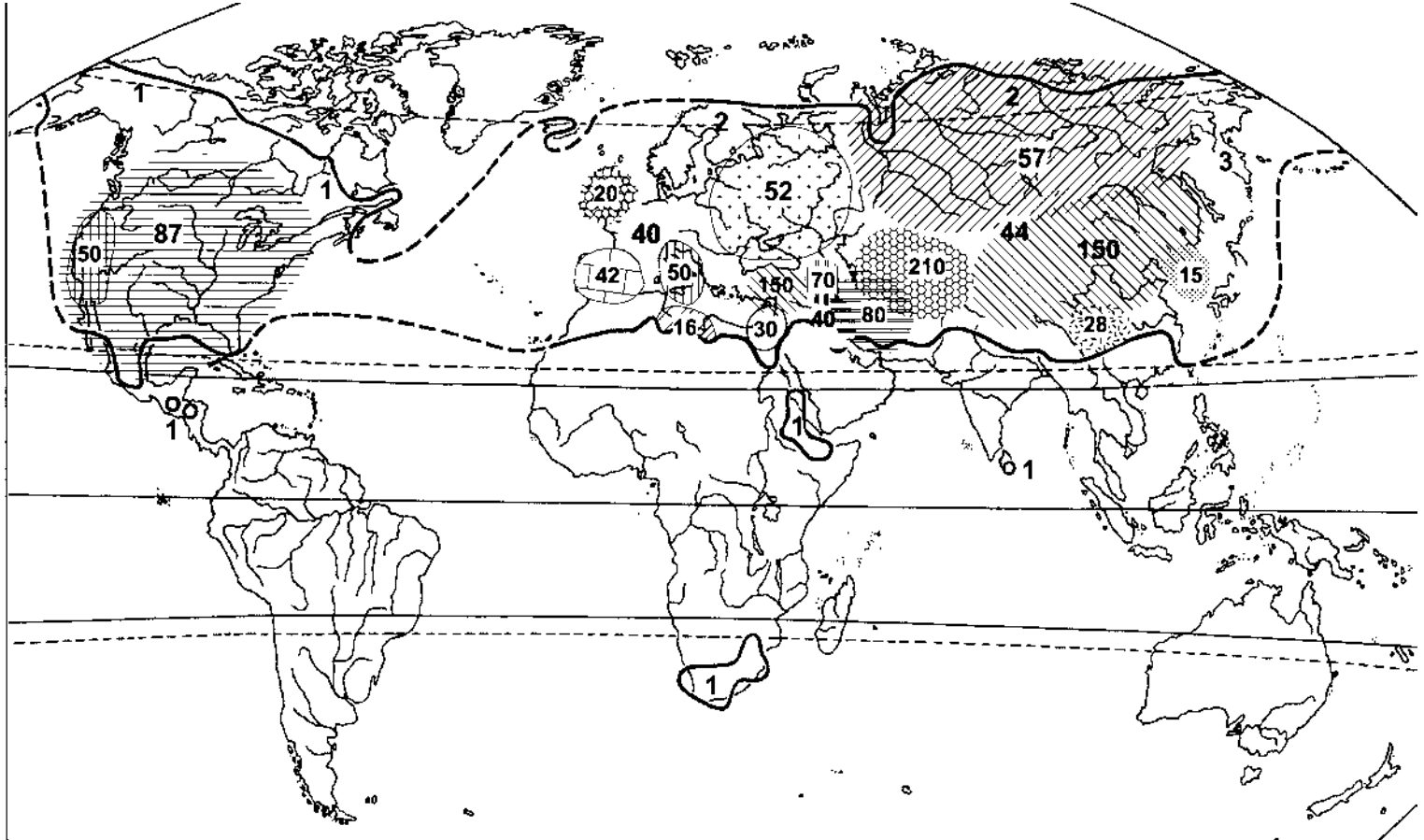
Fig. 1.1. World distribution of wild species of the genus *Allium*. The numbers on the map indicate the number of species found in each region.

species even occur in the subarctic belt, e.g. *A. schoenoprasum* L., and a few alliums are scattered in mountains or highlands within the subtropics and tropics. Only *A. dregeanum* Kth. has been described from the southern hemisphere (South Africa) (de Sarker *et al.*, 1997).

A region of especially high species diversity stretches from the Mediterranean basin to Central Asia and Pakistan (Fig. 1.1). A second, less pronounced centre of species diversity occurs in western North America. These centres of diversity possess differing percentages of the several subgroups of the genus and are thus clearly distinguishable in taxonomic terms.

Evolution of the genus has been accompanied by ecological diversification. The majority of species grow in open, sunny, rather dry sites in arid and moderately humid climates. However, *Allium* species have adapted to many other ecological niches. Different types of forests, European subalpine pastures and moist subalpine and alpine grasslands of the Himalayan and Central Asian high mountains all contain some *Allium* species, and gravelly places along river-banks do as well. Even saline and alkaline environments are tolerated by some taxa.

Allium species from these diverse habitats exhibit a parallel diversity in their rhythms of growth (phenology). Spring-, summer- and autumn-flowering taxa exist. There are short- and long-living perennials, species with one or several annual cycles of leaf formation, and even continuously leafing ones. Species may show summer or winter dormancy. For many species (named 'ephemeroids'), annual growth is limited to a very short period in spring and early summer when the cycle from leaf sprouting to seed maturation is completed in 2 or 3 months.

Conditions suitable for seed germination vary between species. Seed dormancy is variable between wild species. For most species the germinability of the seeds seems to be limited to a few years, unless the seed is stored under cold and very dry conditions, when its life can be greatly extended.

The genus is of great economic significance because it includes several important vegetable crops and ornamental species.

However, in contrast, some *Allium* species are noxious weeds of cultivated ground. The cultivated *Allium* crop species are listed in Table 1.1.

Generally, all plant parts of alliums may be consumed by humans (except perhaps the seeds), and many wild species are exploited by the local inhabitants. These natural resources are often improperly managed at the present time (see Section 2.3.4), and overcollecting caused severe decline of wild sources in the past. Very probably, both protection and the rational use of wild plants growing close to settlements, as well as the transfer of plants into existing garden plots (as explained below under *A. cepa*) (Hanelt, 1990), may all have been important at the initial stages of domestication. Further human and natural selection then led to the development of the different plant types present in several cultivated species.

Domestication did not change the ploidy status of onion, shallot, garlic and many other diploid species, and introgression of other species only rarely played a role during the selection processes. The same seems to be true for the cultivated taxa of *A. ampeloprasum*, which apparently arose from ancestors of different ploidy levels (see Section 4.2).

However, cultivated strains of *A. ramosum* and *A. chinense* include diploids, triploids and tetraploids. Because diploid and tetraploid wild strains exist, polytopic, i.e. at different places (and at several times), domestication of *A. ramosum* seems probable. The history of domestication of *A. chinense* is still being disputed. Either the existence of wild strains in Central and East China is accepted, or cultivars are traced back to the closely related wild species *A. komarovianum* Vved. Participation of other wild species, such as *A. thunbergii* G. Don, seems possible (Hanelt, 2001).

Domestication of wild plants is still continuing. *A. komarovianum* was reportedly taken again into cultivation as a vegetable in North Korea quite recently (Hanelt, 2001), and the case of *A. pskemense* is described below (Section 3.4). Some species listed below (Section 4) have also been recently taken into cultivation, but usually exact data are lacking.

Table 1.1. Cultivated *Allium* species and their areas of cultivation.

Botanical names of the crop groups	Other names used in the literature	Area of cultivation	English names
A. altaicum Pall.	*A. microbulbum* Prokh.	South Siberia	Altai onion
A. ampeloprasum L.			
Leek group	*A. porrum* L., *A. ampeloprasum* var. *porrum* (L.) J. Gay	Mainly Europe, North America	Leek
Kurrat group	*A. kurrat* Schweinf. ex Krause	Egypt and adjacent areas	Kurrat, salad leek
Great-headed garlic group	*A. ampeloprasum* var. *holmense* (Mill.) Aschers. et Graebn.	Eastern Mediterranean, California	Great-headed garlic
Pearl-onion group	*A. ampeloprasum* var. *sectivum* Lued.	Atlantic and temperate Europe	Pearl onion
Tarée group		Iran	Tarée irani
A. canadense L.		Cuba	Canada onion
A. cepa L.			
Common onion group	*A. cepa* ssp. *cepa*/var. *cepa*, *A. cepa* ssp. *australe* Kazakova	Worldwide	Onion, common onion
Ever-ready onions	*A. cepa* var. *perutile* Stearn	Great Britain	Ever-ready onion
Aggregatum group	*A. ascalonicum* auct. hort., *A. cepa* var. *aggregatum* G. Don, var. *ascalonicum* Backer, ssp. *orientalis* Kazakova	Nearly worldwide	Shallot, potato onion, multiplier onion
A. consanguineum Kunth		North-East India	
A. × cornutum Clem. ex Vis.*	*A. cepa* var. *viviparum* auct.*	Locally in South Asia, Europe, Canada, Antilles	
A. chinense G. Don	*A. bakeri* Regel	China, Korea, Japan, South-East Asia	Rakkyo, Japanese scallions
A. fistulosum L.		East Asia, temperate Europe and America	Japanese bunching onion, Welsh onion
A. hookeri Thw.		Bhutan, Yunnan, North-West Thailand	
A. kunthii G. Don	*A. longifolium* (Kunth) Humb.	Mexico	
A. macrostemon Bunge	*A. uratense* Franch., *A. grayi* Regel	China, Korea, Japan	Chinese garlic, Japanese garlic
A. neapolitanum Cyr.	*A. cowanii* Lindl.	Central Mexico	Naples garlic
A. nutans L.		West and South Siberia, Russia, Ukraine	
A. obliquum L.		West Siberia, East Europe	Oblique onion
A. oschaninii O. Fedtsch.		France, Italy	French shallot*
A. × proliferum (Moench) Schrader			
East Asian group	*A. aobanum* Araki, *A. wakegi* Araki	China, Japan, South-East Asia	Wakegi onion
Eurasian group	*A. cepa* var. *viviparum* (Metzg.) Alef., *A. cepa* var. *proliferum* (Moench) Alef.	North America, Europe, North-East Asia	Top onion, tree onion, Egyptian onion, Catawissa onion
A. pskemense B. Fedtsch.		Uzbekistan, Kyrgyzstan, Kazakhstan	

Continued.

Table 1.1. *Continued.*

Botanical names of the crop groups	Other names used in the literature	Area of cultivation	English names
A. ramosum L.	*A. odorum* L., *A. tuberosum* Rottl. ex Sprengel	China and Japan, worldwide now	Chinese chive, Chinese leek
A. rotundum L.	*A. scorodoprasum* ssp. *rotundum* (L.) Stearn	Turkey	
A. sativum L.			Garlic
Common garlic group	*A. sativum* var. *sativum*, *A. sativum* var. *typicum* Regel	Mediterranean area, also worldwide	
Longicuspis group	*A. longicuspis* Regel	Central to South and East Asia	
Ophioscorodon group	*A. sativum* var. *ophioscorodon* (Link) Döll	Europe, also worldwide	
A. schoenoprasum L.	*A. sibiricum* L.	Worldwide in temperate areas	Chive
A. ursinum L.		Central and North Europe	Ramsons
A. victorialis L.	*A. microdictyon* Prokh., *A. ochotense* Prokh.	Caucasus, Japan, Korea, Europe (formerly)	Long-root onion, long-rooted garlic
A. wallichii Kunth	*A. platyphyllum* Diels, *A. lancifolium* Stearn	East Tibet	

* See Friesen and Klaas (1998).

As with many ancient cultivated plants, only a limited amount of circumstantial evidence and no hard facts are available on the evolutionary history of cultivated alliums. Sculptural and painted representations from ancient Egypt support the assumption that onion, garlic and leek were already cultivated at that time. However, it is impossible to pursue these traces during antiquity because many plant names of that era cannot with certainty be assigned to particular species of plants. Unfortunately, a great part of the recent and historical diversity of onion, garlic and several other *Allium* crops, such as chives, was developed during that time and therefore will remain obscure.

1.3 Phylogeny and classification

Recent estimations accept about 750 species in the genus *Allium* (Stearn, 1992), and 650 more synonymous species names exist (Gregory *et al.*, 1998). It is important to divide this large number of species into smaller units or groups for practical purposes. This is also theoretically justified because the genus consists of groups differing in phylogenetic history, in geographical affinity and in evolutionary state and age.

The early monographer of *Allium*, Regel (1875, 1887), grouped the 285 species he accepted into six sections, which trace back to informal groups established by Don (1832). A more recent classification was proposed by Hanelt *et al.* (1992), including six subgenera, 57 sections and subsections. In this scheme, the authors combined some essential ideas from earlier classifications and our own research data as a landmark at the beginning of the molecular research era.

Later, regional revisions on Mediterranean section *Allium* (Mathew, 1996), Central Asia (Khassanov, 1997), China (Xu and Kamelin, 2000) and North America (McNeal and Jacobsen, 2002) supplemented the partly outdated older ones available for Europe (Stearn, 1980; Pastor and Valdes, 1983), most parts of Asia (Vvedensky and Kovalevskaya, 1971; Wendelbo, 1971; Matin, 1978; Kollmann, 1984; Friesen, 1988) and Africa (Wilde-Duyfjes, 1976). The latest compilation of *Allium* names (Gregory *et al.*, 1998) allows us

to trace information across the different species concepts, the complicated classifications and the nomenclatural incongruities presented in earlier classifications.

1.3.1 Evolutionary lineages

The genus *Allium* is generally adapted to arid conditions. This makes it difficult to select natural evolutionary lineages using easily discernible characteristics. Phylogenetically different structures, e.g. leaf blades with one or two rows of vascular bundles, are often hidden by morphological similarities forced by functional reasons. Therefore, the traditional infrageneric classifications include homoplasies, i.e. excess changes resulting from parallel or convergent evolution, and do not necessarily represent evolutionary lineages.

- In the past, detailed investigations using modern methods have contributed more supportive data to evaluate and establish evolutionary lineages, and have resulted in more elaborate classifications with more and necessarily smaller groups. However, many facts remain open to interpretation, and neither the phylogenetically most basic *Allium* group nor the evolutionary lineages could be precisely determined (Hanelt *et al.*, 1992). Thus, the unknown phylogenetic connections between the taxonomic groups remain the most prominent problem of all *Allium* classification studies.
- Most recently, molecular studies have resulted in independent data on the evolutionary history of the genus (see Fig. 8.1, Klaas and Friesen, Chapter 8, this volume). Three main evolutionary lines were detected: (i) subgenus *Amerallium sensu* Hanelt *et al.* (1992), subgenus *Nectaroscordum*, subgenus *Microscordum*; (ii) subgenus *Melanocrommyum sensu* Hanelt *et al.* (1992), subgenus *Caloscordum*, subgenus *Anguinum*; and (iii) subgenus *Rhizirideum sensu stricto*, subgenus *Butomissa*, subgenus *Cepa*, subgenus *Allium s. str.*, subgenus *Reticulatobulbosa s. str.*

The taxonomically unclear subgenus *Bromatorrhiza* (Hanelt *et al.*, 1992) was an artificial assemblage (Samoylov *et al.*, 1999).

Its members are now considered to belong to the subgenera *Amerallium* (sect. *Bromatorrhiza*) and *Rhizirideum* (sects *Cyathophora* and *Coleoblastus*).

Based on molecular data, the phylogenetic information now available allows us to conclude that the bulbous subgenera *Amerallium* and *Melanocrommyum* represent more ancient lines. The development of elongated rhizomes and of false bulbs are advanced character states (synapomorphies), as are fistulose leaves in the sections *Cepa* and *Schoenoprasum*. This new classification mainly uses well-known taxonomic groups and names, but several sections have been given another rank or another formal circumscription. The accepted subgenera are characterized as follows.

1.3.2 Subgenera with a basal chromosome number of x = 7

Subgenus Amerallium. Subgenus *Amerallium* is not exclusively a New World group, although its name may seem to indicate this. Several sections are Eurasian (European, Mediterranean, Himalayan). Nevertheless, molecular data have verified the monophyly of this subgenus as well as the distinctness of both geographical subgroups (Samoylov *et al.*, 1999). Most species of subgenus *Amerallium* produce true bulbs but others have bulbs on rhizomes. Vegetative anatomy and other characters, including molecular data, strongly support its separate status. The basic chromosome number x = 7 dominates, and yet x = 8, 9 and 11 also occur in several morphologically derived groups.

Subgenus Microscordum. The monotypic East Asian section *Microscordum* shares anatomical and morphological characters with the species of subgenus *Amerallium*, although the plants are tetraploids ($2n = 32$) on the basic number x = 8. Molecular data have verified the systematic position close to the subgenera *Amerallium* and *Nectaroscordum*.

Subgenus Nectaroscordum. A basic chromosome number of x = 9 and the special and unique characters of most flower parts and of

other morphological traits were the main arguments for separating this oligotypic group at generic level. However, leaf anatomical characters and molecular data suggest a close relationship to subgenus *Amerallium*.

1.3.3 Subgenera with a basal chromosome number of x = 8

RHIZOMATOUS PLANTS. All rhizomatous species with x = 8 chromosomes share many characters and have been included in the classical subgenus *Rhizirideum s. lato* (Hanelt *et al.*, 1992). Rhizomes have always been considered an indication of primitive or ancestral origin, irrespective of the existing morphological diversity (Cheremushkina, 1992). However, dendrograms based on molecular data (Mes *et al.*, 1997; Friesen *et al.*, 1999a; Fig. 1.2) showed several clades with rhizomatous species being 'dislocated' between clades of the bulbous subgenera *Melanocrommyum* and *Allium*. This fact provides evidence that rhizomes are not necessarily ancestral, and may have evolved and developed independently several times.

Irrespective of the different phylogenetic status, rhizomatous alliums are adapted to similar ecological conditions and have much in common in their horticultural traits. For practical reasons, the '*Rhizirideum* group' will remain a handy and workable unit for a long time.

Subgenus Rhizirideum s. str. This small subgenus comprises several oligotypic sections to which Eurasian steppe species belong, as well as others which show the most diversity in South Siberia and Mongolia. A few species, which would perhaps best be separated as subgenus *Cyathophora*, formerly incorrectly included in the subgenus *Bromatorrhiza*, are distributed in Tibet and the Himalayas.

Subgenus Anguinum. The morphologically well characterized section *Anguinum* is disjunctively distributed in high mountains from south-western Europe to East Asia, and also in north-eastern North America. The plants possess well-developed rhizomes and show a distinct and unique type of simple seed testa sculpture (Kruse, 1988). According to molecular studies, the subgenus is more closely related to the bulbous subgenus *Melanocrommyum* than to any other *Allium* lineage.

Subgenus Butomissa. This small and unique subgenus includes only a few species, which partly inhabit the Siberian–Mongolian–North Chinese steppes, while other species are distributed in the mountains from East Asia to Central Asia and up to the eastern Mediterranean area.

Subgenus Cepa. Species with fistulose leaves, often well-developed bulbs and short vertical rhizomes dominate. Several species of the well-known sections *Cepa* and *Schoenoprasum* occupy most of the Eurasian continent, but most species are distributed in the mountain belt from the Alps and Caucasus to East Asia.

Subgenus Reticulatobulbosa. This is the largest segregate from subgenus *Rhizirideum sensu lato* (*s. lato*), characterized by narrow linear leaves and reticulate bulb tunics. The centre of diversity of the different species-rich sections is located in South Siberia and Central Asia, with wide extensions into adjacent regions of Asia, Europe, Tibet and the Himalayas. Species from section *Scorodon s. str.* (*A. moschatum*) are bulbous but with a well-developed small rhizome. Molecular data support their inclusion in this subgenus.

BULBOUS PLANTS

Subgenus Allium. The subgenus *Allium* is the largest one of the genus and originates exclusively from the Old World. The section *Allium* shows the strongest species diversity: it mainly ranges from the Mediterranean to Central Asia. The section *Codonoprasum* has a centre of diversity in the Mediterranean area. The section *Scorodon* in the broad sense was an artificial assemblage, and its reclassification into several sections, mainly distributed in the Irano-Turanian floristic region (Khassanov, 1997), is supported by molecular data.
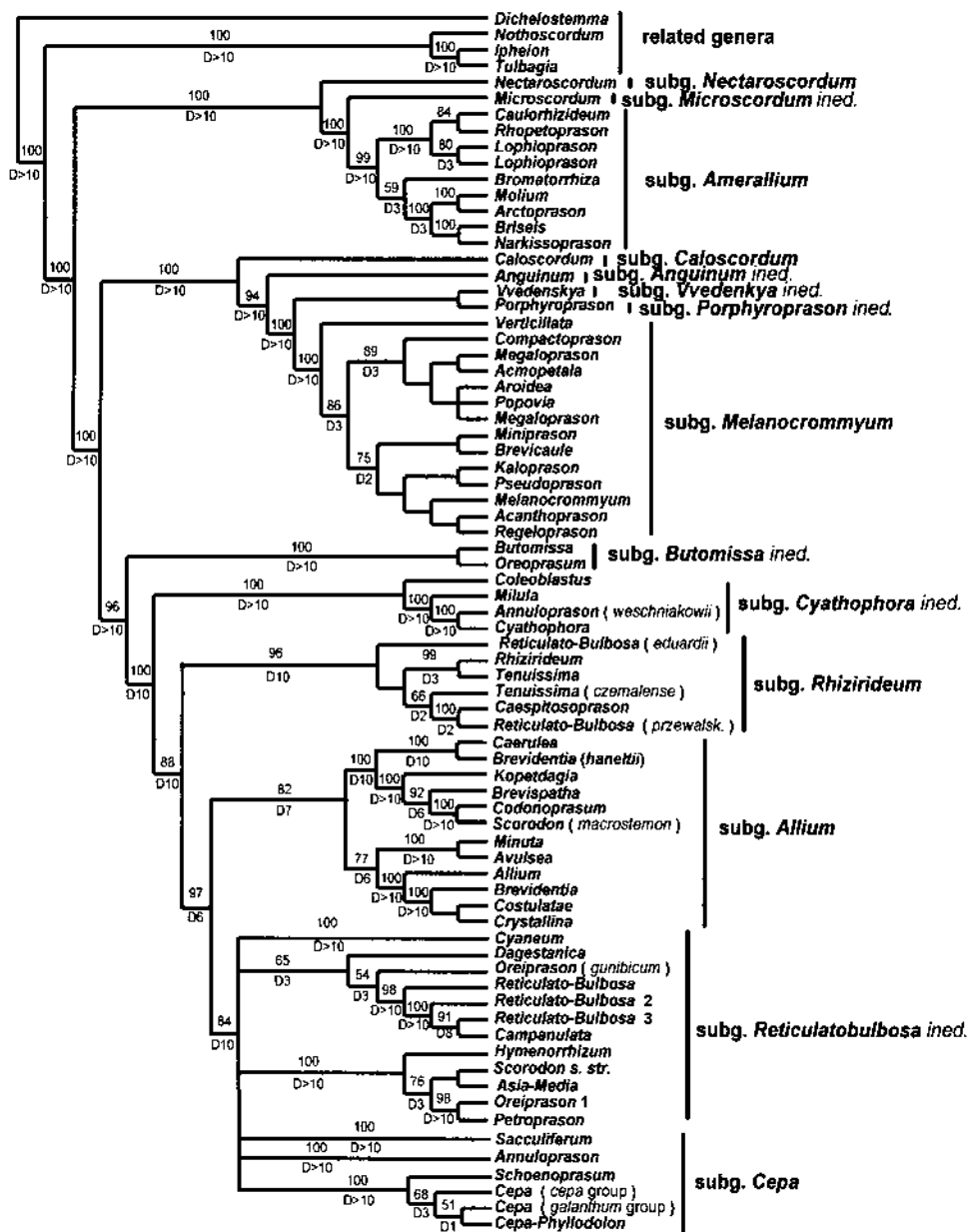
Fig. 1.2. Dendrogram of the genus *Allium* based on molecular markers (strict consensus tree, internal transcribed spacer (ITS) sequences; some group names are provisional). The less advanced groups are close to the related genera (above), the most advanced ones on the opposite side (below).

Subgenus Melanocrommyum. The phenotypically extremely variable subgenus *Melanocrommyum* is well delimited and thus occupies a special evolutionary branch of the genus. For instance, all hitherto investigated species contain only a few cysteine sulphoxides and inactive alliinase, and many plants of this taxon are therefore odourless (Keusgen, 1999). Apparently, rather recently the number and diversity of taxa rapidly

increased in the very arid climates of the Near and Middle East to Central Asia. Its recent geographical speciation centre in Central Asia (*c.* 36–40°N, 66–70°E) was identified and confirmed by molecular markers (Mes *et al.*, 1999). The reticulate phylogenies of several groups explain the existence of small but polyphyletic groups, which conflict with the conventional use of taxonomic categories. A pragmatic taxonomic classification of the subgenus is still awaited.

Subgenus Caloscordum. Only three species distributed in East Asia belong to this small but well-characterized group. Morphological reasons to separate it at subgeneric level rather close to the subgenus *Melanocrommyum* are supported by molecular data. The distantly related sections *Vvedenskya* and *Porphyroprason* would also best be raised to subgeneric rank.

2. The Section *Cepa* (Mill.) Prokh.

This small group includes the two economically important cultivated species, *A. cepa* L. and *A. fistulosum* L. The section shares several morphological and molecular characters with the section *Schoenoprasum*, and is only distantly related to most of the other rhizomatous species.

2.1 Morphology, distribution and ecology

The species are characterized by cylindrical, fistulose, distichous leaves. The cylindrical to globose bulbs are composed of several leaf-bases and are covered by membranous skins. The sheath part of the leaves forms a pseudostem, which hides a great part of the above-ground scape. The inflated scape is fistulose and terminates with a multi-flowered head-like inflorescence. Bracteoles are present at the bases of the pedicels. The spathe is short and the flowers are campanulate or with spreading tepals. The inner stamens are strongly widened at the base, where they may possess short teeth. The stigma is capitate. The triloculate ovary has septal nectaries with distinct nectariferous pores, and two ovules per locule, which develop into angular seeds. Usually, axillary

daughter bulbs are developed on short rhizomes, building up rather large tufts. A gradual reduction of the rhizome can be seen within the section, leading finally to the flat, disc-like corm or basal plate of the common onion, *A. cepa*.

The wild species of the section *Cepa* occur within the Irano-Turanian floristic region, mainly in the mountainous areas of the Tien-Shan and Pamir-Alai. Occurrences in neighbouring floristic provinces are marginal extensions of the main area. The exceptions are *A. altaicum* and *A. rhabdotum*, which grow in the mountains of southern Siberia and Mongolia and in the eastern Himalayas, respectively (Hanelt, 1985; Friesen *et al.*, 1999b). For details, see Fig. 1.3.

The wild taxa of section *Cepa* are petrophytes, which always grow in open plant formations, such as rocks, rock crevices, stony slopes, river-banks, gravelly deposits and similar sites with a shallow soil layer. Their occurrence is not strongly correlated either to the mineral content or pH of the soil or to particular plant-sociological associations or vegetation types. This distribution pattern often results in groups of small populations (Levichev and Krassovskaja, 1981; Hanelt, 1985). However, the occurrence of large populations has also been reported (Hanelt, 1990).

Unlike some other *Allium* species from the same area, taxa of the section *Cepa* have a fairly long annual growth period and are not ephemeroids. Leaf growth begins after the frost has ceased in the spring, and may be next limited by low temperatures in the following autumn and winter. Species growing in arid areas have a weak, drought-induced summer dormancy but this is easily broken by summer rainfall. Therefore, they commonly lack leaf blades during bloom in summer. All the wild taxa of this section have a prolonged juvenile phase, lasting 3–10 years, before the first flowers are produced (Hanelt, 1985).

These species have long been gathered by local people, who use the bulbs and leaves for food or preserve them for winter use. Often, large-scale collection for commercial or semi-commercial purposes still continues. This has resulted in the disappearance of

species from many localities, and a shrinking of their population sizes (Hanelt, 1990). Taxa of more local distribution are seriously endangered or threatened by the rapidly decreasing number of localities at which they occur. Therefore, they were listed in the 'Red Books' of the former Soviet Union and of all Central Asian republics. This situation is serious, because all wild species of the section *Cepa* are the secondary gene pool of *A. cepa* and *A. fistulosum*. The evaluation and exploitation of these genetic resources could contribute significantly to the improvement of these two cultivated species (see Kik, Chapter 4, this volume).

2.2 Cytological limitations

The species of the section *Cepa* are diploid (2*n* = 16), although the occasional occurrence of individual tetraploid bulbs has been reported. Contrary to what is found in some other *Allium* groups, the chromosomes are metacentric or submetacentric and differ only somewhat in length. Only the satellite chromosome pair is subtelocentric (subacrocentric), the satellites being attached to the short arms. Most species of the section *Cepa* have very small dotlike satellites, as in other subgroups of the genus, apart from *A. fistulosum* and *A. altaicum*, which both possess significantly larger satellites. Similar fluorochrome and Giemsa-stained chromosome banding patterns occur in the whole section. However, marker chromosomes with specific intercalary bands on some chromosomes, as well as differences in total length of the chromosome complement were detected (Ohle, 1992; van Raamsdonk and de Vries, 1992b). In spite of the morphological and cytological similarities between the species of section *Cepa*, there are strong crossing barriers between them, which prevent interspecific gene flow even where sympatric distribution of two species occurs.

2.3 Grouping of the species

Section *Cepa* belongs to the morphologically, karyologically and biochemically well-circumscribed *Allium* groups, whose coherence has additionally been demonstrated by molecular data (Pich *et al.*, 1996; Klaas, 1998). The main morphological species-specific characters were presented by van Raamsdonk and de Vries (1992a, b).

The taxa of the section fall into three groups on the basis of morphological and geographical differences (Hanelt, 1985). However, the results of crossing experiments (van Raamsdonk and de Vries, 1992a) and of recent molecular studies show the isolated position of *A. oschaninii* as a sister group to the *A. cepa/A. vavilovii* evolutionary lineage (Friesen and Klaas, 1998). Therefore, the *Cepa* alliance is proposed as a fourth informal group.

1. *Galanthum* alliance. White flowers with spreading tepals and filaments above the adnation to the tepals, coalescent into a narrow ring, are characteristic. Nectariferous tubes end in a tangentially widened pocket. Flowering plants have only about two to four assimilating leaves per shoot. Scapes are evenly inflated. The species show a disjunctive distribution in the Irano-Turanian region.
2. *Oschaninii* alliance. White flowers with spreading tepals and filaments without the above-mentioned ring are characteristic. Nectariferous pores are also pocket-like. There are greater numbers of cylindrical leaves, usually four to nine, and a bubble-like swelling in the lower half of the scape. Distribution is concentrated in the Turkestanian province.
3. *Cepa* alliance. The taxa share most characters with the *Oschaninii* alliance but the flowers may also be greenish and the leaves are initially flat or semi-cylindrical. Distribution is mainly Turkmenian–Iranian.
4. *Altaicum* alliance. These species have campanulate to broadly tubular flowers of a whitish–transparent colour. Filaments are distinctly longer than in the other alliances and do not coalesce into a ring. Nectariferous tubes end in a simple lateral hole. Few leaves are present, and the scapes are evenly inflated. Main distribution is in South Siberia and Mongolia and possibly in Himalaya.

2.4 Enumeration of the species

2.4.1 Galanthum *alliance*

Allium galanthum *Kar. et Kir.* This *Allium* is widely distributed in north-east Kazakhstan to the northern Tien-Shan chains, with isolated occurrences east and south of that area. It has the most continental distribution of all species of the section and occurs mainly within the desert zone.

Allium farctum *Wendelbo.* This is a recently described species from the mountains of West Pakistan, East Afghanistan and the marginal area of West Himalaya. The distribution is not yet fully known. Although morphologically similar to *A. galanthum*, the seed-coat structure is as in the *Oschaninii* alliance (Kruse, 1988). Morphological reasons exclude this species as a possible progenitor of the common onion (Hanelt, 1990).

Allium pskemense *B. Fedtsch.* This is an endangered local species from the western Tien-Shan range, where the borders of Kyrgyzstan, Uzbekistan and Kazakhstan meet. Inhabitants of this area collect the bulbs and sometimes transplant the species and cultivate it in their gardens (Levichev and Krassovskaja, 1981). It has rather large bulbs with a very pungent taste.

2.4.2 Oschaninii *alliance*

Allium oschaninii *O. Fedtsch.* This species is distributed in the transitional area from Central to South-West Asia (Fig. 1.3), with isolated occurrences in north-eastern Iran (Hanelt, 1985). It is often found only in inaccessible places, because the leaves are eaten by livestock and its large bulbs are collected by local inhabitants. The plants are morphologically very variable and sometimes resemble *A. cepa*. It was formerly thought to be conspecific with it (*A. cepa* var. *sylvestre* Regel), but recent molecular studies show it to be a sister group to the *A. cepa/A. vavilovii* evolutionary lineage (Friesen and Klaas, 1998).

Unexpectedly, the latter report gave convincing molecular evidence that the 'French grey shallot' is a domesticate of *A. oschaninii*. This divergent form is highly esteemed for its excellent taste, and has been cultivated in southern France and Italy for a long time (Messiaen *et al.*, 1993; D'Antuono, 1998; Rabinowitch and Kamenetsky, Chapter 17, this volume).

Allium praemixtum *Vved.* This recently described species is endemic in the south-western marginal chains of the Tien-Shan range, on both sides of the border between Tajikistan and Uzbekistan. Its classification is still in doubt because it differs from *A. oschaninii* only by some minor morphological characters.

2.4.3 Cepa *alliance*

Allium vavilovii *M. Pop. et Vved.* This is an endangered local species of the central Kopetdag range in Turkmenia (Fig. 1.4) and North-East Iran. Its bubble-like hollow stem is similar to that of *A. oschaninii* but the leaves are completely flat and falcate. Molecular analysis revealed that it is the closest known relative of the common onion (Friesen and Klaas, 1998; Fritsch *et al.*, 2001).

Allium asarense *R.M. Fritsch et Matin.* Only very recently this species was identified at a single place in the Elburz range west of Tehran, where it grows on very steep scree and rocky slopes. The plants have semi-cylindrical, falcate, not inflated leaves, a stem with a bubble-like inflation (Fig. 1.5) and small semi-globose umbels with small greenish, brown-flushed flowers. Initially it was believed to represent another subspecies of *A. vavilovii*, but molecular studies assigned it to be a basal group of the *A. cepa/A. vavilovii* evolutionary lineage, which deserves species status (Friesen and Klaas, 1998; Fritsch *et al.*, 2001).

Allium cepa *L.* A variable plant cultivated worldwide. Unknown in the wild, although sometimes naturalized (see Section 3).
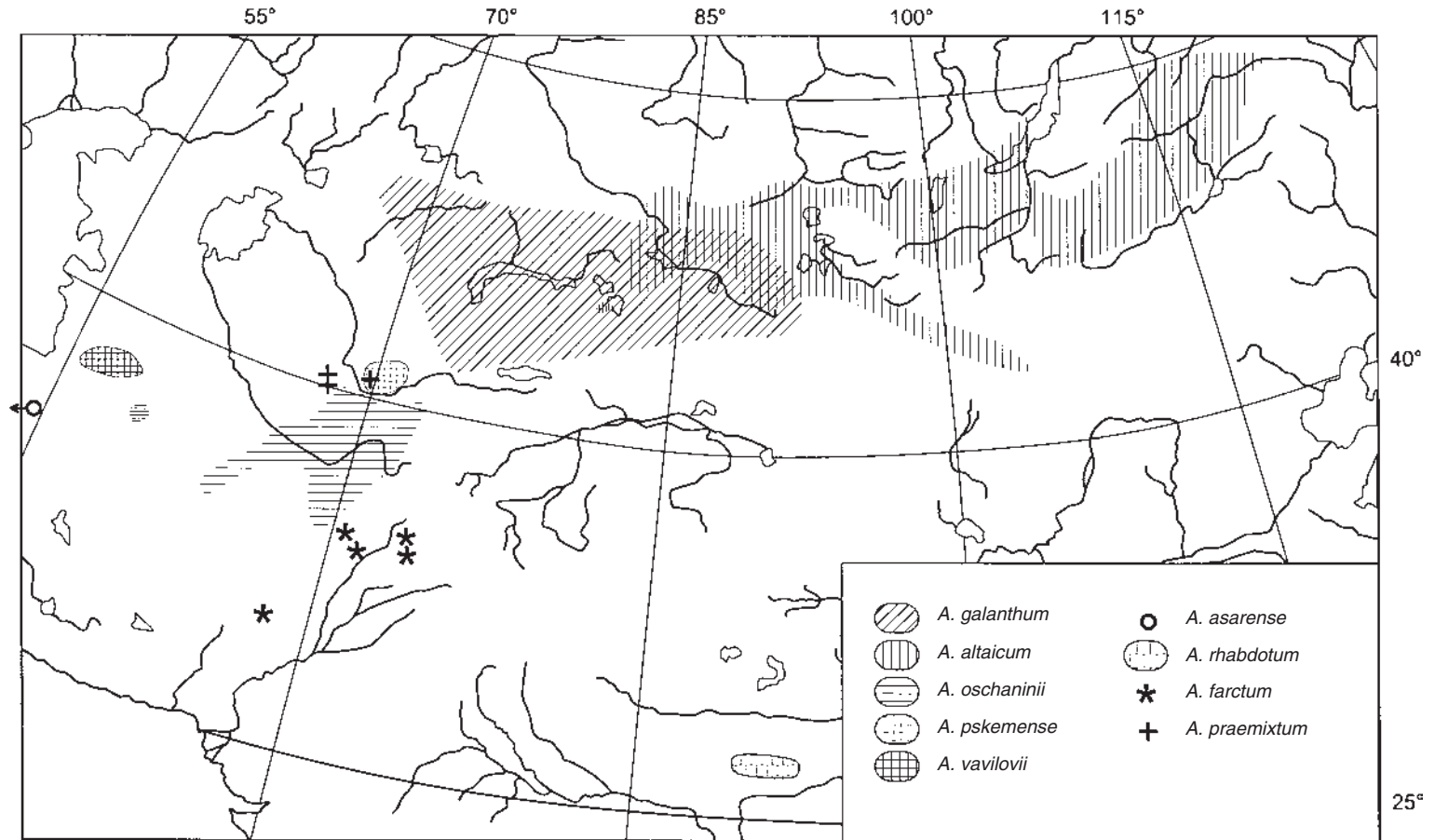
Fig. 1.3. Natural distribution of wild species of section *Cepa*.

Legend:
- *A. galanthum*
- *A. altaicum*
- *A. oschaninii*
- *A. pskemense*
- *A. vavilovii*
- *A. asarense*
- *A. rhabdotum*
- *A. farctum*
- *A. praemixtum*

Fig. 1.4. *Allium vavilovii* on a scree slope, Kopetdag range, Turkmenia.

2.4.4 Altaicum *alliance*

Allium altaicum *Pall.* This is the most widely distributed species of the section. It occurs in the mountains of southern Siberia, North and Central Mongolia to the Trans-Baikal and in the upper Amur region. The bulbs are extremely frost-resistant. Populations are often threatened by mass collection for food. Occasionally plants are transplanted into backyard gardens (N. Friesen, personal observations). *Allium microbulbum* Prokh., which was described decades ago as a cultivated plant in the Trans-Baikal area, may refer to such casual domesticates.

Allium altaicum is a variable species, having at least two phylogenetically distinct morphotypes. It is the wild progenitor of *A. fistulosum*, which was most probably selected from populations near the southernmost border of its natural area (Friesen *et al.*, 1999b), confirming earlier assumptions about its domestication in North China. Literature sources refer to domestication more than 2000 years ago (cited in Maaß, 1997a).

Allium fistulosum *L.* This is a variable cultivated species, of primary importance in China, Korea and Japan (Inden and Asahira, 1990). It is grown mainly for the slender bulbs and basal parts of the pseudostem, which are much esteemed as fresh or cooked vegetables. In the West it is more rarely grown, mainly for the fresh green leaves, and is eaten as a salad onion (scallion).

2.4.5 Insufficiently known and hybrid taxa

Allium rhabdotum *Stearn.* A recently described species, known so far only from herbarium collections made in Bhutan in the eastern Himalayas (Stearn, 1960). It possibly belongs to the *Altaicum* alliance (Hanelt, 1985) but needs more thorough study from living plants.

Allium roylei *Baker.* Formerly only known as a very rare species from north-west India. One *A. roylei* strain was introduced into the European research scene in the 1960s. All living plants investigated in Europe trace back to this single fertile strain. It crosses

Fig. 1.5. *Allium asarense* under cultivation at Gatersleben, Germany.

easily with *A. cepa* and *A. fistulosum*, and shares a high degree of genetic similarity with other taxa of section *Cepa*. However, most morphological characters differ remarkably from others in this section and are much more similar to those of section *Oreiprason*. The study of other wild populations is essential (Klaas, 1998). Recent evidence indicates that *A. roylei* might have a hybrid origin, as its nuclear DNA profile is related to species of the section *Cepa* but its chloroplast DNA profile to the section *Schoenoprasum* (van Raamsdonk *et al.*, 1997, 2000).

Allium × proliferum (Moench) Schrad. It has been shown recently that some minor cultivated taxa, formerly thought to be varieties of *A. cepa* or *A. fistulosum*, or which were described as distinct species, are in fact hybrids of these two species. Analysis of the karyotypes (Schubert *et al.*, 1983), biochemical and molecular data (Havey, 1991; Friesen and Klaas, 1998) and isozyme analysis (Maaß, 1997a) have univocally confirmed the hybrid nature of the plants in question. Top onion and the Wakegi onion are two diploid hybrid types, both having the same parentage. Therefore, they should be combined into one (hybridogenic) nothospecies, according to the rules of botanical nomenclature.

It should be noted that there exist topset-producing forms of *A. cepa* (Jones and Mann, 1963) and *A. fistulosum* (Havey, 1992), which have originated by minor genetic changes and not by species hybridization.

Top onion, tree onion, Egyptian onion, Catawissa onion. These plants are hybrids between *A. fistulosum* and the common onion type of *A. cepa*, and were named *A. × proliferum* in its narrow sense. Most or all of the flowers in an inflorescence do not develop, but some bulbils (topsets) grow instead. These may sprout while still on the mother plant. Flowers, if developed, are completely sterile. The plants are widely cultivated in home gardens in North America, Europe and north-eastern Asia for their topsets and young sprout leaves. A seed-fertile tetraploid strain having the same parental species is known and consumed as scallions ('Beltsville Bunching') (McCollum, 1976).

The origin and place of domestication remain unsolved. Chinese scripts and the overlapping areas of both *A. cepa* and *A. fistulosum* in north-western China suggest a Chinese origin (Hanelt, 1990) but comparison of isozyme patterns supports a possible polytopic origin (Maaß, 1997a).

Wakegi onion. The Wakegi onion is used as a green salad onion and has been cultivated for centuries in China, Japan and South-East Asia. It is completely sterile (although the inflorescence is normal, if developed) and is therefore reproduced only vegetatively. It is a hybrid between shallot (the *Aggregatum* type of *A. cepa*) and *A. fistulosum* as maternal parent (Tashiro *et al.*, 1995). Arifin *et al.* (2000), using material from Indonesia, concluded from restriction fragment length polymorphism (RFLP) analysis of amplified *matK* gene from chloroplast DNA (cpDNA) that *A. × wakegi* originated from shallot as maternal parent and Japanese bunching onion as paternal parent, as well as from the reciprocal cross.

Triploid viviparous onions Allium × cornutum *Clem. ex Vis.* Another type of sterile viviparous onions with a more slender stature and pinkish-flushed flowers is locally cultivated in Tibet, Jammu, Croatia, Central and West Europe, Canada and the Antilles. The plants are triploids. Unanimously, *A. cepa* is accepted as donor of two chromosome sets. The source of the third chromosome set is still disputed. However, *A. fistulosum* is rejected as the second parent (Havey, 1991; Friesen and Klaas, 1998). Puizina *et al.* (1999) proposed *A. roylei*, which was not accepted by Maaß (1997b) and Friesen and Klaas (1998).

3. *Allium cepa* L.

3.1 Description and variability

Allium cepa is cultivated mainly as a biennial, but some types are treated as perennials. It is propagated by seeds, bulbs or sets (small bulbs). Bulbs have a reduced disc-like rhizome at the base. Scapes are up to 1.8 m

tall and gradually tapering from an expanded lower part. The leaves have rather short sheaths and differ in size and are near circular in cross-section but somewhat flattened on the adaxial side. The umbel is subglobose, dense, many-flowered (50 to several hundred) and with a short persistent spathe. Pedicels are equal and much longer than the white and star-like flowers with spreading tepals. Stamens are somewhat exserted, and the inner ones bear short teeth on both sides of the broadened base. The fruit is a capsule approximately 5 mm long.

The wide variation in bulb characteristics indicates intensive selection. Bulb weight may be up to l kg in some southern European cultivars, and the shape covers a wide range from globose to bottle-like and to flattened-disciform. The colour of the membranous skins may be white, silvery, buff, yellowish, bronze, rose red, purple or violet. The colour of the fleshy scales can vary from white to bluish-red. There is also much variation in flavour, the keeping ability of the bulbs and the ability to produce daughter bulbs in the first season. Great variability in ecophysiological growth pattern has developed. There exist varieties adapted to bulbing in a wide range of photoperiodic and temperature conditions (see Bosch Serra and Currah, Chapter 9, and Currah, Chapter 16, this volume). Similarly, adaptation exists for bolting and flowering in a broad range of climates, but non-bolting strains are found in many shallots (Hanelt, 1986a; Kamenetsky and Rabinowitch, Chapter 2, and Rabinowitch and Kamenetsky, Chapter 17, this volume). Organs not selected for by humans, e.g. the flower and the capsule, have been very little affected by domestication and exhibit no striking variations.

3.2 Infraspecific classification

The great variability within the species has led to different proposals for infraspecific groupings, whose historical development has been discussed in detail by Hanelt (1990). Kazakova (1978) presented the most recent version of a classical system which held shallots apart at species level and recognized three formal subspecies, eight formal varieties and 17 cultivar groups (named conculta) based exclusively on quantitative characters. This rather cumbersome classification of *A. cepa* involves statistical methods. The characteristics used are affected strongly by environment and need to be tested in a range of climates. Also, in modern breeding, many 'classical' cultivar groups have been crossed and the boundaries between the different taxa are becoming blurred, making it difficult to place material within the scheme.

The broadly accepted concept of the species *A. cepa* used here includes races with many lateral bulbs and/or shoots, which rarely bolt, and which are partly seed-sterile, namely shallots and potato onions. Other morphological and karyological characters, isozyme and molecular-marker patterns are almost identical to those of *A. cepa* (Hanelt, 1990; Maaß, 1997a, b; Klaas, 1998). Here a simple informal classification will be applied, similar to that of Jones and Mann (1963), accepting two large and one small horticultural groups. The advantages of flexibility and the lack of nomenclature constraints have been discussed in detail elsewhere (Hanelt, 1986b). This approach is convenient for both breeders and horticulturists.

3.2.1 Common onion group

The variability of the species, as discussed above, occurs mainly in this group, economically the most important *Allium* crop. It includes hundreds of open-pollinated traditional and modern cultivars, F_1 hybrids and local races, cultivated in most regions of the world. The bulbs are large and normally single, and plants reproduce from seeds or from seed-grown sets. The majority of cultivars grown for dry bulbs belong to this group, as do salad or pickling onions. In many countries, gene erosion has recently accelerated with the widespread introduction of high-quality, high-yielding F_1 hybrids. However, great diversity still exists in North India and Pakistan, in the former Soviet Union, European and Middle Asian republics, in the Middle East and in the

eastern and south-eastern parts of the Mediterranean area (Astley *et al.*, 1982; Bosch Serra and Currah, Chapter 9, and Currah, Chapter 16, this volume).

3.2.2 Aggregatum group

The bulbs are smaller than in common onions, and several to many form an aggregated cluster. Traditional reproduction is almost exclusively vegetative via daughter bulbs, though recently lines of seed-reproduced shallots have been developed (see Rabinowitch and Kamenetsky, Chapter 17, this volume).

The group is of minor economic importance. Locally adapted clones and cultivars are grown mainly in home gardens in Europe, America and Asia for dry bulbs and, more rarely, for green leaves. Cultivation on a larger scale takes place in France, Holland, England and Scandinavia, in Argentina and in some tropical regions, e.g. West Africa, Thailand, Sri Lanka and other South-East Asian countries, and the Caribbean area. In France and other European countries, as well as in the USA, shallots are favoured for their special flavour. In tropical areas, shallots are used as onion substitutes because of their ability to propagate vegetatively and their short growth cycle, and perhaps because they are resistant to local diseases. The variability within this group is poorly represented in gene-bank collections, where the capacity for carrying latent viruses formerly made them a dubious asset. This problem can be solved by meristem culture, followed by *in vitro* propagation (Keller *et al.*, 2000), or by establishing seed-propagated cultivars (Rabinowitch and Kamenetsky, Chapter 17, this volume).

Shallots are the most important subgroup of the Aggregatum group and the only ones grown commercially to any extent. They produce aggregations of many small, narrowly ovoid to pear-shaped bulbs, which often have red-brown (coppery) skins. The plants have narrow leaves and short scapes (see Rabinowitch and Kamenetsky, Chapter 17, this volume).

Not easily distinguishable from shallots are the potato or multiplier onions. They differ from shallots (though many intermediate forms exist) by their larger bulb size, by fewer daughter bulbs, which remain enclosed by the skin of the mother bulb for longer than in the shallots, and often by their somewhat flattened shape. They are cultivated in home gardens in Europe, North America, the Caucasus, Kazakhstan and the south-east of European Russia (Kazakova, 1978), and commercially in Brazil and southern India (Currah, Chapter 16, this volume).

3.2.3 Ever-ready onion group

This third group of *A. cepa* may be distinguished from the other two by its prolific vegetative growth and by the lack of a dormant period. Bulbs or leaves can be gathered at all times of the year. It is used mainly as a salad onion and was commonly cultivated in British gardens in the mid-20th century. Detailed descriptions were given by Stearn (1943) and Jones and Mann (1963). Isozyme (Maaß, 1997a) and molecular-marker patterns (Friesen and Klaas, 1998) fall inside the variability of the common onion group.

3.3 Evolutionary lineages

Only a few hard facts plus some circumstantial evidence are available to help us to trace the evolutionary history of *A. cepa*. The ancestral group from which *A. cepa* must have originated includes only the wild taxa of the *Oschaninii* and *Cepa* alliances (see Section 3.4). They share with *A. cepa* many morphological characters and have in common the special sculpturing of the seed-coat (Kruse, 1988). The current natural distribution of this alliance indicates that domestication of *A. cepa* probably started in the Middle East (Hanelt, 1990).

Recent molecular data support the conclusion of Hanelt (1990), who assigned only *A. vavilovii* as the closest wild relative of *A. cepa* (Friesen and Klaas, 1998; Fritsch *et al.*, 2001). However, the immediate ancestor remains as yet unknown. The recent discovery of *A. asarense* in northern Iran (see

Section 3.4) nurtures once more the scientists' hope of discovering the direct wild ancestor of the onion, perhaps in a very restricted refugial area.

Abandonment of *A. oschaninii* as a possible ancestor will shift the probable area of domestication of the common onion in a south-westerly direction, approximating to the ancient advanced civilizations of the Near East, where the earliest evidence of common onions and garlic comes from. Therefore, we concur with Hanelt (1990), who proposed that the South-West Asian gene centre of *A. cepa* should be acknowledged as the primary centre of domestication and variability. Other regions, such as the Mediterranean basin, where onions exhibit a great variability, are secondary centres.

3.4 History of domestication and cultivation

Prehistoric remains of cultivated plants are often extremely helpful for reconstructing their evolution and history. This is especially true for long-living seed crops, such as cereals, but much less so for species like the bulb onion, which have little chance of long-term preservation. Therefore, one has to rely mostly upon written records, carvings and paintings. Hence, the picture one obtains of the history of such species is fragmentary, at least for the earlier epochs. The conventional wisdom on the history of cultivation of the common onion has been summarized by Helm (1956), Jones and Mann (1963), Kazakova (1978) and Havey (1995) and was briefly discussed by Hanelt (1990). Hence, only a very short review is given here.

Allium cepa is one of the oldest cultivated vegetables, recorded for over 4000 years. The earliest records come from Egypt, where it was cultivated at the time of the Old Kingdom. Onions appear as carvings on pyramid walls and in tombs from the third and fourth dynasties (2700 BC), indicating their importance in the daily diet of many people. The biblical records of the Exodus (1500 BC) are also well known. From Mesopotamia there is evidence of cultivation in Sumer at the end of the third millennium

BC. This, together with the records from Egypt, indicates that the initial domestication began earlier than 4000 years ago.

The current exploitation of *A. pskemense* can be used as an illustration of how early cultivation of the onion might have started. This species is consumed by inhabitants of the Pskem and Chatkal valleys, who frequently transplant it from the wild to their gardens, where it is cultivated and propagated (Levichev and Krassovskaja, 1981). Perhaps, thousands of years ago, overcollecting made bulbs of the onion's ancestor scarce, thus stimulating their transfer into gardens and so initiating domestication (Hanelt, 1986a). Further human and natural selection probably favoured a change in allometric growth pattern towards bulbs, a shortening of the life cycle of the plants to bienniality and adaptation to many environments (Hanelt, 1990).

In India there are reports of onion in writings from the 6th century BC. In the Greek and Roman Empires, it was a common cultivated garden plant. Its medicinal properties and details on cultivation and recognition of different cultivars were described. It is thought that the Romans, who cultivated onions in special gardens (*cepinae*), took onions north of the Alps, as all the names for onion in West and Central European languages are derived from Latin. Different cultivars of onion are listed in garden catalogues from the 9th century AD, but the onion became widespread as a crop in Europe only during the Middle Ages and was probably introduced into Russia in the 12th or 13th century.

The onion was among the first cultivated plants taken to the Americas from Europe, beginning with Columbus in the Caribbean. Later it was imported several times and established in the early 17th century in what is now the northern USA. Europeans took the species to East Asia during the 19th century. The indigenous cultivated species of this region, especially *A. fistulosum*, are still more widespread and popular for culinary uses there.

This history of cultivation applies solely to the common onion group. The Aggregatum group is poorly documented in historical

records. Most probably, the 'Ascalonian onions' of the authors of antiquity were not shallots. The first reliable records are from the 12th and 13th centuries in France and 16th and 17th centuries in England and Germany. In the herbals of that time, there are good illustrations of this group (Helm, 1956).

4. Other Economic Species

4.1 Garlic and garlic-like forms

4.1.1 Allium sativum L.

Garlic is the second most important *Allium* species. It is grown worldwide in all temperate to subtropical (and mountainous tropical) areas as an important spice and medicinal plant. The bulb, composed of few to many densely packed elongated side bulbs ('cloves'), is the main economic organ, and the fresh leaves, pseudostems and bulbils (topsets) are also consumed by humans. Enzymatic decomposition products of alliin, present in all plant parts, have antibacterial and antifungal activity (see Keusgen, Chapter 15, this volume) and cause the intense and specific odour.

Like onion, garlic has been used by humans from very ancient times, when the historical traces fade away and cannot be followed either to a wild ancestor or even to the exact area of domestication. For taxonomic reasons, its wild ancestor (if still extant, or its close relatives) should grow anywhere in an area from the Mediterranean to southern Central Asia. Wild-growing and profusely flowering garlic with long protruding anthers has been described as *Allium longicuspis* Regel from Central Asia. However, such long filaments are developed in all investigated garlic groups if flower development is artificially forced by removing the bulbils in the umbel at a very early stage (Maaß, 1996; Kamenetsky and Rabinowitch, Chapter 2, this volume). Vegetative descendants of 'wild' garlic resemble common bolting garlic types, which have long been cultivated (R.M. Fritsch, personal observation). Thus, no reliable character remains to maintain *A. longicuspis* at species level, but proponents

continue to regard it as the truly wild ancestor of garlic (Lallemand *et al.*, 1997). More recently, a remarkable similarity to garlic of the Turkish wild species *A. tuncelianum* was detected, denoting this taxon as another candidate for the wild ancestor (Mathew, 1996; Etoh and Simon, Chapter 5, this volume).

Unlike the case of the seed-bearing onion, the lost ability for generative multiplication has led to a much more restricted morphological and genetic variation in garlic, irrespective of the large area where it is in cultivation. Contrary to former formal infraspecific classifications, recent proposals classify the many existing selections into informal cultivar groups (Maaß and Klaas, 1995; Lallemand *et al.*, 1997). Most garlic from Central Asia belongs to the rather diverse *Longicuspis* group (large bolting plants, many small topsets, to some extent still fertile cultivars). They might have been the genetic pool from which the other cultivar groups developed – the *subtropical* and *Pekinense* subgroups (smaller plants, few large topsets) – which possibly developed under the special climatic conditions of South, South-East and East Asia; the Mediterranean *Sativum* group (bolting and non-bolting types, large topsets); and the *Ophioscorodon* group from Central and East Europe (long coiling scapes, few large topsets).

4.1.2 Allium ampeloprasum L., great-headed garlic group

This hexaploid seed-sterile domesticate of *A. ampeloprasum* is locally cultivated in Asia Minor to Iran and Caucasus, and sporadically in California and in other regions of America and Europe. These plants appear to be 'siblings' of garlic with somewhat less intensive odour and taste. They develop large cloves, which are used for both consumption and multiplication. The new sprouts bulb and flower in the first year (in subtropical Israel and California) of cultivation from autumn to spring (H.D. Rabinowitch, Israel, 2000, personal communication) or the second year (in the temperate zone) as a summer crop (van der Meer, 1997; Hanelt, 2001).

4.1.3 Allium macrostemon *Bunge*

Native in the northern central parts of China and Mongolia, this species is grown for the garlic-like taste of its leaves and bulbs. Some strains flower normally and produce fertile seeds (*A. uratense*; in Korea and Japan the synonym *A. grayi* is still sometimes in use), but others develop only bulbils (topsets) (*A. macrostemon s. str.*). Apparently it is a local domesticate of China that reached Korea and Japan earlier than true garlic. In recent times it has become a neglected crop because of its low yield (Hanelt, 2001).

4.2 Taxa of Asiatic origin

4.2.1 Allium ampeloprasum *alliance*

Allium ampeloprasum s. lato is a very variable species (or a group of closely related taxa) widely distributed in the Mediterranean basin. In ancient times, tetraploid populations from the eastern part of its area of distribution were domesticated as vegetables and spice plants. The plants multiply by seeds, apart from pearl onions and great-headed garlic, which are mainly propagated by bulbs/cloves. Formerly named at species level (see Table 1.1), informal classification into cultivar groups is proposed (Hanelt, 2001).

KURRAT GROUP. A leek-like vegetable, used mainly in Egypt and some neighbouring Arab countries, where the rather narrow leaves are used fresh as salad or as a condiment in special dishes (Mathew, 1996; van der Meer, 1997; Hanelt, 2001). The fertile plant freely crosses with leek to produce fertile hybrids, which were utilized in a leek-breeding programme for resistance to leek yellow-stripe virus in Holland by the late Q.P. van der Meer (H.D. Rabinowitch, personal communication).

TARÉE GROUP. A similar use as a condiment is reported for narrow-leafed Caucasian strains of leek and for Tarée cultivated in northern Iran (van der Meer, 1997), which are sometimes included in the Kurrat group (Hanelt, 2001).

LEEK GROUP. Although probably already cultivated in ancient Egypt, in recent times this annual crop has mainly been commercially produced in West and Central Europe, being less important in other European countries, North America and temperate Asia, and is sporadically grown elsewhere. The plants are broad-leaved and stocky. Pseudostems and the basal leaf parts of juvenile plants are mainly consumed as cooked vegetables or condiments (van der Meer and Hanelt, 1990; van der Meer, 1997; Hanelt, 2001; De Clercq and Van Bockstaele, Chapter 18, this volume). When grown as a biennial, leek develops basal bulbs in the second year (van der Meer and Hanelt, 1990; van der Meer, 1997).

PEARL-ONION GROUP. Currently only under small-scale cultivation in house gardens in Central and South Europe, the rather small and slender plants develop large numbers of small subglobular daughter bulbs, which are pickled as a spice (van der Meer, 1997; Hanelt, 2001).

4.2.2 East Asian onions

ALLIUM HOOKERI THWAIT. Naturally distributed in Tibet and North-West China, this species is also cultivated by several non-Chinese tribes in mountainous regions from Bhutan to Yunnan and North-West Thailand. Mainly the fleshy roots but also the leaves are used as vegetables and for soups, fried or pickled (Hanelt, 2001).

ALLIUM RAMOSUM L. (INCLUDING *A. TUBEROSUM* ROTTL. EX SPRENGEL). In East Asia (*A. tuberosum*; local name: Nira) and Central Asia (*A. ramosum*; local name: Djusai) are widely cultivated for the leaves and the flowering umbels, which combine garlic and sweet flavours and are used for soups, salads and other traditional Chinese and Japanese dishes. The plants were taken by immigrants to many other countries. In recent times this species has started to become more popular in Central and West Europe where the leaves are said to have therapeutic effects on tumours (van der Meer, 1997). Its culture and uses in the Orient were described by Saito (1990).

A. tuberosum is usually accepted as the crop species. However, *A. ramosum* (early-flowering, large tepals) and *A. tuberosum* (late-flowering, small tepals) are related by all kinds of transitional forms. Most cultivated strains are tetraploids or triploids; they often develop seeds apomictically (facultative apomicts). Recent molecular data (N. Friesen, unpublished) clearly segregate all cultivated strains as a sister group to the wild species.

ALLIUM CHINENSE G. DON. This kind of oriental garlic, also called rakkyo, is cultivated in China, Korea, Japan, Vietnam, Indonesia and other countries of South-East Asia as a minor or moderately important crop. It is an ancient crop in China, from where it spread to Japan, probably at the end of the first millennium AD (Hanelt, 2001). The domestication history of rakkyo is still being disputed (see Section 1.2). Immigrants from East Asia introduced it into the Americas.

The bulbs are mostly used for pickles and, more rarely, boiled or used as a medicine. The uses and cultivation methods of rakkyo were described by Toyama and Wakamiya (1990).

ALLIUM WALLICHII KUNTH. This species grows wild in the East Himalayas and Tibet to south-west, south and central China. In eastern Tibet, it is grown as a vegetable in traditional home gardens (Hanelt, 2001).

ALLIUM CONSANGUINEUM KUNTH. In its area of natural distribution in West and Central Himalayas, this species is collected from the wild as a vegetable and spice plant. Minor cultivation for the edible leaves was reported from north-eastern India (Hanelt, 2001).

ALLIUM OBLIQUUM L. This tall species grows wild from East Europe to Central Siberia and north-western China, where it is often collected as a substitute for garlic. For a long time it has traditionally been grown for the bulbs in home gardens in West Siberia. Recently it has also become attractive as a medicinal plant in Europe (Hanelt, 2001).

4.3 Chives and locally important onions from other areas

4.3.1 Allium schoenoprasum *L.*

Chives are naturally distributed in most parts of the northern hemisphere (they are the most widely distributed *Allium* of all). In Europe, the young leaves are appreciated as an early vitamin source in spring and are used as a condiment for salads, sauces and special dishes (Poulsen, 1990; van der Meer, 1997; Hanelt, 2001). The species is extremely polymorphous and is being developed by commercial breeders as both a vegetable and an ornamental. Cultivation probably began in Italy, from where it was distributed to Central and West Europe in the early Middle Ages (Helm, 1956), but independent beginnings of cultivation are assumed for Japan and perhaps elsewhere (Hanelt, 2001).

4.3.2 Allium nutans *L.*

In its natural area of distribution from West Siberia to the Yenisei area, it has been collected as a wild vegetable since ancient times. It is transplanted and grown for that reason in home gardens of West Siberia and the Altai mountains. Its cultivation has spread during recent decades to other parts of Russia and the Ukraine (van der Meer, 1997; Hanelt, 2001).

4.3.3 Allium canadense *L.*

This variable species is naturally widespread in North America east of the 103rd meridian. Formerly much collected by native American tribes and later by European settlers, it was introduced to Cuba, where it is locally grown in home gardens as a vegetable (Hanelt, 2001).

4.3.4 Allium kunthii *G. Don*

Wild growing in Mexico and Texas, this species is (semi-)cultivated for its bulbs by the Tarahumara and Tzeltal tribes of Mexico (Hanelt, 2001).

4.3.5 Allium ursinum *L.*

A species which is naturally widespread in temperate Europe to the Caucasus, the leaves and bulbs are sometimes collected for their garlic-like flavour. In earlier centuries, this species was cultivated as a vegetable, medicinal and spice plant in Central and North Europe. Cultivation trials have also been started in recent times. In Germany and mountainous regions of Caucasus it is sometimes transplanted into home gardens (Hanelt, 2001).

4.3.6 Allium neapolitanum *Cyr.*

A common species in the Mediterranean region, which in the past has escaped from cultivation as an ornamental in other warmer countries. It is currently cultivated in Central Mexico, where bulbs and leaves are salted or fried as condiments for several dishes (Hanelt, 2001).

4.3.7 Allium victorialis *L.*

In Europe and Caucasus this polymorphous species grows wild at high altitudes, but in East Asia it usually grows in the forest belt. In former centuries in several European mountain areas, it was cultivated as a medicinal and fetish plant. In Caucasus it is occasionally sown or transplanted in home gardens as a vegetable (Hanelt, 2001). The leaves are often collected in Siberia and the Russian Far East for fresh use, or the basal parts are preserved with salt for the winter period. Recently, it has been offered as a vegetable in catalogues of Japanese seed firms, and it was also introduced in Korea (Hanelt, 2001).

4.3.8 Species of uncertain cultivation status

About two dozen more alliums than mentioned above are collected as wild vegetables and medicinal and spice plants. Several of them were also sporadically cultivated, but the attempts were usually unsuccessful (e.g. *A. triquetrum* (Hanelt, 2001)) or were abandoned (e.g. *A. stipitatum*). Former cultivation is assumed for topset-bearing forms of *A. ampeloprasum* L. and *A. scorodoprasum* L. (Stearn, 1980), but the incomplete old records do not permit exact determination as to the nature of the tested plants (Helm, 1956). Certainly, more species than mentioned in this chapter are potential crops of local importance (van der Meer, 1997).

5. Conclusions

Allium is a species-rich and taxonomically complicated genus. Modern classifications accept more than 750 species and about 60 taxonomic groups at subgeneric, sectional and subsectional ranks.

Recent molecular data provide evidence for three main evolutionary lines. The most ancient line contains bulbous plants, with only rarely a notably elongated rhizome, while the other two lines contain both rhizomatous and bulbous taxa. Thus, the presence of elongated rhizomes is an advanced character state, which developed several times independently. However, probably most sections with rhizomatous species will be retained provisionally together in one subgenus for practical reasons.

Further progress in compiling a phylogenetically based natural *Allium* classification will mainly depend on the accessibility of living material from the hitherto under-investigated arid areas of South-West, southern Central and western East Asia.

Common onion and garlic are species of worldwide economic importance and they consist of several infraspecific groups. Their cultivation traces back to very ancient times, and thus their direct wild ancestors and places of domestication remain unknown. Other *Allium* species of minor economic importance, such as leek, chives, etc., as well as about two dozen species and hybrids grown sporadically or in restricted regions only, have been mostly taken into cultivation in the historical period.

In this time of increasing general mobility and easy contact between peoples and continents, not only formerly unknown fruits and vegetables but also condiments, such as *A. tuberosum*, have been recently introduced, especially into Europe and

North America. New data about the beneficial effects of the fresh greens of these and other alliums will further accelerate their acceptance as part of a healthy daily diet and support their use as phytopharmaceuticals. Therefore, in the future cultivation of minor species, as well as cultivation trials of hitherto uncultivated species, will be enhanced without changing the dominant position of common onion and garlic, and locally of rakkyo and other traditional species. Domestication of other interesting wild *Allium* taxa will be necessary in the future in order to protect their natural resources from overexploitation.

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