1 Introduction to Edible Alliums: Evolution, Classification and Domestication

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1. The Genus *Allium* L.

1.1. General characteristics

The Angiosperm Phylogeny Group (APG) classified *Allium* L. as the only member of the monotypic tribe Allieae within the subfamily Allioideae of the Amaryllidaceae (Chase *et al.*, 2016; Fig. 1.1).

Allium Linnaeus (1753, p. 294) is one of the largest monocotyledonous genera with ~1000 accepted species (Goevarts *et al.*, 2020), and the numbers keep growing with annual additions of over 10 new species.

Allium is a genus of perennial, mostly bulbous, plants characterized by:

- underground storage organs: bulbs, rhizomes or swollen roots;
- bulbs: often on rhizomes; true bulbs (1–2 extremely thickened prophylls (bladeless 'true scales') or false bulbs (thickened basal sheaths and prophylls); several membranous, fibrous or coriaceous tunics; annual or perennial roots;
- rhizomes: rarely runner-like condensed or elongated with very diverse branching patterns;
- leaves: basally arranged, consisting of a basal sheath and terminal blade, often covering the scape and thus appearing cauline;
- bracts: two to several, often fused into an involucre ('spathe');
- inflorescence: fasciculate to often umbel- or head-like (rarely spicate), (one) few-to many-flowered, loose to dense;
- flowers: pediceled, actinomorphic, hypogynous, trimerous of very diverse shape;
- tepals: in two slightly differentiated whorls, free or basally united;
- stamens: two whorls, sometimes basally (or up to two-thirds) connected, the inner often widened and/or toothed;
- ovary: trilocular, three septal nectaries of various shapes, two or more curved (campylotropous) ovules/locule, sometimes diverse apical appendages (crests and horns) developing into a loculicidal capsule dehiscing along the carpels' midrib;
- style: single, with slender, capitate or, rarely, trilobed stigma;
- seeds: angular to globular, black (phytomelan epidermal layer), extremely variable shape, and coat ornamentation;
- karyology: predominant basic chromosome numbers x = 8 and x = 7 (rarely x = 9 or x = 10) with polyploidy in both predominant series; chromosome morphology differs with taxonomic groups.

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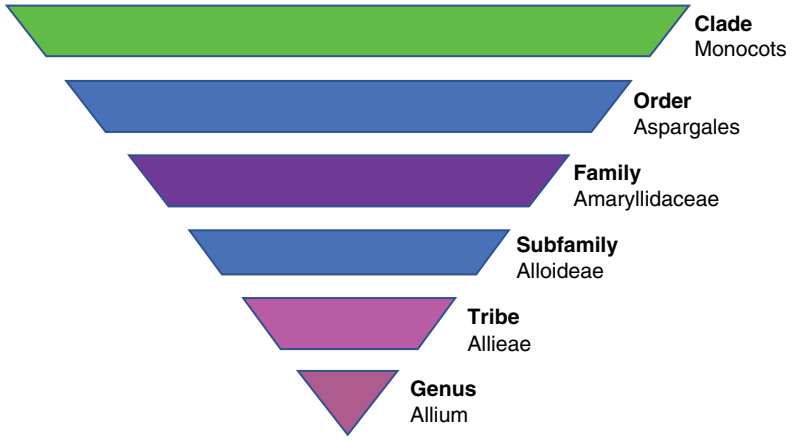

Fig. 1.1. APG IV taxonomic classification of *Allium* hierarchy. (Angiosperm Phylogeny Group; Chase *et al*., 2016)

Shape, size, colour and texture of rhizomes, bulbs, roots, leaf blades (e.g. flat, channelled, terete or fistulose, sheath/lamina ratio), scapes, spathes, inflorescences, tepals (mostly white, rose to deep purple/violet, rarely blue or yellow), stamens, ovaries and seeds vary considerably with species. The same is true for the anatomy, cross-sections and internal structure of all plant parts.

Basal bulblets and topsets are important vegetative propagules.

Most *Allium* species are allogamous and spontaneous interspecific hybridization is not rare, but strong crossing barriers exist in some groups, even between morphologically similar species.

1.2. Distribution and ecology

Natural distribution of the genus *Allium* occurs in the northern hemisphere over the holarctic region from the dry subtropics to the boreal zone. Its major centre of diversity stretches from the Mediterranean basin to Central Asia and west China and a second but smaller one (~100 species) in North America (from Alaska to Mexico) (Fig. 1.2).

One or two species inhabit the subarctic belt (e.g. *Allium schoenoprasum* L.), and a few are scattered in subtropical and tropical mountains or highland (e.g. Vietnam and Myanmar: *Allium wallichii* Kunth (Quang *et al.*, 2020); Sri Lanka: *A. hookeri* Thwaites; east Sudan to northern Somalia: *A. spathaceum* Steud. ex A. Rich. (De Wilde-Duyfjes, 1976)). Indications of some Chilean (*A. juncifolium* – invalid name) and Brazilian (*A. sellowianum* – synonym of *Nothscordum bivalve* (L.) Britton) *Allium*s (Block, 2010) are not supported by others and are erroneous.

A single *Allium* (*A. synnotii* G.Don (syn. *A. dregeanum* Kunth)) of unknown origin has been described in South Africa, either a modification of *A. ampeloprasum* L. introduction by early European and North African settlers (De Wilde-Duyfjes, 1976) or South African indigenous plants (Mathew, 1996; Germishuizen and Meyer, 2003), which is rather unlikely (Friesen, 2007) as it exhibits the highest number of chromosomes for the genus (2n=64 and 80; De Sarker *et al.*, 1997) and because it has an almost identical intergenic spacer of the ribosomal DNA (ITS) to the European species *Allium scorodoprasum* L. and *A. rotundum* L., section *Allium* (Friesen *et al.*, 2006; Hirschegger *et al.*, 2010; NCBI GenBank Accession AJ411962). *Allium synnotii* is possibly a descendent of *Allium scorodoprasum* and/or related species introductions by early European settlers followed by hybridization, polyploidization and/or other manipulation. This question remains open.

1.3. Phylogeny and classification

Advances in molecular phylogenetics have revolutionized our understanding of *Allium* taxonomy and evolution. The overwhelming morphological diversity is mirrored by a complicated taxonomic structure consisting of 15 subgenera

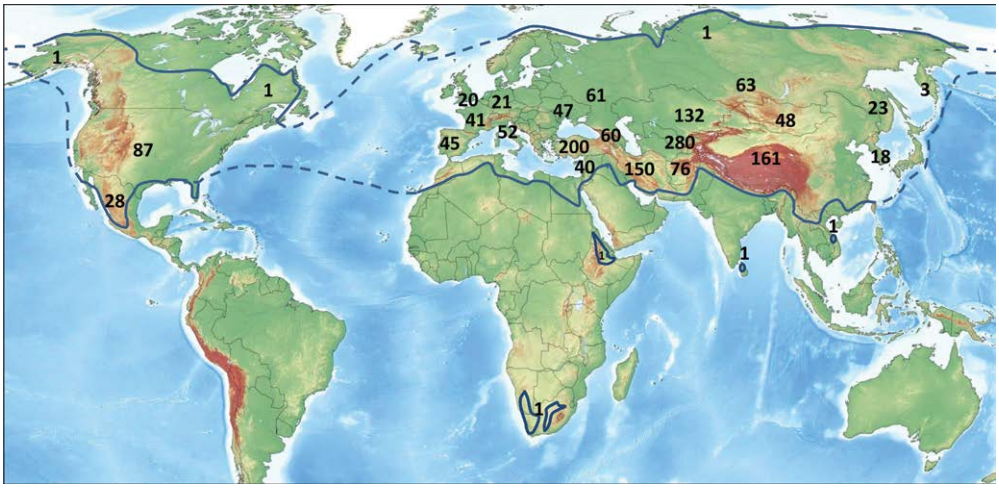

Fig. 1.2. World distribution of wild *Allium* species. The figures indicate the number of local species/regions.

and 72 sections (Friesen *et al.*, 2006) of three evolutionary lineages (Fritsch and Friesen, 2002; Friesen *et al.*, 2006).

The oldest lineage, subg. *Nectaroscordum*, subg. *Microscordum* and subg. *Amerallium*, has one row of vascular bundles and subepidermal laticifers in the leaf blades (Fritsch, 1988). Both first mentioned subgenera show bulbose species and there is a great morphological resemblance in many features (also karyological with x = 9 or x = 8). The subgenus *Amerallium* includes also rhizomatous groups of American and European species and its basic chromosome number is x = 7; secondary there is also x = 8 and x = 11.

The second lineage, subg. *Anguinum*, subg. *Vvedenskya*, subg. *Porphyroprason*, subg. *Caloscordum* and subg. *Melanocrommyum*, has a basic chromosome number of x = 8. Subgenus *Anguinum* is the only rhizomatous representative here. Blades are mostly flat (cylindrical blade occurs in the monotypic subg. *Vvedenskya* and subg. *Caloscordum*), and the laticifers are generally on the inner border of the palisade parenchyma (Friesen *et al.*, 1986). In the leaf blades of subg. *Anguinum* and *Porphyroprason*, one or two rows of vascular bundles occur, while two oppositely oriented rows of vascular bundles are present in subg. *Melanocrommyum*, at least on the ventral side (Fritsch, 1988).

The youngest evolutionary lineage with seven subgenera (x = 8) have laticifers on the inner border of the palisade parenchyma. Leaf blades are often flat, and have two oppositely oriented rows of randomly distributed vascular bundles at the top, except for subgenus *Cyathophora* (with one row of vascular bundles). Less common are cylindrical leaf blades as in the common onion, with a ring of vascular bundles and thread-like leaf blades. The species-poor rhizomatous subgenera *Butomissa*, *Cyathophora* and *Rhizirideum* in the narrowest sense are less specialized.

More specialized is the bulbous subgenus *Allium* with three subgroups, corresponding to the classic sections *Allium*, *Codonoprasum* and the inhomogeneous *Scorodon s.l.* The latter is divided into several small, partly oligotypic sections: *Avulsea, Brevidentia, Coerulea, Costulatae, Crystallina, Eremoprasum, Kopetdagia, Longivaginata, Mediasia, Minuta, Multicaulia* and *Pallasia* (Khassanov, 1996, 2000, 2018; Fritsch *et al.*, 1998; Friesen *et al.*, 2006). Most derived molecular features are shown by the rhizomatous subgenera *Reticulatobulbosa*, *Polyprason* and *Cepa*.

This classification employed almost exclusively known names, even if several taxonomic groups were united, others received higher rank and were applied in the narrow sense.

Lately, more *Allium* sections were combined and described: *Longibidentata* (R.M. Fritsch in Khassanov and Fritsch, 1994, p. 974); R.M. Fritsch (2009, p. 465), *Decipientia* (Omelczuk, 1962, p. 71), *Asteroprason* and *Procerallium* (Fritsch *et al.*, 2010, pp. 168, 184, 199), *Unicaulia* and *Haneltia* (Khassanov *et al.*, 2011, p. 174), *Rechingeria* (Khassanov *et al.*, 2013,

p. 214), *Kingdonia* and *Trifurcatum* (Huang *et al.*, 2014, pp. 283, 284, respectively), *Tulipifolia* (Friesen *et al.*, 2021). Some sections have been assembled according to the latest phylogenetic data (Friesen *et al.*, 2020).

All subsequent phylogenetic studies (Li *et al.*, 2010; Wheeler *et al.*, 2013; Li *et al.*, 2016; Hauenschild *et al.*, 2017; Costa *et al.*, 2020; Jimenez *et al.*, 2020; Xie *et al.*, 2020) confirmed the genus division into three major evolutionary lineages and the monophyletic origin of all subgenera included in the two older evolutionary lineages. Only Namgung *et al.* (2021) showed a paraphyletic situation in subgenus *Melanocrommyum*, based on the very doubtful position of *Allium nigrum*.

The phylogenetic relationships in the youngest lineage are less clear (Li *et al.*, 2016; Hauenschild *et al.*, 2017; Friesen *et al.*, 2020; Xie *et al.*, 2020), as analyses of most species from subgenera *Allium*, *Rhizirideum*, *Cepa* and *Polyprason* show paraphyletic characters, as demonstrated by the SplitsTree network with over 300 nrITS sequences, with species representatives from every accepted section of the genus *Allium* (Fig. 1.3).

Little is known of the taxonomy and genetic diversity within some well-established subgenera and sections (Friesen, 2007). However, reliable taxonomic and bio-geographic analyses are available for the sections *Schoenoprasum* (Friesen and Blattner, 2000) and *Cepa* (Gurushidze *et al.*, 2007), subgenus *Melanocrommyum* (Gurushidze *et al.*, 2010; Fritsch 2012, 2016), section *Sacculiferum* (Choi and Oh, 2011), the American species of subgenus *Amerallium* (Nguyen *et al.*, 2008; Wheeler *et al.*, 2013; Mashayekhi and Columbus, 2014), section *Oreiprason* (Seregin *et al.*, 2015), section *Coerulea* (Khassanov *et al.*, 2013), subgenus *Anguinum* (Herden *et al.*, 2016), subgenus *Cyathophora* (Li *et al.*, 2016), section *Rhizirideum* (Sinitsyna *et al.*, 2016), section *Daghestanica* (Xie *et al.*, 2019, 2020), *Caloscordum* (Yang *et al.*, 2017), section *Rhizomatosa* (Friesen *et al.*, 2020), sections *Decipientia* and *Tulipifolia* (Friesen *et al.*, 2021),

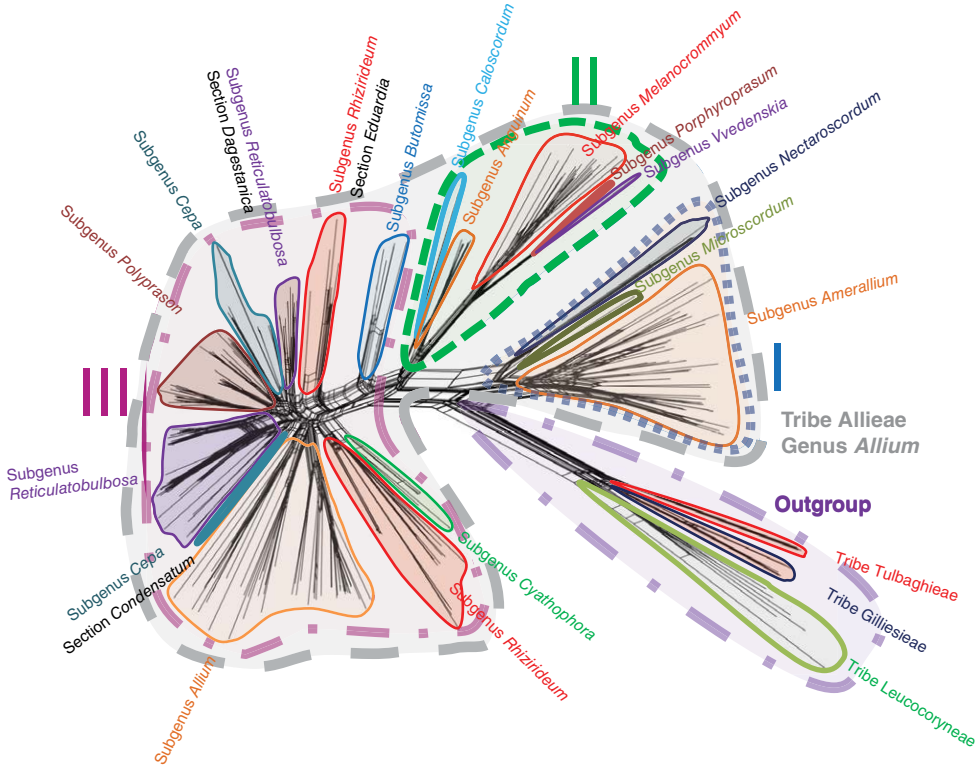

Fig. 1.3. The SplitsTree network of the tribe Allieae, based on nrITS sequences of >300 *Allium* species.

the Eurasian species of subgenus *Amerallium* (Friesen *et al.*, in preparation).

It is important to include all species in phylogenetic analysis to solve the paraphyly issue in some third evolution lineage taxa, and results from both nuclear and plastid genomes are very useful in tracking down the evolutionary hybridogenic events within the genus.

The enormous size of *Allium* nuclear genomes precludes full sequencing soon, while the entire plastid genome has already been published for >60 *Allium* species (Filushin *et al.*, 2016, 2018; Lee *et al.*, 2017; Xie *et al.*, 2019, 2020; Yang *et al.*, 2019; Yusupov *et al.*, 2020; Namgung *et al.*, 2021), as well as the transcriptome of the nine *Allium* species nuclear genome (Zhu *et al.*, 2017). The deeper and broader the genus phylogeny is examined, the more examples of the incongruence between nuclear and plastid phylogenies emerge, which indicate hybridogenic events in the earlier phases of the genus phylogeny (Li *et al.*, 2016; Han *et al.*, 2019; Xie *et al.*, 2019, 2020; Yusupov *et al.*, 2020; Friesen *et al.*, 2021).

1.4. Time of origin

Large discrepancies exist in estimated divergence times of the genus *Allium* – from 11 up to 52.2 mya, mainly due to differences in fossil placement, the dating methods used and the fact that no *Allium* fossil records exist. Published data is therefore based on a secondary calibration point estimated for other monocotyledons (Chen *et al.*, 2013; Li *et al.*, 2016; Hauenschild *et al.*, 2017; Costa *et al.*, 2020; Xie *et al.*, 2020). We trust that employment of nrITS substitution rates for herbaceous annual/perennial angiosperms is the most appropriate means to accomplish the task (Kay *et al.*, 2006). *Paleoallium*, a single fossil (*c.*49 mya) from Washington State, USA (Pigg *et al.*, 2018), of another genus of Amaryllidaceae is unlikely an *Allium*, yet it could be used for calibration. Such analyses with confidence in secondary calibration points often show that certain plant groups are younger than expected. The discrepancies in the origin and age of the angiosperms were confirmed (Coiro *et al.*, 2019; Li *et al.*, 2019). In my opinion, of the published datings, only Costa *et al.* (2020) with 52.2 mya (58.1–44.4 mya: 95% HPD) provided a close estimate of the actual genesis age of the genus *Allium*. The intercontinental disjunction hypothesis in the Allioideae tribes as the result of the vicariance after the Gondwana break-up is also discussed for the first time (Costa *et al.*, 2020). Using an extensive molecular clock analysis covering 800 monocots, Janssen and Bremer (2004) proposed an earlier genesis age for subfamily Allioideae (87 mya). Based on the analysis of the genus *Allium* subgenera distribution, the out-of-India hypothesis (Briggs, 2003; Bossuyt *et al.*, 2006; Datta-Roy and Karanth, 2009; Costa *et al.*, 2020) could also be validated. Most overlaps in the subgenera distribution are concentrated to the north of the Himalayas (Tian Shan, Karakorum, Tibet) and from there some migrated west (e.g. *Melanocrommyum*) and east (*Butomissa*, *Cyathophora*). Some monotypic subgenera grow only in Central Asia north of the Himalayas (e.g. *Vvedenskya*, *Porphyroprason*), others only in eastern Asia (e.g. *Caloscordum* and *Microscordum*) or only in west Asia and southeast Europe (*Nectaroscordum*). Some subgenera (*Cepa*, *Rhizirideum, Reticulatobulbosa*) are distributed in Europe and Asia, but exhibit the greatest diversity in Asia, north of the Himalayas. Others have disjunction centres in the Mediterranean, east Asia and North America (*Amerallium* and *Anguinum*). The migration to North America probably occurred several times from Asia via the Bering Land Bridge (Huang *et al.*, 2014; Herden *et al.*, 2016), as did *Allium schoenoprasum* (subgenus *Cepa*, section *Schoenoprasum*), the only native representative of the third lineage in North America (Friesen and Blattner, 2000) (Fig. 1.4).

2. Edible Alliums

2.1. Edible *Allium*

The genus *Allium*'s economic significance depends on several important vegetable crops (onion, garlic, leek, bunching onion, Chinese chive and others) and ornamental species mostly belong to the third evolutionary line (Galmarini, 2017) (Table 1.1), while man consumes wild-growing species of the three evolutionary lineages.

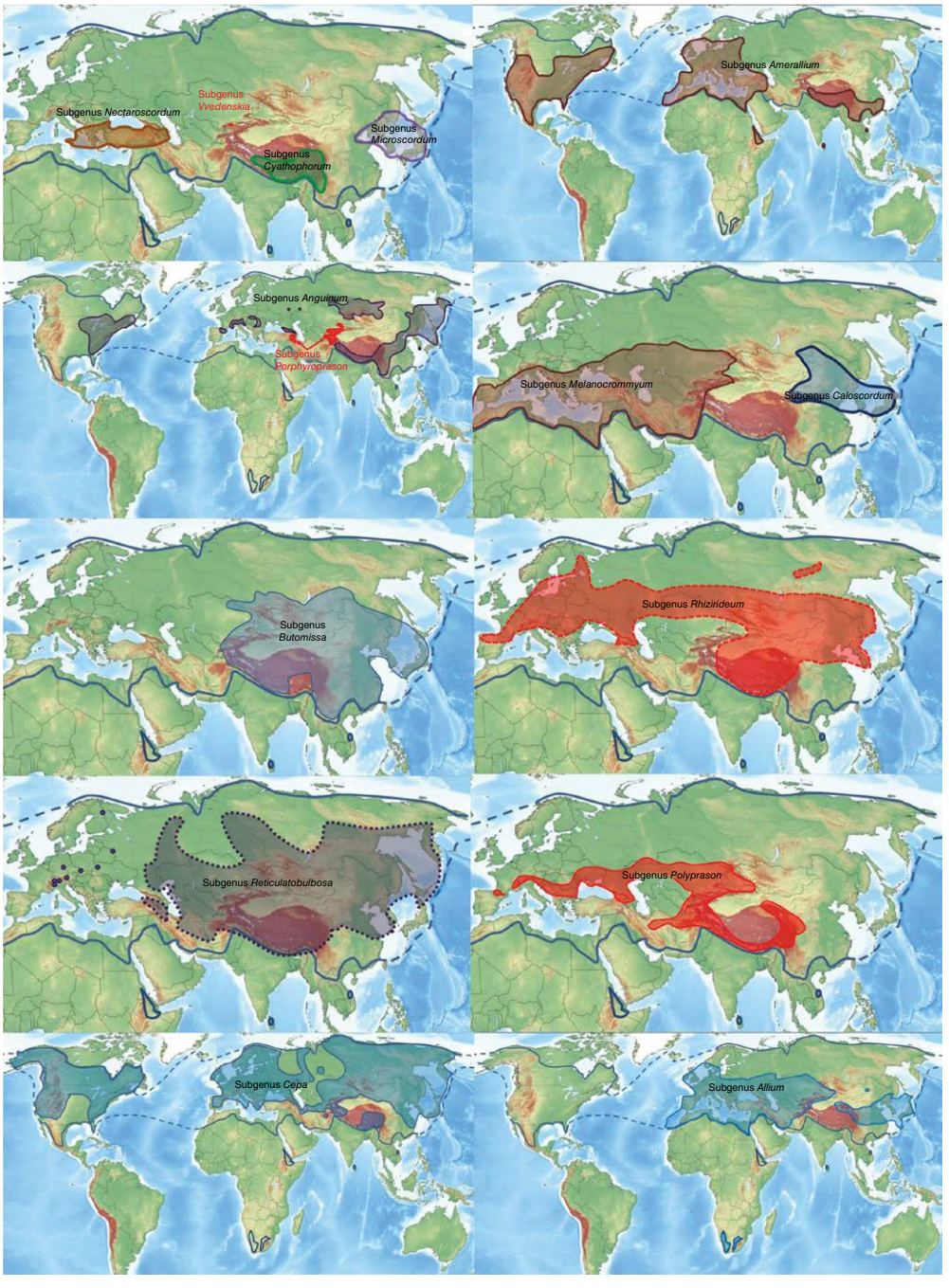

Fig. 1.4. Distribution of the subgenera of the genus *Allium*.

Generally, all parts of all *Allium* species may be consumed by humans. Many taste good, yet some are less edible or even unpalatable, e.g. members of subg. *Nectaroscordum* that taste and smell like burnt rubber.

Many wild species are consumed locally, depending on size, availability and taste. The following provides a shortlist of human-consumed wild species. Mongolia: *Allium mongolicum* Regel; Siberia: *A. microdictyon* Prokh.; Russian Far

Table 1.1. Allium crop species and their areas of cultivation.

Evolution lineage/ Subgenera/ Section	Botanical names of the crop groups	Other names used in the literature	Area of cultivation	English names
I/*Amerallium*/ *Bromatorrhiza*	*A. hookeri* Thw.		Butan, Yunnan, northwest Thailand	
I/*Amerallium*/ *Bromatorrhiza*	*A. wallichii* Kunth	*A. platyphyllum* Diels, *A. lancifolium* Stearn	East Tibet	
I/*Amerallium*/ *Rhopetoprason*	*A. kunthii* G.Don		Mexico	
I/*Amerallium*/ *Amerallium*	*A. canadense* L.		Cuba	
I/*Amerallium*/ *Molium*	*A. neapolitanum* Cyr.		Mexico	Naples garlic
III/*Allium*/*Allium*	*A. ampeloprasum* L. s.l.			
	Leek group	*A. porrum* L., *A. ampeloprasum* var. *porrum* (L.) J.Gay	Mainly Europe and North America	Leek
	Kurrat group	*A. kurrat* Schweinf. ex Krause	Egypt and adjacent areas	Kurrat, salad leek
	Great-headed garlic group - *A. ampeloprasum* var. ampeloprasum	*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
III/*Allium*/*Allium*	*A. tuncelianum* (Kollmann) N.Özhatay, Mathew & Şiraneci		Turkey	Tunceli garlic***
III/*Allium*/*Allium*	*A. sativum* L.	*A. longicuspis* Regel	Worldwide	garlic
III/*Allium*/*Allium*	*A. rotundum* L.	*A. scorodoprasum* ssp. *rotundum* (L.) Stearn	Turkey	
III/*Allium*/ *Scorodon*	*A. macrostemon* Bunge	*A. uratense* Franch., *A. grayi* Regel	China, Korea, Japan	Chinese garlic, Japanese garlic
III/*Butomissa*/ *Butomissa*	*A. tuberosum* Rottl. ex Sprengel*		China, Japan, Central Asia, worldwide now	Chinese chive
III/*Cepa*/ *Schoenoprasum*	*A. schoenoprasum* L.		Worldwide in temperate areas	Chive

Continued

Table 1.1. Continued.

Evolution lineage/ Subgenera/ Section	Botanical names of the crop groups	Other names used in the literature	Area of cultivation	English names
III/*Cepa*/*Cepa*	*A. cepa* L. Common onion group Ever-ready onions Aggregatum group	*A. cepa*. ssp. *cepa*/ var. *cepa A. cepa* ssp. *australe* Trofimez ex Kazakova *A. cepa* var. *perutile* Stearn *A. ascalonicum* auct. hort. *A. cepa* var. *aggregatum* G.Don, var. *ascalonicum* Backer *A. cepa* ssp. *orientalis* Kazakova	Worldwide/Great Britain Nearly worldwide	onion, common onion ever-ready onion shallot, potato onion, multipler onion
III/*Cepa*/*Cepa*	*A. fistulosum* L.		East Asia, temperate Europe and North America	bunching onion, Welsh onion
	A. × cornutum Clem. ex Vis.**	*A. cepa* var. *viviparum* auct.**	Locally in south Asia, Europe, Canada, Antilles, China, Korea, Japan, southeast Asia	
III/*Cepa*/*Cepa*	*A. oschaninii* O.Fedtsch.		France, Italy	French shallot**
III/*Cepa*/*Cepa*	*A . proliferum* (Moench.) Schrader east Asian group Eurasian group	*A. aobanum* Araki, *A. wakegi* Araki, *A. cepa* var. *viviparum* (Metzg.) Alef., *A. cepa* var. *proliferum* (Moench)Alef.	China, Japan, south-east Asia North America, Europe, northeast Asia	Wakegi onion, top onion, tree onion, Egyptian onion, Catawissa onion
III/*Cepa*/*Cepa*	*A. pskemense* B.Fedtsch.		Uzbekistan, Kyrgyzstan, Kazakhstan	
III/*Cepa*/ *Sacculiferum*	*A. chinense* G.Don	*A. bakeri* Regel	China, Korea, Japan, Southeast Asia	Rakkyo, Japanese scallions

*see Blattner and Friesen (2006); Oyuntsetseg *et al*. (2012); **see Friesen and Klaas (1998); ***see Ipek *et al*. (2008); Kizil and Khawar (2017).

East: *A. ochotense* Prokh.; USA and east Canada: *A. tricoccum*; China: *A. prattii*; south Siberia and Mongolia, south Ural and Altai: *A. altaicum* Pall., *A. microdictyon* Prokh., *A. obliquum* L.; east Siberia and Mongolia: *A. ramosum* L.; Europe: *A. ursinum* L.; Yunnan and Sichuan, China: *A. omeiense* Z.Y. Zhu; India (Kashmir), Afghanistan and Pakistan: *A. humile* Kunth; Uzbekistan: *A. suworowii* Regel and *A. tschimganicum* B. Fedtsch.; Tajikistan: *A. giganteum* Regel; Pakistan and Afghanistan: *A. roylei* Stearn; west Siberia and east Kazakhstan: *A. nutans* L.; south Ural and north Kazakhstan: *A. angulosum* L.; northwest India: *A. consanguineum* Kunth (Keusgen *et al.*, 2008; Ozturk *et al.*, 2012; Fritsch and Abbasi, 2013; Ju *et al.*, 2013; Kang *et al.*, 2013). These natural resources are often improperly managed, and over-collected with consequent severe population decline.

2.2. Domestication

Domestication probably started by both protection and the rational use of wild plants, followed by transplanting into gardens (Hanelt, 1990). Human selection and natural events resulted in the development of variation now common in several cultivated species.

The cultivation of domesticated *Allium* species (onion, garlic and others) during ancient times is well covered (Helm, 1956; Jones and Mann, 1963; Havey, 1995; Ekşi *et al.*, 2020). Here I will discuss another aspect: the location of the crops in the genus' phylogenetic system, and whether its progenitor exists in nature. Were the crop plants' domestication a single or multiple event?

2.3. Onions (section *Cepa*)

Allium section *Cepa* comprises ten wild species (*A. altaicum, A. asarense, A. farctum, A. galanthum, A. oschaninii, A. praemixtum, A. pskemense, A. rhabdotum, A. roylei, A. vavilovii* and the cultivated *A. cepa* (bulb onion) and *A. fistulosum* (bunching onion), all of which are consumed by man as condiment vegetables.

The wild taxa inhabit the Irano-Turanian floristic region, mainly in the Tian-Shan and Pamiro-Alai regions. Occurrences in neighbouring floristic provinces are only marginal extensions. The exceptions are *A. altaicum* and *A. rhabdotum*, which inhabit southern Siberia and the Mongolian mountains and the eastern Himalayas, respectively (Stearn, 1960; Fritsch and Friesen, 2002; Gurushidze *et al.*, 2007).

2.3.1 Common onion

The wild progenitor and origin of the common onion are not clear. Nuclear ITS sequences analyses revealed that *Allium vavilovii* that crosses freely with *A. cepa* is its genetically closest related species (Gurushidze *et al.*, 2007). These clear results confirm earlier studies on chloroplast data (Havey, 1992), yet morphological characterization contradicts this conclusion. *Allium cepa* has thick, fistulous, slightly bent leaves, and a somewhat biconical inflated scape, resembling the species of the other clades of section *Cepa*. *Allium vavilovii* and *A. asarense*, however, have flat, sickle-shaped leaves and bubble-like inflation of the scape. These discrepancies between molecular and morphological characterizations and the similarity between *A. cepa* and *A. oschaninii* might imply a sense of a hybrid origin of the common onion.

Strong crossing barriers exist between *A. oschaninii* and both *A. vavilovii* and *A. cepa*, while *A. vavilovii* crosses to some extent with *A. galanthum* and *A. fistulosum* (van Raamsdonk *et al.*, 2003). Leaves and scape morphologies of common onion are similar to *A. galanthum*, but the morphologically distinct *A. fistulosum* crosses better with *A. cepa*. Apart from these morphological inconsistencies the high variation of ITS sequences within *A. cepa* cannot result only from multiple domestication events but indicate an extended history of hybridization (Gurushidze *et al.*, 2007). Complete CP genome sequencing in seven section *Cepa* species, unfortunately without *A. vavilovii*, showed *A. galanthum* as the next related species to *A. cepa* (Yusupov *et al.*, 2020). This confirms the possible hybridogenic origin of *A. cepa*.

To finally clarify the *A. cepa* origin, genome sequencing of several accessions of all section *Cepa* species from different distribution areas is required.

2.3.2 Bunching onion (Allium fistulosum *L.*)

RAPD and PCR RFLP data confirmed the monophyletic origin of *A. fistulosum* from *A. altaicum* (Friesen *et al.*, 1999). This variable vegetable is common in China, Japan and Korea (Inden and Asahira, 1990), where the slender bulbs and basal parts of the pseudostem are much esteemed as fresh or cooked vegetables. In the west, it is consumed mostly as fresh green leaves forced in the wintertime.

2.3.3 Allium × proliferum *(Moench) Schrad. (top onion, tree onion, Egyptian onion, Catawissa onion, Wakegi onion)*

These *A. fistulosum* × *A. cepa* hybrids (Schubert *et al.*, 1983; Havey, 1991; Maaß, 1997a; Friesen and Klaas, 1998) mostly fail to develop flowers. The few buds that reach anthesis are sterile and some topsets develop on the receptacle. The crops are popular in North America, Europe and northeastern Asia home gardens for their topsets and young leaves. Hanelt (1990) suggested a Chinese origin, but morphological differences and genetic diversity in the top onion support a

polytopic origin (Maaß, 1997a). Indeed, *A. cepa* and *A. fistulosum* are often cultivated side-by-side, hence multiple hybridizations possibly occurred.

2.3.4 *Triploid onion* (Allium × cornutum *Clementi ex Visiani*)

Another sterile viviparous onion with a slender stature and pinkish-flushed flowers is cultivated in Tibet, Jammu, Croatia, central and western Europe, Canada and the Antilles. *Allium cepa* is accepted as one donor of these triploids (Havey, 1991; Maaß, 1997b; Friesen and Klaas, 1998), and *Allium roylei* was proposed as another parent (Puizina and Papeš, 1996). Fredotović *et al.* (2014) confirmed the above and proposed *A. pskemense* as the third parent, and that Jammu, Afghanistan or Pakistan are the monophyletic origin of the triploid species.

2.3.5 *French grey shallot*

French grey shallot cv. Grise de la Drôme has long been cultivated in southern France and Italy (Messiaen *et al.*, 1993; D'Antuono, 1998; Rabinovich and Kamenetsky, 2002. Messiaen *et al.* (1993) described the plants and, based on scape and umbel morphologies, proposed relationships with *A. oschaninii*. Maaß (1996) ruled out *A. cepa* relationship but proposed *A. oschaninii* or *A. vavilovii* as origins. Friesen and Klaas (1998) used both genomic *in situ* hybridization and fingerprint method RAPD and concluded that most grey shallot chromosomes originated from *A. oschaninii* and one-and-a-half chromosome arms from either *A. cepa* or *A. vavilovii*. All analysed grey shallot clones by fingerprinting were identical, hence monophyletic origin is very likely, but no information is available on where and when domestication occurred.

2.4. Garlic (*A. sativum*)

Like cultivated garlic, wild populations of *Allium longicuspis* Regel are sterile. The two plants are practically indistinguishable and are thus considered synonyms (Maaß and Klaas, 1995; Ipek *et al.*, 2003; Shemesh-Mayer and Kamenetsky-Goldstein, 2019; POWO, 2020). Supposedly, the transition to vegetative reproduction resulted from selections for earliness and large bulbs (Kamenetsky *et al.*, 2005; Shemesh-Mayer and Kamenetsky-Goldstein, 2019), and fertility was restored by physiological manipulations, experimentally (Pooler and Simon, 1994) and in open fields (Etoh and Simon, 2002; Kamenetsky *et al.*, 2004a; Kamenetsky *et al.*, 2007; Shemesh-Mayer and Kamenetsky-Goldstein, 2019).

It was suggested that *A. longicuspis* is the direct wild-growing ancestor of *A. sativum* (Vvedensky, 1944; Etoh and Ogura, 1984; Pooler and Simon, 1993; Maaß and Klaas, 1995; Mathew, 1996; Hong, 1999) and also that it is feral cultivated garlic since it grows along roads and in places of abandoned settlements in Central Asia (Etoh and Simon, 2002; Fritsch and Friesen, 2002; Klaas and Friesen, 2002; Kamenetsky *et al.*, 2004b).

The Turkish wild species *A. tuncelianum* (Kollmann) Özhatay, B.Mathew & Siraneci, assumed the wild progenitor of garlic (Mathew, 1996), is only distantly related and cannot be the progenitor (Ipek *et al.*, 2008).

2.5. Leek and relatives

Allium ampeloprasum L. *sensu lato* represents extremely variable polyploid complexes of several wild and cultivated taxa commonly grown across the Mediterranean basin through the Middle East into middle Asia and China (Kollmann, 1971; Wendelbo, 1971; Mathew, 1996; Hanelt, 2001). Bothmer (1970) introduced the concept of *A. ampeloprasum* complex, a group of closely related species including *A. ampeloprasum*, *A. bourgeaui* Rech. fil. and *A. commutatum* Guss, and later on added *A. atroviolaceum* Boiss to the list (Bothmer, 1974), and *A. polyanthum* should also be included in the complex (Guern *et al.*, 1991).

Cloning nrITS fragments of the hexaploid great-headed garlic and tetraploid leek revealed that both are allopolyploids with different parent species in their genomes (Hirschegger *et al.*, 2010), while the tetraploid minor crop taxa (Kurrat, Taree Irani and pearl onion) are related to leek. *Allium ampeloprasum* L. lectotype is from Island Flat Holm, UK (BM. Herb. Sloan 152, folio 153). Plants of the Flat Holm vegetable cultivar (Dr T. Rich, London, 2021, personal communication) are sterile hexaploids 2n=48 (De Sarker

et al., 1997). Hence, the name *A. ampeloprasum* L. s. str. should only apply to great-headed garlic and other *A. ampeloprasum* hexaploid plants, but leek should be named *Allium porrum* L. Nevertheless, this does not clarify the nomenclatural, taxonomic and phylogenetic issues of the *A. ampeloprasum* polyploid complex. Further genomic studies are needed to elucidate the subtleties in the origin of polyploid species in this complex followed by a thorough nomenclature and morphological processing including all relevant taxa. Hence, the questions of where and how crop species leek and great-headed garlic came about remain open.

2.6. Chinese chive (*Allium tuberosum* Rottl. ex Sprengel)

Domestication of Chinese chive occurred in northern China more than 3000 years ago (Hanelt, 2001) and currently it is the second-most economically important *Allium* crop in eastern Asia. *A. ramosum* L. is considered to be ancestral to the crop species (Hanelt, 1988). Since both are tetraploids (2n=32) that have similar morphology. Hanelt (2001) merged them into *A. ramosum*. Phenetic, cladistic and multivariate analyses of RAPD data revealed an unexpected relationship between wild *A. ramosum* and domesticated plants (Blattner and Friesen, 2006). Yet molecular data separated wild and crop populations as sister species.

Molecular data points to northern China as the most suitable site for the domestication of the diploid progenitor population but not the diploid *A. ramosum* from east Mongolia (Oyuntsetseg *et al.*, 2012).

The high *A. tuberosum* genetic variability is attributed to either multiple parallel domestications – namely, different populations contributed to the crop's gene pool – or post-domestication hybridization events with advanced wild populations (Blattner and Friesen, 2006).

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Appendix 1. Currently Accepted Infrageneric Groups in *Allium* L.

First evolutionary lineage

1. Subgenus *Nectaroscordum* (Lindl.) Asch. et Graebn., Type: *A. siculum* Ucria
Sect. *Nectaroscordum* (Lindl.) Gren. et Godr., Type: *A. siculum* Ucria
2. Subgenus *Microscordum* (Maxim.) N. Friesen, Type: *A. monanthum* Maxim
Sect. *Microscordum* Maxim., Type: *A. monanthum* Maxim
3. Subgenus *Amerallium* Traub., Type *A. canadense* L.
American sections:*
Sect. *Amerallium* Traub, Type: *A. canadense* L.
Sect. *Rhophetoprason* Traub, Type: *A. glandulosum* Link et Otto
Sect. *Lophioprason* Traub, Type: *A. sanbornii* Wood.
Sect. *Caulorhizideum* Traub, Type: *A. validum* S.Wats
East Asian sections
Sect. *Bromatorrhiza* Type: *A. wallichii* Kunth
Sect. *Kingdonia* X.J. He et D.Q. Huang, Type: *A. kingdonii* Stearn
Mediterranean sections
Sect. *Ophioscorodon* (Wallr.)Endl., Type: *A. ursinum* L.
Sect. *Narkissoprason* Type: *A. insubricum* Boiss. et Reut.
Sect. *Molium* G. Don, Type: *A. roseum* L.
Sect. *Briseis* (Salisb.) Stearn, Type: *A. triquetrum* L.
Sect. *Chamaeprason* F. Hermann, Type: *A. chamaemoly* L.
Sect. *Rhynchocarpum* Brullo, Type: *A. ruhmerianum* Asch. ex E.A. Durand et Barratte

*Modern authors divide American species from the subgenus *Amerallium* not into sections but into alliances (Saghir *et al.,* 1960; McNeal and Jacobsen, 2002; Nguyen *et al.,* 2008; Wheeler *et al.,* 2013).

Second evolutionary lineage

4. Subgenus *Caloscordum* (Herb.) R.M. Fritsch, Type: *A. neriniflorum* (Herb.) Baker
Sect. *Caloscordum* (Herb.) Baker, Type: *A. neriniflorum* (Herb.) Baker
5. Subgenus *Anguinum* (G.Don ex Koch) N. Friesen, Type: *A. victorialis* L.
Sect. *Anguinum* G. Don ex Koch, Type: *A. victorialis* L.
6. Subgenus *Porphyroprason* (Ekberg) R.M. Fritsch, Type: *A. oreophilum* C.A.Mey.
Sect. *Porphyroprason* Ekberg, Type: *A. oreophilum* C.A.Mey.
7. Subgenus *Vvedenskya* (Kamelin) R.M. Fritsch, Type: *A. kujukense* Vved.
Sect. *Vvedenskya* Kamelin, Type: *A. kujukense* Vved.
8. Subgenus *Melanocrommyum* (Webb et Berth.) Rouy. Type: *A. nigrum* L.
Sect. *Melanocrommyum* Webb et Berth. Type: *A. nigrum* L.
Sect. *Acmopetala* R.M. Fritsch, Type: *A. backhousianum* Regel
Sect. *Megaloprason* Wendelbo, Type: *A. rosenbachianum* Regel
Sect. *Regeloprason* Wendelbo, Type: *A. regelii* Trautv.
Sect. *Kaloprason* Koch, Type: *A. caspium* (Pall.) M. Bieb.
Sect. *Acanthoprason* Wendelbo, Type: *A. akaka* S.G.Gmel. ex Schult. et Schult. f.
Sect. *Compactoprason* R.M. Fritsch, Type: *A. giganteum* Regel
Sect. *Pseudoprason* (Wendelbo) K. Perss. et Wendelbo, Type: *A. koelzii* (Wendelbo) K. Perss. et Wendelbo
Sect. *Miniprason* R.M. Fritsch, Type: *A. karataviense* Regel
Sect. *Brevicaule* R.M.Fritsch, Type: *A. sergii* Vved.

Sect. *Thaumasioprason* Wendelbo, Type: *A. mirum* Wendelbo
Sect. *Verticillata* Kamelin, Type: *A. verticillatum* (Regel) Regel
Sect. *Acaule* R.M. Fritsch, Type: *A. hexaceras* Vved.
Sect. *Aroidea* F.O.Khass. et R.M. Fritsch, Type: *A. aroides* Popov & Vved.
Sect. *Popovia* F.O. Khass. et R.M. Fritsch, Type: *A. gypsaceum* Popov & Vved.
Sect. *Longibidentata* (R.M. Fritsch) R.M. Fritsch, Type: A. *fetissowii* Regel
Sect. *Asteroprason* R.M. Fritsch, Type: *A. elburzense* Wendelbo
Sect. *Procerallium* R.M. Fritsch, Type: *A. stipitatum* Regel
Sect. *Stellata* (F.O. Khass. et R.M. Fritsch) R.M. Fritsch, Type: *A. taeniopetalum* Popov & Vved
Sect. *Decipientia* (Omelczuk) R.M. Fritsch, Type: *A. decipiens* Fisch. ex Schult. & Schult.f.
Sect. *Tulipifolia* R.M. Fritsch & N. Friesen, Type: *A. tulipifolium* Ledeb.

Third evolutionary lineage

9. Subgenus *Butomissa* (Salisb.) N. Friesen, Type: *A. ramosum* L.
Sect: *Butomissa* (Salisb.) Kamelin, Type: *A. ramosum* L.
Sect. *Trifurcatum* X.J. He et D.Q.Huang, Type: A. *trifurcatum* (F.T. Wang & Tang) J.M. Xu
Sect. *Austromontana* N. Friesen, Type: *A. oreoprasum* Schrenk
10. Subgenus *Cyathophora* (R.M. Fritsch) R.M. Fritsch, Type: *A. cyathophorum* Bur. et Franch.
Sect. *Cyathophora* R.M. Fritsch, Type: *A. cyathophorum* Bur. et Franch.
Sect. *Milula* (Prain) N. Friesen, Type: *A. spicatum* (Prain) N. Friesen
Sect. *Coleoblastus* Ekberg, Type: *A. mairei* H.Lev.
11. Subgenus *Rhizirideum* (G. Don ex Koch) Wendelbo, Type: *A. senescens* L.
Sect. *Rhizirideum* G. Don ex Koch, Type: *A. senescens* L.
Sect. *Tenuissima* (Tsagolova) Hanelt, Type: *A. tenuissimum* L.
Sect. *Rhizomatosa* Egorova emend N. Friesen (incl. syn. sect. *Caespitosoprasum* N. Friesen), Type: *A. caespitosum* Sievers ex Bong. et C.A.Mey
Sect. *Eduardia* N. Friesen, Type: *A. eduardii* Stearn
12. Subgenus *Allium* Type: *A. sativum* L.
Sect. *Allium* Type: *A. sativum* L.
Sect. *Codonoprasum* Koch, Type: *A. oleraceum* L.
Sect. *Avulsea* F.O. Khass., Type: *A. griffithianum* Boiss.
Sect. *Brevidentia* F.O. Khass. et Yengal., Type: *A. brevidens* Vved.
Sect. *Coerulea* (Omelczuk) F.O. Khass., Type: *A. coeruleum* Pall.
Sect. *Costulatae* F.O. Khass. et Yengal., Type: *A. filidens* Regel.
Sect. *Haneltia* F.O. Khass., Type: *A. haneltii* F.O. Khass. & R.M. Fritsch.
Sect. *Crystallina* F.O. Khass. et Yengal., Type: *A. crystallinum* Vved.
Sect. *Eremoprasum* (Kamelin) F.O. Khass., R.M. Fritsch et N. Friesen, Type: *A. sabulosum* Stev. ex Bunge
Sect. *Kopetdagia* F.O. Khass., Type: *A. kopetdagense* Vved.
Sect. *Longivaginata* (Kamelin) F.O. Khass., R.M. Fritsch et N. Friesen, Type: *A. longivaginatum* Wendelbo
Sect. *Mediasia* F.O. Khass., Yengal. et N. Friesen, Type: *A. turkestanicum* Regel
Sect. *Minuta* F.O. Khass., Type: *Allium minutum* Vved.
Sect. *Multicaulia* F.O. Khass. et Yengal., Type: *A. borszczowii* Regel
Sect. *Pallasia* (Tzag.) F.O. Khass., R.M. Fritsch et N. Friesen, Type: *A. pallasii* Murray
Sect. *Unicaulia* F.O. Khass., Type: *Allium kotschyi* Boiss.
Sect. *Rechingeria* F.O. Khass. & Tirkasheva, Type: *A. rechingeri* Wendelbo

13. Subgenus *Cepa* (Mill.) Radić, Type: *A. cepa* L.
- Sect. *Cepa* (Mill.) Prokh., Type: *A. cepa* L.
- Sect. *Schoenoprasum* Dumort., Type: *A. schoenoprasum* L.
- Sect. *Annuloprason* Egorova, Type: *A. fedschenkoanum* Regel
- Sect. *Sacculiferum* P.P. Gritz., Type: *A. sacculiferum* Maxim.
- Sect. *Flavovirens* Q.Q. Li & X.J. He, Type: *A. flavovirens* Regel (nomen nudum)
- Sect. *Condensatum* N. Friesen, Type: *A. condensatum* Turch.

14. Subgenus *Polyprason* Radić, Type: *A. moschatum* L.
- Sect. *Scorodon* Koch, Type: *A. moschatum* L.
- Sect. *Oreiprason* F. Hermann, Type: *A. saxatile* M. Bieb.
- Sect. *Falcatifolia* N. Friesen, Type: *A. carolinianum* Redouté
- Sect. *Daghestanica* (Tscholok.) N. Friesen, Type: *A. daghestanicum* Grossg.

15. Subgenus *Reticulatobulbosa* (Kamelin) N. Friesen, Type: *A. lineare* L.
- Sect. *Reticulatobulbosa* Kamelin, Type: *A. lineare* L.
- Sect. *Campanulata* Kamelin, Type: *A. xiphopetalum* Aitch.
- Sect. *Scabriscapa* (Tscholok.) N. Friesen, Type: *A. scabriscapum* Boiss.
- Sect. *Nigrimontana* N. Friesen, Type: *A. drobovii* Vved.
- Sect. *Sikkimensia* (Traub) N. Friesen, Type: *A. sikkimense* Baker