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PHYLOGENY AND NEW INTRAGENERIC CLASSIFICATION OF *ALLIUM* (ALLIACEAE)
BASED ON NUCLEAR RIBOSOMAL DNA ITS SEQUENCES

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ABSTRACT

The internal transcribed spacer region (ITS) of nuclear ribosomal DNA was sequenced from 195 representative species of *Allium*, two species of *Nothoscordum*, and one species each of *Ipheion*, *Dichelostemma*, and *Tulbaghia*. Within the *Allium* species the lengths of the ITS regions were in a range from 612 to 661 base pairs and pairwise genetic distances reached up to 46%. The ITS data supported the inclusion of *Nectaroscordum*, *Caloscordum*, and *Milula* into *Allium*. Subgenera *Rhizirideum* and *Allium*, as well as sects. *Reticulobulbosa* and *Oreiprason* were non-monophyletic taxa. Based on the phylogenetic relations, a new classification of genus *Allium* consisting of 15 monophyletic subgenera is presented. Sections *Microscordum*, *Anguinum*, *Porphyroprason*, *Vvedenskya*, *Butomissa*, *Cyathophora*, and *Reticulobulbosa* are raised to subgeneric rank. Sections *Austromontana* N. Friesen, *Eduardia* N. Friesen, *Mediasia* F. O. Khassanov, S. C. Yengalycheva et N. Friesen, *Nigrimontana* N. Friesen, *Falcatifolia* N. Friesen, and *Condensatum* N. Friesen are newly described. Series *Daghestanica*, *Pallasia*, and *Scabriscapa*, as well as subsections. *Eremoprasum*, *Longivaginata*, and *Sikkimensia* are raised to sectional rank. A taxonomic conspectus of *Allium* at sectional level is given.

Key words: *Allium*, classification, evolution, internal transcribed spacer, phylogenetic analysis, taxonomy.

INTRODUCTION

Allium L. is probably the largest genus of the petaloid monocotyledons, comprising some 750 species (Stearn 1992). The genus is characterized by having bulbs enclosed in membranous (sometimes finally fibrous) tunics, free or almost free tepals, and often a subgynobasic style. Most species produce remarkable amounts of cysteine sulphoxides causing the well-known characteristic odor and taste. The genus is naturally distributed only in the Northern Hemisphere, mainly in regions that are seasonally dry. It has a main center of diversity in southwest and central Asia and a second smaller one in North America. *Allium* includes some economically important species like common onion, garlic, chives, and leek under worldwide cultivation, and also species with medicinal properties and others of horticultural merit (Fritsch and Friesen 2002). *Allium* is a member of family Alliaceae subfamily Allioideae Herb. (Fay and Chase 1996). Takhtajan (1987, 1997) placed Alliaceae in the order Amaryllidales close to Hyacinthaceae and Amaryllidaceae. After Fay and Chase (1996) and Friesen et al. (2000) subfamily Allioideae consist only of *Allium* (including *Caloscordum* Herb., *Milula* Prain, and *Nectaroscordum* Lindl.).

No comprehensive monograph of the genus has been compiled since Regel's in 1875 and the taxonomy is complicated, with a proliferation of synonyms and disagreement as to the subdivision of the genus. The history of infrageneric classification begins prior to Linnaeus (1753) who accepted 30 species in three alliances. Later studies recognized an increasing number of infrageneric groups together with an enlarged number of species: 6 sections (which trace back to informal groups established by Don in 1832) and 262 spe-

cies (Regel 1875); 9 sections and 228 species for the former USSR (Vvedensky 1935) alone; 3 subgenera, 36 sections and subsections and ca. 600 species (Traub 1968); 6 subgenera, 44 sections and subsections (Kamelin 1973); 6 subgenera, 50 sections and subsections for 600–700 species (Hanelt et al. 1992). In this last mentioned paper, subgen. *Rhizirideum* was explicitly regarded as a polyphyletic assemblage of different phylogenetic lines, and subgen. *Allium* as containing three main entities: the very diverse but insufficiently subdivided sect. *Scorodon*, the more homogenous and distinctly specialized sect. *Codonoprasum*, and (the largest among them) sect. *Allium* separated by other morphological and phenetic specializations. The latter two sections were regarded as phylogenetically young groups. Up to now about 1400 species names have been proposed, often from inadequate or incomplete material, which have later proven synonymous with existing species (Gregory et al. 1998).

A first approach to structure the genus *Allium* by molecular markers was published by Linne von Berg et al. (1996) who conducted a chloroplast DNA RFLP analysis. They recognized the then established subgenera, but found that subgen. *Amerallium* and *Bromatorrhiza* could not be clearly distinguished. A closer investigation of the *Amerallium*–*Bromatorrhiza* complex (Samoylov et al. 1995, 1999) proved again the polyphyletic state of subgen. *Bromatorrhiza*, which had to be integrated into subgen. *Amerallium* (all species with $x = 7$) and subgen. *Rhizirideum* (species with $x = 8$). The distribution of *Amerallium* species in the Old and New World was also reflected in these phylogenetic data, as well as in an internal transcribed spacer region (ITS) sequence analysis of Dubouzet and Shinoda (1999). Mes et al. (1999) included 29 species of *Allium* and 7 species of related genera

in a phylogenetic study using restriction fragment length polymorphism (RFLP) data from polymerase chain reaction (PCR) amplified chloroplast DNA. In this analysis the large subgen. *Rhizirideum* and *Allium*, which had still remained largely intact in the previously published studies, proved to be polyphyletic, and *Nectaroscordum siculum* was placed in *Allium*. Although some sections in the monophyletic subgen. *Melanocrommyum* appeared then artificial, the taxonomy at the level of sections remained more or less intact. Dubouzet et al. (1997) proposed a first molecular phylogeny of subgen. *Rhizirideum* based on nuclear DNA markers. Their results largely confirmed the taxonomic system of Hanelt et al. (1992). However, no species from outside the analyzed subgenus were included in this study, nor in some other recent phylogenetic analyses (subgen. *Melanocrommyum*: Dubouzet and Shinoda 1998; subgen. *Rhizirideum*: van Raamsdonk et al. 2000), thus preventing unambiguous circumscriptions of these subgenera.

Another important aspect in several molecular phylogenetic studies is the quality of the studied plant material. Often research was conducted on seeds obtained from botanical gardens or seed companies, mostly from free-pollinated specimens. In our experience over 60% of such materials were wrongly determined or had hybrid origins, thus impeding phylogenetic studies (Friesen et al. 1999) when used without further confirmation of their status.

Here we present a study where we used sequence data of the ITS region of nuclear ribosomal DNA (nrDNA) to assess phylogenetic relationship of the entire genus *Allium*. Furthermore, to evaluate the proposed poly- or paraphyletic origin of some *Allium* subgenera and sections (Mes et al. 1997, 1999; Klaas and Friesen 2002), we used a relatively dense taxon sample, representing all major groups of the genus. The ITS region, including the 5.8S nrDNA and the two spacers ITS-1 and ITS-2, has proven to be an excellent source of information from the nuclear genome in plants at the intrageneric level (e.g., Baldwin 1992; Baldwin et al. 1995; Dubouzet and Shinoda 1999; Friesen et al. 2000; Blattner 2004). We also provide a new intrageneric classification of *Allium* based on our ITS data, but also integrate earlier molecular studies to circumscribe monophyletic taxa. We do not intend to discuss details below the section level here. Analyses of the biogeography of the genus and several subgeneric groups, as well as a discussion of the hybrid origin of *Allium* taxa, will be published elsewhere.

MATERIALS AND METHODS

Plant Material

In this investigation 221 samples representing 196 species of genus *Allium*, and one species each of the outgroup genera *Ipheion* Raf., *Tulbaghia* L., and *Dichelostemma* Kunth, and two species of *Nothoscordum* Kunth (Fay and Chase 1996; Mes et al. 1997; Friesen et al. 2000) were studied. Most of the accessions were selected from the *Allium* living collection of the Department of Taxonomy, IPK Gatersleben. This collection comprises more than 340 species, mostly with multiple accessions per species. Most of these accessions were collected from naturally occurring populations. The accession numbers H600 and higher represent herbarium specimens (herbaria: TASH, GAT, NS, and LE). Accession num-

ber, the taxonomical classification (Hanelt et al. 1992), and origin of species examined are indicated in Table 1. Subgenera *Rhizirideum* and *Allium* were represented by 165 accessions and representatives of each of the 37 sections of the subgen. *Amerallium*, *Caloscordum*, *Nectaroscordum*, and *Melanocrommyum* were included. ITS sequences for some species from subgen. *Amerallium* (*Allium roseum* L., *A. chamaemoly* L., *A. neapolitanum* Cirillo, *A. zebdanense* Boiss. et Noë, *A. validum* S. Wats., *A. sanbornii* A. Wood, *A. stellatum* Ker., *A. bolanderi* S. Wats., *A. dichlamydeum* E. L. Greene, *A. unifolium* Kell., *A. hyalinum* M. K. Curran, and *A. amplexens* Torr.) were taken from Dubouzet and Shinoda (1999). In all cases when accessions were placed in preliminary trees at an unexpected position, additional accessions of the same species were analyzed to corroborate the phylogenetic affiliation of the species.

Molecular Methods

DNA was isolated with the NucleoSpin Plant kit (Macherey-Nagel, Düren, Germany) according to the instructions of the manufacturer. The concentration of the extracted DNA was checked on an agarose gel. Isolated DNAs were used directly in PCR amplifications. For most samples, the nrDNA ITS region (ITS-1, 5.8S nrDNA subunit, and ITS-2) was amplified using primers ITS-A and ITS-B (Blattner 1999). ITS-1 and ITS-2 were amplified separately when DNAs from herbarium sheets were used, in these cases under inclusion of primers ITS-A together with ITS-C, and ITS-B with ITS-D (Blattner 1999). PCR was carried out in a Grant Autogene II thermo-cycler (Grant Instruments, Cambridge, UK) programmed as: 95°C for 2 min [55°C for 30 sec, 70°C for 1 min, 95°C for 20 sec]₃₂ 70°C for 7 min. Amplification was carried out with 1 Unit Taq DNA polymerase (Boehringer, Mannheim, Germany) in the supplied reaction buffer, 0.2 mM of each dNTP, 50 pmol of each primer and 10–25 ng of total DNA in 50 µL reaction volume. The PCR products were separated on an agarose gel and purified with the NucleoSpin Gel Extraction kit (Macherey-Nagel, Düren, Germany). After checking DNA concentration on a 1.8% agarose gel, about 40 ng PCR product was used in a 10 µL cycle sequencing reaction with the ABI BigDye Terminator Kit (Applied Biosystems, Foster City, California, USA) according to the instructions of the manufacturer. The internal primers ITS-SF, ITS-SR (Blattner et al. 2001), and partly also ITS-C and ITS-D were used as sequencing primers. The sequencing reactions were analyzed on ABI377 DNA sequencers (Applied Biosystems).

Data Analysis

Forward and reverse sequences from every individual were manually edited with CHROMAS* vers. 1.5 software (Technelysium Pty. Ltd., Tweantin, Queensland, Australia) and combined in single consensus sequences. The sequences of all 221 samples were aligned with CLUSTALX (Thompson et al. 1997) and the alignment was manually adjusted where necessary. Phenetic and cladistic analyses were conducted in PAUP* vers. 4.0b10 (Swofford 2002), model-based analyses with Bayesian inference (BI) in MrBayes 3.0b4 (Ronquist and Huelsenbeck 2003). Different models of sequence evolution were first evaluated with Modeltest

Table 1. New and traditional classifications for *Allium* species with investigated EMBL accessions and chromosome numbers. The traditional classification shown is as accepted by Hanelt et al. (1992), or according to description if described later. TAX refers to accession numbers of the Taxonomic *Allium* Reference Collection of the IPK, Gatersleben, Germany. Herbarium specimens are marked with "H" and herbarium acronym. Origin is given by country and locality or botanical garden (BG). If origin of BG accession is known it is noted in brackets []. Nucleotide Sequence Database accession numbers of the ITS sequences were given under EMBL.

New classification Subgenus/Section	Traditional classification Subgenus/Section	Species	2n	TAX	Origin	EMBL
<i>Allium</i>	<i>Allium</i>					
<i>Allium/Allium</i>	<i>Allium/Allium</i>	<i>A. ampeloprasum</i> L.	32	2198	BULGARIA: Arkutino	AJ411888
<i>Allium/Allium</i>	<i>Allium/Allium</i>	<i>A. atroviolaceum</i> Boiss.	32	5376	TURKEY: vil. Antalya, Saklikent	AJ411884
<i>Allium/Allium</i>	<i>Allium/Allium</i>	<i>A. dregeanum</i> Kunth	64	5722	SOUTH AFRICA	AJ411962
<i>Allium/Allium</i>	<i>Allium/Allium</i>	<i>A. iranicum</i> (Wendelbo) Wen- delbo	32	3969	IRAN: Asara, Elburz Range, Karaj Valley	AJ411961
<i>Allium/Allium</i>	<i>Allium/Allium</i>	<i>A. sativum</i> L.	16	1319	TAJKISTAN: BG Dushanbe	AJ411901
<i>Allium/Allium</i>	<i>Allium/Allium</i>	<i>A. scorodoprasum</i> L.	16	2290	BULGARIA: Plovdiv	AJ412713
<i>Allium/Allium</i>	<i>Allium/Allium</i>	<i>A. sphaerocephalon</i> L.	16	5337	TURKEY: vil. Denizli, Boz Dagi	AJ412717
<i>Allium/Mediasia</i>	<i>Allium/Allium</i>	<i>A. turkestanicum</i> Regel	16	3366	UZBEKISTAN: Malguzar Mts., Dzhizakh	AJ411968
		<i>A. turkestanicum</i> Regel	16	5049	KAZAKHSTAN: Karatau Range, Mt. Ul- ken-Burul	AJ412718
<i>Allium/Avulsea</i>	<i>Allium/Scorodon</i>	<i>A. griffithianum</i> Boiss.	16	3660	UZBEKISTAN: Zaravshan Range, Pass Takhta-Karachi	AJ411862
<i>Allium/Avulsea</i>	<i>Allium/Scorodon</i>	<i>A. umbilicatum</i> Boiss.	16	2646	IRAN: BG Tehran [Moshaj]	AJ412719
<i>Allium/Brevidentia</i>	<i>Allium/Brevidentia</i>	<i>A. brevidens</i> Vved.	16	5037	UZBEKISTAN: vil. Zevar, SW Hissar Range	AJ412721
<i>Allium/?</i> (perhaps a new section)	<i>Allium/Brevidentia</i>	<i>A. haneltii</i> Khassanov et R. M. Fritsch		5796	UZBEKISTAN: Chatkal Range, Kuram Mts., Chorkesar	AJ412725
<i>Allium/Brevispatha</i>	<i>Allium/Brevispatha</i>	<i>A. margaritae</i> B. Fedtsch.		H658	KAZAKHSTAN: Chu-Ili Mts., Kurdai Pass (GAT)	AJ412732
<i>Allium/Brevispatha</i>	<i>Allium/Brevispatha</i>	<i>A. cupanii</i> Raf. subsp. <i>hirtova-</i> <i>ginatum</i> (Kunth) Stearn	16	5336	TURKEY: vil. Denizli, Boz Dagi	AJ412737
<i>Allium/Caerulea</i>	<i>Allium/Scorodon</i>	<i>A. caeruleum</i> Pall.	16	1525	RUSSIA: BG Moscow	AJ411903
		<i>A. caeruleum</i> Pall.	16	3735	KAZAKHSTAN: Chu-Ili Mts., Kurdai Pass	AJ412729
<i>Allium/Caerulea</i>	<i>Allium/Scorodon</i>	<i>A. caesium</i> Schrenk	32	2561	TAJKISTAN: Turkestan Range, Kusavlisai	AJ412731
<i>Allium/Caerulea</i>	<i>Allium/Scorodon</i>	<i>A. elegans</i> Drob.	16	3688	KAZAKHSTAN: Karatau Range, Mt. Ul- ken-tura	AJ412730
<i>Allium/Caerulea</i>	<i>Allium/Scorodon</i>	<i>A. litvinovii</i> Drob. ex Vved.	16	3339	KIRGIZSTAN: Alai Range, Pass Chigirchik	AJ412727
<i>Allium/Codonoprasum</i>	<i>Allium/Codonoprasum</i>	<i>A. flavum</i> L.	16	3230	AUSTRIA: BG Linz	AJ411926
<i>Allium/Codonoprasum</i>	<i>Allium/Codonoprasum</i>	<i>A. kunthianum</i> Vved.	16	2579	GEORGIA: Tbilisi, Narikala	AJ412734
<i>Allium/Codonoprasum</i>	<i>Allium/Codonoprasum</i>	<i>A. melanatherum</i> Pančić		3092	UK: BG Reading	AJ412739
<i>Allium/Codonoprasum</i>	<i>Allium/Codonoprasum</i>	<i>A. paniculatum</i> L.	16	3828	ITALY: Sardinia, La Corte	AJ411949
<i>Allium/Codonoprasum</i>	<i>Allium/Codonoprasum</i>	<i>A. rupestre</i> Steven		5302	TURKEY: vil. Kastamonu, Ayli-Dagi Mts.	AJ412733
<i>Allium/Costulatae</i>	<i>Allium/Allium</i>	<i>A. filidens</i> Regel	16	3674	KAZAKHSTAN: W foothills of Karatau Range	AJ412723
<i>Allium/Costulatae</i>	<i>Allium/Allium</i>	<i>A. filidentiforme</i> Vved. ex Kasht. et Nikitin	16	2573	TAJKISTAN: Turkestan Range, Shakhris- tan Pass	AJ412722
<i>Allium/Crystallina</i>	<i>Allium/Allium</i>	<i>A. crystallinum</i> Vved.		3662	UZBEKISTAN: SW Hissar Range, Derbent	AJ412724
<i>Allium/Kopetdagia</i>	<i>Allium/Scorodon</i>	<i>A. erenoprasum</i> Vved.	16	5243	UZBEKISTAN: Aktau Mts.	AJ412726
<i>Allium/Kopetdagia</i>	<i>Allium/Scorodon</i>	<i>A. kopetdagense</i> Vved.	16	5802	TURKMENISTAN: Kopetdag Mts.	AJ411950
<i>Allium/Minuta</i>	<i>Allium/Scorodon</i>	<i>A. parvulum</i> Vved.		5055	KIRGIZSTAN: Talas-Alatau Range, Talas	AJ412720
<i>Allium/Pallasia</i>	<i>Allium/Scorodon</i>	<i>A. schoenoprasoides</i> Regel	16	2903	KAZAKHSTAN: Trans-Ili Range, Valley Almaatinka	AJ412728
<i>Allium/Pallasia</i>	<i>Allium/Scorodon</i>	<i>A. tanguticum</i> Regel	16	3779	CHINA: Tibet	AJ411893
<i>Polyprason/Scorodon</i>	<i>Allium/Scorodon</i> s.s.	<i>A. moschatum</i> L.	16	H654	GEORGIA: Tbilissi (GAT)	AJ411872

Table 1. Continued.

New classification Subgenus/Section	Traditional classification Subgenus/Section	Species	2n	TAX	Origin	EMBL
<i>Polyprason/Scorodon</i>	<i>Allium/Scorodon</i>	<i>A. inaequale</i> Janka		5752	S RUSSIA: Krasnodar, W Caucasus	AJ412735
<i>Polyprason/Scorodon</i>	<i>Allium/Scorodon</i>	<i>A. pamiricum</i> Wendelbo		H657	PAKISTAN: Karakorum (GAT)	AJ412736
<i>Allium/?</i> (perhaps a new section)	<i>Allium/Scorodon</i> s.l.	<i>A. macrostemon</i> Bunge	16	2369	MONGOLIA: Somon Matad	AJ412738
<i>Vvedenskya/Vvedenskya</i>	<i>Allium/Vvedenskya</i>	<i>A. kujukense</i> Vved.	20	3625	KAZAKHSTAN: Karatau Range, Pass Kuyuk	AJ411947
<i>Amerallium</i>	<i>Amerallium</i>					
<i>Amerallium/Amerallium</i>	<i>Amerallium/Amerallium</i>	<i>A. drummondii</i> Regel	14	0200	SWEDEN: BG Uppsala	AJ411908
<i>Amerallium/Arctoprasum</i>	<i>Amerallium/Arctoprasum</i>	<i>A. ursinum</i> L.	14	1350	GERMANY: Thuringia, Keula	AJ412744
<i>Amerallium/Briseis</i>	<i>Amerallium/Briseis</i>	<i>A. paradoxum</i> (M. Bieb.) G. Don	16	1657	GERMANY: BG Leipzig	AJ412741
<i>Amerallium/Briseis</i>	<i>Amerallium/Briseis</i>	<i>A. triquetrum</i> L.	16	3269	N TUNESIA: Tell-Atlas Range	AJ412742
<i>Amerallium/Bromatorrhiza</i>	<i>Bromatorrhizal/Bromatorrhiza</i>	<i>A. hookeri</i> Thwaites	22	2013	CHINA: Prov. Yunnan, Kunming, house garden	AJ250297
<i>Amerallium/Bromatorrhiza</i>	<i>Bromatorrhizal/Bromatorrhiza</i>	<i>A. wallichii</i> Kunth	14	2441	GERMANY: Gesellschaft der Staudenfreunde	AJ250294
<i>Amerallium/Caulorhizideum</i>	<i>Amerallium/Caulorhizideum</i>	<i>A. brevistylum</i> S. Watson	14	2811	SWEDEN: BG Göteborg [USA: Utah]	AJ412763
<i>Amerallium/Caulorhizideum</i>	<i>Amerallium/Caulorhizideum</i>	<i>A. goodingii</i> Ownbey	14	3471	USA: Pepperell, M. McDonough [Arizona]	AJ411930
<i>Amerallium/Lophioprason</i>	<i>Amerallium/Lophioprason</i>	<i>A. cernuum</i> Roth	14	0682	GERMANY: 'Wyoming Pink', Gesellschaft der Staudenfreunde	AJ250289
<i>Microscordum/Microscordum</i>	<i>Amerallium/Microscordum</i>	<i>A. monanthum</i> Maxim.	32	5617	RUSSIA: Far East, Khabarovsk, Ussuri lowland	AJ411943
		<i>A. monanthum</i> Maxim.	32	5618	RUSSIA: Far East, Vladivostok	AJ412745
<i>Amerallium/Molium</i>	<i>Amerallium/Molium</i>	<i>A. moly</i> L.	14	1117	GERMANY: Gatersleben, house garden	AJ412743
<i>Amerallium/Molium</i>	<i>Amerallium/Molium</i>	<i>A. subhirsutum</i> L.	14	0023	ITALY: BG Palermo [Adiacenze di Petralia]	AJ411912
<i>Amerallium/Narkissoprason</i>	<i>Amerallium/Narkissoprason</i>	<i>A. insubricum</i> Boiss. et Reut.	14	0230	GERMANY: BG Marburg	AJ250291
<i>Nectaroscordum/Nectaroscordum</i>	<i>Nectaroscordum</i>	<i>A. bulgaricum</i> (Janka) Prodan	18	3220	UK: Wokingham, R. Dadd	AJ412747
<i>Nectaroscordum/Nectaroscordum</i>	<i>Nectaroscordum</i>	<i>A. siculum</i> Ucria	18	2192	BULGARIA: Distr. Burgas, Nos Emine	AJ250299
<i>Amerallium/Rhopetoprasum</i>	<i>Amerallium/Rhopetoprasum</i>	<i>A. fimbriatum</i> S. Watson var. <i>purdyi</i> Eastw.		3487	USA: D. McNeal, Stockton [California, Lake Co.]	AJ411932
<i>Amerallium/Rhopetoprasum</i>	<i>Amerallium/Rhopetoprasum</i>	<i>A. glandulosum</i> Link. et Otto	28	3045	FRANCE: Montpellier, C.M. Messiaen	AJ412746
<i>Caloscordum/Caloscordum</i>	<i>Caloscordum/Caloscordum</i>	<i>A. neriniflorum</i> (Herb.) Baker	16	2379	EAST MONGOLIA: Somon Chalchgol	AJ411913
		<i>A. neriniflorum</i> (Herb.) Baker	16	2797	RUSSIA: BG Novosibirsk [Dauria, Onon River]	AJ411916
<i>Melanocrommyum</i>	<i>Melanocrommyum</i>					
<i>Melanocrommyum/Acmopetala</i>	<i>Melanocrommyum/Acmopetala</i>	<i>A. backhousianum</i> Regel	16	1502	TAJIKISTAN: BG Khorog	AJ411964
<i>Melanocrommyum/Acmopetala</i>	<i>Melanocrommyum/Acmopetala</i>	<i>A. suworowii</i> Regel	16	3652	KAZAKHSTAN: Chu-Ili Mts., Georgievka	AJ411934
<i>Melanocrommyum/Aroidea</i>	<i>Melanocrommyum/Thaumasio-prason</i>	<i>A. aroides</i> Popov et Vved.	16	2517	UZBEKISTAN: BG Tashkent	AJ411915
<i>Melanocrommyum/Brevicaule</i>	<i>Melanocrommyum/Miniprasum</i>	<i>A. sergii</i> Vved.	16	3680	KAZAKHSTAN: Karatau Range, Valley Ikonzu	AJ411936
<i>Melanocrommyum/Compactoprasum</i>	<i>Melanocrommyum/Compactoprasum</i>	<i>A. komarowii</i> Lipsky	16	3133	TAJIKISTAN: Saravshan Range, Lake Iskanderkul	AJ411967
<i>Melanocrommyum/Kaloprasum</i>	<i>Melanocrommyum/Kaloprasum</i>	<i>A. cristophii</i> Trautv.	16	1920	UK: BG Manchester	AJ411966
<i>Melanocrommyum/Megaloprasum</i>	<i>Melanocrommyum/Megaloprasum</i>	<i>A. sarawschanicum</i> Regel	16	3673	UZBEKISTAN: Zaravshan Range, Pass Takhta-Karachi	AJ411935

Table 1. Continued.

New classification Subgenus/Section	Traditional classification Subgenus/Section	Species	2n	TAX	Origin	EMBL
<i>Melanocrommyum/Megaloprason</i>	<i>Melanocrommyum/Megaloprason</i>	<i>A. stipitatum</i> Regel	16	2257	TAJIKISTAN: Hissar Range, Romit Reservation	AJ411911
<i>Melanocrommyum/Melanocrommyum</i>	<i>Melanocrommyum/Melanocrommyum</i>	<i>A. nigrum</i> L.	16	1650	GERMANY: BG Leipzig	AJ411965
<i>Melanocrommyum/Melanocrommyum</i>	<i>Melanocrommyum/Melanocrommyum</i>	<i>A. noëanum</i> Reut. ex Regel	16	3940	IRAN: Prov. Azerbaijan, Miyaneh	AJ411970
<i>Melanocrommyum/Miniprason</i>	<i>Melanocrommyum/Miniprason</i>	<i>A. karataviense</i> Regel	18	2989	UZBEKISTAN: Chatkal Range, Chilchenboa Mts.	AJ411922
<i>Melanocrommyum/Popovia</i>	<i>Melanocrommyum/Melanocrommyum</i>	<i>A. gypsaceum</i> Popov et Vved.	16	3661	UZBEKISTAN: SW Hissar Range, Dekhkanabad	AJ411969
<i>Porphyroprason/Porphyroprason</i>	<i>Melanocrommyum/Porphyroprason</i>	<i>A. oreophilum</i> C. A. Mey.	16	0348	AUSTRIA: BG Graz	AJ411931
<i>Melanocrommyum/Pseudoprason</i>	<i>Melanocrommyum/Pseudoprason</i>	<i>A. cardiostemon</i> Fisch. et C. A. Mey.	16	3947	NW IRAN: Lake Orumiye, Ghushch	AJ411971
<i>Melanocrommyum/Regeloprason</i>	<i>Melanocrommyum/Regeloprason</i>	<i>A. regelii</i> Trautv.	16	5255	TURKMENISTAN: Central Kopetdag, Gyaurs	AJ411972
<i>Melanocrommyum/Verticillata</i>	<i>Melanocrommyum/Verticillata</i>	<i>A. verticillatum</i> Regel	16	2182	TAJIKISTAN: Gazimajlik Range, Ganjino	AJ411910
<i>Anguinum/Anguinum</i>	<i>Rhizirideum/Anguinum</i>	<i>A. microdictyon</i> Prokh.	16	1300	RUSSIA: BG Kirovsk [Altai]	AJ411859
<i>Anguinum/Anguinum</i>	<i>Rhizirideum/Anguinum</i>	<i>A. ovalifolium</i> Hand.-Mazz.	16	5092	CHINA: Prov. Quinghai, Beisha National Park	AJ411882
<i>Anguinum/Anguinum</i>	<i>Rhizirideum/Anguinum</i>	<i>A. tricocum</i> Sol.	16	2582	USA: Glencoe, J. F. Swenson	AJ411917
<i>Anguinum/Anguinum</i>	<i>Rhizirideum/Anguinum</i>	<i>A. victoralis</i> L.	16	2673	GEORGIA: Caucasus	AJ411919
<i>Cepal/Annuloprason</i>	<i>Rhizirideum/Annuloprason</i>	<i>A. atosanguineum</i> Kar. et Kir.	16	2912	KAZAKHSTAN: Trans-Ili Range, Valley Almaatinka	AJ411864
<i>Cepal/Annuloprason</i>	<i>Rhizirideum/Annuloprason</i>	<i>A. fedschenkoanum</i> Regel	16	2560	TAJIKISTAN: Turkestan Range, Kusavlisai	AJ411916
<i>Cepal/Annuloprason</i>	<i>Rhizirideum/Annuloprason</i>	<i>A. fedschenkoanum</i> Regel	16	H618	KIRGYZSTAN: Alai Mts. (GAT)	AJ411894
<i>Cepal/Annuloprason</i>	<i>Rhizirideum/Annuloprason</i>	<i>A. monadelphum</i> Turcz. ex Kar. et Kir.	16	H643	RUSSIA: East Siberia, Chentei (NSK)	AJ411955
<i>Cepal/Annuloprason</i>	<i>Rhizirideum/Annuloprason</i>	<i>A. semenowii</i> Regel		H628	KIRGIZSTAN: Centr. Than-Schan (TASH)	AJ411897
<i>Cepal/Annuloprason</i>	<i>Rhizirideum/Annuloprason</i>	<i>A. weschniakowii</i> Regel		H641	KIRGIZSTAN: Issyk-kul (TASH)	AJ411946
<i>Butomissa/Butomissa</i>	<i>Rhizirideum/Butomissa</i>	<i>A. ramosum</i> L.	32	2735	KAZAKHSTAN: BG Alma-Ata	AJ250295
<i>Butomissa/Butomissa</i>	<i>Rhizirideum/Butomissa</i>	<i>A. ramosum</i> L.	32	2755	RUSSIA: Buryatia, Lake Gusinoe	AJ250293
<i>Butomissa/Butomissa</i>	<i>Rhizirideum/Butomissa</i>	<i>A. tuberosum</i> Rottl. ex Spreng.	32	2454	INDIA: Kashmir, Ladakh	AJ411914
<i>Rhizirideum/Caespitosoprason</i>	<i>Rhizirideum/Caespitosoprason</i>	<i>A. bidentatum</i> Fisch. ex Prokhorov	32	2365	MONGOLIA: Somon Erdenetsagan	AJ411861
<i>Rhizirideum/Caespitosoprason</i>	<i>Rhizirideum/Caespitosoprason</i>	<i>A. bidentatum</i> Fisch. ex Prokhorov	32	3163	RUSSIA: Altai Mts., Czemal	AJ311868
<i>Rhizirideum/Caespitosoprason</i>	<i>Rhizirideum/Caespitosoprason</i>	<i>A. dentigerum</i> Prokhorov	16	5091	CHINA: Prov. Quinghai, Xining	AJ411958
<i>Rhizirideum/Caespitosoprason</i>	<i>Rhizirideum/Caespitosoprason</i>	<i>A. mongolicum</i> Regel	16	2373	MONGOLIA: Tamsarbulag	AJ411883
<i>Rhizirideum/Caespitosoprason</i>	<i>Rhizirideum/Caespitosoprason</i>	<i>A. polyrrhizum</i> Turcz. ex Regel	32	2359	MONGOLIA: Aimak centre Baruun urt, Talbulagu	AJ250296
<i>Rhizirideum/Caespitosoprason</i>	<i>Rhizirideum/Caespitosoprason</i>	<i>A. subangulatum</i> Regel		H604	MONGOLIA: Gobi Altai Mts. (GAT)	AJ411870
<i>Reticulotubulbosal/Campanulata</i>	<i>Rhizirideum/Campanulata</i>	<i>A. drepanophyllum</i> Vved.	16	2791	UZBEKISTAN: Chatkal Range, Bashkysylsai	AJ411854
<i>Reticulotubulbosal/Campanulata</i>	<i>Rhizirideum/Campanulata</i>	<i>A. jodanthum</i> Vved.	16	1330	TAJIKISTAN: Hissar Range, Kondara Valley	AJ411902
<i>Reticulotubulbosal/Campanulata</i>	<i>Rhizirideum/Campanulata</i>	<i>A. minorensis</i> ined.		H679	KIRGIZSTAN: Talas Alatau Range (GAT)	AJ412748
<i>Reticulotubulbosal/Campanulata</i>	<i>Rhizirideum/Campanulata</i>	<i>A. sordidiflorum</i> Vved.		H630	TAJIKISTAN: Sanglok Mts. (TASH)	AJ411899

Table 1. Continued.

New classification Subgenus/Section	Traditional classification Subgenus/Section	Species	2n	TAX	Origin	EMBL
<i>Reticulotubulosa/Campanulata</i>	<i>Rhizirideum/Campanulata</i>	<i>A. tenuicaule</i> Regel		H632	TAJIKISTAN: Hissar Range (TASH)	AJ411887
<i>Reticulotubulosa/Campanulata</i>	<i>Rhizirideum/Campanulata</i>	<i>A. teretifolium</i> Regel		H633	KAZAKHSTAN: Dzhungar Alatau Range (TASH)	AJ411886
<i>Reticulotubulosa/Campanulata</i>	<i>Rhizirideum/Campanulata</i>	<i>A. xiphopetalum</i> Aitch. et Baker	16	1070	SWEDEN: BG Göteborg	AJ411858
<i>Cepal/Cepa</i>	<i>Rhizirideum/Cepa</i>	<i>A. altaicum</i> Pall.	16	0339	LITHUANIA: BG Kaunas	AJ411928
		<i>A. altaicum</i> Pall.	16	2760	RUSSIA: Sayan Mts, Tuva, Erzin	AJ412749
		<i>A. altaicum</i> Pall.	16	5561	RUSSIA: Altai Mts., Yuzhno-Chuisky Range	AJ412750
<i>Cepal/Cepa</i>	<i>Rhizirideum/Cepa</i>	<i>A. asarense</i> R. M. Fritsch et Martin	16	3900	IRAN: Elburz Range, Karaj Valley, Asara	AJ411937
<i>Cepal/Cepa</i>	<i>Rhizirideum/Cepa</i>	<i>A. cepa</i> L.	16	4878	GERMANY: 'Stuttgarter Riesen'	AJ411944
<i>Cepal/Cepa</i>	<i>Rhizirideum/Cepa</i>	<i>A. cepa</i> aggregatum cultivar group	16	1810	USA: Glencoe, J. F. Swenson	AJ411906
<i>Cepal/Cepa</i>	<i>Rhizirideum/Cepa</i>	<i>A. fistulosum</i> L.	16	41388	JAPAN: 'Long White Tokyo'	AJ411918
<i>Cepal/Cepa</i>	<i>Rhizirideum/Cepa</i>	<i>A. galanthum</i> Kar. et Kir.	16	1729	KAZAKHSTAN: BG Alma-Ata	AJ411905
<i>Cepal/Cepa</i>	<i>Rhizirideum/Cepa</i>	<i>A. oschaninii</i> B. Fedtsch.	16	5016	KIRGIZSTAN: Turkestan Range, Dargun	AJ411940
<i>Cepal/Cepa</i>	<i>Rhizirideum/Cepa</i>	<i>A. praemixtum</i> Vved.	16	5712	TAJIKISTAN: Mogoltau Range, Spa massif	AJ411873
<i>Cepal/Cepa</i>	<i>Rhizirideum/Cepa</i>	<i>A. pskemense</i> B. Fedtsch.	16	1994	DENMARK: BG Copenhagen	AJ411907
<i>Cepal/Cepa</i>	<i>Rhizirideum/Cepa</i>	<i>A. vavilovii</i> Popov et Vved.	16	5238	TURKMENISTAN: C. Kopetdag Range, Chuli	AJ411839
<i>Cepal/Cepa</i>	<i>Rhizirideum/Cepa</i>	<i>A. vavilovii</i> Popov et Vved.	16	5239	TURKMENISTAN: C. Kopetdag Range, Chuli	AJ411840
<i>Cyathophoral/Coleoblastus</i>	<i>Bromatorrhizal/Coleoblastus</i>	<i>A. mairei</i> Levl.	16	2104	SWITZERLAND: BG Zurich	AJ250298
<i>Cyathophoral/Cyathophora</i>	<i>Bromatorrhizal/Cyathophora</i>	<i>A. cyathophorum</i> Bur. et Franch.	16	2824	NORWAY: BG Oslo	AJ250286
		<i>A. cyathophorum</i> Bur. et Franch.	16	2825	NORWAY: BG Oslo	AJ411889
<i>Cyathophoral/Milula</i>	<i>Milula</i>	<i>A. spicatum</i> (Prain) N. Friesen	16	H680	CHINA: Tibet, Tsangpo Valley (OSBU)	AJ250285
		<i>A. spicatum</i> (Prain) N. Friesen	16	H682	CHINA: Tibet, Upper Cuamda Chu (OSBU)	AJ250284
<i>Polyprason/Falcatifolia</i>	<i>Rhizirideum/Oreiprason</i>	<i>A. carolinianum</i> DC.	16	2570	TAJIKISTAN: Hissar Range, Anzob Pass	AJ250290
<i>Cepal/Condensatum</i>	<i>Rhizirideum/Oreiprason</i>	<i>A. condensatum</i> Turcz.	16	5619	RUSSIA: Far East, Khabarovsk, Ussuri lowland	AJ412752
		<i>A. condensatum</i> Turcz.	16	H663	EAST MONGOLIA: (GAT)	AJ412752
<i>Polyprason/Daghestanica</i>	<i>Rhizirideum/Oreiprason</i>	<i>A. daghestanicum</i> Grossh.	16	1741	GEORGIA: BG Bakuriani, [Daghestan]	AJ411850
<i>Polyprason/Daghestanica</i>	<i>Rhizirideum/Oreiprason</i>	<i>A. ericetorum</i> Thore	16	1547	GERMANY: BG Leipzig	AJ311867
<i>Polyprason/Daghestanica</i>	<i>Rhizirideum/Oreiprason</i>	<i>A. gunibicum</i> Miscz. ex Grossh.	16	2333	GEORGIA: Caucasus, Chevsuretia, Dusheti	AJ411890
<i>Butomissa/Austromontana</i>	<i>Rhizirideum/Oreiprason</i>	<i>A. gilgiticum</i> Wang et Tang		H600	PAKISTAN: Karakorum Range (GAT)	AJ411942
<i>Polyprason/Falcatifolia</i>	<i>Rhizirideum/Oreiprason</i>	<i>A. hymenorrhizum</i> Ledeb.	16	3135	TAJIKISTAN: Saravshan Range, Lake Iskanderkul	AJ411879
<i>Polyprason/Oreiprason</i>	<i>Rhizirideum/Oreiprason</i>	<i>A. kaschianum</i> Regel	16	2418	TAJIKISTAN: BG Chorog [Pamir, Shakh-darya Mts.]	AJ412754
<i>Polyprason/Oreiprason</i>	<i>Rhizirideum/Oreiprason</i>	<i>A. kurssanovii</i> Popov	16	1612	KAZAKHSTAN: Trans-Ili Range, Medeo	
<i>Rhizirideum/Oreiprason</i>	<i>Rhizirideum/Oreiprason</i>	<i>A. ochroleucum</i> Waldst. et Kit.	16	3763	SLOVENIA: Steiner Alps	AJ411856
		<i>A. ochroleucum</i> Waldst. et Kit.	16	5578	SLOVENIA: BG Ljubljana [Julijske Alps]	AJ412755
<i>Polyprason/Daghestanica</i>	<i>Rhizirideum/Oreiprason</i>	<i>A. ochroleucum</i> subsp. <i>pseudosuaveolens</i> Zahar.	16	2827	ROMANIA: BG Cluj-Napoca	AJ411863
<i>Polyprason/Oreiprason</i>	<i>Rhizirideum/Oreiprason</i>	<i>A. petraeum</i> Kar. et Kir.	16	3040	KAZAKHSTAN: Chu-Ili Mts., Pass Kurdai	AJ411952

Table 1. Continued.

New classification Subgenus/Section	Traditional classification Subgenus/Section	Species	2n	TAX	Origin	EMBL
<i>Polyprason/Falcatifolia</i>	<i>Rhizirideum/Oreiprason</i>	<i>A. platyspathum</i> Schrenk	16	2905	KAZAKHSTAN: Trans-Ili Range, Valley Almaatinka	AJ411878
<i>Polyprason/Falcatifolia</i>	<i>Rhizirideum/Oreiprason</i>	<i>A. platyspathum</i> subsp. <i>ambly- ophyllum</i> (Kar. et Kir.) N. Friesen	16	2396	RUSSIA: BG Novosibirsk	AJ411875
<i>Polyprason/Oreiprason</i>	<i>Rhizirideum/Oreiprason</i>	<i>A. roylei</i> Stearn	16	5152	CZECH REPUBLIK: Olomouc	AJ411945
<i>Polyprason/Oreiprason</i>	<i>Rhizirideum/Oreiprason</i>	<i>A. setifolium</i> Schrenk		H629	UZBEKISTAN: (GAT)	AJ411898
<i>Polyprason/Daghestanica</i>	<i>Rhizirideum/Oreiprason</i>	<i>A. suaveolens</i> Jacq.	16	1603	ITALY: BG Padua	AJ411874
<i>Polyprason/Oreiprason</i>	<i>Rhizirideum/Oreiprason</i>	<i>A. talassicum</i> Regel	16	3376	CHINA: Prov. Xingiang	AJ411865
<i>Polyprason/Oreiprason</i>	<i>Rhizirideum/Petroprason</i>	<i>A. obliquum</i> L.	16	3158	RUSSIA: Altai Mts., Lake Teletskoe	AJ412753
<i>Reticulatobulbosa/Sikkimensia</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. beesianum</i> W. W. Sm.	32	2211	DENMARK: BG Copenhagen,	AJ411860
<i>Reticulatobulbosa/Reticulato- bulbosa</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. chamarense</i> M. Ivanova	16	H645	MONGOLIA: Chentei (GAT)	AJ411957
<i>Reticulatobulbosa/Reticulato- bulbosa</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. clathratum</i> Ledeb.	32	3165	RUSSIA: Altai Mts., Chernal	AJ411855
<i>Reticulatobulbosa/Sikkimensia</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. cyaneum</i> Regel	32	3872	GERMANY: BG Tuebingen	AJ411880
<i>Reticulatobulbosa/Nigrimontana</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. drobovii</i> Vved.		H622	UZBEKISTAN: Ugamskij Chr. (TASH)	AJ411895
<i>Rhizirideum/Eduardia</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. eduardii</i> Stearn	16	2761	RUSSIA: Sayan Range, Tuva, Erzin	AJ411959
		<i>A. eduardii</i> Stearn	16	2745	RUSSIA: Sayan Range, Tuva, Erzin	AJ412756
<i>Reticulatobulbosa/Reticulato- bulbosa</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. flavidum</i> Ledeb.	16	H644	RUSSIA: Altai (GAT)	AJ411956
<i>Cyathophora/Coleoblastus</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. kingdonii</i> Stearn		H691	CHINA: Tibet (OSBU)	AJ250298
<i>Reticulatobulbosa/Reticulato- bulbosa</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. kuramense</i> F. O. Khassanov et N. Friesen	16	5703	UZBEKISTAN: Chatkal Range, Kuram Mts., Chorkesar	AJ411868
<i>Reticulatobulbosa/Reticulato- bulbosa</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. leucocephalum</i> Turcz.	16	H660	RUSSIA: Burjatia, Dzhida (NSK)	AJ412757
<i>Reticulatobulbosa/Reticulato- bulbosa</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. lineare</i> L.	16	5816	N KAZAKHSTAN: vil. Kievskoe	AJ411951
		<i>A. lineare</i> L.	16	H624	KAZAKHSTAN: (GAT)	AJ411951
<i>Reticulatobulbosa/Reticulato- bulbosa</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. malyshevii</i> N. Friesen	16	H653	RUSSIA: Tuva, Sengilen (GAT)	AJ412758
<i>Rhizirideum/Reticulatobulbosa</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. montibaicalense</i> N. Friesen	16	3390	RUSSIA: Buryatia, NW Baikal, Muzhinai	AJ411838
		<i>A. montibaicalense</i> N. Friesen	16	H603	RUSSIA: North Baikal (GAT)	AJ411871
<i>Reticulatobulbosa/Nigrimontana</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. oreoprasoides</i> Vved.		H627	UZBEKISTAN: West Than-Shan (TASH)	AJ41189
<i>Butomissa/Austromontana</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. oreoprasum</i> Schrenk	16	3643	KAZAKHSTAN: Trans-Ili Range, Turgen Valley	AJ411867
		<i>A. oreoprasum</i> Schrenk	16	5000	KIRGIZSTAN: Talas-Alatau Range, Pass Otmek	AJ411933
<i>Rhizirideum/Caesptosoprasum</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. przewalskianum</i> Regel	32	5089	CHINA: Prov. Quinghai, Lake Koko Nor	AJ411852
<i>Reticulatobulbosa/Reticulato- bulbosa</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. rupestristepposum</i> N. Friesen	16	5737	RUSSIA: Lake Baikal, Goloustnoe	AJ411869
<i>Reticulatobulbosa/Scabri- scapa</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. scabriscapum</i> Boiss.	16	3898	IRAN: Prov. Tehran, Merdabat	AJ411881
<i>Reticulatobulbosa/Sikkimensia</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. sikkimense</i> Baker		H670	CHINA: SE Tibet, Lhasa (GAT)	AJ411885
<i>Reticulatobulbosa/Reticulato- bulbosa</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. splendens</i> Schult. et Schult. f.	48	3384	RUSSIA: Buryatia, NW shore of Lake Bai- kal	AJ411927
<i>Reticulatobulbosa/Reticulato- bulbosa</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. strictum</i> Schrad.	48	5404	RUSSIA: upper Enisey River, Shushenskoe	AJ411951
<i>Reticulatobulbosa/Flavi- scordum</i>	<i>Rhizirideum/Reticulatobulbosa</i>	<i>A. sulphureum</i> Vved.		H648	TAJIKISTAN: Pamiro-Alai, Gasimaylik (LE)	AJ412759

Table 1. Continued.

New classification Subgenus/Section	Traditional classification Subgenus/Section	Species	2n	TAX	Origin	EMBL
<i>Reticulobulbosa/Flaviscordum</i>	<i>Rhizirideum/Reticulobulbosa</i>	<i>A. trachyscordum</i> Vved.	16	3998	KIRGIZSTAN: Talas, Talas-Alatau Range	AJ411857
<i>Reticulobulbosa/Reticulobulbosa</i>	<i>Rhizirideum/Reticulobulbosa</i>	<i>A. ubsicolum</i> Regel	32	2769	RUSSIA: Tuva, Erzin, Sayan Range	AJ411960
<i>Rhizirideum/Rhizirideum</i>	<i>Rhizirideum/Rhizirideum</i>	<i>A. albidum</i> Fisch. ex Bieb.	16	3765	AUSTRIA: BG Graz [Serbia, Deliblatska Pescara]	AJ411841
<i>Rhizirideum/Rhizirideum</i>	<i>Rhizirideum/Rhizirideum</i>	<i>A. albidum</i> Fisch. ex Bieb.	16	1977	GEORGIA: Caucasus Range, Chevsuretia, Mutso	AJ411892
		<i>A. albidum</i> Fisch. ex Bieb.	16	3470	USA: Pepperell, M. McDonough [NE Turkey]	AJ411954
<i>Rhizirideum/Rhizirideum</i>	<i>Rhizirideum/Rhizirideum</i>	<i>A. angulosum</i> L.	16	2778	N KAZAKHSTAN: vil. Kievskoe	AJ250287
<i>Rhizirideum/Rhizirideum</i>	<i>Rhizirideum/Rhizirideum</i>	<i>A. austrosibiricum</i> N. Friesen	16	2747	RUSSIA: Tuva, Ersin, Sayan Range	AJ411832
<i>Rhizirideum/Rhizirideum</i>	<i>Rhizirideum/Rhizirideum</i>	<i>A. flavescens</i> Bess.	16	5736	N KAZAKHSTAN: vil. Kievskoe	AJ411842
<i>Rhizirideum/Rhizirideum</i>	<i>Rhizirideum/Rhizirideum</i>	<i>A. incensiodorum</i> Radić	16	3764	AUSTRIA: BG Graz	AJ411866
<i>Rhizirideum/Rhizirideum</i>	<i>Rhizirideum/Rhizirideum</i>	<i>A. lusitanicum</i> Lam.	32	2927	GERMANY: Harz, Benzingerode	AJ411831
<i>Rhizirideum/Rhizirideum</i>	<i>Rhizirideum/Rhizirideum</i>	<i>A. nutans</i> L.	32	3161	RUSSIA: Gorno-Altai, Altai Mts.	AJ411924
<i>Rhizirideum/Rhizirideum</i>	<i>Rhizirideum/Rhizirideum</i>	<i>A. rubens</i> Schrad.	16	1609	KAZAKHSTAN: Temirtau	AJ411904
		<i>A. rubens</i> Schrad.	16	3401	RUSSIA: Altai Mts., Sailugem	AJ411891
<i>Rhizirideum/Rhizirideum</i>	<i>Rhizirideum/Rhizirideum</i>	<i>A. senescens</i> L.	32	2750	RUSSIA: Buryatia, Lake Gusinoe	AJ411834
<i>Rhizirideum/Rhizirideum</i>	<i>Rhizirideum/Rhizirideum</i>	<i>A. spirale</i> Willd.	32	1968	NORTH KOREA: BG Wonsan [Prov. S-Hwanghe]	AJ411833
<i>Rhizirideum/Rhizirideum</i>	<i>Rhizirideum/Rhizirideum</i>	<i>A. stellerianum</i> Willd.	32	5738	RUSSIA: Muchor, Lake Baikal	AJ411963
<i>Rhizirideum/Rhizirideum</i>	<i>Rhizirideum/Rhizirideum</i>	<i>A. togashii</i> Hara	16	5221	USA: Pepperell, M. McDonough	AJ411843
<i>Rhizirideum/Rhizirideum</i>	<i>Rhizirideum/Rhizirideum</i>	<i>A. tuvinicum</i> (N. Friesen) N. Friesen	16	2744	RUSSIA: Tuva, Erzin, Sayan Range	AJ411853
<i>Cepal/Sacculiferum</i>	<i>Rhizirideum/Sacculiferum</i>	<i>A. chinense</i> G. Don	24	2015	CHINA: Prov. Yunnan, Kunming, market	AJ411848
		<i>A. chinense</i> G. Don	32	3407	JAPAN: Fukui, local strain	AJ411948
<i>Cepal/Sacculiferum</i>	<i>Rhizirideum/Sacculiferum</i>	<i>A. komarovianum</i> Vved.		H646	RUSSIA: Far East (LE)	AJ412760
<i>Cepal/Sacculiferum</i>	<i>Rhizirideum/Sacculiferum</i>	<i>A. thunbergii</i> G. Don	16	1963	NORTH KOREA: BG Wonsan [Kumgangsan Range, Prov. Kanwon]	AJ411849
<i>Cepal/Schoenoprasum</i>	<i>Rhizirideum/Schoenoprasum</i>	<i>A. altynolicum</i> N. Friesen	32	0433	GERMANY: Quedlinburg, breeder's strain	AJ411939
<i>Cepal/Schoenoprasum</i>	<i>Rhizirideum/Schoenoprasum</i>	<i>A. karelinii</i> Poljak.	16	2592	JAPAN: Tsukuba Research Station	AJ411876
<i>Cepal/Schoenoprasum</i>	<i>Rhizirideum/Schoenoprasum</i>	<i>A. ledebourianum</i> Schult. et Schult. f.	16	3170	RUSSIA: Altai Mts., Cholzun	AJ411925
<i>Cepal/Schoenoprasum</i>	<i>Rhizirideum/Schoenoprasum</i>	<i>A. maximowiczii</i> Regel	16	2772	RUSSIA: Buryatia, Romanovka	AJ411877
<i>Cepal/Schoenoprasum</i>	<i>Rhizirideum/Schoenoprasum</i>	<i>A. oliganthum</i> Kar. et Kir.	16	3201	KAZAKHSTAN: Lake Zajsan	AJ411835
<i>Cepal/Schoenoprasum</i>	<i>Rhizirideum/Schoenoprasum</i>	<i>A. schmitzii</i> Coutinho	16	5226	USA: Pepperell, M. McDonough	AJ412761
<i>Cepal/Schoenoprasum</i>	<i>Rhizirideum/Schoenoprasum</i>	<i>A. schoenoprasum</i> subsp. <i>latiorifolium</i> (Pau) R. Martinez et al.	32	5432	SPAIN: Sierra de Guadarrama, Mt. Penarala	AJ411837
<i>Cepal/Schoenoprasum</i>	<i>Rhizirideum/Schoenoprasum</i>	<i>A. schoenoprasum</i> L.	16	3446	RUSSIA: Far East, Peninsula Chukotka	AJ411836
		<i>A. schoenoprasum</i> L.	16	4214	GERMANY: 'Mittelgrober'	AJ411938
<i>Rhizirideum/Tenuissima</i>	<i>Rhizirideum/Tenuissima</i>	<i>A. anisopodium</i> Ledeb.	16	2349	MONGOLIA: Aimak Chentij, Zargalanchan	AJ411847
<i>Rhizirideum/Tenuissima</i>	<i>Rhizirideum/Tenuissima</i>	<i>A. tenuissimum</i> L.	16	3249	NORTH KOREA: BG Pyongyang	AJ411846
<i>Rhizirideum/Tenuissima</i>	<i>Rhizirideum/Tenuissima</i>	<i>A. vodopjanovae</i> N. Friesen	16	5402	RUSSIA: W Sayan Range, Khakasia	AJ411942
		<i>A. vodopjanovae</i> N. Friesen	16	3192	RUSSIA: Altai Mts., Ust-Koksa, Kyrlyk	AJ411845
<i>Ipheion</i>	<i>Ipheion</i>	<i>I. uniflorum</i> (Graham) Raf.	12	3458	NETHERLAND: BG Amsterdam	AJ250288
<i>Tulbaghia</i>	<i>Tulbaghia</i>	<i>T. simmleri</i> Beauv. (= <i>T. fragrans</i> Verdoorn)	12	2165	UK: London, Chelsea Physic Garden	AJ250300
<i>Nothoscordum</i>	<i>Nothoscordum</i>	<i>N. bivalve</i> (L.) Britton	18	2621	UK: Wellesbourne, HIS	AJ250300
		<i>N. gracile</i> (Ait.) Stearn	18	0494	SWEDEN: BG Göteborg	AJ250301
<i>Dichelostemma</i>	<i>Dichelostemma</i>	<i>D. multiflorum</i> (Benth.) Heller		2471	USA: California, BG Berkeley [Shasta Co.]	AJ412714

vers. 3.06 (Posada and Crandall 1998) and TrN + Γ distances were calculated, which were analyzed with the neighbor-joining algorithm (NJ). Two parsimony analysis (MP) algorithms were used: Fitch parsimony and generalized parsimony, weighting transversions vs. transitions 2:1 (Swoford et al. 1996). We conducted heuristic searches with simple and with 100 random addition sequences and tree bisection reconnection (TBR) branch swapping. For Bayesian inference six chains were run for 1 million generations under a GTR + Γ model of sequence evolution, sampling a tree every 100 generations. The first 2001 (nonstationary) trees were discarded and 8000 trees were used for the calculation of posterior probabilities. To allow the calculation of statistical support of the clades with MP a reduced data set was used, including only representative accession from each group found in the strict consensus tree of the first analysis. Thus, 100 accessions were included, which resulted in the same relative tree topology as in the analyses of the entire data set. Support was tested with BI and bootstrap analyses (Felsenstein 1985), involving 1000 bootstrap resamples in neighbor-joining analysis and 200 resamples in parsimony analysis. Decay indices (Bremer 1988) were also calculated for this data set. *Dichelostemma multiflorum* was in all analyses defined as outgroup taxon.

RESULTS

ITS Sequences

Within the 195 *Allium* species the lengths of the ITS region ranged from 612 base pairs (bp) in *A. cyathophorum* to 661 bp in *A. triquetrum*, though for most sequences the length was 640 ± 10 bp. The outgroup species had relatively longer ITS regions than *Allium*: *Ipheion uniflorum* 658 bp, *Tulbaghia fragrans* 659 bp, *Nothoscordum gracile* 671 bp, *N. bivalve* 672 bp, and *Dichelostemma multiflorum* 675 bp. GC contents of the ITS region were between 42–46% in *Allium*, and between 47–51% in the outgroup genera. Aligning the individual sequences resulted in an alignment of 778 bp length. Of these, 116 characters were constant, 66 variable characters were parsimony uninformative, and 596 were parsimony informative. In ITS-1, 81% of sequence positions were variable, in ITS-2 75%, and even in the 5.8S nrDNA, 23% variable positions could be found. The inclusion of outgroups increased the amount of variable sites only by about 5%. Pairwise genetic distances were between 1% (among species from one section) to 53% between *A. haneltii* (subgen. *Allium*) and *A. bulgaricum* (subgen. *Nectaroscordum*).

Phylogenetic Analyses

Generalized parsimony analysis of the ITS data produced 78,300 equally parsimonious trees (length = 5525 steps, including parsimony uninformative characters, consistency index (CI) 0.2878, retention index (RI) 0.8036, when all 221 accessions were included. The consensus tree was generally congruent with the result of Fitch parsimony and is available from the authors on demand. Analyses of a reduced data set (Fig. 1), comprising 100 representative taxa from all clades found in the initial analyses resulted in 20 MP trees (length = 4110 steps, CI = 0.3348, RI = 0.6940). The strict consensus trees of the parsimony analyses were also congruent

with the results of model-based and phenetic analyses of the respective data sets. Statistical support of the branches from bootstrap (BS) and decay analyses (D), and BI posterior probabilities (PP) were given for the reduced data set in Fig. 1, 2.

Allium is a monophyletic group, clearly separated from the outgroup species (100% BS and PP, $d > 10$). Two major clades were found within *Allium*, comprising subgen. *Nectaroscordum* ($x = 9$), *Amerallium* ($x = 7$) together with sect. *Microscordum* ($x = 8$, *A. monanthum*) (Fig. 1: node 1) on one side and all other *Allium* taxa on the other side (all $x = 8$). This latter group is divided in two sister clades, subgen. *Caloscordum*, *Melanocrommyum* and sect. *Anguinum* (Fig. 1: node 2) and subgen. *Allium* and *Rhizirideum* (Fig. 1: node 3). The species of former subgen. *Bromatorrhiza* occur at two different positions in the tree: sect. *Bromatorrhiza* (*A. wallichii* and *A. hookeri*, $x = 7$) are clearly placed in subgen. *Amerallium* and species of sects. *Coleoblastus* (*A. kingdonii* and *A. mairei*, $x = 8$) and *Cyathophora* (*A. cyathophorum*, $x = 8$) fall in the large clade comprising *Rhizirideum* and *Allium*. Subgenera *Rhizirideum* and *Allium* are subdivided in seven monophyletic groups that have different relationships: sect. *Anguinum* is sister group of subgen. *Melanocrommyum*, sect. *Butomissa* (including some species from sect. *Reticulobulbosa*) is sister group to the rest of subgen. *Rhizirideum* and *Allium*, sects. *Cyathophora*, *Coeloblastus*, and *Milula* are sister group to all other sections of subgenera *Rhizirideum* and *Allium*, sects. *Rhizirideum*, *Caespitosoprason*, *Tenuissima*, and *A. eduardii* (sect. *Reticulobulbosa*) are sister group to the remaining sections of subgen. *Rhizirideum* and *Allium*, most species from subgen. *Allium* form a monophyletic clade, excluding the species from sect. *Scorodon* s.s. and *A. turkestanicum*. *Allium kujukense* (sect. *Vvedenskya*) is clearly placed in one clade with subgen. *Melanocrommyum*. The rest of subgen. *Rhizirideum* with sect. *Scorodon* s.s. and *A. turkestanicum* form a clade that consists of well-supported small sections with unresolved interrelationships.

Phylogenetic analysis supported a monophyletic origin of most circumscribed sections in subgen. *Rhizirideum* and *Allium*, with some exceptions. The morphologically variable sects. *Scorodon*, *Reticulobulbosa*, and *Oreiprason* were polyphyletic and some morphologically “difficult” species, such as *A. turkestanicum*, *A. condensatum*, *A. eduardii*, and *A. przewalskianum* showed unexpected relationships outside their former sections.

Species of sect. *Reticulobulbosa* appear in three groups, (i) *Reticulobulbosa* s.s., (ii) a small group of the four species (*A. trachyscordum*, *A. scabriscapum*, *A. sulphureum*, and *A. drobovii*), which are more closely related to sect. *Campanulata*, and (iii) all Chinese-Himalayan species with blue flowers (*A. beesianum*, *A. forrestii*, *A. aciphyllum*, *A. sikkimense*, and *A. cyaneum*), which form an isolated clade with unresolved relationships.

Species of sect. *Oreiprason* are split into four clades: (i) the east Asian species *A. condensatum*, (ii) *A. obliquum*, *A. petraeum*, and *A. talassicum*, (iii) the central Asian group with *A. platyspathum*, *A. filifolium*, *A. carolinianum*, *A. kashchianum*, and *A. hymenorrhizum*, and (iv) the Caucasian–European clade with *A. gunibicum*, *A. ericetorum*, *A. daghestanicum*, *A. ochroleucum*, and *A. suaveolens*.

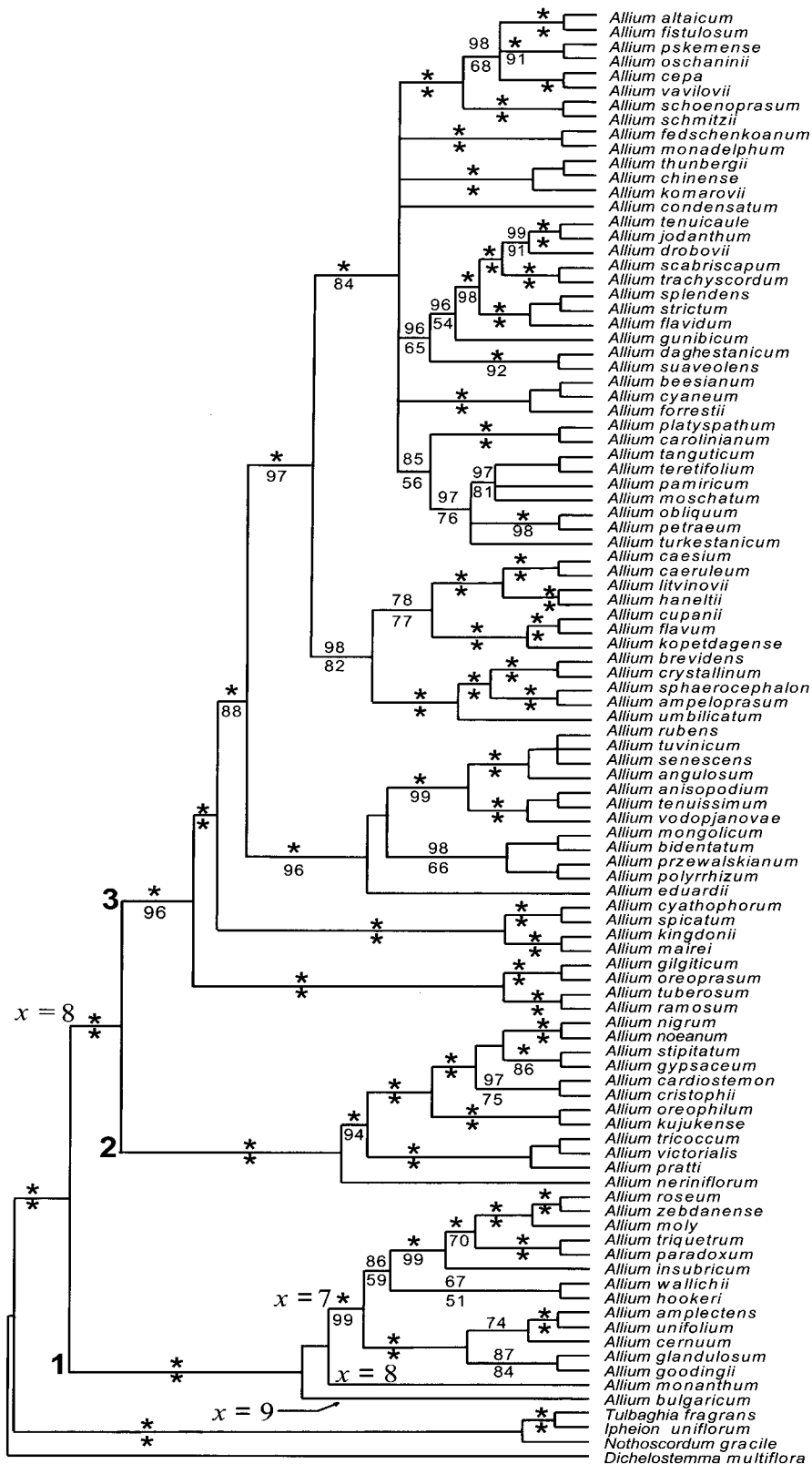


Fig. 1.—Strict consensus tree of 20 most parsimonious trees from the analysis of nrDNA ITS sequences of 100 *Allium* accessions. Bootstrap values (>50%) are given above the branches; BI posterior probabilities are shown below. Values of 100% are depicted by asterisks. The basic chromosome numbers of the *Allium* species are shown above the branches.

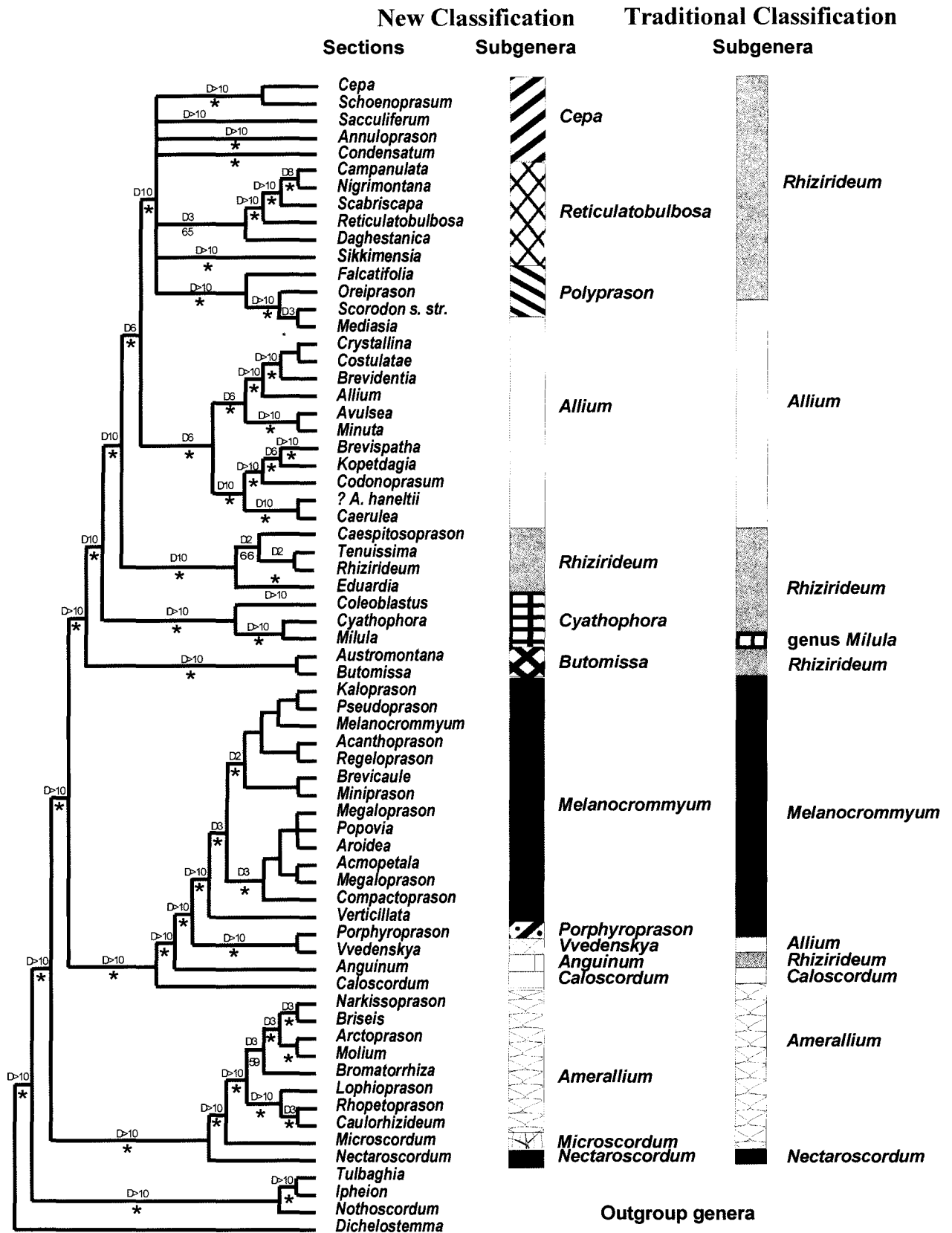


Fig. 2.—Modified consensus tree from Fig. 1 to represent the sects. of *Allium* instead of the species on the tips of the tree. Bootstrap values (>50%) are given below the branches, decay indices above. Bootstrap values higher than 75% are represented by asterisks. The new and old intrageneric classification of the genus is depicted to the right.

Polyploids and Hybrid Taxa

Twenty-eight *Allium* species (14%) included in the analysis were polyploids (see Table 1). In the worst case in terms of phylogenetic analysis, these might be allopolyploids resulting from hybridization events, thus combining different ITS types in the same nucleus. Due to their reticulate structure, hybrid taxa cannot be placed correctly in a dichotomous tree and might even disturb parts in the phylogenetic tree adjacent to the hybrid (Friesen and Blattner 2000). To analyze the influence of polyploid taxa on our phylogenetic reconstruction, we excluded all polyploid species from the analysis. This resulted in only small differences within the terminal clades (i.e., within sections), but did not change the relationships among these clades. The ITS sequences were mostly obtained by direct sequencing of PCR products, resulting in a small number of sequence positions with polymorphic base composition. Only in some species like *A. hookeri* ($2n = 22$) or *A. splendens* ($2n = 48$), where no clear sequences could be obtained via direct sequencing, the PCR fragments were cloned prior to sequencing. In these cases the differences among the cloned sequences from one individual were relatively small and all sequences grouped in the same clade in the phylogenetic tree. As our aim in this study was to define the major groups in *Allium* and not phylogenetic analyses within sections, we left all polyploid taxa in the analysis.

Taxonomic Conclusions and Classification

The molecular results strongly suggest that a natural classification of *Allium* must recognize many more well separated main groups than hitherto were accepted at the subgeneric level. Additionally, several of the traditional sections proved to be artificial. Thus, a modern classification that is in accord with the above given phylogeny must necessarily introduce new groups and new names. In order to insure nomenclatural stability, it seemed most appropriate to use as often as possible already known names although at differing hierarchical levels. Following the nomenclatural rules of the International Code of Botanical Nomenclature (ICBN) (Greuter et al. 2000), we apply some hitherto unused but valid names. The subgenera are listed according to their position in the phylogenetic dendrogram (Fig. 2). A nomenclatural conspectus of the genus *Allium* at sectional level is given as Appendix 1. For representative taxa see Fig. 3–26.

ALLIUM subgen. NECTAROSCORDUM (Lindl.) Asch. et Graebn., Syn. Mitteleur. Fl. 3: 96, 166 (1905).—TYPE: *A. siculum* Ucria (= *N. siculum* (Ucria) Lindl.) (Fig. 3).

Genus *Nectaroscordum* Lindl., *Edwards's Bot. Reg.* 9: t. 1913 (1836); subgen. *Nectaroscordum* (Lindl.) Traub, *Pl. Life (Stanford)* 24: 162 (1968), comb. superfl.; sect. *Nectaroscordum* (Lindl.) Gren. et Godr., *Fl. France* 3: 212 (1855–56).

At least two species belong to this group. The western Mediterranean-type species and the southwest Asian *A. tripedale* Trautv. (Kudrjashova 2003) are certainly distinct taxa, but there is controversy as to whether *A. bulgaricum*, *A. dioscorides* Sibth. et Sm., and *A. meliophilum* Juz. (endemic of the Crimea) might be only eastern Mediterranean variants of the type species or good species.

The joint occurrence of several specific characters was the main argument to regard *Nectaroscordum* as a genus of its own: large and 3–7-veined tepals, the long triangular innermost sheath leaf surrounding the scape, a wider than long ovary, the lower half of which is sunken into the funnel-like widened tip of pedicels, multiovulate locules stretching in a nearly horizontal direction (Stearn 1955, 1978), heavy seeds (thousand kernel weight [TKW] of about 6 g) with three sharp edges, as well as a basic chromosome number of $x = 9$. Especially large and many-lobed nectaries mounding in a wide secretory channel near the tip of the nectary are unique. All these characters imply at least a very long and separate phylogeny. Apparently only some common characters of leaf anatomy (Fritsch 1988) support the close relationship to subgen. *Amerallium* that is shown by molecular analyses.

ALLIUM subgen. **MICROSCORDUM** (Maxim.) N. Friesen, comb. et stat. nov.—TYPE: *A. monanthum* Maxim.

Basionym: *Allium* sect. *Microscordum* Maxim., *Bull. Acad. Imp. Sci. Saint-Petersbourg* 31(1): 109 (1886).

This group is monotypic occurring only in eastern Asia. Morphological characters of bulbs, bulb tunics, leaves and flowers are similar to species of subgen. *Amerallium*, but one- or two-flowered inflorescences and also the feathery ends of stigmatic lobes are unique within the genus *Allium*. The same is true for the occurrence of dioecy, which developed only at the diploid level (Noda and Kawano 1988). The plants show also a special chromosome pattern at different ploidy levels based on $x = 8$.

ALLIUM subgen. AMERALLIUM Traub, *Pl. Life (Stanford)* 24: 159 (1968).—TYPE: *A. canadense* L.

Subgen. *Bromatorrhiza* Ekberg, *Bot. Not.* 122: 58 (1969), pro parte.—TYPE: *A. wallichii* Kunth; subgen. *Molium* (G. Don) Wendelbo, *Bot. Not.* 122: 26 (1969).—TYPE: *A. neapolitanum* L.; subgen. *Caulorhizideum* (Traub) Kamelin, *Florogenet. analiz. est. fl. gorn. Sredn. Azii*: 245 (1973).—TYPE: *A. validum* S. Wats.; subgen. *Chamaeprason* (F. Hermann) Garbari, *Taxon* 24: 541 (1975).—TYPE: *A. chamaemoly* L.

Besides the sections mentioned above as synonymous subgenera, the American sects. *Lophoprason* (Fig. 4), *Amerallium*, and *Rhophetoprason*, as well as the Old World sects. *Arctoprasum* (Fig. 5), *Briseis*, *Narkissoprason*, *Molium* (Fig. 7) and *Bromatorrhiza* (Fig. 6) are included. Section *Rhynchocarpum* possibly also belongs here. Molecular data underline the existence of two sister alliances: a rather diverse Old World and a derived New World one. Nevertheless, both are a monophyletic unit, which agrees with a uniform electrophoretic banding pattern of salt-soluble seed storage proteins (Maass 1992). Bulbous and rhizomatous species occur in both alliances. This may explain why different types of growth form and shoot foliation exist, but irregular insertion of cataphylls into the foliage leaf sequence was only observed in subgen. *Amerallium* (Kruse 1992a). All species share a special anatomy of vegetative parts (one row of vascular bundles, absence of palisade parenchyma, and subepidermal position of laticifers; Fritsch 1988). Furthermore, the dominating basic chromosome number of $x = 7$ strongly supports its separate status, although $x = 8, 9$, and 11 also

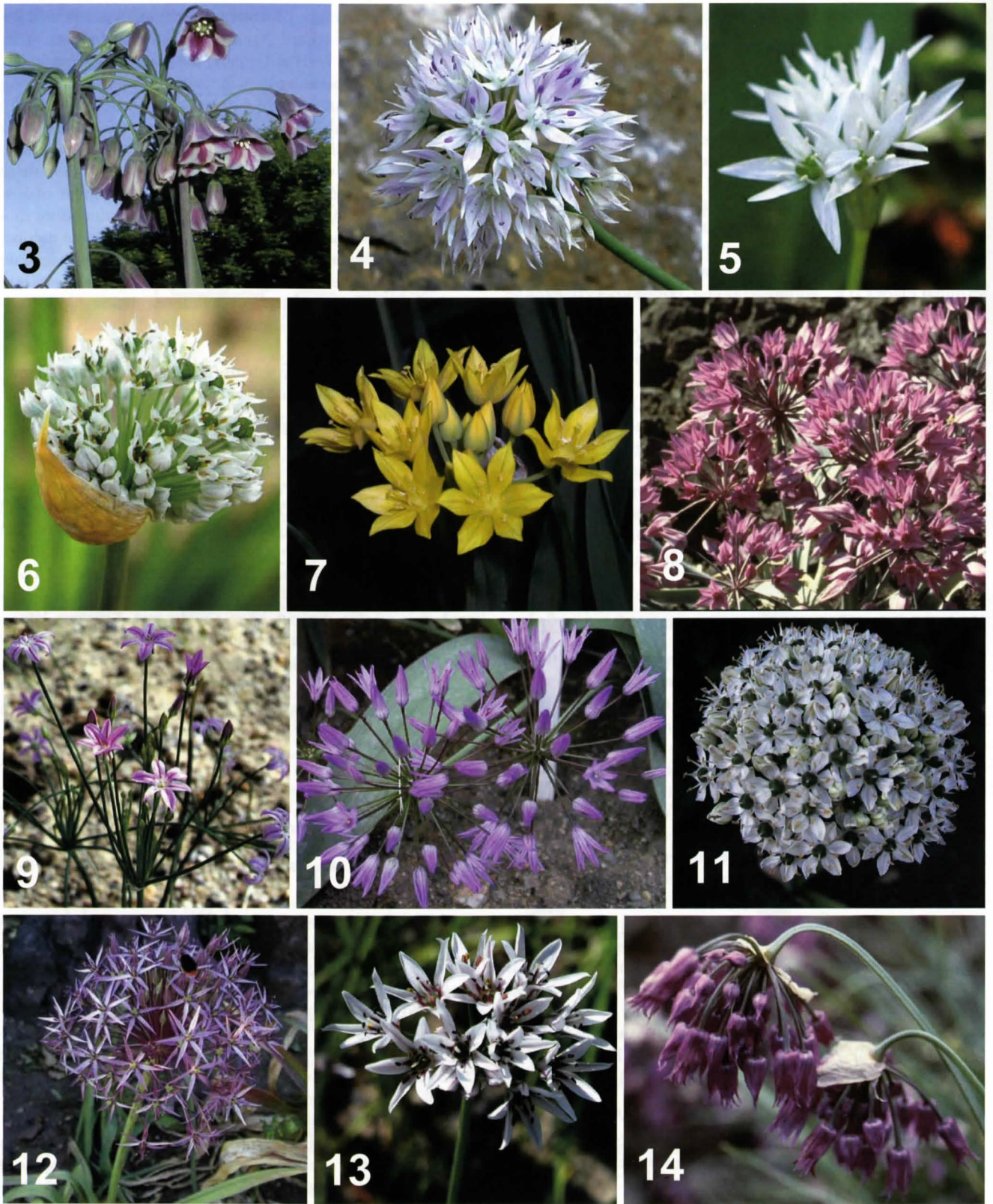


Fig. 3–14.—Plant portraits.—3. *Allium siculum* (sect. *Nectaroscordum*).—4. *A. amplexens* Torr. (sect. *Lophioprason*).—5. *A. ursinum* (sect. *Arctoprason*).—6. *A. hookeri* (sect. *Bromatorrhiza*).—7. *A. moly* (sect. *Molium*).—8. *A. oreophilum* (sect. *Porphyroprason*).—9. *A. neriniflorum* (sect. *Caloscordum*).—10. *A. cupuliferum* Regel (sect. *Regeloprason*).—11. *A. nigrum* (sect. *Melanocrommyum*).—12. *A. cristophii* (sect. *Kaloprason*).—13. *A. ramosum* (sect. *Butomissa*).—14. *A. cyathophorum* (sect. *Cyathophora*).

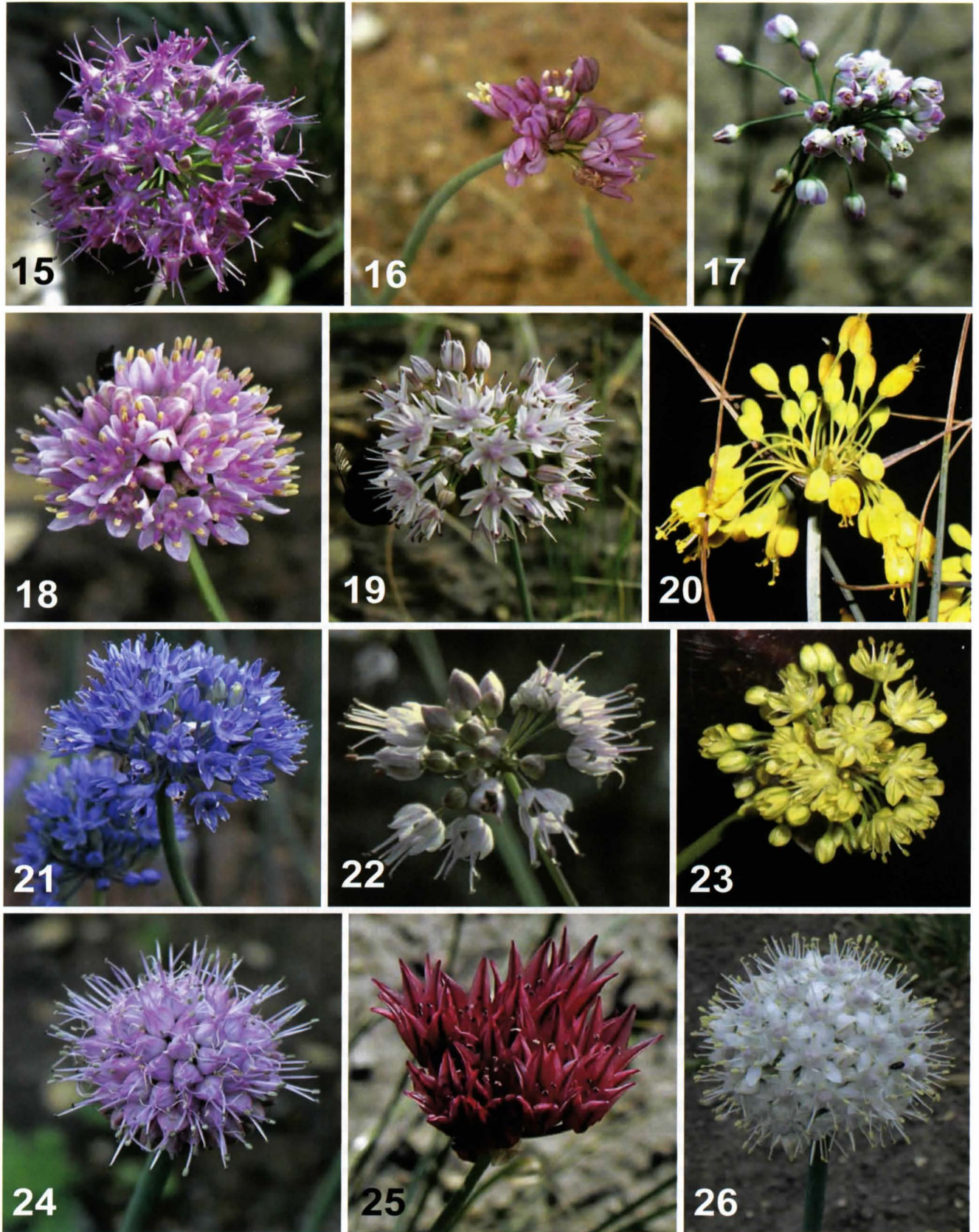


Fig. 15–26.—Plant portraits.—15. *Allium przewalskianum* (sect. *Caespitosoprasum*).—16. *A. mongolicum* (sect. *Caespitosoprasum*).—17. *A. tenuissimum* (sect. *Tenuissima*).—18. *A. incensiodorum* (sect. *Rhizirideum*).—19. *A. eduardii* (sect. *Eduardia*).—20. *A. flavum* (sect. *Codonoprasum*).—21. *A. caeruleum* (sect. *Caerulea*).—22. *A. ericetorum* (sect. *Daghestanica*).—23. *A. scabriscapum* (sect. *Scabriscapa*).—24. *A. carolinianum* (sect. *Falcatifolia*).—25. *A. inconspicuum* Vved. (sect. *Campanulata*).—26. *A. galanthum* (sect. *Cepa*).

occur in several morphologically derived *Amerallium* groups. DNA content per genome is commonly high, ranging from 45–60 pg 2C DNA content but some species of sects. *Caulorhizideum*, *Lophioprason*, *Molium*, and *Bromatorrhiza* range between 30–40 pg (Ohri et al. 1998). The nectaries show a rather uniform shape and position and excrete mainly through short spurs. This simple structure differs only slightly from sect. *Rhizirideum*. A more advanced nectarial structure was stated for rhizomatous species only (Fritsch 1992b).

Hypogeal seed germination, the unique *A. ursinum* seedling type, and large chromosomes with an exceptionally high 2C DNA content of nearly 64 pg characterize sect. *Arctoprasum* as a rather old alliance with a separate position. A very short leaf sequence beginning with a foliage leaf composed of a thickened basal sheath with storage function, a narrow petiole, and a rather wide lamina is followed by a cataphyll and a second foliage leaf without basal storage function. The lamina is exceptional for the whole genus *Allium*; the upper and lower side show reversed anatomical structures and are also reversed positioned. All these morphological characters are certainly signs of a highly generalized specialization. Nevertheless, molecular data show only small differences between sect. *Arctoprasum* and other sections.

Section *Bromatorrhiza* is characterized by knobby thickenings of the cortex cell walls of the roots (Fritsch 1992a), uniovulate locules (Hanelt 1992), and by a rather low DNA content of about 30 pg 2C DNA content (Ohri et al. 1998). All these characters as well as the more specialized structure of the nectary and excretory tube (Fritsch 1992b) underline a rather advanced evolutionary state.

ALLIUM subgen. CALOSCORDUM (Herb.) R. M. Fritsch, *Kew Bull.* **49**: 560 (1994).—TYPE: *A. neriniflorum* (Herb.) Baker (Fig. 9).

Genus *Caloscordum* Herb., *Edwards's Bot. Reg* **30**: 64 (1844); sect. *Caloscordum* (Herb.) Baker, *J. Bot.* **3**: 290 (1874).

It is an oligotypic group with three species in east Asia. It shares multiovulate locules, subterranean leaf sheaths, and the presence of relatively large inner vascular bundles in the scapes (Friesen et al. 1986; Fritsch 1993) with subgen. *Melanocrommyum* where three-lobed stigmata are rare and such bulbs (composed of several storage leaves) do not occur. Shape and position of nectaries and excretory tubes are similar to those hitherto found in several subgenera. However, according to our molecular data subgen. *Caloscordum* is most closely related to subgen. *Anguinum*. Simple characters of seed testa cells are an almost even and slightly verrucose periclinal wall and straight anticlinal walls (Kruse 1984, 1988), supporting this relationship morphologically.

ALLIUM subgen. **Anguinum** (G. Don ex Koch) N. Friesen, comb. et stat. nov.—TYPE: *A. victorialis* L.

Basionym: *Allium* sect. *Anguinum* G. Don ex Koch, Synopsis Deutsch. Schweiz. Fl.: 714 (1837).

In this subgenus two distinct groups exist. One with a Eurasian-American distribution (*A. victorialis* alliance, including *A. tricocum*) and the second restricted to east Asia

(*A. prattii*, *A. ovalifolium*, and others). The plants have a prominent rhizome and develop lateral shoots of first order, only. The leaf sequence begins with several elongated cataphylls without lamina, followed without transitional types, by two or three foliage leaves having a distinct petiole part between basal sheath and the rather wide lamina (Kruse 1992a). Seed germination is hypogeal, and the *A. victorialis*-type of seedlings is only present in this subgenus (Druselmann 1992). Narrow, branched, and lengthwise twisted septal nectaries (Fritsch 1992b), a nearly identical width of the rhizodermal and exodermal cells, and exodermal cell walls with exceptionally high suberin content are section-specific anatomical root characters (Fritsch 1992a). The locules are uniovulate, a character that occurs sporadically in the genus *Allium* and may reflect adaptation to mesophytic herb layers of forest associations (Hanelt 1992). Hence, it is morphologically and anatomically a rather distinct and specialized section, but the seed testa sculpturing is very simple (Kruse 1984, 1988), sharing most characters with sect. *Caloscordum*. Serological data point to close relationships to subgen. *Melanocrommyum* and *Butomissa* (Hanelt et al. 1992), which might indicate an ancient origin of the group.

ALLIUM subgen. **Porphyroprason** (Ekberg) R. M. Fritsch, comb. et stat. nov.—TYPE: *A. oreophilum* C. A. Mey. (Fig. 8).

Basionym: *Allium* sect. *Porphyroprason* Ekberg, *Bot. Not.* **122**: 65 (1969).

Several specific morphological characters such as planar venation of leaf blades, occurrence of up to three veins in the outer tepals, a tripartite stigma, 3–4 ovules per locule, and evenly granulous periclinal walls as well as only slightly undulate anticlinal walls of the seed testa cells characterize this monotypic group. Shape and position of nectaries and excretory tubes do not differ from that often met within subgen. *Melanocrommyum*, but the leaf blades do not show the regular pairwise position of opposite vascular bundles, typical for that subgenus. Also, serological characters underline a rather isolated position, which is closer to subgen. *Melanocrommyum* s.l. than to any other alliance (Hanelt et al. 1989). The phylogenetical distance to subgen. *Vvedenskya* is very small, and both may have a common but very ancient ancestor.

ALLIUM subgen. **Vvedenskya** (Kamelin) R. M. Fritsch, comb. et stat. nov.—TYPE: *A. kujukense* Vved.

Basionym: *Allium* sect. *Vvedenskya* Kamelin, *Florogenet. analiz est. fl. gorn. Sredn. Azii*: 243 (1973).

It is also a monotypic group. The locules are multiovulate as often found in subgen. *Melanocrommyum*, and also the shape of the narrowly campanulate flowers is most similar to *A. gypsaceum* of sect. *Popovia*. Especially the lax inflorescence with rather few flowers and the small subglobose bulbs with several stalked side bulbs and membranous tunics do not differ much from *A. oreophilum*. However, the scape and the cylindrical and tubular leaves of *A. kujukense* are densely ribbed and bear short hairs differing thus considerably from that species. These morphological characters, and also nearly smooth periclinal walls, and Omega-like undu-

late anticlinal walls of the seed testa cells (Kruse unpubl. data) are similar to subgen. *Allium* s.l. That relationship is, however, not supported by molecular data, which might indicate that these character states are either plesiomorphic or evolved independently in both groups.

Three southwest Asian species included here by Khassanov (2000) very probably belong to sect. *Kopetdagia* of subgen. *Allium*.

ALLIUM subgen. MELANOCROMMYUM (Webb et Berth.) Rouy, Fl. France 2: 378 (1910).—TYPE: *A. nigrum* L. (Fig. 11).

Sect. *Molium* sensu Vved. et auct. Ross., pro parte majore, non s.s.

Although large and morphologically extremely diverse, it is a monophyletic group. The complicated taxonomic structure may result from reticulate evolution (Mes et al. 1997, 1999). This might also explain that group-specific chromosomal characters are largely missing (Fritsch and Astanova 1998). However, current molecular studies did not confirm the dominance of reticulate structures (Blattner pers. comm.) but will only result in a new classification proposal after completion. Therefore, the morphologically based classification at sectional level proposed by Khassanov and Fritsch (1994) is applied here. The relations inside the species-rich sect. *Melanocrommyum* remained unclear because only very few species could be studied as living plants. Preliminary results of the above mentioned molecular investigation showed that this section and also the below named large ones are conglomerates of distantly related subgroups (Blattner pers. comm.). The sects. *Acmopetala*, *Megaloprason*, *Regeloprason* (Fig. 10) *Kaloprason* (Fig. 12), and *Acanthoprason* are rather large with about 15–35 species each, while sects. *Compactoprason*, *Pseudoprason*, *Miniprason*, *Brevicaule*, *Thaumasoprason*, and *Verticillata* are oligotypic including 2–8 species each. Sects. *Acaule*, *Aroidea*, and *Povovia* are monotypic.

All members show epigeal germination with seedlings of the *A. karataviense*-type (Druselmann 1992) and share a regular pairwise position of opposite vascular bundles in supra- and often also subterranean leaf parts. The basal sheath part of the foliage leaves is commonly not visible above the soil. Very often this sheath is only partially or not closed and may then show connections between the margins of consecutive leaves (Kruse 1992a). The cell walls of the root endodermis are thickened all around ("O-type"; Fritsch 1992a). None of these character states occur in any other subgenus. A strongly unreduced, salt-soluble seed storage protein with molecular weight of 65,000–70,000 was found in this subgenus only (Maass 1992). Although most species show multiovulate locules in the ovary, two ovules per locule were reported for sect. *Megaloprason* (Hanelt 1992), and pseudo-uniovulate locules are characteristic for sect. *Compactoprason*. DNA values are rather uniform and moderately high in a range of 40–50 pg 2C DNA content although a few taxa have only about 30 pg (Ohri et al. 1998). These low values, as well as exceptionally low TKW (Hanelt 1992) were found in species of the rather specialized sects. *Regeloprason* and *Kaloprason*. Hence also in subgen. *Melanocrommyum* derived groups have lower DNA content than more ancient ones, and the contrary conclusion by Ohri et al. (1998) cannot be upheld. Most commonly the nectaries

are located only in the lower half of the ovaries and excrete through spurs or rather short tubes. The excretory tubes are most often downward bent and end in the angle between ovary and tepals, rarely somewhat higher. These are simpler character states than present in subgen. *Reticulobulbosa* and *Cepa*. However, lobed nectaries were found in a few species but this variation was apparently not correlated with their taxonomic position (Fritsch 1992b). Multiveined tepals, mentioned in the description of *A. koelzii* (Wendelbo) K. M. Perss. et Wendelbo of sect. *Pseudoprason*, apparently evolved independently in subgen. *Nectaroscordum* and *Porphyroprason* and possess no taxonomic significance for these groups.

A few aberrant characters are shown by the basal sect. *Verticillata*: the leaf blades (the sheaths are completely entire) are longitudinally dissected into thread-like parts. This leaf shape is unique at least among the members of Alliaceae, and probably also in the entire Asparagales. Seed testa cells show strongly crumpled periclinal walls without central prominent sculptures and shortly but variably undulate anticlinal walls. This character combination is not known from any other species in *Melanocrommyum* or related subgenera (Kruse 1994). The seed testa of *A. aroides*, the only species of sect. *Aroidea*, is also exceptional in having flat periclinal walls with evenly verrucose ornamentation, and nearly straight anticlinal walls (Kruse 1994). The seed testa cells of all other species of subgen. *Melanocrommyum* and *Allium* (as far as studied to date) are very similar showing convex periclinal walls with several large prominent sculptures and verrucose ornamentation, combined with S- to Omega-like undulate anticlinal walls (Kruse 1992b).

ALLIUM subgen. **BUTOMISSA** (Salisb.) N. Friesen, comb. et stat. nov.—TYPE: *A. ramosum* L. (= *A. tataricum* L. f.) (Fig. 13).

Basionym: genus *Butomissa* Salisb., Gen. Pl. fragm. cont. part Liriogamae: 90 (1866).

Butomissa is a small group. The typical sect. *Butomissa* contains two genetic entities, which morphologically overlap (Blattner and Friesen 2006). They inhabit the Siberian–Mongolian–North Chinese steppes. It is still being discussed whether they represent one or two species. The growth form (Kruse 1992a) and chromosome morphology are as simple as in sect. *Rhizirideum* (Friesen 1988), but multiovulate locules (with a mean of 3.2 ovules per locule in *A. ramosum*) and rather high TKW (mean 4.1 g; Hanelt 1992) as well as serological data show relations to subgen. *Melanocrommyum* and subgen. *Anguinum*. Molecular data suggest subgen. *Butomissa* occupies a position between these subgenera closer to subgen. *Cyathophora* and subgen. *Rhizirideum*. Position, shape, and excretory tube of the nectaries show rather simple character states (Fritsch 1992b).

ALLIUM subgen. BUTOMISSA sect. **AUSTROMONTANA** N. Friesen, sect. nov.—TYPE: *A. oreoprasum* Schrenk.

Bulbi gregari rhizomati horizontali robusti insidentes, tunicis reticulatis. Folia plana linearia, prope basin scapi congesta. Tepala rosea nervo atropurpureo.

Bulbs aggregated, outer tunics reticulate. Rhizome hori-

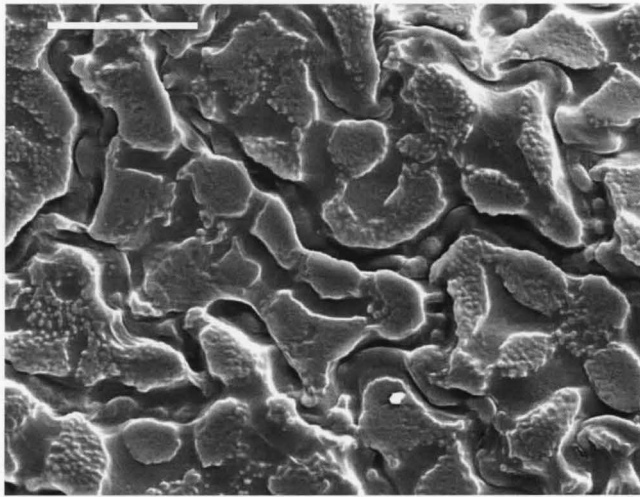


Fig. 27.—Seed surface of *Allium oreoprasum*. Scale bar = 20 μm .

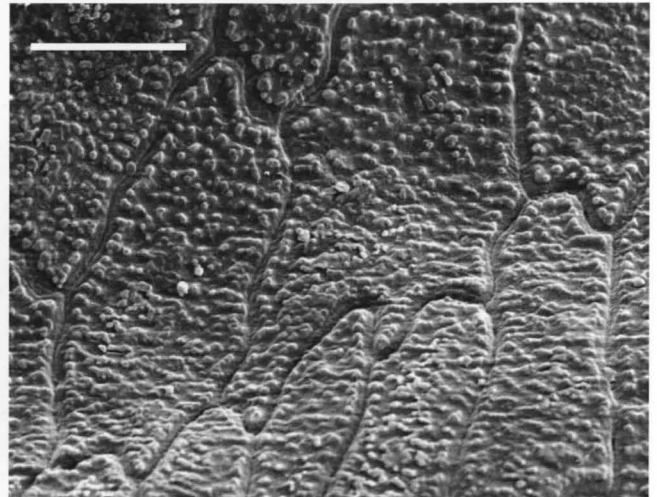


Fig. 28.—Seed surface of *Allium ramosum*. Scale bar = 20 μm .

zontal, well developed. Leaves flat, linear, aggregated in lower part of scape. Tepals pink with a dark purple nerve.

This section contains two species (*A. oreoprasum* Schrenk and *A. gilgiticum* Wang & Tang) occurring in the mountains from eastern to central Asia up to the borderline of the eastern Mediterranean area. The seed testa of *A. oreoprasum* (Fig. 27) is very comparable to *A. ramosum* (Fig. 28) and *A. tuberosum* of subgen. *Butomissa*, differing only by the verrucose ornamentation of the periclinal walls.

ALLIUM subgen. Cyathophora (R. M. Fritsch) R. M. Fritsch, comb. et stat. nov.—TYPE: *A. cyathophorum* Bur. et Franch. (Fig. 14).

Basionym: *Allium* sect. *Cyathophora* R. M. Fritsch, *Kew Bull.* **49**: 561 (1994).

Subgen. *Bromatorrhiza* Ekberg, *Bot. Not.* **122**: 58 (1969), pro parte, excl. sect. *Bromatorrhiza*.

The oligotypic sects. *Cyathophora* and *Coleoblastus* and the monotypic sect. *Milula* belong to this small and solely Asian (Tibet and the Himalayas) group. Though the leaf bases seem somewhat inflated, thickened parts with storage function and storage leaves are absent (Kruse 1992a) and also a bulb is missing. All species share only one row of identically orientated vascular bundles in the leaf blades combined with the presence of palisade parenchyma and subcortical laticifers, which is perhaps the most ancient character combination in the genus (Fritsch 1988). As far as known, all species have biovulate locules (Hanelt 1992). The elongated inflorescence of *A. spicatum* (Prain) N. Friesen attracts special attention, though all other characters tested agree completely with the other species of this subgenus. The roots are less specialized than those of the other sections showing evenly and not knot-like thickened cortex cell walls (Friesen et al. 2000). Growth form and foliation of *A. cyathophorum* seems slightly more advanced than in sect. *Rhizirideum* showing ramification up to lateral shoots of third order (with inflorescences on those of first and second order) and rarely transitional leaf forms with somewhat reduced lamina but no cataphylls (Kruse 1992a). Structures of nec-

tary and excretory tube also show a more advanced state than in sect. *Rhizirideum* (Fritsch 1992b).

ALLIUM subgen. RHIZIRIDEUM (G. Don ex Koch) Wendelbo, *Bot. Not.* **122**: 25 (1969), s.s.—TYPE: *A. senescens* L.

Subgen. *Steiptoprason* Radić, *Razpr. Slov. Akad. Znan. Umetn., Razr. Nar. Vede.* [SAZU] **31**: 250, 251 (1990).—TYPE: *A. incensiodorum* Radić.

Though this subgeneric name has been used for groups with extremely different circumscriptions, it must remain in use because of nomenclatural reasons. We regard it as a comparatively small subgenus comprising currently about 37 species including the sects. *Rhizirideum* (Fig. 18), *Caespiotoprason* (Fig. 15, 16), *Tenuissima* (Fig. 17), *Rhizomatosa*, and the new monotypic sect. *Eduardia*. These are Eurasian steppe taxa showing the most diversity in southern Siberia and Mongolia. Only a few species are distributed in Europe, reaching Portugal as their western-most outpost, and some species such as *A. anisopodium* (sect. *Tenuissima*), *A. spirale* (sect. *Rhizirideum*) occur also in Korea and far eastern Russia, as well as *A. togashii* (sect. *Rhizirideum*) in Japan. The growth form is simple because only foliage leaves with a complete lamina are developed (Kruse 1992a). Also, the growth rhythm presents a rather ancestral state in these sections (Hanelt et al. 1992). The simple form of nectaries without an excretory tube (Fritsch 1992b) and differing karyotypes in every section (Friesen 1988) underline this phylogenetically rather ancient state. The occurrence of several ploidy levels in the *A. senescens* alliance (sect. *Rhizirideum*) is connected with the origin of several young species, showing thus a secondary radiation in this group (Friesen 1992).

ALLIUM subgen. RHIZIRIDEUM sect. Eduardia N. Friesen, sect. nov.—TYPE: *A. eduardii* Stearn (Fig. 19).

Bulbi conici gregari ad rhizoma repens insidentes. Spatha in rostrum longum attenuata, rostrum fere triplo basi longiorum. Umbella hemisphaerica pauciflora laxa.

Bulbs several, conical, borne on creeping rhizome. Spathe with long beak, nearly three times longer than base. Umbel hemispherical, few flowered, lax.

The shape of the nectaries is identical to sect. *Rhizirideum*, but the presence of a long excretory tube (Fritsch 1992b), fibrous bulb tunics, and a deviating chromosome morphology (Friesen 1988) support the taxonomic separation.

ALLIUM subgen. ALLIUM.—TYPE: *A. sativum* L.

Subgen. *Codonoprasum* (Rchb.) Zahariadi, Problems Balkan Flora: 230 (1976).—TYPE: *A. oleraceum* L.

This is the largest subgenus of *Allium* comprising by far the largest number of species. Molecular data support the division into two main groups.

One refers to the “classical” sect. *Allium* that has tripartite inner filaments and only one thick storage cataphyll. Often more chromosomes than in other subgenera have exceptionally long satellites (Hanelt et al. 1992), which characterize this group karyologically. The rather recent splitting of the mainly oligotypic sects. *Caerulea* (Fig. 21), *Crystallina*, *Multicaulea*, *Spathulata*, and *Brevidentia* by Khassanov (1996, 2000) is widely supported by molecular data, whereas the informal groups proposed by Mathew (1996) are not reflected in our molecular analyses. Inclusion of *A. haneltii* F. O. Khassanov et R. M. Fritsch in sect. *Brevidentia* (Fritsch et al. 1998) must be revised as Fig. 2 shows. Nevertheless, sect. *Allium* remains the most species-rich in the genus. An inflorescence with numerous long bracteoles, paper-like bulb tunics, a symmetric karyotype with small satellites, and straight anticlinal walls of seed testa cells characterize sect. *Spathulata* as less specialized among these sections (Fritsch et al. 1998).

The second group is morphologically more diverse and comprises less closely related sections. The rather distinct sects. *Codonoprasum* (Fig. 20), *Brevispatha*, and *Kopetdagia* as well as segregates of bulbous species of the “classical” sect. *Scorodon* in a broad sense belong to it. These species often have two or more cataphylls in the bulbs and a different shape and position of the nectaries and excretory tubes (Fritsch 1992b). However, only small differences of the growth form to sect. *Allium* exist (Kruse 1992a).

Four sections were invalidly combined by Khassanov (2000) and will be validated here:

ALLIUM subgen. ALLIUM sect. **Eremoprasum** (Kamelin) F. O. Khassanov, R. M. Fritsch et N. Friesen, comb. et stat. nov.—TYPE: *A. sabulosum* Stev.

Basionym: *Allium* subsect. *Eremoprasum* Kamelin, Florogenet. analiz est. fl. gorn. Sredn. Azii: 237 (1973).

ALLIUM subgen. ALLIUM sect. **Longivaginata** (Kamelin) F. O. Khassanov, R. M. Fritsch et N. Friesen, comb. et stat. nov.—TYPE: *A. longivaginatum* Wendelbo.

Basionym: *Allium* subsect. *Longivaginata* Kamelin, Florogenet. analiz est. fl. gorn. Sredn. Azii: 238 (1973).

ALLIUM subgen. ALLIUM sect. **Pallasia** (Tzag.) F. O. Khassanov, R. M. Fritsch et N. Friesen, comb. et stat. nov.—TYPE: *A. pallasii* Murr.

Basionym: *Allium* ser. *Pallasia* Tzagolova, *Novosti Sist. Vyssh. Nizsh. Rast.*: 53 (1977).

ALLIUM subgen. ALLIUM sect. **Mediasia** F. O. Khassanov, S. C. Yengalycheva et N. Friesen, sect. nov.—TYPE: *A. turkestanicum* Regel.

Scapus 50–100 cm altus. Folia in numero 4–6, laminae lineares 1–1.5 cm latae. Inflorescentia denseque subglobosa, multiflora. Perigonii late campanulati phylla obtusa. Filamenta perigonii breviora subulata, interiora inferne denticulata. Stylus exsertus. Ovarium rotundato-tripartitum, rubrum.

Plant 50–100 cm tall. Leaves 4–6, 1–2.5 cm broad, linear. Inflorescence subspherical, dense, many-flowered. Flowers campanulate, tepals obtuse. Filaments slightly longer than tepals, inner filaments basally obovate. Style exserted. Ovary subspherical with three furrows, red.

This section is monotypic. However, *A. yuchuanense* Y. Z. Zhao & J. Y. Chao from China may possibly also belong here.

Scape length, leaf shape and number, as well as the bipartite spathe with a moderately long beak of *A. turkestanicum* are rather similar to the garlic alliance of sect. *Allium*. However, the campanulate perianth, inner filaments with an obovate basal lamina and very short lateral cusps, ovoid bulbs, 3-lobed pinkish ovaries with deep pocket-like mounds of nectarial tubes, some anatomical and embryological characters (Khassanov et al. in prep.), as well as seed testa cells having a narrow anticlinal field and slightly convex periclinal walls with granulate sculptures (Kruse unpubl. data) do not fit that section. This specific combination of characters is known from several rhizomatous groups and may underline an ancient hybridogenous origin of this taxon. Section *Mediasia* is included here because the bulbous character dominates.

ALLIUM subgen. **Reticulobulbosa** (Kamelin) N. Friesen, comb. et stat. nov.—TYPE: *A. lineare* L.

Basionym: *Allium* sect. *Reticulato-bulbosa* Kamelin, Florogenet. analiz est. fl. gorn. Sredn. Azii: 239 (1973).

Sections *Reticulobulbosa*, *Campanulata*, and the new sects. *Scabriscapa*, *Nigrimontana*, and *Sikkimensia* belong to this subgenus. They display much similarity in vegetative morphology, as reticulate or at least fibrous tunics and narrowly linear leaf blades, and much diversity of flower characters. The shoot foliation is advanced beginning with two to five cataphylls having an extremely reduced lamina, followed by transitional leaves with reduced lamina, and finally foliage leaves with a complete lamina (Kruse 1992a). A many-layered root exodermis with strongly thickened cell walls (Fritsch 1992a), as well as the broad and phloem-rich inner vascular bundles of the scape (Fritsch 1993) are only typical for sect. *Campanulata* and a few more species from the other sections.

ALLIUM subgen. RETICULOBULBOSA sect. **Scabriscapa** (Tscholok.) N. Friesen, comb. et stat. nov.—TYPE: *A. scabriscapum* Boiss. (Fig. 23).

Basionym: *Allium* ser. *Scabriscapa* Tscholok, *Zametki Sist. Geogr. Rast.* 31: 42 (1975).

Allium scabriscapum (including *A. ericoleum* Vved.), *A. sulphureum*, and *A. trachyscordum* represent this section. Except for the latter species, they have bright yellow flowers.

ALLIUM subgen. RETICULATOBULBOSA sect. **Nigrimontana** N. Friesen, sect. nov.—TYPE: *A. drobovii* Vved.

Folia plana, linearia, altitudine caulis non superantia. Tepala albivirescentia vel albo-roseola purpureo-nervata. Stamina integra.

Leaves flat, linear, shorter than scape. Tepals greenish-white or pinkish-white with red nerves. Filaments entire.

Here belong *A. drobovii* and *A. oreoprasoides*, endemic species from Karatau Mountains, Kazakhstan. They occupy an isolated position next to sect. *Campanulata*. Shape of the nectaries and excretory tubes are similar but not identical to those of sect. *Campanulata* (Fritsch 1992b).

ALLIUM subgen. RETICULATOBULBOSA sect. **Sikkimensia** (Traub) N. Friesen, comb. et stat. nov.—TYPE: *A. sikkimensense* Baker.

Basionym: *Allium* subsect. *Sikkimensia* Traub, *Pl. Life (Stanford)* **28**: 136 (1972).

This section is characterized by blue flowers and occurs mainly in southwestern and southern China.

ALLIUM subgen. POLYPRASON Radić, *Razp. Slov. Akad. Znanosti Umetn., Razr. Nar. Vede.* [SAZU] **31**: 250, 253 (1990).—TYPE: *A. moschatum* L.

This subgenus comprises mainly the former sect. *Oreiprason* in the broad sense of Kamelin (1973), and sect. *Sco-rodon* in the strict sense (possessing bulbs with rhizomes; subsect. *Moschata* (Omelcz.) Tscholok.). We accept sect. *Oreiprason* s.s. to include sect. *Petroprason* (though the scape anatomy is more similar to sect. *Rhizirideum*; Fritsch 1993), and segregate the new sects. *Falcatifolia* and *Daghestanica*. All taxa possess papery to leathery bulb tunics sometimes breaking into strips in the upper part. The growth form is as advanced as described above for subgen. *Reticulatobulbosa*, but *A. moschatum* is exceptional in missing cataphylls (Kruise 1992a). Rather similar nectaries and excretory tubes strongly support grouping of the above-mentioned sections and subsections. Surprisingly, nectarial characters of the sections united now under subgen. *Reticulatobulbosa* do not differ much (Fritsch 1992b).

The name proposed by Radić must be used because of nomenclatural reasons although, the original Latin characterization denies, incorrectly, the presence of a rhizome.

ALLIUM subgen. POLYPRASON sect. **Falcatifolia** N. Friesen, sect. nov.—TYPE: *A. carolinianum* DC. (Fig. 24).

Rhizoma breve, verticale. Bulbus semper fere solitarius vel interdum gregarius tunicis coriaceis vel scariosis. Folia plana plerumque falcata vel linearia.

Rhizome short, vertical. Bulbs usually single or sometimes several, with coriaceous or scarios tunicis. Leaves flat, usually falcate or linear.

The species of this section are found growing in the montane to subalpine belt of Central Asian mountains. They are characterized by strong rhizomes, which enable the species to survive in steep scree and rubble slopes. The more or less falcate leaf blades may be narrow or rather broad.

ALLIUM subgen. POLYPRASON sect. **Daghestanica** (Tscholok.)

N. Friesen, comb. nov.—TYPE: *A. daghestanicum* Grossh.

Basionym: *Allium* ser. *Daghestanica* Tscholok., *Zametki Sist. Geogr. Rast.* **25**: 83 (1965).

This section consists of two geographical alliances. The first one contains the Caucasian species *A. daghestanicum* and *A. gunibicum*, having thin thread-like leaves and beginning with anthesis only in autumn. *Allium ericetorum* (Fig. 22), *A. ochroleucum*, *A. kermesinum* Rchb., and *A. suaveolens* belong to the second (European) alliance distributed from the eastern Alps to the Pyrenees. These plants show semicylindrical or narrowly linear leaves, are flowering in summer, and are the only group of the subgenus having bulb tunics splitting into longitudinal stripes (but not into fibers).

ALLIUM subgen. CEPA (Mill.) Radić, *Razp. Slov. Akad. Znanosti Umetn., Razr. Nar. Vede.* [SAZU] **31**: 250, 251 (1990).—TYPE: *A. cepa* L.

This subgenus comprises taxa with fistulous leaves and scapes although a few species are exceptional in having more or less flat leaf blades. The sects. *Cepa* (Fig. 26), *Schoenoprasum* s.s., *Annuloprason*, *Sacculiferum*, and the new monotypic sect. *Condensatum* are included. Their close relationship has already been stated by Hanelt et al. (1992). Bulbs are mostly well developed, although a large size as in sect. *Cepa* is exceptional. They also share a 4- to 6-fold number of vascular bundles outside the scape sclerenchyma compared to inside (Fritsch 1993). Reticulate or fibrous bulb tunics do not occur in this group. Position and shape of the nectaries is variable, but the excretory tubes are always specially shaped (Fritsch 1992b). All investigated members of sect. *Cepa* (in the circumscription of Hanelt 1985) share a specific satellite DNA sequence that had evolved already in the progenitor forms (Pich et al. 1996).

Chromosomal and molecular characters favor a position of *A. roylei* in subsect. *Cepa*, but morphological characters of inflorescence, flower parts, and seed testa unequivocally support exclusion from this section as member of sect. *Oreiprason*. Only the study of newly introduced natural accessions may possibly elucidate the true taxonomic state of this taxon (Fritsch and Friesen 2002).

ALLIUM subgen. CEPA sect. **Condensatum** N. Friesen, sect. nov.—TYPE: *A. condensatum* Turcz.

Bulbi solitarii rhizomati brevi insidentes. Folia semicylindrica fistulosa longitudinaliter profunde sulcata. Inflorescentia globosa compacta multiflora. Tepala flaveola viridi-nervata.

Bulbs borne singly on a short rhizome. Leaves semicylindrical, deeply grooved, fistulous. Umbel globose, compact, many flowered. Perianth pale yellow with greenish nerves.

This monotypic section has a very slender habit, thread-like leaves, and membranous bulb tunics. It occurs from eastern Siberia and Mongolia north to Korea and Japan.

DISCUSSION

Phylogenetic analysis of the ITS region from 221 accessions representing 196 *Allium* and five outgroup species revealed several intrageneric taxa of *Allium* as poly- or para-

phyletic. These findings are mostly in accord with the results from other molecular studies as reviewed in Klaas and Friesen (2002). Our taxon sample covers roughly one-quarter of the known *Allium* species, assembled to represent all groups and paying particular attention to putative or known non-monophyletic groups in earlier classification systems. We also included most of the "difficult" species with uncertain taxonomic affiliation to provide a firm basis for a phylogenetic classification of the genus.

Our data showed *Allium* to be monophyletic when *Milula* (Friesen et al. 2000) and *Nectaroscordum* (Fay and Chase 1996) were included in the genus. A conspicuous feature of the ITS data were the very high genetic distances (>40%) within *Allium*. Values above 40% often characterize the most distant genera within subfamilies or even families (e.g., Baldwin et al. 1995; Hsiao et al. 1999; Noyes and Rieseberg 1999) in ITS analyses, while intrageneric distances in other plant families are mostly less than 10% (Baldwin et al. 1995). Large genetic distances were not restricted to the ITS region, but were also found in chloroplast *rbcL-atpB* sequences (Klaas and Friesen 2002). These findings suggest that the genus *Allium* is of ancient origin and molecular evolution was not accompanied by the rise of pronounced morphological divergence and accompanying higher taxonomic categories (Friesen et al. 2000). The pronounced molecular differences together with the extant distribution area of *Allium* indicate an origin of the genus early in the Tertiary (Friesen et al. 2000; in prep.). Thus in age and genetic variation the genus *Allium* resembles plant families in other groups of the angiosperms. Although a split of *Allium* into several genera would result in better comparability of equal taxonomic categories among different plant families, we rejected this possibility as: (1) *Allium* in its current circumscription is monophyletic, and (2) a change would necessitate a tremendous amount of new taxon designations. More than 30 generic names described between 1754 and 1869 refer to *Allium* species and would have to be examined according to the current rules of botanical nomenclature. Also (current as well as former) sectional and subsectional names would have to be proved concerning correctness of affiliation and circumscription. The determination of correct types for all these groups would become an extremely complicated work. As only the current subgen. *Allium* (about 300 species) would remain unaltered, roughly 500 new binomials and the same high number of new synonyms would have to be recognized, just to shift the former problems to another level. This, we think, would not contribute to a widely accepted and long-term stable taxonomic system for *Allium*.

The adequate classification of the phylogenetically complicated genus *Allium* requires, in our opinion, about 70 infrageneric taxa at the subgeneric and sectional levels to cover morphologically definable monophyletic groups. This seems an inconveniently high number, with the result that dealing with *Allium* may necessitate time-consuming and occasionally frustrating navigation through long keys and extended comparisons of characters. However, as the majority of our proposed changes concern the polyphyletic subgen. *Rhizirideum*, the split into six new subgenera created morphologically relatively homogenous groups. The presence of a visible rhizome was the key character of former subgen. *Rhizirideum*, although morphology and growth form of these

rhizomes is quite different among the different clades. All species from sect. *Anguinum* have an ascending rhizome, the species from sect. *Rhizirideum* s.s. have a horizontal rhizome, and species from sect. *Cepa* have a short vertical rhizome. Rhizomes were thought to be a basal character in *Allium* and that within subgen. *Rhizirideum* long rhizomes were the primitive character state and short or nearly reduced rhizomes to be advanced (Hanelt et al. 1992). However, the diversity of rhizome forms could not be correlated with other morphological characters used as markers for phylogenetic relationships in former subgen. *Rhizirideum* or the entire genus *Allium*. Our phylogenetic analysis indicates that rhizomes evolved several times independently in the groups of former subgen. *Rhizirideum*, which explains the different rhizome forms in these groups. A correlation between the occurrence of rhizomes and habitat preferences exists, as well as between rhizome morphology and different life forms (Cheremushkina 1992, 2001). Furthermore, our newly defined sections of former subgen. *Rhizirideum* are also monomorphic with regard to the bulb tunics, thus avoiding contradicting character distribution in former subgen. *Rhizirideum* (Hanelt et al. 1992). Generally, the new classification will allow a sound interpretation of character states in *Allium* and thus allows us to find correlations between morphological structures and their ecological or phylogenetic relevance.

The conspectus (Appendix 1) proposes to divide *Allium* into 15 subgenera and 56 sections (without type sections). The approximate number of species is given for every subgenus. We believe this to be helpful because one may find very different species numbers for *Allium* in recent books and papers, ranging from 450 to approximately 750. The number given for subgen. *Amerallium* is based on the most recent and excellent revision for America (McNeal and Jacobsen 2002). All other numbers were concluded from our own studies during fieldwork and with living collections, as well as from good herbarium specimens. Unfortunately, we were not able to study all described taxa from living plants, and could only estimate the true state of several species names from descriptions and incomplete dry specimens. Thus, the sum of all species numbers given exceeds 800, which is possibly somewhat too high, but a number of about 780 *Allium* species seems currently a realistic estimation.

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Appendix 1. Taxonomic conspectus of the genus *Allium* L.*First Evolutionary Line*

1. Subgen. NECTAROSCORDUM (Lindl.) Asch. et Graebn.—TYPE: *A. siculum* Ucria (ca. 3 spp.).
 - 1.1. Sect. NECTAROSCORDUM (Lindl.) Gren. et Godr.—TYPE: *A. siculum* Ucria.
2. Subgen. **Microscordum** (Maxim.) N. Friesen.—TYPE: *A. monanthum* Maxim. (monotypic).
 - 2.1. Sect. MICROSCORDUM Maxim.—TYPE: *A. monanthum* Maxim.
3. Subgen. AMERALLIUM Traub.—TYPE: *A. canadense* L. (ca. 135 spp.).
 - 3.1. Sect. AMERALLIUM Traub.—TYPE: *A. canadense* L. (2 subsects.).
 - 3.2. Sect. LOPHIOPRASON Traub.—TYPE: *A. sanbornii* Wood.
 - 3.3. Sect. RHOPHETOPRASON Traub.—TYPE: *A. glandulosum* Link et Otto.
 - 3.4. Sect. ARCTOPRASUM Kirschl. (*Ophioscorodon* (Wallr.) Endl.).—TYPE: *A. ursinum* L.
 - 3.5. Sect. BRISEIS (Salisb.) Stearn.—TYPE: *A. triquetrum* L.
 - 3.6. Sect. BROMATORRHIZA Ekberg.—TYPE: *A. wallichii* Kunth.
 - 3.7. Sect. CAULORHIZIDEUM Traub.—TYPE: *A. validum* S. Watson
 - 3.8. Sect. CHAMAEPRASON Herm.—TYPE: *A. chamaemoly* L.
 - 3.9. Sect. MOLIMUM G. Don ex Koch.—TYPE: *A. roseum* L. (2 subsects.).
 - 3.10. Sect. NARKISSOPRASON (F. Herm.) Kamelin.—TYPE: *A. narcissiflorum* Vill.
 - ? 3.11. Sect. RHYNCHOCARPUM Brullo.—TYPE: *A. ruhmerianum* Asch.
 - ? 3.12. Sect. TRIPTERA Kamelin et Seisums, nom. nud.—TYPE: *A. tripterum* Nasir.

Second Evolutionary Line

4. Subgen. CALOSCORDUM (Herb.) R. M. Fritsch.—TYPE: *A. neriniflorum* (Herb.) Baker (ca. 3 spp.).
 - 4.1. Sect. CALOSCORDUM (Herb.) Baker.—TYPE: *A. neriniflorum* (Herb.) Baker.
5. Subgen. **Anguinum** (G. Don ex Koch) N. Friesen.—TYPE: *A. victorialis* L. (ca. 12 spp.).
 - 5.1. Sect. ANGUINUM G. Don ex Koch.—TYPE: *A. victorialis* L.
6. Subgen. **Porphyrprason** (Ekberg) R. M. Fritsch.—TYPE: *A. oreophilum* C. A. Mey. (monotypic).
 - 6.1. Sect. PORPHYROPRASON Ekberg.—TYPE: *A. oreophilum* C. A. Mey.
7. Subgen. **Vvedenskya** (Kamelin) R. M. Fritsch.—TYPE: *A. kujukense* Vved. (monotypic).
 - 7.1. Sect. VVEDENSKYA Kamelin.—TYPE: *A. kujukense* Vved.
8. Subgen. MELANOCROMMYUM (Webb et Berth.) Rouy.—TYPE: *A. nigrum* L. (ca. 140 spp.).
 - 8.1. Sect. MELANOCROMMYUM Webb et Berth.—TYPE: *A. nigrum* L.
 - 8.2. Sect. ACANTHOPRASON Wendelbo.—TYPE: *A. akaka* Gmel.
 - 8.3. Sect. ACAULE R. M. Fritsch.—TYPE: *A. hexaceras* Vved.
 - 8.4. Sect. ACMOPETALA R. M. Fritsch.—TYPE: *A. backhousianum* Regel (7 subsects.).
 - 8.5. Sect. AROIDEA F. O. Khassanov et R. M. Fritsch.—TYPE: *A. aroides* Vved. et Popov.
 - 8.6. Sect. BREVICAULE R. M. Fritsch.—TYPE: *A. sergii* Vved.
 - 8.7. Sect. COMPACTOPRASON R. M. Fritsch.—TYPE: *A. giganteum* Regel (3 subsects.).
 - 8.8. Sect. KALOPRASON C. Koch.—TYPE: *A. caspium* (Pall.) M. Bieb. (4 subsects.).
 - 8.9. Sect. MEGALOPRASON Wendelbo.—TYPE: *A. rosenbachianum* Regel (3 subsects.).
 - 8.10. Sect. MINIPRASON R. M. Fritsch.—TYPE: *A. karataviense* Regel.
 - 8.11. Sect. POPOVIA F. O. Khassanov et R. M. Fritsch.—TYPE: *A. gypsaceum* Popov et Vved.
 - 8.12. Sect. PSEUDOPRASON (Wendelbo) K. M. Perss. et Wendelbo.—TYPE: *A. koelzii* (Wendelbo) K. M. Perss. et Wendelbo.
 - 8.13. Sect. REGELOPRASON Wendelbo.—TYPE: *A. regelii* Trautv. (2 subsects.).
 - 8.14. Sect. THAUMASIOPRASON Wendelbo.—TYPE: *A. mirum* Wendelbo.
 - 8.15. Sect. VERTICILLATA Kamelin.—TYPE: *A. verticillatum* Regel.

Third Evolutionary Line

9. Subgen. **Butomissa** (Salisb.) N. Friesen.—TYPE: *A. ramosum* L. (ca. 4 spp.).
 - 9.1. Sect. BUTOMISSA (Salisb.) Kamelin.—TYPE: *A. ramosum* L.
 - 9.2. Sect. **Austromontana** N. Friesen.—TYPE: *A. oreoprasum* Schrenk.
10. Subgen. **Cyathophora** (R. M. Fritsch) R. M. Fritsch.—TYPE: *A. cyathophorum* Bur. et Franch. (ca. 5 spp.).
 - 10.1. Sect. CYATHOPHORA R. M. Fritsch.—TYPE: *A. cyathophorum* Bur. et Franch.
 - 10.2. Sect. COLEOBLASTUS Ekberg.—TYPE: *A. mairei* Lévl.
 - 10.3. Sect. MILULA (Prain) N. Friesen.—TYPE: *A. spicatum* (Prain) N. Friesen.
11. Subgen. RHIZIRIDEUM (G. Don ex Koch) Wendelbo s.s.—TYPE: *A. senescens* L. (ca. 37 spp.).
 - 11.1. Sect. RHIZIRIDEUM G. Don ex Koch s.s.—TYPE: *A. senescens* L.
 - 11.2. Sect. CAESPITOSOPRASON N. Friesen.—TYPE: *A. polyrrhizum* Siev.
 - 11.3. Sect. RHIZOMATOSA Egor.—TYPE: *A. caespitosum* Siev.
 - 11.4. Sect. TENUISSIMA (Tzagolova) Hanelt.—TYPE: *A. tenuissimum* L.
 - 11.5. Sect. **Eduardia** N. Friesen.—TYPE: *A. eduardii* Stearn.

Appendix 1. Continued.

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12. Subgen. **ALLIUM**.—TYPE: *A. sativum* L. (ca. 300 spp.).
- 12.1. Sect. **ALLIUM** (including sect. **COSTULATAE** F. O. Khassanov et S. C. Yengalycheva).—TYPE: *A. sativum* L.
 - 12.2. Sect. **BREVIDENTIA** F. O. Khassanov et S. C. Yengalycheva.—TYPE: *A. brevidens* Vved.
 - 12.3. Sect. **CRYSTALLINA** F. O. Khassanov et S. C. Yengalycheva.—TYPE: *A. crystallinum* Vved.
 - 12.4. Sect. **MULTICAULEA** F. O. Khassanov et S. C. Yengalycheva.—TYPE: *A. lehmannianum* Merckl.
 - 12.5. Sect. **SPATHULATA** F. O. Khassanov et R. M. Fritsch.—TYPE: *A. spathulatum* F. O. Khassanov et R. M. Fritsch.
 - 12.6. Sect. **Mediasia** F. O. Khassanov, S. C. Yengalycheva et N. Friesen.—TYPE: *A. turkestanicum* Regel.
 - 12.7. Sect. **AVULSEA** F. O. Khassanov.—TYPE: *A. rubellum* M. Bieb.
 - 12.8. Sect. **BREVISPATHA** Valsecchi.—TYPE: *A. parciflorum* Viv.
 - 12.9. Sect. **CAERULEA** (Omelcz.) F. O. Khassanov.—TYPE: *A. caeruleum* Pall.
 - 12.10. Sect. **CODONOPRASUM** Rchb.—TYPE: *A. oleraceum* L. (2 subsects.).
 - 12.11. Sect. **Eremoprasum** (Kamelin) F. O. Khassanov, R. M. Fritsch et N. Friesen.—TYPE: *A. sabulosum* Stev.
 - 12.12. Sect. **KOPETDAGIA** F. O. Khassanov.—TYPE: *A. kopetdagense* Vved.
 - 12.13. Sect. **Longivaginata** (Kamelin) F. O. Khassanov, R. M. Fritsch et N. Friesen.—TYPE: *A. longivaginatum* Wendelbo.
 - 12.14. Sect. **MINUTA** F. O. Khassanov.—TYPE: *A. minutum* Vved.
 - 12.15. Sect. **Pallasia** (Tzagolova.) F. O. Khassanov, R. M. Fritsch et N. Friesen.—TYPE: *A. pallasii* Murr.
13. Subgen. **Reticulobulbosa** (Kamelin) N. Friesen.—TYPE: *A. lineare* L. (ca. 80 spp.).
- 13.1. Sect. **RETICULATOBULBOSA** Kamelin s.s.—TYPE: *A. lineare* L.
 - 13.2. Sect. **CAMPANULATA** Kamelin.—TYPE: *A. xiphopetalum* Aitch.
 - 13.3. Sect. **Scabriscapa** (Tscholok.) N. Friesen.—TYPE: *A. scabriscapum* Boiss.
 - 13.4. Sect. **Nigrimontana** N. Friesen.—TYPE: *A. drobovii* Vved.
 - 13.5. Sect. **Sikkimensia** (Traub) N. Friesen.—TYPE: *A. sikkimense* Baker.
14. Subgen. **POLYPRASON** Radić.—TYPE: *A. moschatum* L. (ca. 50 spp.).
- 14.1. Sect. **SCORODON** Koch s.s.—TYPE: *A. moschatum* L.
 - 14.2. Sect. **OREIPRASON** F. Herm. (including sect. **Petroprason** F. Herm.).—TYPE: *A. saxatile* M. Bieb.
 - 14.3. Sect. **Falcatifolia** N. Friesen.—TYPE: *A. carolinianum* DC.
 - 14.4. Sect. **Daghestanica** (Tscholok.) N. Friesen.—TYPE: *A. daghestanicum* Grossh. (2 subsects.).
15. Subgen. **CEPA** (Mill.) Radić.—TYPE: *A. cepa* L. (ca. 30 spp.).
- 15.1. Sect. **CEPA** (Mill.) Prokh.—TYPE: *A. cepa* L.
 - 15.2. Sect. **ANNULOPRASON** T. V. Egorova.—TYPE: *A. fedtschenkoanum* Regel.
 - 15.3. Sect. **Condensatum** N. Friesen.—TYPE: *A. condensatum* Turcz.
 - 15.4. Sect. **SACCULIFERUM** P. P. Gritz.—TYPE: *A. thunbergii* G. Don (*A. sacculiferum* Maxim.).
 - 15.5. Sect. **SCHOENOPRASUM** Dumort.—TYPE: *A. schoenoprasum* L.
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