Phylogeny and New Intrageneric Classification of Allium (Alliaceae) Based on Nuclear Ribosomal DNA ITS Sequences

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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, Dicholostemma, 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. Reticulatobulbosa and Oreiphrax were non-monophyletic taxa. Based on the phylogenetic relations, a new classification of genus Allium consisting of 15 monophyletic subgenera is presented. Sections Microscordium, Anguinum, Porphyroprason, Vvedenska, Butomissa, Cyathophora, and Reticulatobulbosa are raised to subgeneric rank. Sections Austromontana N. Friesen, Eduardia N. Friesen, Mediasia F. O. Khassanov, S. C. Yenaghcheva et N. Friesen, Nigermontana N. Friesen, Falcatifolia N. Friesen, and Condensatum N. Friesen are newly described. Series Daghestanica, Pallisia, and Scabriskapa, as well as subsects. Eremoprason, 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 about 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 sulphotides 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 Aliioidea 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 Alliioidea 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 species (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. Codonoprason, 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. *Rhzizideum* 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. *Rhzizideum* 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. *Rhzizideum*: 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 paraplyletic origin of some *Allium* subgenera and sections (Mes et al. 1997, 1999; Klaas and Friesen 2002), we used a relatively dense taxon sample, representing most 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 sequence evolution were first evaluated with Modeltest (Posada and Crandall 1998) and combined in single consensus sequences. The sequences 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 *Iphelion* Raf., *Tulbaghia* L., and *Dichelostenma* Kunth, and two species of *Nectaroscordum* 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 numbers of sequence evolution were first evaluated with Modeltest

**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], 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 10μL 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-8F, ITS-8R (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 CLUSTAL_X (Thompson et al. 1997) and the alignment was manually adjusted where necessary. Phylogenetic 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 [ ].

| New classification | Traditional classification | Species | 2n | TAX | Origin | EMBL |
|--------------------|-----------------------------|---------|----|-----|--------|------|
| Allium/Allium       | Allium                      | A. ampoloprasum L. | 32 | 2198 | BULGARIA: Arkutino | AJ411888 |
| Allium/Allium       | Allium/Allium               | A. atroviolaceum Boiss. | 32 | 5576 | TURKEY: vil. Antalya, Saklikent | AJ411894 |
| Allium/Allium       | Allium/Allium               | A. dregeanum Kunth | 64 | 5722 | SOUTH AFRICA | AJ411962 |
| Allium/Allium       | Allium/Allium               | A. iranicum (Wendelbo) Wendelbo | 32 | 3969 | IRAN: Asara, Elburz Range, Karaj Valley | AJ411961 |
| Allium/Allium       | Allium/Allium               | A. sativum L. | 16 | 1319 | TAJIKISTAN: BG Dushanbe | AJ411901 |
| Allium/Allium       | Allium/Allium               | A. scorodoprasum L. | 16 | 2290 | BULGARIA: Plovdiv | AJ412713 |
| Allium/Allium       | Allium/Allium               | A. sphaerocephalum L. | 16 | 5337 | TURKEY: vil. Denizli, Boz Dagi | AJ412717 |
| Allium/Allium       | Allium/Allium               | A. turkestanicum Regel | 16 | 3366 | UZBEKISTAN: Malguzar Mts., Dzhizakh | AJ411968 |
| Allium/Allium       | Allium/Allium               | A. turkestanicum Regel | 16 | 5049 | KAZAKHSTAN: Karatau Range, Mt. Ulden-Burul | AJ412718 |
| Allium/Avulaea       | Allium/Scorodon             | A. griffithianum Boiss. | 16 | 3660 | UZBEKISTAN: Zaravshan Range, Pass Takhta-Karachi | AJ411862 |
| Allium/Avulaea       | Allium/Scorodon             | A. umbilicatum Boiss. | 16 | 2646 | IRAN: BG Tehran [Mosha] | AJ412719 |
| Allium/Brevidentia   | Allium/Brevidentia          | A. brevivens Vved. | 16 | 5037 | UZBEKISTAN: vil. Zevar, SW Hissar Range | AJ412721 |
| Allium/Brevidentia   | Allium/Scorodon             | A. hanelitii Khasanov et R. M. Fritsch | 5796 | | | |
| Allium/Brevipathea   | Allium/Brevipathea          | A. margaritae B. Fedtsch. | H658 | | KAZAKHSTAN: Chu-Ili Mts., Kuram Mts., Chorkeser | AJ412725 |
| Allium/Brevipathea   | Allium/Brevipathea          | A. cupanii Raf. subsp. hirtovaginatum (Kunth) Stearn | 16 | 5336 | TURKEY: vil. Demizli, Boz Dagi | AJ412737 |
| Allium/Caerulea      | Allium/Scorodon             | A. caeruleum Pall. | 16 | 1525 | RUSSIA: BG Moscow | AJ411903 |
| Allium/Caerulea      | Allium/Scorodon             | A. caeruleum Pall. | 16 | 3735 | KAZAKHSTAN: Chu-Ili Mts., Kurdam Pass | AJ412729 |
| Allium/Caerulea      | Allium/Scorodon             | A. caesium Schrenk | 32 | 2561 | TAJIKISTAN: Turkestan Range, Kusavlsai | AJ412731 |
| Allium/Caerulea      | Allium/Scorodon             | A. elegans Drob. | 16 | 3688 | KAZAKHSTAN: Karatau Range, Mt. Ulken-tura | AJ412730 |
| Allium/Caerulea      | Allium/Scorodon             | A. litinovii Drob. ex Vved. | 16 | 3339 | KIRGIZSTAN: Alaí Range, Pass Chigirichik | AJ412727 |
| Allium/Caerulea      | Allium/Scorodon             | A. flavum L. | 16 | 3230 | AUSTRIA: BG Linz | AJ411926 |
| Allium/Caerulea      | Allium/Scorodon             | A. melantherum Vved. | 16 | 2579 | GEORGIA: Tbilisi, Narikala | AJ412712 |
| Allium/Caerulea      | Allium/Scorodon             | A. melanantherum Panicé | 3092 | | UK: BG Reading | AJ412739 |
| Allium/Caerulea      | Allium/Scorodon             | A. paniculatum L. | 16 | 3828 | ITALY: Sardinia, La Corte | AJ411949 |
| Allium/Caerulea      | Allium/Scorodon             | A. rupestre Steven | 16 | 5302 | TURKEY: vil. Kastamonu, AYLI-DAGI Mts. | AJ412733 |
| Allium/Costulatae    | Allium/Allium               | A. filidens Regel | 16 | 3674 | KAZAKHSTAN: W foothills of Karatau Range | AJ412723 |
| Allium/Costulatae    | Allium/Allium               | A. filidentiforme Vved. ex Kashl. et Nikitin | 16 | | TAJIKISTAN: Turkestan Range, Shakhrisam Range | AJ412722 |
| Allium/Crystallina   | Allium/Allium               | A. crystallinum Vved. | 16 | 2573 | TAJIKISTAN: Turkestan Range, Shakhrisam Pass | AJ412722 |
| Allium/Kopetadagia   | Allium/Scorodon             | A. eremoasprum Vved. | 16 | 5243 | UZBEKISTAN: SW Hissar Range, Derbent | AJ412724 |
| Allium/Kopetadagia   | Allium/Scorodon             | A. kopetadagense Vved. | 16 | 5802 | UZBEKISTAN: Aktuu Mts. | AJ412726 |
| Allium/Minuta        | Allium/Scorodon             | A. parvulum Vved. | 16 | 5055 | TURKMENISTAN: Kopetdag Mts. | AJ411950 |
| Allium/Pallasia      | Allium/Scorodon             | A. schonepnoprassioide Regel | 16 | 2903 | KIRGIZSTAN: Talat-Altaiu Range, Talas | AJ412720 |
| Allium/Pallasia      | Allium/Scorodon             | A. tanguticum Regel | 16 | 3779 | KAZAKHSTAN: Trans-Altaiu Range, Valley | AJ412728 |
| Polyprason/Scorodon  | Allium/Scorodon s.s.        | A. moschatum L. | 16 | 2654 | CHINA: Tibet | AJ411893 |
| Polyprason/Scorodon  | Allium/Scorodon s.s.        | A. moschatum L. | 16 | 2654 | GEORGIA: Tbilissi (GAT) | AJ411872 |
| New classification Subgenus/Section | Traditional classification Subgenus/Section | Species | 2n | TAX | Origin | EMBL   |
|------------------------------------|---------------------------------------------|---------|-----|-----|--------|--------|
| Polyprason/Scorodon Allium/Scorodon | A. inaequale Janka                          | 5752    | S   | RUSSIA: Krasnodar, W Caucasus | AJ412735 |
| Polyprason/Scorodon Allium/Scorodon | A. panicicum Wendelbo                       | 1657    | PAKISTAN: Karakorum (GAT)      | AJ412736 |
| Allium? (perhaps a new section)     | A. macrostemon Bunge                        | 16      | MONGOLIA: Somon Matal          | AJ412738 |
| Vvedenskya/Vvedenskya Allium/Vvedenskya | A. kujukense Vved.                         | 20      | KAZAKHSTAN: Karatau Range, Pass Kuyuk | AJ411947 |
| Amerallium/Sordin/Microsordum       | A. flavum Maxim.                            | 5617    | RUSSIA: Far East, Khabarovsky, Ussuri Lowland | AJ411943 |
| Amerallium/Sordin/Microsordum       | A. flavum Maxim.                            | 5618    | RUSSIA: Far East, Vladivostock | AJ412745 |
| Amerallium/Molinum/Microsordum      | A. moly L.                                  | 1117    | GERMANY: Gatersleen, house garden | AJ412743 |
| Amerallium/Molinum/Microsordum      | A. subhirsutum L.                           | 1117    | ITALY: BG Palermo [Adiacenze di Petralia] | AJ411912 |
| Amerallium/Narkissoprason           | A. insubricum Boiss. et Reut.               | 1117    | GERMANY: ‘Wyoming Pink’, Gesellschaft der Staudenfreunde | AJ250298 |
| Nectaroscordum/Compactosordum       | A. neriflorum (Herb.) Baker                 | 2397    | USA: D. McNeal, Stockton [California, Lake Co.] | AJ411932 |
| Melanocrommyum/Acroprason           | A. backhausianum Regel                      | 1502    | TAJIKISTAN: BG Khorog          | AJ412746 |
| Melanocrommyum/Acroprason           | A. savorowii Regel                          | 16      | KAZAKHSTAN: Chu-Ili Mts., Georgievka | AJ411934 |
| Melanocrommyum/Papilosa             | A. aroids Popov et Vved.                    | 2517    | UZBEKISTAN: BG Tashkent        | AJ411915 |
| Melanocrommyum/Thaumato-           | A. sergii Vved.                             | 16      | KAZAKHSTAN: Karatau Range, Valley Ikonizu | AJ411936 |
| Melanocrommyum/Brevicaule           | A. komarowii Lipsky                         | 16      | TAJIKISTAN: Saravshan Range, Lake Is-kanderkul | AJ411967 |
| Melanocrommyum/Compactosordum       | A. cristophii Trautv.                       | 16      | UK: BG Manchester              | AJ411966 |
| Melanocrommyum/Brevicaule           | A. sarawuschanicum Regel                    | 16      | UZBEKISTAN: Zaravshan Range, Pass Takhta-Karachi | AJ411935 |
| New classification Subgenus/Section | Traditional classification Subgenus/Section | Species | 2n | TAX | Origin | EMBL |
|-----------------------------------|---------------------------------------------|---------|----|-----|--------|------|
| Melanocrommyum/Megalo-prason      | Melanocrommyum/Megalo-prason                | A. stipitatum Regel | 16 | 2257 | TAJIKISTAN: Hissar Range, Romit Reservation | AJ411911 |
| Melanocrommyum/Melano-crommyum    | Melanocrommyum/Melano-crommyum              | A. nigrum L. | 16 | 1650 | GERMANY: BG Leipzig | AJ411965 |
| Melanocrommyum/Miniprason         | Melanocrommyum/Miniprason                    | A. noeanum Reut. ex Regel | 16 | 3940 | IRAN: Prov. Azerbaijan, Miyaneh | AJ411970 |
| Melanocrommyum/Popovia            | Melanocrommyum/Popovia                      | A. gypsaceum Popov et Vved. | 16 | 3661 | UZBEKISTAN: SW Hissar Range, Dakhkanabad | AJ411969 |
| Porphyrprason/Porphyrprason       | Porphyrprason/Porphyrprason                  | A. oreophilum C. A. Mey. | 16 | 0348 | AUSTRIA: BG Graz | AJ411931 |
| Melanocrommyum/Pseudo-prason      | Melanocrommyum/Pseudo-prason                 | A. regelii Trautv. | 16 | 5255 | TURKMENISTAN: Central Kopetdag, Gyaurus | AJ411972 |
| Anguinum/Anguinum                 | Rhizirideum/Anguinum                         | A. microdictyon Prokh. | 16 | 1300 | RUSSIA: BG Kirovsk [Altai] | AJ411859 |
| Anguinum/Anguinum                 | Rhizirideum/Anguinum                         | A. ovatifolium Hand.-Mazz. | 16 | 5092 | CHINA: Prov. Qinghai, Beisha National Park | AJ411882 |
| Anguinum/Anguinum                 | Rhizirideum/Anguinum                         | A. tricoccum Sol. | 16 | 2582 | USA: Glencoe, J. F. Swenson | AJ411917 |
| Anguinum/Anguinum                 | Rhizirideum/Anguinum                         | A. victoriais L. | 16 | 2673 | GEORGIA: Caucasus | AJ411919 |
| Cepal/Annuloprason                | Rhizirideum/Annuloprason                     | A. atrasanguineum Kar. et Kir. | 16 | 2912 | KAZAKHSTAN: Trans-Ili Range, Valley Almaatinka | AJ411864 |
| Cepal/Annuloprason                | Rhizirideum/Annuloprason                     | A. fedschenkoanum Regel | 16 | 2560 | TAJIKISTAN: Turkestan Range, Kusavlisai | AJ411916 |
| Cepal/Annuloprason                | Rhizirideum/Annuloprason                     | A. monadelphum Turcz. ex Kar. et Kir. | 16 | 1643 | KIRGYZSTAN: Alai Mts. (GAT) | AJ411894 |
| Cepal/Annuloprason                | Rhizirideum/Annuloprason                     | A. semenowii Regel | H628 | KIRGYZSTAN: Centr. Than-Schan (TASH) | AJ411897 |
| Cepal/Annuloprason                | Rhizirideum/Annuloprason                     | A. weschniakowii Regel | H641 | KIRGYZSTAN: Issyk-kul (TASH) | AJ411946 |
| Butomissa/Butomissa               | Rhizirideum/Butomissa                        | A. ramosum L. | 32 | 2735 | KAZAKHSTAN: BG Alma-Ata | AJ250295 |
| Butomissa/Butomissa               | Rhizirideum/Butomissa                        | A. ramosum L. | 32 | 2735 | RUSSIA: Buryatia, Lake Gusinoe | AJ250293 |
| Butomissa/Butomissa               | Rhizirideum/Butomissa                        | A. tuberosum Rottl. ex Spreng. | 32 | 2454 | INDIA: Kashmir, Ladakh | AJ411914 |
| Rhizirideum/Caespitosoprason      | Rhizirideum/Caespitosoprason                 | A. bidentatum Fisch. ex Prokhorov | 32 | 2365 | MONGOLIA: Somon Erdenetsegan | AJ411861 |
| Rhizirideum/Caespitosoprason      | Rhizirideum/Caespitosoprason                 | A. bidentatum Fisch. ex Prokhorov | 32 | 3163 | RUSSIA: Altai Mts., Czemal | AJ311868 |
| Rhizirideum/Caespitosoprason      | Rhizirideum/Caespitosoprason                 | A. dentigerum Prokhorov | 16 | 5091 | CHINA: Prov. Qinghai, Xining | AJ411958 |
| Rhizirideum/Caespitosoprason      | Rhizirideum/Caespitosoprason                 | A. mongolicum Regel | 16 | 2373 | MONGOLIA: Tamsarbulag | AJ411883 |
| Rhizirideum/Caespitosoprason      | Rhizirideum/Caespitosoprason                 | A. polyphyllum Turcz. ex Regel | 32 | 2359 | MONGOLIA: Aimak centre Barun urt, Talbulaq | AJ250296 |
| Reticulatobulbosa/Campanulata     | Reticulatobulbosa/Campanulata                | A. subangulatum Regel | H604 | MONGOLIA: Gobi Altai Mts. (GAT) | AJ411870 |
| Reticulatobulbosa/Campanulata     | Reticulatobulbosa/Campanulata                | A. drepanophyllum Vved. | 16 | 2791 | UZBEKISTAN: Chatkal Range, Bashkysylsai | AJ411854 |
| Reticulatobulbosa/Campanulata     | Reticulatobulbosa/Campanulata                | A. jodanithium Vved. | 16 | 1330 | TAJIKISTAN: Hissar Range, Kondara Valley | AJ411902 |
| Reticulatobulbosa/Campanulata     | Reticulatobulbosa/Campanulata                | A. minorensis ined. | H679 | KIRGYZSTAN: Talas Alatau Range (GAT) | AJ12748 |
| Reticulatobulbosa/Campanulata     | Reticulatobulbosa/Campanulata                | A. sordidiflorum Vved. | H630 | TAJIKISTAN: Sanglok Mts. (TASH) | AJ411899 |
| New classification Subgenus/Section | Traditional classification Subgenus/Section | Species | 2n | TAX | Origin | EMBL |
|-------------------------------------|--------------------------------------------|---------|-----|-----|--------|------|
| Reticulatobulbosa/Campanulata       | Rhizirideum/Campanulata                    | A. tenaicaule Regel | H632 | TAJIKISTAN: Hissar Range (TASH) | AJ411887 |
| Reticulatobulbosa/Campanulata       | Rhizirideum/Campanulata                    | A. tereifolium Regel | H633 | KAZAKHSTAN: Dzhungar Alatau Range (TASH) | AJ411886 |
| Reticulatobulbosa/Campanulata       | Rhizirideum/Campanulata                    | A. xiphopetalum Aitch. et Baker | 16 | 1070 | SWEDEN: BG Göteborg | AJ411858 |
| Cepa/Cepa                           | Rhizirideum/Cepa                           | A. altaicum Pall. | 16 | 0339 | LITHUANIA: BG Kaunas | AJ411928 |
| Cepa/Cepa                           | Rhizirideum/Cepa                           | A. alaicum Pall. | 16 | 2760 | RUSSIA: Sayan Mts, Tuva, Erzin | AJ412749 |
| Cepa/Cepa                           | Rhizirideum/Cepa                           | A. alaicum Pall. | 16 | 5561 | RUSSIA: Altai Mts., Yuzhno-Chuisky Range | AJ412750 |
| Cepa/Cepa                           | Rhizirideum/Cepa                           | A. asarense R. M. Fritsch et Matin | 16 | 3900 | IRAN: Elburz Range, Karaj Valley, Asara | AJ411937 |
| Cepa/Cepa                           | Rhizirideum/Cepa                           | A. cepa L. | 16 | 4878 | GERMANY: ‘Stuttgarter Riesen’ | AJ411944 |
| Cepa/Cepa                           | Rhizirideum/Cepa                           | A. cepa aggregatum cultivar group | 16 | 1810 | USA: Glencoe, J. F. Swenson | AJ411906 |
| Cepa/Cepa                           | Rhizirideum/Cepa                           | A. fistulosum L. | 16 | 41388 | JAPAN: ‘Long White Tokyo’ | AJ411918 |
| Cepa/Cepa                           | Rhizirideum/Cepa                           | A. galanthum Kar. et Kir. | 16 | 1729 | KAZAKHSTAN: BG Alma-Ata | AJ411905 |
| Cepa/Cepa                           | Rhizirideum/Cepa                           | A. oschaninii B. Fedtsch. | 16 | 5016 | KIRGIZSTAN: Turkestan Range, Dargun | AJ411940 |
| Cepa/Cepa                           | Rhizirideum/Cepa                           | A. praenixicum Vved. | 16 | 5712 | TAJIKISTAN: Mogoltau Range, Spa massif | AJ411873 |
| Cepa/Cepa                           | Rhizirideum/Cepa                           | A. pskemense B. Fedtsch. | 16 | 1994 | DENMARK: BG Copenhagen | AJ411907 |
| Cepa/Cepa                           | Rhizirideum/Cepa                           | A. vavilovii Popov et Vved. | 16 | 5238 | TURKMENISTAN: C. Kopetdag Range, Chuli | AJ411839 |
| Cepa/Cepa                           | Rhizirideum/Cepa                           | A. vavilovii Popov et Vved. | 16 | 5239 | TURKMENISTAN: C. Kopetdag Range, Chuli | AJ411840 |
| Cyathophora/Coleoblastus Bromatorrhiza/Coleoblastus | A. mairei Lev. | 16 | 2104 | SWITZERLAND: BG Zurich | AJ250298 |
| Cyathophora/Cyathophora Bromatorrhiza/Cyathophora | A. cyathophorum Bur. et Franch. | 16 | 2824 | NORWAY: BG Oslo | AJ250286 |
| Cyathophora/Milula Milula           | A. spicatum (Prain) N. Friesen | 16 | 2825 | NORWAY: BG Oslo | AJ411889 |
| Polyprason/Falcatifolia Rhizirideum/Oreiprason | A. carolinianum DC. | 16 | H680 | CHINA: Tibet, Tsangpo Valley (OSBU) | AJ230285 |
| Polyprason/Falcatifolia Rhizirideum/Oreiprason | A. spicatum (Prain) N. Friesen | 16 | H682 | CHINA: Tibet, Upper Cuamda Chu (OSBU) | AJ250284 |
| Polyprason/Condensatum Rhizirideum/Oreiprason | A. condensatum Turcz. | 16 | 2570 | TAJIKISTAN: Hissar Range, Anzob Pass | AJ250290 |
| Polyprason/Condensatum Rhizirideum/Oreiprason | A. condensatum Turcz. | 16 | 5619 | RUSSIA: Far East, Khabarovsk, Ussuri lowland | AJ412752 |
| Polyprason/Daghestanica Rhizirideum/Oreiprason | A. daghestanicum Grossh. | 16 | H663 | EAST MONGOLIA: (GAT) | AJ412752 |
| Polyprason/Daghestanica Rhizirideum/Oreiprason | A. ericetorum Thore | 16 | 1741 | GEORGIA: BG Bakuriani, [Daghestan] | AJ411850 |
| Polyprason/Daghestanica Rhizirideum/Oreiprason | A. ganibicum Miscz. ex Grossh. | 16 | 1547 | GERMANY: BG Leipzig | AJ311867 |
| Polyprason/Daghestanica Rhizirideum/Oreiprason | A. ganibicum Miscz. ex Grossh. | 16 | 2333 | GEORGIA: Caucasus, Chevsureti, Dusheti | AJ411890 |
| Butomissa/Austromontana Rhizirideum/Oreiprason | A. gigiticum Wang et Tang | 16 | H600 | PAKISTAN: Karakorum Range (GAT) | AJ411942 |
| Polyprason/Falcatifolia Rhizirideum/Oreiprason | A. hymenorrhizum Ledebo | 16 | 3135 | TAJIKISTAN: Saravshan Range, Lake Iskanderkul | AJ411879 |
| Polyprason/Oreiprason Rhizirideum/Oreiprason | A. kaschianum Regel | 16 | 2418 | TAJIKISTAN: BG Chorog [Pamir, Shakh-darya Mts.] | AJ412754 |
| Polyprason/Oreiprason Rhizirideum/Oreiprason | A. kaschianum Regel | 16 | 1612 | KAZAKHSTAN: Trans-Ili Range, Medeo | AJ411856 |
| Polyprason/Oreiprason Rhizirideum/Oreiprason | A. ochroleucum Waldst. et Kit. | 16 | 3763 | SLOVENIA: Steiner Alps | AJ411856 |
| Polyprason/Oreiprason Rhizirideum/Oreiprason | A. ochroleucum Waldst. et Kit. | 16 | 5578 | SLOVENIA: BG Ljubljana [Julische Alps] | AJ412755 |
| Polyprason/Oreiprason Rhizirideum/Oreiprason | A. ochroleucum subsp. pseudossuaveolens Zahar. | 16 | 2827 | ROMANIA: BG Cluj-Napoca | AJ411863 |
| Polyprason/Oreiprason Rhizirideum/Oreiprason | A. petraeum Kar. et Kir. | 16 | 3040 | KAZAKHSTAN: Chu-Ili Mts., Pass Kurdi | AJ411952 |
| New classification | Traditional classification | Species | 2n | TAX | Origin | EMBL |
|--------------------|---------------------------|---------|----|-----|--------|------|
| Polyprason/Falcatifolia | Rhizirideum/Oreiprason | A. platyspathum Schrenk | 16 | 2905 | KAZAKHSTAN: Trans-Ili Range, Valley Almaatinka | AJ411878 |
| Polyprason/Falcatifolia | Rhizirideum/Oreiprason | A. platyspathum subsp. ambylophyllum (Kar. et Kir.) N. Friesen | 16 | 2396 | RUSSIA: BG Novosibirsk | AJ411875 |
| Polyprason/Oreiprason | Rhizirideum/Oreiprason | A. roylei Stearn | 16 | 5152 | CZECH REPUBLIK: Olomouc | AJ411945 |
| Polyprason/Oreiprason | Rhizirideum/Oreiprason | A. setifolium Schrenk | 16 | H629 | UZBEKISTAN: (GAT) | AJ411898 |
| Polyprason/Daghestantica | Rhizirideum/Oreiprason | A. suaveolens Jacq. | 16 | 1603 | ITALY: BG Padua | AJ411874 |
| Polyprason/Oreiprason | Rhizirideum/Oreiprason | A. talassicum Regel | 16 | 3376 | CHINA: Prov. Xingjiang | AJ411865 |
| Polyprason/Oreiprason | Rhizirideum/Oreiprason | A. obliquum L. | 16 | 3158 | RUSSIA: Altai Mts., Lake Teletskoe | AJ4112753 |
| Reticulatobulbosa/Sikkimensia | Rhizirideum/Reticulatobulbosa | A. beeシアNum W. W. Sm. | 32 | 2211 | DENMARK: BG Copenhagen | AJ411860 |
| Reticulatobulbosa/Reticulatobulbosa | Rhizirideum/Reticulatobulbosa | A. chamaerense M. Ivanova | 16 | H645 | MONGOLIA: Chentei (GAT) | AJ411937 |
| Reticulatobulbosa/Reticulatobulbosa | Rhizirideum/Reticulatobulbosa | A. clathratum Ledeb. | 32 | 3165 | RUSSIA: Altai Mts., Chemal | AJ411855 |
| Reticulatobulbosa/Sikkimensia | Rhizirideum/Reticulatobulbosa | A. e. cyaneum Regel | 32 | 3872 | GERMANY: BG Tuebingen | AJ411880 |
| Reticulatobulbosa/Reticulatobulbosa | Rhizirideum/Reticulatobulbosa | A. d. d. Stearn | 16 | H622 | UZBEKISTAN: Ugamskij Chr. (TASH) | AJ411895 |
| Rhizirideum/Eduardia | Rhizirideum/Reticulatobulbosa | A. eduardii Stearn | 16 | 2761 | RUSSIA: Sayan Range, Tuva, Erzin | AJ411959 |
| Reticulatobulbosa/Reticulatobulbosa | Rhizirideum/Reticulatobulbosa | A. eduardii Stearn | 16 | 2745 | RUSSIA: Sayan Range, Tuva, Erzin | AJ4112756 |
| Reticulatobulbosa/Reticulatobulbosa | Rhizirideum/Reticulatobulbosa | A. eduardii Stearn | 16 | H644 | RUSSIA: Altai (GAT) | AJ411956 |
| Cyathophora/Coleoblastus | Rhizirideum/Reticulatobulbosa | A. kingdonii Stearn | 16 | H691 | CHINA: Tibet (OSBU) | AJ250298 |
| Reticulatobulbosa/Reticulatobulbosa | Rhizirideum/Reticulatobulbosa | A. k. F. O. Khassanov et N. Friesen | 16 | 5703 | UZBEKISTAN: Chatkal Range, Kuram et N. Friesen, Chorkesar | AJ411868 |
| Reticulatobulbosa/Reticulatobulbosa | Rhizirideum/Reticulatobulbosa | A. leucocapum Turcz. | 16 | H660 | RUSSIA: Burjatia, Dzhida (NSK) | AJ4112757 |
| Reticulatobulbosa/Reticulatobulbosa | Rhizirideum/Reticulatobulbosa | A. lineare L. | 16 | 5816 | N KAZAKHSTAN: vil. Kvievskoe | AJ411951 |
| Reticulatobulbosa/Reticulatobulbosa | Rhizirideum/Reticulatobulbosa | A. lineare L. | 16 | H624 | KAZAKHSTAN: (GAT) | AJ411951 |
| Reticulatobulbosa/Reticulatobulbosa | Rhizirideum/Reticulatobulbosa | A. m. N. Friesen | 16 | H653 | RUSSIA: Tuva, Sengilen (GAT) | AJ412758 |
| Rhizirideum/Reticulatobulbosa | Rhizirideum/Reticulatobulbosa | A. m. N. Friesen | 16 | 3390 | RUSSIA: Buryatia, NW Baikal, Muzhinai | AJ411838 |
| Reticulatobulbosa/Reticulatobulbosa | Rhizirideum/Reticulatobulbosa | A. m. N. Friesen | 16 | H603 | RUSSIA: North Baikal (GAT) | AJ411871 |
| Reticulatobulbosa/Nigrimonstana | Rhizirideum/Reticulatobulbosa | A. oreoprasoides Vved. | 16 | H627 | UZBEKISTAN: West Than-Shan (TASH) | AJ411889 |
| Butomissus/Austromontana | Rhizirideum/Reticulatobulbosa | A. oreoprasum Schrenk | 16 | 3643 | KAZAKHSTAN: Trans-Ili Range, Turgen Valley | AJ411867 |
| Reticulatobulbosa/Reticulatobulbosa | Rhizirideum/Reticulatobulbosa | A. oreoprasum Schrenk | 16 | 5000 | KIRGIZSTAN: Talas-Alatau Range, Pass Otme | AJ411933 |
| Rhizirideum/Canesploropson | Rhizirideum/Reticulatobulbosa | A. przewalskianum Regel | 32 | 5089 | CHINA: Prov. Qinghai, Lake Koko Nor | AJ411852 |
| Reticulatobulbosa/Reticulatobulbosa | Rhizirideum/Reticulatobulbosa | A. r. N. Friesen | 16 | 5737 | RUSSIA: Lake Baikal, Golousnok | AJ411869 |
| Reticulatobulbosa/Scabri-scapa | Rhizirideum/Reticulatobulbosa | A. s. Boiss. | 16 | 3898 | IRAN: Prov. Tehran, Merdabat | AJ411881 |
| Reticulatobulbosa/Sikkimensia | Rhizirideum/Reticulatobulbosa | A. sikkimensis Baker | 48 | H670 | CHINA: SE Tibet, Lhasa (GAT) | AJ411885 |
| Reticulatobulbosa/Reticulatobulbosa | Rhizirideum/Reticulatobulbosa | A. s. Schult. et Schult. f. | 48 | 3384 | RUSSIA: Buryatia, NW shore of Lake Bai- kal, f. | AJ411927 |
| Reticulatobulbosa/Reticulatobulbosa | Rhizirideum/Reticulatobulbosa | A. strictum Schrad. | 48 | 5404 | RUSSIA: upper Enisey River, Shushenskoe | AJ411951 |
| Reticulatobulbosa/Flavi-scordum | Rhizirideum/Reticulatobulbosa | A. sulphureum Vved. | 16 | H648 | TAJIKISTAN: Pamiro-Alai, Gasimaylik | AJ412759 |
| New classification Subgenus/Section | Traditional classification Subgenus/Section | Species | 2n | TAX  | Origin | EMBL |
|------------------------------------|-------------------------------------------|---------|----|------|--------|------|
| Reticulatobulbosa/Flavi-scorbium    | Rhizirideum/Reticulatobulbosa             | A. trachyscorbium Vved. | 16 | 3998 | KIRGIZSTAN: Talas, Talas-Alatau Range | AJ411857 |
| Reticulatobulbosa/Reticulato-bulbosa| Rhizirideum/Reticulatobulbosa             | A. abscolum Regel      | 32 | 2769 | RUSSIA: Tuva, Erzin, Sayan Range   | AJ411960 |
| Rhizirideum/Rhizirideum            | Rhizirideum/Rhizirideum                  | A. albidum Fisch. ex Bieb. | 16 | 3765 | AUSTRIA: BG Graz [Serbia, Deliblatska Pecara] | AJ411841 |
| Rhizirideum/Rhizirideum            | Rhizirideum/Rhizirideum                  | A. angulosum          | 16 | 1977 | GEORGIA: Caucasus Range, Chevsuretia, Matso | AJ411892 |
| Rhizirideum/Rhizirideum            | Rhizirideum/Rhizirideum                  | A. albidum Fisch. ex Bieb. | 16 | 3470 | USA: Pepperell, M. McDonough [NE Tur- key] | AJ411954 |
| Rhizirideum/Rhizirideum            | Rhizirideum/Rhizirideum                  | A. angulosum L.       | 16 | 2778 | N KAZAKHSTAN: vil. Kiewskoe             | AJ250287 |
| Rhizirideum/Rhizirideum            | Rhizirideum/Rhizirideum                  | A. austrosibiricum N. Friesen | 16 | 2747 | RUSSIA: Tuva, Erzin, Sayan Range       | AJ411832 |
| Rhizirideum/Rhizirideum            | Rhizirideum/Rhizirideum                  | A. flavescens Bess.   | 16 | 5736 | N KAZAKHSTAN: vil. Kiewskoe             | AJ411842 |
| Rhizirideum/Rhizirideum            | Rhizirideum/Rhizirideum                  | A. incensiodorum Radic | 16 | 3764 | AUSTRIA: BG Graz                     | AJ411866 |
| Rhizirideum/Rhizirideum            | Rhizirideum/Rhizirideum                  | A. luxitunicum Lam.   | 32 | 2927 | GERMANY: Harz, Benzingerode              | AJ411831 |
| Rhizirideum/Rhizirideum            | Rhizirideum/Rhizirideum                  | A. nutans L.          | 32 | 3161 | RUSSIA: Gorno-Altaisk, Altai Mts.       | AJ411924 |
| Rhizirideum/Rhizirideum            | Rhizirideum/Rhizirideum                  | A. rubens Schrad.     | 16 | 1699 | KAZAKHSTAN: Temirtau                  | AJ411904 |
| Rhizirideum/Rhizirideum            | Rhizirideum/Rhizirideum                  | A. rubens Schrad.     | 16 | 3401 | RUSSIA: Altai Mts., Sailagem             | AJ411891 |
| Rhizirideum/Rhizirideum            | Rhizirideum/Rhizirideum                  | A. senescens L.       | 32 | 2750 | RUSSIA: Buryatiya, Lake Gusinoe         | AJ411834 |
| Rhizirideum/Rhizirideum            | Rhizirideum/Rhizirideum                  | A. spirale Wild.      | 32 | 1968 | NORTH KOREA: BG Wonsan [Prov. S-Hwanghe] | AJ411833 |
| Rhizirideum/Rhizirideum            | Rhizirideum/Rhizirideum                  | A. stellerianum Willd. | 32 | 5738 | N RUSSIA: Muchor, Lake Baikal           | AJ411963 |
| Rhizirideum/Rhizirideum            | Rhizirideum/Rhizirideum                  | A. togoshibi Hara     | 16 | 5221 | USA: Pepperell, M. McDonough               | AJ411843 |
| Rhizirideum/Rhizirideum            | Rhizirideum/Rhizirideum                  | A. trovincum (N. Friesen) N. Friesen | 16 | 2744 | RUSSIA: Tuva, Erzin, Sayan Range       | AJ411853 |
| Cepa/Saccifilferum                 | Rhizirideum/Saccifilferum                | A. chinense G. Don    | 24 | 2015 | CHINA: Prov. Yunnan, Kunming, market   | AJ411848 |
| Cepa/Saccifilferum                 | Rhizirideum/Saccifilferum                | A. chinense G. Don    | 32 | 3407 | JAPAN: Fukui, local strain              | AJ411948 |
| Cepa/Saccifilferum                 | Rhizirideum/Saccifilferum                | A. komarosvianum Vved. | 32 | 5646 | RUSSIA: Far East (LE)       | AJ412760 |
| Cepa/Saccifilferum                 | Rhizirideum/Saccifilferum                | A. thunbergii G. Don  | 16 | 1963 | NORTH KOREA: BG Wonsan [Kumgang-san Range, Prov. Karwon] | AJ411849 |
| Cepa/Schoenoprasum                 | Rhizirideum/Schoenoprasum               | A. altaicolicum N. Friesen | 32 | 0433 | GERMANY: Quedlinburg, breeder's strain | AJ411939 |
| Cepa/Schoenoprasum                 | Rhizirideum/Schoenoprasum               | A. karelinii Poljak.  | 16 | 2592 | JAPAN: Tsukuba Research Station       | AJ411876 |
| Cepa/Schoenoprasum                 | Rhizirideum/Schoenoprasum               | A. ledebouriason Schult. et Schult. f. | 16 | 3170 | RUSSIA: Altai Mts., Cholzun            | AJ411925 |
| Cepa/Schoenoprasum                 | Rhizirideum/Schoenoprasum               | A. maximowiczii Regel | 16 | 2772 | RUSSIA: Buryatiya, Romanovka        | AJ411877 |
| Cepa/Schoenoprasum                 | Rhizirideum/Schoenoprasum               | A. oliganthum Kar. et Kir. | 16 | 3201 | KAZAKHSTAN: Lake Zajsan                | AJ411835 |
| Cepa/Schoenoprasum                 | Rhizirideum/Schoenoprasum               | A. schmitzii Coutinho | 16 | 5226 | USA: Pepperell, M. McDonough           | AJ412761 |
| Cepa/Schoenoprasum                 | Rhizirideum/Schoenoprasum               | A. schoenoprasum subsp. la-tiorifollum (Pau) R. Martinez et al. | 32 | 5432 | SPAIN: Sierra de Guadarrama, Mt. Penarala | AJ411837 |
| Cepa/Schoenoprasum                 | Rhizirideum/Schoenoprasum               | A. schoenoprasum L.   | 16 | 3446 | RUSSIA: Far East, Peninsula Chukotka   | AJ411836 |
| Rhizirideum/Tenuissima             | Rhizirideum/Tenuissima                  | A. schoenoprasum L.   | 16 | 4214 | GERMANY: ‘Mittelgrober’                | AJ411938 |
| Rhizirideum/Tenuissima             | Rhizirideum/Tenuissima                  | A. anisopodium Ledebe. | 16 | 2349 | MONGOLIA: Aimak Chentij, Zargalant-chan | AJ411847 |
| Rhizirideum/Tenuissima             | Rhizirideum/Tenuissima                  | A. tenuissimun L.     | 16 | 3249 | NORTH KOREA: BG Pyongyang              | AJ411846 |
| Rhizirideum/Tenuissima             | Rhizirideum/Tenuissima                  | A. vodopyanovae N. Friesen | 16 | 5402 | RUSSIA: W Sayan Range, Khakasia       | AJ411942 |
| Rhizirideum/Tenuissima             | Rhizirideum/Tenuissima                  | A. vodopyanovae N. Friesen | 16 | 3192 | RUSSIA: Altai Mts., Ust-Koksa, Kyrlyk   | AJ411845 |
| Ipheion                            | Ipheion                                 | I. uniflorum (Graham) Raf. | 12 | 3458 | NETHERLAND: BG Amsterdam             | AJ250288 |
| Tulbaghia                          | Tulbaghia                               | T. simleri Beav. (= T. fra-grans Verdoorn) | 12 | 2165 | UK: London, Chelsea Physic Garden     | AJ250300 |
| Nothoscorodum                      | Nothoscorodum                           | N. bivalve (L.) Britton | 18 | 2621 | SWEDEN: BG Göteborg                   | AJ250301 |
| Dichelostemma                      | Dichelostemma                           | D. multiflorum (Benth.) Heller | 18 | 0494 | USA: California, BG Berkeley [Shasta Co.] | AJ412714 |
vers. 3.06 (Posada and Crandall 1998) and TrN + $\Gamma$ 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 (Swofford 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 + $\Gamma$ model of sequence evolution, sampling a tree every 100 generations. The first 200 (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*: *Iphion 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 rDNA, 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. hanetii* (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 *Cyaithophora* (*A. cyaithophorum*, 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. *Reticulatobulbosa*) is sister group to the rest of subgen. *Rhizirideum* and *Allium*, sects. *Cyathophora*, *Coleoblastus*, and *Milula* are sister group to all other sections of subgenera *Rhizirideum* and *Allium*, sects. *Rhizirideum*, *Caespitosoprasion*, *Tenuissima*, and *A. eduardii* (sect. *Reticulatobulbosa*) 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*, *Reticulatobulbosa*, 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. *Reticulatobulbosa* appear in three groups, (i) *Reticulatobulbosa* s.s., (ii) a small group of the four species (*A. trachyscordum*, *A. scribiscapum*, *A. sulphureum*, and *A. drobovii*), which are more closely related to sect. *Campanulata*, and (iii) all Chinese-Himalayan species with blue flowers (*A. beeianum*, *A. forrestii*, *A. aciphyllum*, *A. sikkimenense*, 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. filfolium*, *A. carolinianum*, *A. kaschianum*, and *A. hymenorrhizum*, and (iv) the Caucasian-European clade with *A. gunibicum*, *A. ericetorum*, *A. daghestanicum*, *A. ochroleucum*, and *A. suaveolens*.  

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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.
Polypliods and Hybrid Taxa

Twenty-eight Allium species (14%) included in the analysis were polypliods (see Table 1). In the worst case in terms of phylogenetic analysis, these might be allopliods 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 polypliod taxa on our phylogenetic reconstruction, we excluded all polypliod 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 polypliod 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 assure 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 Graechn., 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., Bull. Acad. Imp. Sci. Saint-Pétersbourg 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. Chamaeprasion (F. Hermann) Garbari, Taxon 24: 541 (1975).—TYPE: A. chamaemoly L.

Besides the sections mentioned above as synonymous subgenera, the American sects. Lophioprasion (Fig. 4), Amerallium, and Rhophoetoprasion, as well as the Old World sects. Arctoprasum (Fig. 5), Briseis, Narkissoprasion, Molium (Fig. 7) and Bromatorrhiza (Fig. 6) are included. Section Rhynchoscarpus possibly also belongs here. Molecular data underline the existence of two sister alliances: a rather divergent 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. Arctoprasum).—6. *A. hookeri* (sect. Bromatorrhiza).—7. *A. moly* (sect. Molium).—8. *A. oreophilum* (sect. Porphyroprason).—9. *A. nerinilorum* (sect. Caloscordum).—10. *A. cupuliferum* Regel (sect. Regeloprasum).—11. *A. nigrum* (sect. Melanocrommyum).—12. *A. cristophii* (sect. Kaloprasum).—13. *A. ramosum* (sect. Butomissa).—14. *A. cyathophorum* (sect. Cyathophora).
Fig. 15–26.—Plant portraits.—15. *Allium przewalskianum* (sect. *Caespitosoprason*).—16. *A. mongolicum* (sect. *Caespitosoprason*).—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. *Caulorhizeum*, *Lophioprason*, *Melium*, 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. *Rhizideum*. A more advanced nectarial structure was stated for rhizomatous species only (Fritsch 1992b).

Hyogepal 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, subtaneous 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* var. *vendexyi* 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. tricoccum*) 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 type, by two or three foliage leaves having a distinct petiole part between basal sheath and the rather wide lamina (Kruse 1992a). Seed germination is hypogean, and the *A. victorialis*-type of seedlings is only present in this subgenus (Drusellmann 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. *Caloscordium*. Serological data point to close relationships to subgen. *Melanocrommyum* and *Bromotomosia* (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. gypscapeum* of sect. *Popovia*. Especially the lax inflorescence with rather few flowers and the small subglobe bulbs with several stalked side bulbs and membranous tunicas 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. Kopetadagia of subgen. Allium.

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

Sect. Melium 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, Megaleoprasum, Regeloprasum (Fig. 10) Kaloprasum (Fig. 12), and Acanthoprasum are rather large with about 15–35 species each, while sects. Compactoprasum, Pseudoprasum, Miniprasum, Brevicaule, Thaumasioprasum, and Verticillata are oligotypic including 2–8 species each. Sects. Acaule, Aroidea, and Popovia 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 species in Melanocrommyum or related subgenera. The seed testa of Melanocrommyum and Allium (as far as studied to date) are very similar showing convex periclinal walls with evenly verrucose ornamentation, and nearly straight anticlinal walls (Kruse 1994). The 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 all other species of subgen. Melanocrommyum and Allium (except 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 the only 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 Butomissia Salisb., Gen. Pl. fragm. cont. part Liriogumae: 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. Rhiizideum (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. Rhiizideum. 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. oreoprassum Schrenk.

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

Bulbs aggregated, outer tunics reticulate. Rhizome hori-
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. gigiticum 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. Butomiissa, 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 (Kruse 1992a). 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 nectarary 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. Umjet., Razr. Nar. Vede. [SAZU] 31: 250, 251 (1990).—TYPE: A. incensidorum 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), Caespitosoprason (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. antispodium (sect. Tenuissima), A. spirale (sect. Rhizirideum) occur also in Korea and far eastern Russia, as well as A. jogashii (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. **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 distinct growth form to sect. *Laza* species often have two or more cataphylls in the bulbs and comprises less closely related sections. The rather distinct *Spathulata* straight anticlinal walls of seed testa cells characterize sect. *Spathulata*.

Brevidentia and *Brevidentia* by Khassanov (1996, 2000) is widely supported by molecular analyses. Inclusion of *A. hanetii* 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 anticalinal 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), *Breviopatha*, and *Kopetdabiga* 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. pallastii* Murr.

Basionym: *Allium* ser. *Pallasia* Tzagolova, Novosti Sist. Vyssh. Nizsh. Rast. 53: 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. Inflорescencia densеque subglobosa, multiflora. Perigonii late campanulati phylla obusa. Filamenta perigonii breviora subulata, interiora inferne denticulata. Stylus exertus. Ovaryum ronduturo-triangularium, rubrum.

Plant 50–100 cm tall. Leaves 4–6, 1–2.5 cm broad, linear. Inflorescence submersical, dense, many-flowered. Flowers campanulate, tepals obtuse. Filaments slightly longer than tepals, inner filaments basally obovate. Style exerted. Ovary submersical 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 other rhizomatous groups and may underlie an ancient hybridogenous origin of this taxon. Section *Mediasia* is included here because the bulbous character dominates.

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

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

Sections *Reticulatobulbosa*, *Campanulata*, and the new sects. *Scabris capita*, *Nigrimontana*, and *Sikkimensis* 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. Reticulatobulbosa sect. Scabris capita** (Tscholok.) N. Friesen, comb. et stat. nov.—**TYPE:** *A. scabriscapum* Boiss. (Fig. 23).

Basionym: *Allium* ser. *Scabris capita* Tscholok, Zamecki Sist. Geogr. Rast. 31: 42 (1975).

*Allium scabriscapum* (including *A. eriocoleum* Vved.), *A. sulphureum*, and *A. trachyscyorum* represent this section. Except for the latter species, they have bright yellow flowers.
**ALLIUM subgen. Reticulatobulbosa sect. Nigrimontana** N. Friesen, sect. nov.—**TYPE:** A. drobовii Vved.

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

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

Here belong A. drobовii 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. Sikkimensis** (Traub) N. Friesen, comb. et stat. nov.—**TYPE:** A. sikkimense Baker.

*Basionym:* Allium subsect. Sikkimensis 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** Радiч, Razp. Slov. Akad. Znanosti Umetn., Razr. Nar. Vede. [SAZU] 31: 250, 253 (1990).—**TYPE:** A. moschatum L.

This subgenus comprises mainly the former sect. Orie­prason in the broad sense of Kamelin (1973), and sect. Sco­rodon in the strict sense (possessing bulbs with rhizomes; subsect. Moschata (Omelcz.) Tscholok.). We accept sect. Or­ieprason 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 (Kru­se 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 Радiч 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 scarious tunics. 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 ericitorum (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.) Радiч, Razp. Slov. Akad. Znanosti Umetn., Razr. Nar. Vede. [SAZU] 31: 250, 253 (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. Or­ieprason. 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 semicyllndrica fistulosae 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-
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. *Anguionum* 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 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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Baldwin, B. G. 1992. Phylogenetic utility of the internal transcribed spacers of nuclear ribosomal DNA in plants: an example from the Compositae. *Molec. Phylogen. Evol.*, 1: 3–16.
Appendix 1. Taxonomic conspectus of the genus *Allium* L.

First Evolutionary Line

1. Subgen. *Nectaroscordum* (Lindl.) Asch. et Graebn.—TYPE: *A. sicolum* Ucria (ca. 3 spp.).
   1.1. Sect. *Nectaroscordum* (Lindl.) Gren. et Godr.—TYPE: *A. sicolum* Ucria.

2. Subgen. *Microscordum* (Maxim.) N. Friesen.—TYPE: *A. monanthum* Maxim. (monotypic).
   2.1. Sect. *Microscordum* Maxim.—TYPE: *A. monanthum* Maxim.

3. Subgen. *Amarella* Traub.—TYPE: *A. canadense* L. (ca. 135 spp.).
   3.1. Sect. *Amarella* Traub.—TYPE: *A. canadense* L. (2 subsects.).
   3.2. Sect. *Lophoprason* Traub.—TYPE: *A. sanbornii* Wood.
   3.3. Sect. *Rhophetoprason* Traub.—TYPE: *A. glandulosum* Link et Otto.
   3.4. Sect. *Arctoprason* Kirschl. (*Ophthalmoscorodon* (Wallr.) Endl.)—TYPE: *A. ursinum* L.
   3.5. Sect. *Briseis* (Salish.) 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. *Molium* G. Don ex Koch.—TYPE: *A. roseum* L. (2 subsects.).
   3.10. Sect. *Narkisoprason* (F. Herm.) Kamelin.—TYPE: *A. narcissiflorum* Vill.
   3.11. Sect. *Rhyncho carpus* Brullo.—TYPE: *A. ruhmerianum* Asch.
   3.12. Sect. *Triptera* Kamelin et Seisums, nom. nud.—TYPE: *A. triptera* Nasir.

Second Evolutionary Line

4. Subgen. *Caloscor dum* (Herb.) R. M. Fritsch.—TYPE: *A. neriflorum* (Herb.) Baker (ca. 3 spp.).
   4.1. Sect. *Caloscor dum* (Herb.) Baker.—TYPE: *A. neriflorum* (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. *Porphyroprason* Ekberg—TYPE: *A. oreophilum* C. A. Mey. (monotypic).
   6.1. Sect. *Porphyroprason* Ekberg.—TYPE: *A. oreophilum* C. A. Mey.

7. Subgen. *Vvedensky a* (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. *Aemopetala* R. M. Fritsch.—TYPE: *A. backhosianum* 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. *Popoivia* 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. *Thaumasoprason* Wendelbo.—TYPE: *A. mirum* Wendelbo.
   8.15. Sect. *Verticillata* Kamelin.—TYPE: *A. verticillatum* Regel.

Third Evolutionary Line

9. Subgen. *Butomissa* (Salish.) N. Friesen.—TYPE: *A. ramosum* L. (ca. 4 spp.).
   9.1. Sect. *Butomissa* (Salish.) 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. *Coryliastus* Ekberg.—TYPE: *A. mairei* Lévl.
    10.3. Sect. *Mallula* (Prain) N. Friesen.—TYPE: *A. spicatum* (Prain) N. Friesen.

11. Subgen. *Rhezridium* (G. Don ex Koch) Wendelbo s.s.—TYPE: *A. senescens* L. (ca. 37 spp.).
    11.1. Sect. *Rhezridium* G. Don ex Koch s.s.—TYPE: *A. senescens* L.
    11.2. Sect. *Caespitosoprason* N. Friesen.—TYPE: *A. polyrhizum* Siev.
    11.3. Sect. *Rhizomatosa* (Ophioscorodon) N. Friesen.—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.

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. BREVIPATHA 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. Eremoprasmum (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. Reticulatobulbosa (Kamelin) N. Friesen.—TYPE: A. lineare L. (ca. 80 spp.).

13.1. Sect. RETICULATOBULBOSA Kamelin s.s.—TYPE: A. lineare L.

13.2. Sect. CAMPA NULATA Kamelin.—TYPE: A. xiphopetalum Aitch.

13.3. Sect. SCABRISCAPA (Tscholok.) N. Friesen.—TYPE: A. scabriscapum Boiss.

13.4. Sect. Nigrimontana N. Friesen.—TYPE: A. drohovii Vved.

13.5. Sect. SIKKIMEN SIA (Traub) N. Friesen.—TYPE: A. sikkimensis Baker.

14. Subgen. Polyprason Radic.—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. CEP A (Mill.) Radic.—TYPE: A. cepa L. (ca. 30 spp.).

15.1. Sect. CEP A (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. Grütz.—TYPE: A. thunbergii G. Don (A. sacculiferum Maxim.).

15.5. Sect. SCHIOENOPRASUM Dumort.—TYPE: A. schoenoprasum L.