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Geographic relations and morphological variation inside molecular clades of Central Asian *Allium* species of subg. *Melanocrommyum* (Amaryllidaceae)*)

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Molecular investigations using Internal Transcribed Spacer (ITS) sequences yieldied a dendrogram presenting about 40 well-separated clades but without resolving the phylogenetic relations of most of these clades. Many clades are composed of several species and subspecies differing morphologically and by geographic origin. About 30 of these clades are described in detail. They comprise about 70 Central Asian species and subspecies which are morphologically characterized. Their phenetic relations to taxa of the same and other clades as well as their current taxonomic affiliation are also discussed.

Fritsch R. M., 2012: Geographische Beziehungen und morphologische Variabilität innerhalb von molekularen Clades mittelasiatischer *Allium*-Arten des subg. *Melanocrommyum* (Amaryllidaceae).
Eine molekulare Analyse der ITS-Sequenzen ergab ein Dendrogramm mit etwa 40 gut getrennten Clades, ohne deren phylogenetischen Beziehungen zueinander klären zu können. Viele Clades enthalten mehrere morphologisch gut trennbare Arten und Unterarten unterschiedlicher geographischer Herkunft. Näher charakterisiert werden etwa 30 dieser Clades, die etwa 70 Taxa aus Mittelasien umfassen. Diese Taxa werden vorgestellt, ihre morphologischen Beziehungen zu ähnlichen Taxa innerhalb und außerhalb des jeweiligen Clades sowie ihre derzeitige taxonomische Einordnung werden diskutiert.

Keywords: *Allium* subg. *Melanocrommyum*, morphology, geographic distribution, molecular relations, classification.

Introduction

Central Asia belongs to the main centre of *Allium* diversity which is also comprising Southwest Asia and Asia Minor. The most recent inventory (Khassanov 2008) counted 224 *Allium* species in Central Asia, and eight more were described during the last three years. More than 70 species belong to subg. *Melanocrommyum* (Webb & Berthel.) Rouy which is the species-richest subgenus in Central Asia.

The post-Linnean taxonomic history of the species affiliated today to this subgenus started in the 19th century when about 25 species were described, most of them by Regel. In the first half of 20th century about 20 species were added mainly by Vvedensky. Up to the 1970th, these species were included in sect. *Molium* G. Don ex Koch following the sectional *Allium* classifications used by Regel and Vvedensky. Only Wendelbo (1969) pointed to many important differences between these species and those taxa forming sect. *Molium* in the strict sense. He accepted both supra-sectional groups at subgeneric level. Kamelin (1973) followed Wendelbo's point of view to accept *Melanocrommyum* at subgeneric level but proposed a different circumscription and partitioning. That proposal was not accepted in the scientific literature during the next decades. Nearly 20 years later, Hanelt et al. (1992) presented another detailed classification of subg. *Melanocrommyum* into 11 sections, among them newly described ones from Central Asia. A detailed study of Central Asian species led Khassanov & Fritsch (1994)

*) Dedicated to Franz Speta on the occasion of his 70th birthday.

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to describe four additional sections finally accepting 16 sections and 19 subsections in subg. *Melanocrommyum*. Another classification of subg. *Melanocrommyum* by SEISUMS (1994) modified KAMELIN's (1973) proposal and accepted five sections and 14 subsections, but one new section and five new subsections were never validly described. During the last six decades about 40 more new species were affiliated by different authors to subg. *Melanocrommyum*, which currently comprises about 160 species and subspecies (FRITSCH et al. 2010).

Application of several molecular markers confirmed generally the circumscription of subg. *Melanocrommyum* proposed by HANELT et al. (1992). Analysis of ITS (internal transcribed spacer of nuclear ribosomal DNA) sequences (FRIESEN at al. 2006) corroborated the monophyly of subg. *Melanocrommyum* when the sections *Porphyroprason* EKBERG, *Vvedenskya* KAMELIN, and *Caloscordum* (HERB.) BAKER are excluded. On the other hand, these sections as well as sect. *Anguinum* G. DON ex KOCH are the closest relatives of subg. *Melanocrommyum*; they were also accepted at subgeneric level. These subgenera constitute together the second, moderately advanced evolutionary lineage of the genus *Allium* (FRIESEN at al. 2006). However, the topology of the rather few *Melanocrommyum* species included showed some conflict with the classification of KHASSANOV & FRITSCH (1994).

A comprehensive molecular investigation allowed to recognize about 40 well separated molecular clades within the subgenus (FRITSCH et al. 2010) and confirmed earlier results (GURUSHIDZE et al. 2008, 2010) that most classical sections are either para- or polyphyletic and must be divided up. Also the addition of about 100 accessions resulted in a similar dendrogram (GURUSHIDZE unpubl.). It consists of a basal grade (Fig. 1, lower part) and a core clade where the exact phylogenetic relations of most subclades representing sections and subsections of subg. *Melanocrommyum* remained as unresolved as shown in FRITSCH et al. (2010). Several sectors of this dendrogram containing species from Central Asia are presented in the Figures 1 (upper part) and 2 to 6. These groups and the species mentioned therein will be introduced and discussed below.

Results

Sections and species of the basal grade

The most basal section *Longibidentata* (R. M. FRITSCH) R. M. FRITSCH comprises two morphologically very similar species occurring in the western Tianshan mountain range, *A. fetisowii* REGEL (feti, Fig. 7) and *A. chychkanense* R.M. FRITSCH (chyc, Fig. 8). The latter taxon differs by shorter and broader leaves and by completely backwards turned tepals. Phylogenetically closely related are the species of sect. *Decipientia* (OMELCZUK) R. M. FRITSCH where most basal the West Caucasian *A. decipiens* FISCH. ex SCHULT. & SCHULT. f. was inserted (only subsp. *quercetorum* SEREGIN [quer] could be investigated, Fig. 9). They are characterized by rose-lilac flowers and narrow linear leaves. The south Siberian *A. viridulum* LEDEB. (virm), rather small plants with narrow leaves, and *A. tulipifolium* Ledeb. (tufo, Fig. 14), larger and rather broad-leafed plants with pale lilac flowers, belong also here. Nested within the latter species is *A. chelotum* WENDELBO (chel, Fig. 12) from the Hyrcanian area of northern Iran. This large species owns also broad leaves but rose-pinkish flowers and striking six-angular ovaries. More separate is the position of another south Siberian species, *A. robustum* KAR. & KIR. (robm) differing by purple flowers (Fig. 10). Within the basal clade, the evolution of ITS sequences is rather congruent with morphological differences at species levels.

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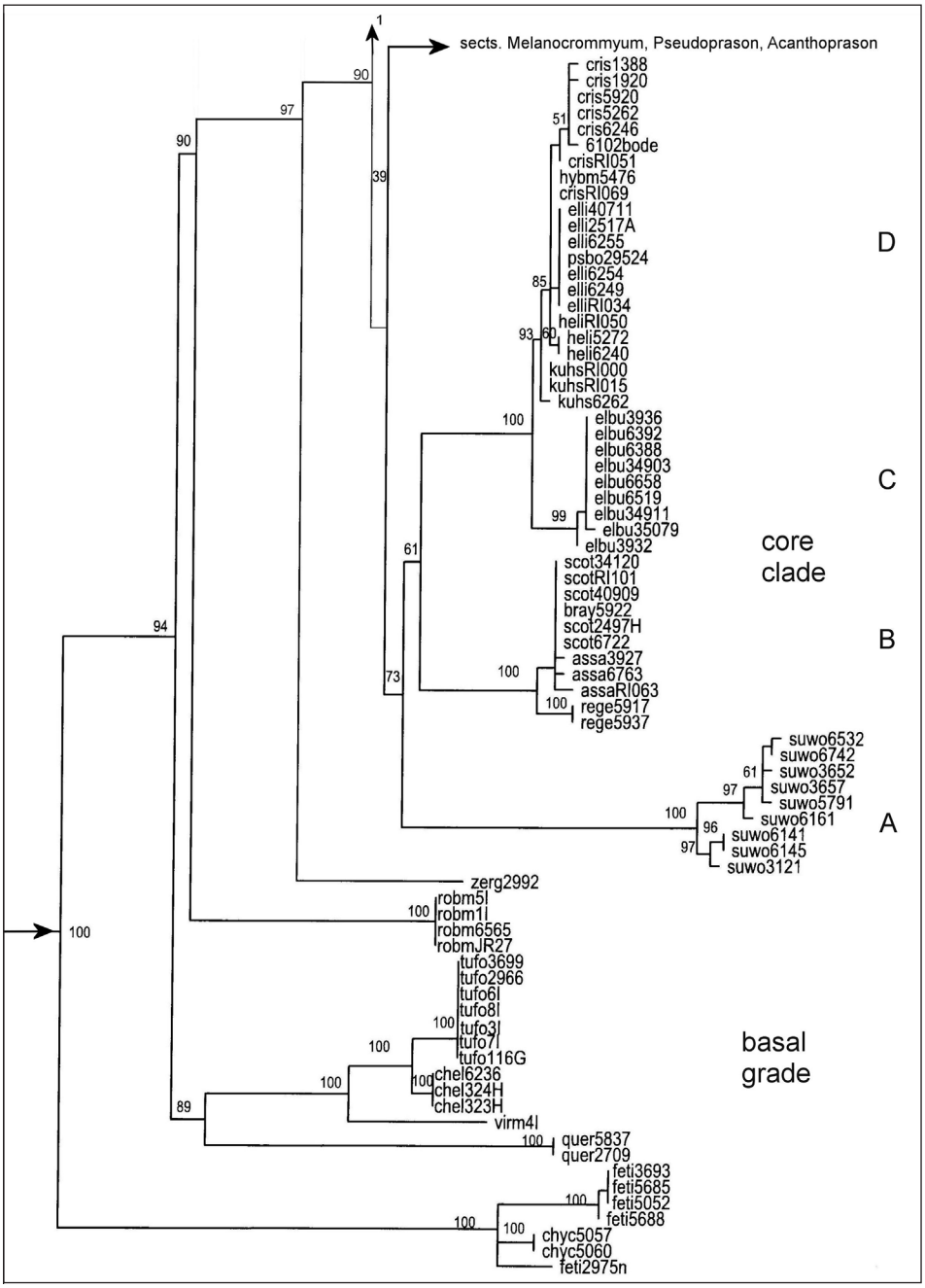

Fig. 1: Basal sector of a RAxML dendrogram based on ITS sequences of subg. *Melanocrommyum* showing the basal grade and the basal part of the core clade. Arrowhead 1 marks the connection to the bottom of Fig. 2. – Abb. 1: Basaler (erster) Abschnitt eines RAxML-Dendrogramms der ITS-Sequenzen von subg. *Melanocrommyum*, der die basalen sukzessiv abzweigenden Linien und den untersten Teil des Haupt-Clades zeigt. Pfeil 1 markiert den Anschluss zur Basis von Abb. 2.

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The only investigated accession of *A. zergericum* F. O. KHASS. & R. M. FRITSCH (zerg) is intermediate between the basal grade and the upper clade at more advanced position. Investigation of more material seems essential to verify this special position. Very peculiar is the whitish-crème tepal color (Fig. 11), but otherwise the plants are similar to those of sect. *Acmopetala* at position M.

Sections and species of the core clade

The core clade contains rather many bifurcations with bootstrap values below 80 and comb-like arrangements. Thus the phylogenetic relations of separated groups remain uncertain, and phylogenetically basal groups cannot be distinguished from advanced ones. Therefore the discussion will refer to the non-informative sequence of main clades in the dendrogram marked by uppercase letters.

The somewhat polymorphous *A. suworowii* REGEL (suwo, Fig. 13) forms a well separated clade (sect. *Megaloprason* WENDELBO subsect. *Spiralitunicata* R. M. FRITSCH) at position A. Our molecular data point to a rather high degree of diversification within this taxon. Despite of often high bootstrap values, the subgroups are not correlated to morphology or geography, and separation of formal infraspecific groups would not be justified.

Allium regelii TRAUTV. (rege, Fig. 18), the type species of sect. *Regeloprason*, forms the most basal subgroup of the clade at position B. This taxon is exceptional for the often multi-storey inflorescence (up to 5 superposed umbels were reported), but the flowers may also be lilac or white. Surprisingly, the other investigated members of this section are scattered over the whole dendrogram in the positions F, G, H, P, Q, R, T, and also inside of sect. *Melanocrommyum* WEBB & BERTHEL. (figure not shown). The reason for this topology is unknown. Perhaps it represents an ancient group whose members developed into different directions (demonstrated by very diverse leaf characters as well as variable density of inflorescences) but retained rather uniform flower characters (FRITSCH et al. 2010).

The second subgroup of clade B comprises Iranian members of sect. *Megaloprason* (subsect. *Humilicognata* R. M. FRITSCH).

The clades at the positions C and D are members of sect. *Asteroprason* R. M. FRITSCH distributed in Iran (until *A. kuhsorkhense* R. M. FRITSCH [kuhs]), and (upper subclade at position D) also in Turkmenistan in the Kopet Dagh mountain range. *Allium helicophyllum* VVED. (heli, Fig. 16) forms a well separated subgroup and differs morphologically by small soft tepals curled in the dry state and the name-giving spirally enrolled upper part of leaves. All other species possess triangular straw-like tepals becoming stiff and prickly by involute margins after anthesis, and straight leaves. Most subgroups were not well supported but separate the Iranian *A. ellisii* BAKER (elli; taxonomically still unclear) from at least two morphotypes of *A. cristophii* TRAUTV. (cris). Figure 15 shows the brownish-flowering form most common on the Iranian part of Kopet Dagh mountain range. Here also the hybrid cultivar ´Globemaster` (hybm5476) is included, but the accessions 6102bode and psbo29524 represent preliminarily named herbarium vouchers.

In the dendrogram follow several subclades comprising members of the sections *Melanocrommyum, Pseudoprason* (WENDELBO) K. PERSS. & WENDELBO, and *Acanthoprason* WENDELBO distributed solely in Southwest Asia and the Mediterranean. Their special morphological features will be discussed in other papers.

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The following sector of the dendrogram is shown in Figure 2. Two clades at position E represent the western subgroup (below) and the eastern subgroup (above) of *A. verticillatum* Regel (vert, Fig. 17). Jointly with *A. viridiflorum* Pobed. (vifl, Fig. 19, one accession between the positions P and Q) it belongs to sect. *Verticillata* Kamelin. These species differ strongly from all other members of subg. *Melanocrommyum* by leaf laminae longitudinally divided into several narrow, thread-like tips appearing as single leaves. Their positions in the dendrogram may represent cases of long-branch attraction (Gurushidze et al. 2008), i.e. inclusion of distantly related items at accidental positions in the dendrogram. Irrespective of the great molecular diversity inside of *A. verticillatum*, the members of both subgroups do not differ morphologically.

Great molecular diversity is also shown by members of sect. *Regeloprason* in the subclades at the positions F and H, but all members share loose inflorescences already when in buds. They grow in very different regions: *Allium cupuliferum* Regel (cupu, position F) occurs only in the mountains north and northeast of Samarkand (Uzbekistan) and is characterized by rather broad and thick leaves and straight tepals (Fig. 21). *Allium subkopetdagense* (R.M. Fritsch & F. O. Khass.) R.M. Fritsch grows along the northern spurs of Kopet Dagh mountain range and is distinguished by narrower and thinner leaves, a looser inflorescence, and by deflexed tepals (Fig. 20). An umbel-like inflorescence and rather pale flowers are special characters of *A. balkhanicum* (R.M. Fritsch & F. O. Khass.) R.M. Fritsch (balk, Fig. 22) which is only known from Great Balkhan massif in western Turkmenistan. Only very distantly related are two still undescribed species (adyl and isak-13Fer) occuring in the Fergan depression in eastern Uzbekistan, but *A. iliense* Regel (ilie) is growing on the northern spurs of western Tian-Shan mountain range in Kazakhstan, and *A. isakulii* R.M. Fritsch & F. O. Khass. (Fig. 23) in the Mogoltau massif in northwestern Tajikistan. The latter two species share very loose, large, and umbel-like inflorescences, but shape and tone of the more or less deep purple flowers are different. Also *A. cathodicarpum* Wendelbo (cath) occurring in Central Iran belongs to this subclade.

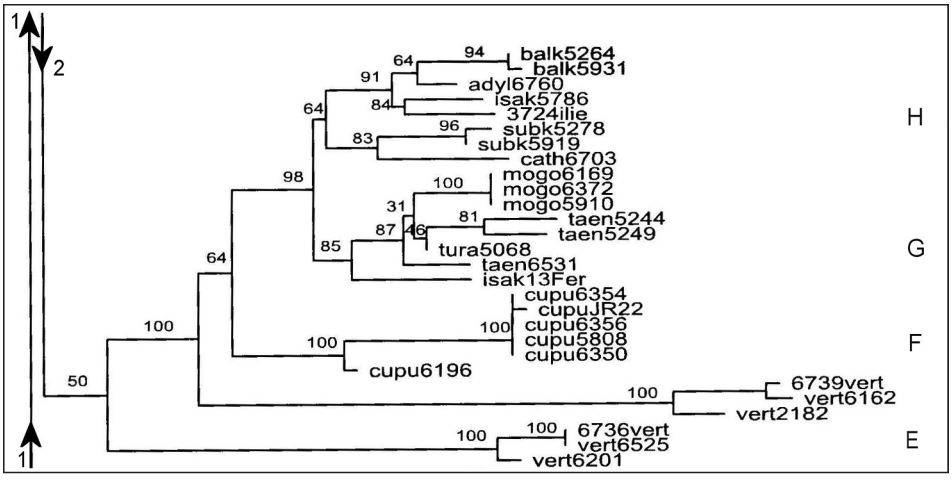

Fig. 2: Upper basal sector of a RAxML dendrogram based on ITS sequences of subg. *Melanocrommyum* showing the core clade at positions E - H. Numbered arrowheads mark the connections to Figs. 1 & 3. – Abb. 2: Zweiter Abschnitt eines RAxML-Dendrogramms der ITS-Sequenzen von subg. *Melanocrommyum*, der die Clades an den Positionen E - H zeigt. Die Pfeile und Nummern markieren die Anschlüsse zu den Abb. 1 und 3.

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Inserted among this group of sect. *Regeloprason* are all members of the monotypic sect. *Stellata* (R.M. FRITSCH & F. O. KHASS.) R.M. FRITSCH, *A. taeniopetalum* VVED. subsp. *taeniopetalum* (taen, Fig. 24), subsp. *mogoltavicum* (VVED.) R.M. FRITSCH & F. O. KHASS. (mogo), and subsp. *turakulovii* R.M. FRITSCH & F. O. KHASS. (tura, Fig. 25). These taxa occur in a strip moving from the mountains east of Tashkent through Mogoltau massif and the northern spurs of Turkestan mountain range to mountains east of Bukhara. Perhaps here the molecular diversity mirrors different ecological preferences and separate areas of distribution, but morphologically these taxa differ mainly by flower color.

The following sector of the dendrogram is shown in Figure 3. The subclade at position I comprises only *A. karataviense* REGEL (kara), the only species of sect. *Miniprasson* R. M. FRITSCH. It was not expected that two accessions from the Tajik bank of Pandj river (kara6133 and kara6147) represent a basal subgroup despite they share pinkish-grey flowers (Fig. 27) with plants from the type location in Kazakhstan. The other accessions from Kyrgyzstan, Uzbekistan (Fig. 26, from Kurama mountain range), and Tajikistan display different flower colors, subsp. *henrikii* RUKSANS (henr9678) has leaves shorter than the scape.

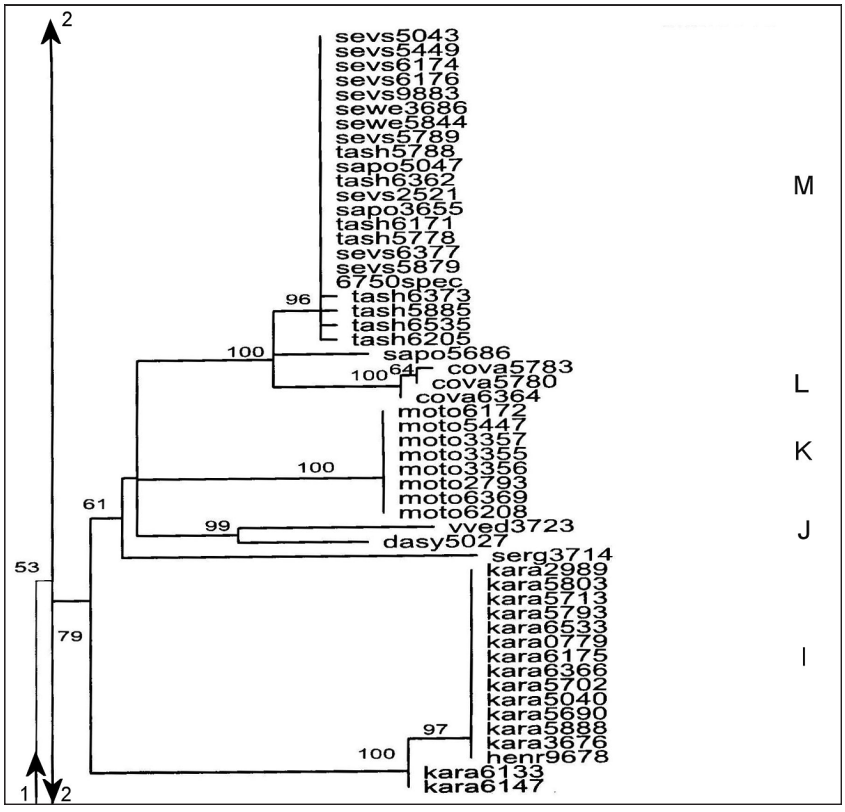

Fig. 3: Lower median sector of a RAxML dendrogram based on ITS sequences of subg. *Melanocrommyum* showing the core clade at positions I–M. Numbered arrowheads mark the connections to Figs. 2 & 4. – Abb. 3: Dritter Abschnitt eines RAxML-Dendrogramms der ITS-Sequenzen von subg. *Melanocrommyum*, der die Clades an den Positionen I–M zeigt. Die Pfeile und Nummern markieren die Anschlüsse zu den Abb. 2 und 4.

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A single accession of *A. sergii* Vved. (serg3714, sect. *Brevicaule* R. M. Fritsch) at position J may represent another case of long branch attraction (explained above). This tiny species from Kazakh Karatau mountain range is characterized by often spirally curled leaves and inconspicuous small yellow flowers. Another member of this sections, *A. chitralicum* F. T. Wang & Tang (chit6153, Fig. 28) was positioned widely apart inside of the clade at position O. That species owns straight leaves and larger whitish flowers. It occurs in the subalpine belt of Pamir and Hindukush mountain ranges. The study of more material of all species of this section would be essential to verify value and taxonomic relationship of sect. *Brevicaule*.

The other subclades at the positions J till M comprise members of sect. *Acmopetala* R. M. Fritsch. *Allium dasyphyllum* Vved. (dasy) and *A. vvedenskyanum* Pavlov (vved, Fig. 29) at position J are moderately tall species characterized by narrow leaves and yellowish or rose-pinkish flowers, resp. Hitherto they were affiliated to subsect. *Acmopetala* R. M. Fritsch (see under position Q below) characterized by a large stature and broad leaves. Perhaps they may represent one or two extra subsection(s) if addition of more material will confirm this position. The morphological diversity of the species at the positions J, K, and L corresponds well to the molecular groups.

Allium tschimganicum O. Fedtsch. s. str. (moto) at position K represents the well separated subsect. *Pharmakoprason* R. M. Fritsch, morphologically characterized by soft, moderately wide leaves and dense heads of pinkish-purple flowers. However, the subgroups at the positions L and M are composed of rather many species. To subsect. *Durovaginata* R.M. Fritsch belong *A. costatovaginatum* Kamelin & Levichev (cova, Fig. 31), characterized by rather short tepals and prominent longitundinal ribs on a sheathy prophyll including the leaf bases also above soil, and *A. severtzovioides* R.M. Fritsch (sevs, Fig. 32), morphologically very similar to *A. tschimganicum* but with a coarse, finely ribbed sheathy prophyll. All other species of subg. *Melanocrommyum* possess thin and smooth sheathy prophylls quickly decaying when the leaves are growing out of the bud stage to larger dimensions. *Allium tashkenticum* F. O. Khass. & R.M. Fritsch (tash) and *A. sewerzowii* Regel (sewe) are members of subsect. *Inornatae* R.M. Fritsch and share strikingly darker filaments than tepals. The first mentioned species grows in the Chatkal mountain range and owns glossy, yellowish-green leaves and yellowish tepals, whereas *A. sewerzowii* occurs in the western Tienshan mountain range and has pink tepals and glaucous, dull and coarse leaves. The only species of subsect. *Albidiflora* R.M. Fritsch, *A. saposhnikovii* Nikitina (sapo, Fig. 35) is a large plant with broad, dull and glaucous leaves and whitish flowers. The remarkable morphological differences between the mentioned species is in contrast to the uniform molecular group at position M (beside the singular position of the accession sapo5686).

Figure 4 shows the sector of the dendrogram continuing the sector of Figure 3. The groups at the positions N and O contain members of sect. *Megaloprason* subsect. *Megaloprason* R. M. Fritsch. *Allium kwakense* (R. M. Fritsch) R. M. Fritsch (kwak, Fig. 36) at position N and *A. rosenbachianum* Regel s. str. (rosb Fig. 37) at position O are molecularly well separated despite they share identical flower characters beside a darker tone of flower color in *A. kwakense*. However, the leaves are different: *A. kwakense* has erect, sub-linear and spirally twisted leaves, *A. rosenbachianum* owns recurved, lanceolate and flat ones. Addition of more accession will be essential to verify the infraspecific groups in these species as well as acceptance of the extremely narrow-leafed *A. insufficiens* Vved. (inss, Fig. 38) as fourth well separated subgroup.

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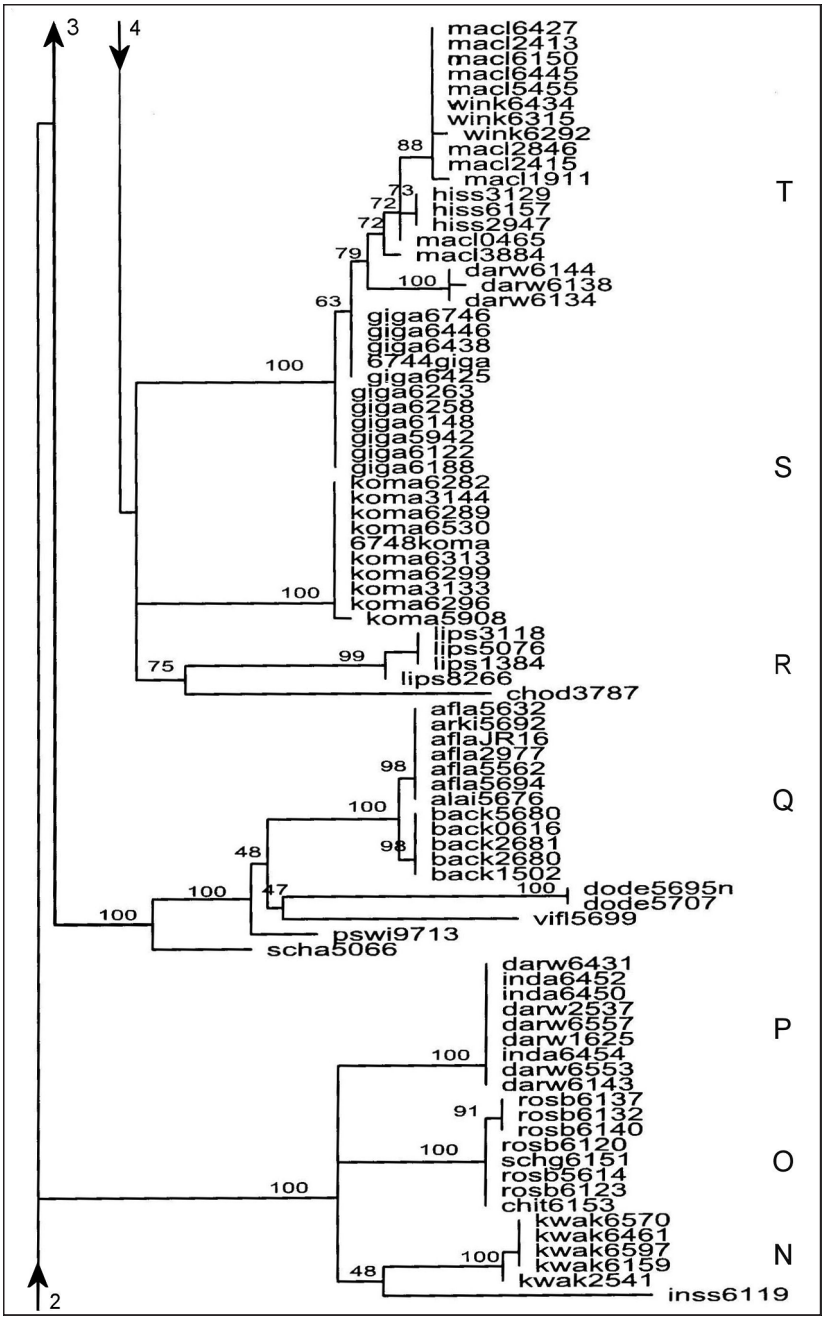

Fig. 4: Median sector of a RAxML dendrogram based on ITS sequences of subg. *Melanocrommyum* showing the core clade at positions N–T. Numbered arrowheads mark the connections to Figs. 3 & 5. – Abb. 4: Vierter (mittlerer) Abschnitt eines RAxML-Dendrogramms der ITS-Sequenzen von subg. *Melanocrommyum*, der die Clades an den Positionen N–T zeigt. Die Pfeile und Nummern markieren die Anschlüsse zu den Abb. 3 und 5.

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Another very well separated subclade contains at position P again two species of sect. *Regeloprason* from the Tajik Darvaz mountain range, the purplish flowering *A. intradarvazicum* R. M. Fritsch (inda, Fig. 39) and *A. darwasicum* Regel (darw, Fig. 40) having crème flowers. Whitish (darw1625) and yellowish-green (darw2537) flowering forms of the latter taxon from Hissar and Vakhsh mountain ranges, respective, do not differ molecularly, but some accessions from Darwaz were inserted basal to position T and represent a cryptic species as analyzed by Gurushidze et al. (2010).

In the subclade at the position Q, another species hitherto affiliated to sect. *Durovaginata*, *A. dodecadontum* Vved. (dode, Fig. 43), is included among members of subsect. *Acmopetala* despite the general appearance is similar to the species of sect. *Longibidentata* positioned in the basal grade. Also *A. schachimardanicum* Vved. (scha, Fig. 44) shares this general appearance. However, some morphological details exclude affiliation to sect. *Longibidentata*: *A. dodecadontum* possess a finely ribbed sheathy prophyll covering the leaf bases and bidentate and ciliate bases of filaments, whereas *A. schachimardanicum* owns a quickly decaying and smooth sheathy prophyll and glabrous filament bases without teeth. As in the cases of the basally separate position of *A. schachimardanicum* and *A. viridiflorum* (vifl, see above discussion of *A. verticillatum* at position E), these positions should be confirmed by additional accessions prior to drawing taxonomic conclusions. Also the position of *A. pseudowinklerianum* R.M. Fritsch & F. O. Khass. (pswi, sect. *Regeloprason*) remains uncertain in this respect.

The separate position of *A. backhousianum* Regel (back, type species of sect. *Acmopetala*, Fig. 45) was expected from morphological reasons. It is a magnificent large species having broad glaucous leaves topped by dense heads of white flowers showing long triangular tepals with curled tips (Fig. 45). The sister group contains less tall species: the broad-leaved *A. aflatunense* B. Fedtsch. s. str. (afla, Fig. 46) is morphologically rather similar to *A. stipitatum* Regel (position Z2) and was formerly affiliated beside it in sect. *Megaloprason* in the old sense, as well as *A. arkitense* R. M. Fritsch (arki) and *A. alaicum* Vved. (alai, Fig. 47), two species possessing narrower leaves. They are more similar in the general appearance to *A. zergericum* (Fig. 11) inserted between basal grade and core clade (see above). *Allium arkitense* owns glabrous leaves and scapes and purplish flowers, *A. alaicum* has pilose leaves and pilose, basally ribbed scapes, and pale pinkish flowers. All mentioned species at position Q occur on the mountain spurs around the Fergan depression in Uzbekistan and Kyrgyzstan.

At position R, again two species of sect. *Regeloprason* were positioned. *Allium lipskyanum* Vved. (lips, Fig. 41) from Hissar mountain range has pink flowers and a dense inflorescence becoming loose after anthesis (Fig. 42). It forms a badly supported subgroup with *A. chodsha-bakirganicum* Gaffarov & Turak. from Turkestan mountain range having yellow flowers and a not changing, condensed inflorescence. Lumping of *A. lipskyanum* with *A. cupuliferum* (at position F, Fig. 21), proposed by some authors, completely ignores remarkably differences in leaf, inflorescence, and flower morphology and is also not supported by molecular data.

The subclade at position S and T include most species of sect. *Compactoprason* R. M. Fritsch which share wide and large leaves and large scapes. *Allium komarowii* Lipsky (koma, Fig. 48), the only species of subsect. *Komaroviana* F. O. Khass. & R.M. Fritsch, forms a separate subclade. It occurs from Hissar mountain range to Turkestan mountain range in Tajikistan and adjacent Uzbekistan roughly between 68° and 69° East and is also morphologically distinct: the scape is rarely more than 60 cm long, and the subglobose in-

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florescence is smaller and less dense (Fig. 48) than those of the species of subsect. *Erectopetala* F. O. KHASS. which compose the second subclade. Here *A. giganteum* REGEL (giga), distributed at lower altitudes from the eastern spurs of Kopet Dagh mountain range in Iran to the Panj valley in the Western Pamir area, occupies the most basal position. It is the largest species and owns the densest and largest flower heads in this group (Fig. 49). Sister are members of sect. *Regeloprason*: the molecularly aberrant accessions of *A. darwasicum* (discussed above) and, at position T, the purplish-flowering species *A. hissaricum* VVED. (hiss, Fig. 52) and *A. winklerianum* REGEL s. str. (wink, Fig. 55). These species occur from Hissar mountain range to Darwaz mountain range in Central Tajikistan but in different altitudes: the slender plants of *A. hissaricum* grow on grassy slopes in the montane belt, while those of *A. winklerianum* are commonly smaller and occupy subalpine to alpine meadows. The same position in the dendrogram shares *A. macleanii* BAKER (macl, Fig. 50) also distributed at higher altitudes from Pamir-Alai mountain area to the Hindukush mountain range in Pakistan. *Allium macleanii* grows not so tall as *A. giganteum* and differs additionally by glossy leaves, a smaller inflorescence, sub-acute tepals, and, pinkish (not purplish), relatively larger filaments. It was surprising to see the morphologically really different *A. macleanii* and *A. winklerianum* in one molecular group.

Two more species of sect. *Compactoprason* are also similar to *A. giganteum* but were inserted in the following clade (Fig. 5) at the positions U and Y. *Allium trautvetterianum* REGEL (trau, Fig. 51) differs by larger and glossy flowers on shorter scapes and occurs only in southern Tajikistan (Vakhsh and Khozratishoh mountain ranges). *Allium majus* VVED. (maju) differs even only by inconspicuous flower characters and grows in the Central and western Hissar mountain range. Its inclusion among members of sect. *Kaloprason* K. Koch at location Y is concordant with its separation as monotypic subsect. *Spiralopetala* F.O. KHASS. & R.M. FRITSCH.

Closer related and sister to *A. trautvetterianum* is *A. sarawschanicum* REGEL (sara, Fig. 54) at position V, the only species of sect. *Megaloprason* subsect. *Keratoprason* R. M. FRITSCH. However, the plants are morphologically much more similar to *A. rosenbachianum* (position O) and differ mainly by straight sub-linear leaves and six radial bulges at the top of the ovaries (Fig. 54). Also *A. sarawschanicum* is widely distributed from Central Kopet Dagh mountain range in Iran and Turkmenistan to the Saravshan and Hissar mountain ranges in Uzbekistan and Tajikistan, but both molecular subgroups comprise accessions from different regions. Our data also underline that the ornamental cultivar ´Stipineva` (hybmineva) is not a hybrid but a mutant of *A. sarawschanicum*.

The well separated subclades at the positions W and X include morphologically well characterized monotypic sections, on the one hand *A. aroides* VVED. (aroi, sect. *Aroidea* F. O. KHASS. & R. M. FRITSCH, Fig. 53) occupying a very restricted area of distribution along the southern slopes of Saravshan mountain range south of Samarkand (Uzbekistan) with an outpost in the northeastern corner of Turkmenistan. It is a moderately small species with flowers similar to *A. verticillatum* (Fig. 17) but on longer pedicels in a larger umbel. On the other hand, at position X *A. gypsaceum* VVED. (gyps, sect. *Popovia* F. O. KHASS. & R. M. FRITSCH, Fig. 56) is positioned, and among them but with low bootstrap support, *A. hexaceras* VVED. (hexa, sect. *Acaule* R. M. FRITSCH). Both latter mentioned species are rather small and occur in somewhat differing regions south of the central chains of Hissar mountain range. *Allium gypsaceum* grows at lower elevations on gypsaceous saline slopes and is characterized by lanceolate, longitudinally folded leaves and narrowly campanulate, ochre flowers with violet (sometimes only slightly purplish) suffused tips. *Allium hexaceras* occupies rocky alpine slopes and owns flat

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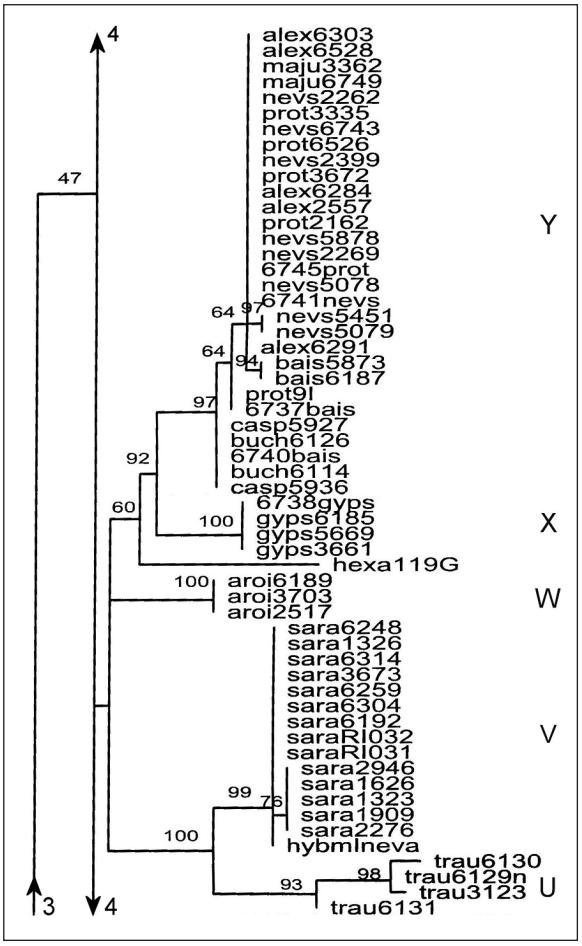

Fig. 5: Second upper sector of a RAxML dendrogram based on ITS sequences of subg. *Melanocrommyum* showing the core clade at positions U - Y. Numbered arrowheads mark the connections to Figs. 4 & 6. – Abb. 5: Fünfter Abschnitt eines RAxML-Dendrogramms der ITS-Sequenzen von subg. *Melanocrommyum*, der die Clades an den Positionen U - Y zeigt. Die Pfeile und Nummern markieren die Anschlüsse zu den Abb. 4 und 6.

linear leaves and bowl-shaped star-like pinkish flowers bearing (name-giving) horn-like outgrowths on the top of the ovaries. Sometimes also the bulge-like outgrowths at the top of ovaries in *A. saraws-chanicum* may appear horn-like on herbarium specimens, but stature of plants as well as shape of outgrowths of both species look very different. It is more probable that this position of the single investigated accession of *A. hexaceras* does not indicate a closer relationship but was accidentally caused by long-branch attraction (see above).

Sister to the subclade at position X are members of sect. *Kaloprason* (position Y). They all share very loose inflorescences with pedicels of striking unequal lengths and basally very weak scapes. When the seeds are ripe, the scapes are breaking near the soil and the infrutescences can be blown by the wind over the soil as "tumble-weeds" shedding the seeds anywhere. Our ITS sequence data do not resolve the phylogenetic structure of this clade. All investigated taxa were united in one clade in spite of morphological differences and affiliations to different subsections. Only accessions from the type locations of *A. caspium* subsp. *baissunense* (Lipsky) F.O. Khass. & R. M. Fritsch (bais5873 and bais6187) and *A. nevskianum* Vved. ex Wendelbo (nevs5079 and nevs5451) form well supported subgroups. *Allium caspium* (Pall.) M. Bieb. subsp. *caspium* (casp, Fig. 57), *A. caspium* subsp. *baissunense* (bais, Fig. 58), and *A. bucharicum* Regel (buch, Fig. 69) belong to subsect. *Kaloprason*. The typical subspecies of *A. caspium* differs mainly by often longer tepals and more intensely colored flower parts from subsp. *baissunense*, but is widely distributed in sand deserts of the Caspian-Balkhash region to the Iranian and Pakistani deserts. Subsp. *baissunense* occurs only on gypsaceous and saline places on the southern foothills of the Hissar mountain range. *Allium bucharicum* differs by up to six narrower leaves and sev-

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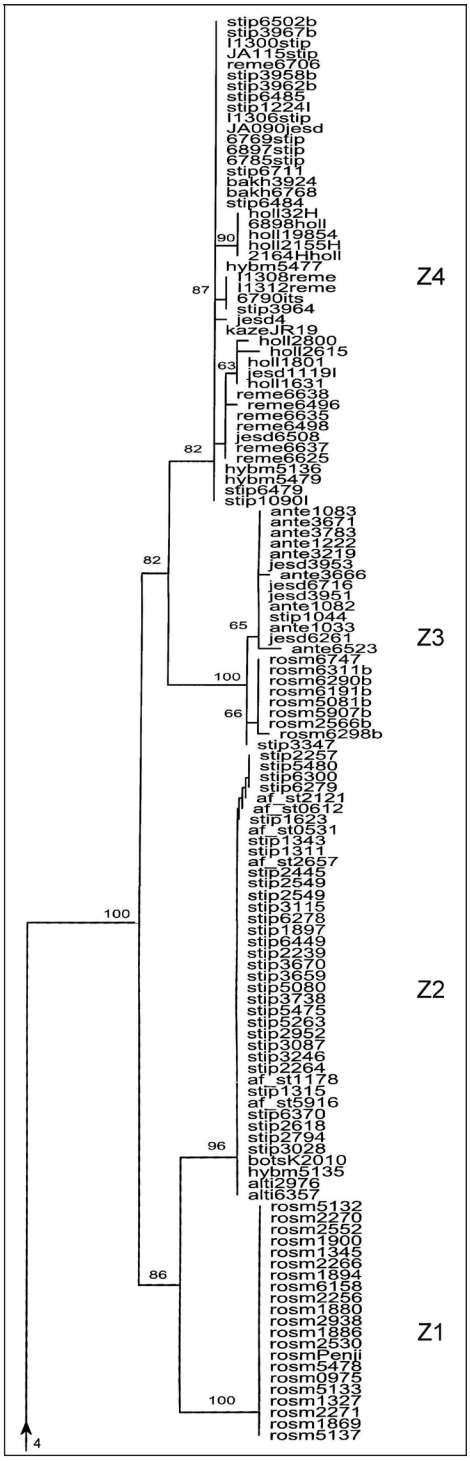

eral flower characters (Fig. 69); it occurs in a rather restricted semi-desert area in southern Tajikistan.

The remaining three species investigated are members of subsect. *Ligulifolia* R. M. FRITSCH. *Allium protensum* WENDELBO (prot, Fig. 60) owns a similar large area of distribution as *A. caspium* subsp. *caspium* but prefers loamy plains. This species has widely funnel-shaped flowers which may be whitish with a green median vein, yellowish-brown with a brown median vein, or pinkish-carmine with a purple median vein. The vicariant species *A. alexeianum* REGEL (alex, Fig. 61), and *A. nevskianum* (nevs, Fig. 62) occur in the central parts of Turkestan and Saravshan mountain ranges, and on the southern slopes of Central to the southwestern Hissar mountain range, respective. They do not much differ when in anthesis (compare Figs. 61 and 62, although *A. nevskianum* may have much paler flowers than Fig. 62 shows), but after anthesis the tepals of *A. alexeianum* become stiff and prickly, those of *A. nevskianum* remain soft becoming only crumbled.

The final clade of the dendrogram is shown in Fig. 6. All investigated species of sect. *Procerallium* R. M. FRITSCH were included in this clade which is divided into four main subclades displaying geographic correlations: Z1 and Z2 contain accessions from Central Asia, Z4 solely from Iran, and Z3 from both regions.

All members of sect. *Procerallium* are large plants sharing more or less dense globular inflorescences composed of large

Fig. 6: Upper sector of a RAxML dendrogram based on ITS sequences of subg. *Melanocrommyum* showing the most upper part of the core clade at positions Z1 - Z4. Arrowhead 4 marks the connection to the top of Fig. 5. – Abb. 6: Oberster Abschnitt eines RAxML-Dendrogramms der ITS-Sequenzen von subg. *Melanocrommyum*, der die Clades an den Positionen Z1 - Z4 zeigt. Pfeil 4 markiert den Anschluss zur Spitze von Abb. 5.

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star-like pink to carmine flowers on subequal pedicels and after anthesis deflexed and spirally crumpled tepals. The ovaries are always stalked with a tuberculate surface. Shape and number of leaves, scape surface, as well as shape and color of tepals and filaments are more variable and delivers species-specific characters.

Perhaps best known in Europe is *A. rosenorum* R. M. Fritsch (rosm, Fig. 63) because bulbs are often sold under the wrong name *A. rosenbachianum* in garden shops. It occurs naturally in the Hissar mountain range in Tajikistan and is characterized by narrow long-lanceolate, strongly canaliculated, recurved leaves, densely ribbed scapes which may reach 1 m length, and basally triangular filaments having pink upper parts. An unresolved molecular problem is the affiliation of this species to two well separated subclades at locations Z1 (accessions from Central Hissar mountain range and those received from flower bulb trade) and Z3 (accessions from West and Southwest Hissar mountain ranges) which are indistinguishable by morphology. Approximately 68° East longitude separates the molecular variants.

A similar case is represented by *A. stipitatum* Regel (stip, Fig. 64) where the investigated accessions from Central Asia and the northern slope of Kopet Dagh mountain range form together the subclade at position Z2, but those from Central and northwestern Iran were included in the subclade at position Z4. Also here all accessions of *A. stipitatum* s. str. are morphologically uniform despite this species is widely distributed from the western Tienshan mountain range in Kazakhstan and the Hindukush mountain range in Afghanistan and Pakistan till the Central Zagros mountain range and the mountains west of lake Orumiyeh in Iran. It is the largest species of sect. *Procerallium* not smaller than *A. giganteum* and *A. backhousianum*. *Allium stipitatum* has a glossy smooth scape, large and broad leaves bearing a very variable indumentums of long hairs (but not rarely only short teeth on the ribs and along the margins are present). It differs from *A. rosenorum* also by broader tepals. Somewhat deviating morphotypes having narrower, hairless leaves, a less dense inflorescence and broader, recurved, and mostly darker tepals were named as *A. altissimum* Regel (alti, Fig. 65), but *A. botschantzevii* Kamelin (bots) differs by a smaller stature and presence of hairs on the scape. The latter species occurs only in a restricted area of southwestern Hissar mountain range in Uzbekistan, but *A. altissimum*-like variants are known from several parts of the whole area of distribution. These and hairless tall forms of *A. stipitatum* often wrongly named *A. aflatunense* (af_st) do not differ molecularly from typical *A. stipitatum* at position Z2. It remains unclear why the accessions stip1044 and stip3347 were included in the subclade at position Z3 - the plants belong clearly to *A. stipitatum*, and also the ITS sequences do not show problematic allocations.

This subclade at position Z3 presents still a third problem, because the sister subclade to *A. rosenorum* contains mainly two subspecies of *A. jesdianum* Boiss. & Buhse; subsp. *angustitepalum* (Wendelbo) F. O. Khass. & R.M. Fritsch (ante, Fig. 66) and subsp. *jesdianum* (jesd) from the type location in the province Yazd, eastern Iran. Also the only investigated accession of *A. oriento-iranicum* Neshati, Zarre & R.M. Fritsch (jesd6261) is positioned here which occurs in the province Khorasan in northeastern Iran. However, *A. jesdianum* subsp. *remediorum* R.M. Fritsch (reme) as well as accessions very similar to the typical subspecies but occurring in the Zagros mountain range of northwestern Iran belong to the subclade at position Z4.

Among the species discussed here, only *A. jesdianum* subsp. *angustitepalum* occurs outside the Iran in northern Afghanistan and in the Kugitang massif of Uzbekistan. It is well discernable from the similar *A. rosenorum* by a lower number of broader leaves, less ribs

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Zu den Abbildungen auf den Seiten 259 bis 262:

Fig. 7–20, Seite 258: Inflorescences of 14 species of *Allium* subg. *Melanocrommyum* (magnifications differ). Fig. 7: *A. fetisowii*; Fig. 8: *A. chychkanense*; Fig. 9: *A. decipiens* subsp. *quercetorum*; Fig. 10: *A. robustum*; Fig. 11: *A. zergericum*; Fig. 12: *A. chelotum*; Fig. 13: *A. suworowii*; Fig. 14: *A. tulipifolium*; Fig. 15: *A. cristophii* (brownish-flowering variant); Fig. 16: *A. helicophyllum*; Fig. 17: *A. verticillatum*; Fig. 18: *A. regelii*; Fig. 19: *A. viridiflorum*; Fig. 20: *A. subkopetdagense*. – Abb. 7–20: Blütenstände von 14 Arten von *Allium* subg. *Melanocrommyum* (nicht im gleichen Maßstab photographiert). Abb. 7: *A. fetisowii*; Abb. 8: *A. chychkanense*; Abb. 9: *A. decipiens* subsp. *quercetorum*; Abb. 10: *A. robustum*; Abb. 11: *A. zergericum*; Abb. 12: *A. chelotum*; Abb. 13: *A. suworowii*; Abb. 14: *A. tulipifolium*; Abb. 15: *A. cristophii* (bräunlich blühende Variante); Abb. 16: *A. helicophyllum*; Abb. 17: *A. verticillatum*; Abb. 18: *A. regelii*; Abb. 19: *A. viridiflorum*; Abb. 20: *A. subkopetdagense*.

Fig. 21–35, Seite 259: Inflorescences of 15 species and subspecies of *Allium* subg. *Melanocrommyum* (magnifications differ). Fig. 21: *A. cupuliferum*; Fig. 22: *A. balkhanicum*; Fig. 23: *A. isakulii*; Fig. 24: *A. taeniopetalum* subsp. *taeniopetalum*; Fig. 25: *A. taeniopetalum* subsp. *turakulovii*; Fig. 26: *A. karataviense* (red form); Fig. 27: *A. karataviense* (pinkish form); Fig. 28: *A. chitralicum*; Fig. 29: *A. vvedenskyanum*; Fig. 30: *A. severtzovioides*; Fig. 31: *A. costatovaginatum*; Fig. 32: *A. tschimganicum*; Fig. 33: *A. tashkenticum*; Fig. 34: *A. sewerzowii*; Fig. 35: *A. saposhnikovii*. – Abb. 21–35: Blütenstände von 15 Arten und Unterarten von *Allium* subg. *Melanocrommyum* (nicht im gleichen Maßstab photographiert). Abb. 21: *A. cupuliferum*; Abb. 22: *A. balkhanicum*; Abb. 23: *A. isakulii*; Abb. 24: *A. taeniopetalum* subsp. *taeniopetalum*; Abb. 25: *A. taeniopetalum* subsp. *turakulovii*; Abb. 26: *A. karataviense* (rot blühende Form); Abb. 27: *A. karataviense* (rosa blühende Form); Abb. 28: *A. chitralicum*; Abb. 29: *A. vvedenskyanum*; Abb. 30: *A. severtzovioides*; Abb. 31: *A. costatovaginatum*; Abb. 32: *A. tschimganicum*; Abb. 33: *A. tashkenticum*; Abb. 34: *A. sewerzowii*; Abb. 35: *A. saposhnikovii*.

Fig. 36–51, Seite 260: Inflorescences of 15 species and subspecies of *Allium* subg. *Melanocrommyum* (magnifications differ). Fig. 36: *A. kwakense*; Fig. 37: *A. rosenbachianum*; Fig. 38: *A. insufficiens*; Fig. 39: *A. intradarvazicum*; Fig. 40: *A. darwasicum*; Fig. 41: *A. lipskyanum* (peak of anthesis); Fig. 42: *A. lipskyanum* (end of anthesis); Fig. 43: *A. dodecadontum*; Fig. 44: *A. schachimardanicum*; Fig. 45: *A. backhousianum*; Fig. 46: *A. aflatunense* s. str.; Fig. 47: *A. alaicum*; Fig. 48: *A. komarowii*; Fig. 49: *A. giganteum*; Fig. 50: *A. macleanii*; Fig. 51: *A. trautvetterianum*. – Abb. 36–51: Blütenstände von 15 Arten und Unterarten von *Allium* subg. *Melanocrommyum* (nicht im gleichen Maßstab photographiert). Abb. 36: *A. kwakense*; Abb. 37: *A. rosenbachianum*; Abb. 38: *A. insufficiens*; Abb. 39: *A. intradarvazicum*; Abb. 40: *A. darwasicum*; Abb. 41: *A. lipskyanum* (in Vollblüte); Abb. 42: *A. lipskyanum* (zu Blühende); Abb. 43: *A. dodecadontum*; Abb. 44: *A. schachimardanicum*; Abb. 45: *A. backhousianum*; Abb. 46: *A. aflatunense* s. str.; Abb. 47: *A. alaicum*; Abb. 48: *A. komarowii*; Abb. 49: *A. giganteum*; Abb. 50: *A. macleanii*; Abb. 51: *A. trautvetterianum*.

Fig. 52–66, Seite 261: Inflorescences of 15 species and subspecies of *Allium* subg. *Melanocrommyum* (magnifications differ). Fig. 52: *A. hissaricum*; Fig. 53: *A. aroides*; Fig. 54: *A. sarawschanicum*; Fig. 55: *A. winklerianum*; Fig. 56: *A. gypsaceum*; Fig. 57: *A. caspium* subsp. *caspium*; Fig. 58: *A. caspium* subsp. *baissunense*; Fig. 59: *A. bucharicum*; Fig. 60: *A. protensum*; Fig. 61: *A. alexeianum*; Fig. 62: *A. nevskianum*; Fig. 63: *A. rosenorum*; Fig. 64: *A. stipitatum*; Fig. 65: *A. altissimum*; Fig. 66: *A. jesdianum* subsp. *angustitepalum*. – Abb. 52–66: Blütenstände von 15 Arten und Unterarten von *Allium* subg. *Melanocrommyum* (nicht im gleichen Maßstab photographiert). Abb. 52: *A. hissaricum*; Abb. 53: *A. aroides*; Abb. 54: *A. sarawschanicum*; Abb. 55: *A. winklerianum*; Abb. 56: *A. gypsaceum*; Abb. 57: *A. caspium* subsp. *caspium*; Abb. 58: *A. caspium* subsp. *baissunense*; Abb. 59: *A. bucharicum*; Abb. 60: *A. protensum*; Abb. 61: *A. alexeianum*; Abb. 62: *A. nevskianum*; Abb. 63: *A. rosenorum*; Abb. 64: *A. stipitatum*; Abb. 65: *A. altissimum*; Abb. 66: *A. jesdianum* subsp. *angustitepalum*.

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only present in the lower part of the scape, and basally rectangular widened filaments which are pure white above.

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