Zeitschrift: Candollea : journal international de botanique systématique = international journal of systematic botany

Herausgeber: Conservatoire et Jardin botaniques de la Ville de Genève

Band: 57 (2002)

Heft: 2

Artikel: Multivariate analysis, systematics, and distribution of Galium sect. Orientigalium Ehrend. (Rubiaceae) in the Caucasus region

Autor: Schanzer, Ivan / Ehrendorfer, Friedrich

DOI: https://doi.org/10.5169/seals-879353

Multivariate analysis, systematics, and distribution of Galium sect. Orientigalium Ehrend. (Rubiaceae) in the Caucasus region

IVAN SCHANZER
&
FRIEDRICH EHRENDORFER

ABSTRACT

SCHANZER, I. & F. EHRENDORFER (2002). Multivariate analysis, systematics, and distribution of Galium sect. Orientigalium Ehrend. (Rubiaceae) in the Caucasus region. *Candollea* 57: 329-357. In English, English abstract.

Galium sect. *Orientigalium* Ehrend. is a species rich and polymorphic clade centred in the western Irano-Oriental region, from where it extends to the Iberian Peninsula in the W, the Lebanon in the S, and the Caucasus region in the N. Preliminary chromosome counts and correlated pollen diameter measurements show that the clade includes several polyploid complexes. One of them, particularly diverse in the Caucasus, is the *G. subvelutinum* alliance. On the basis of an extensive evaluation of morphological differential characters, eighteen populations of this alliance were studied in the field, together with additional herbarium material resulting in a total of four hundred and three individuals scored for twenty differential characters and eventually arranged in twenty-six OTUs. This matrix was subjected to cluster analysis, multidimensional scaling, and discriminant analyses. The resulting tree reveals five major OTU clusters. Their structure, affinities, discontinuities and clinal connections are illustrated by 2-dimensional scatter plots and maps. As a consequence, it is possible to separate two informal species groups within the Caucasian members of the *G. subvelutinum* alliance: the ± suffruticose and more xerophilous *G. mite* group and the ± herbaceous and rather mesophilous *G. hyrcanicum* group. Both apparently contain diploid and polyploid members and are occasionally linked by hybridization. Within the *G. mite* group four species can be recognized, of which *G. armenum* apparently is of hybrid origin. The *G. hyrcanicum* group includes *G. bullatum*, *G. hyrcanicum* agg. (three species) and *G. xylorrhizum* agg. (three species). These aggregates have developed a number of interesting local endemic taxa in the Great Caucasus, which obviously have originated from Irano-Oriental ancestors which first penetrated northward, and then became isolated during the later Pleistocene and Holocene.

KEY-WORDS: Galium sect. *Orientigalium* – Caucasus – Taxonomy – Cluster analysis – Discriminant analysis – Distribution.

1. Introduction

The section *Orientigalium* Ehrend. of the genus *Galium* L. comprises about sixty species which partly form polymorphic polyploid complexes and are distributed in mountains of SW Asia and the Mediterranean. Most of the species are known from Turkey and adjacent N and W Iran, N Iraq, and the Caucasus region. No complete treatment of the section is yet available. After the first description of sect. *Orientigalium* (EHRENDORFER, 1951), a general survey (EHRENDORFER, 1971) and several treatments within regional analyses of *Rubiaceae* have been published: for "Flora Europaea" (EHRENDORFER, 1976), for the Floras of Turkey (EHRENDORFER, 1958; EHRENDORFER & SCHÖNBECK-TEMESY, 1982) and Iraq (EHRENDORFER

CODEN: CNDLAR
ISSN: 0373-2967
57(2) 329 (2002)

& SCHÖNBECK-TEMESY, 1980), and for "Flora Iranica" (EHRENDORFER & al., 2002 in print). Furthermore, there is a note on some taxa of the section in the Caucasus (SCHANZER, 1989).

Earlier treatments of the relevant taxa have been presented by GROSSHEIM for the Flora of the Caucasus (1934), by POBEDIMOVA for the Floras of the USSR (1958) and Azerbaijan (1961), and by MANDENOVA for the Floras of Armenia (1972, 1980) and Georgia (1999). In the recent "Synopsis of the Caucasian Flora" for the *Rubiaceae*, prepared at the Komarov Botanical Institute in St. Petersburg, MIKHEYEV (1992) recognized the following species of sect. *Orientigalium*: *G. grusinum* Trautv. [= *G. incanum* subsp. *elatius* (Boiss.) Ehrend.], and from the *G. subvelutinum* alliance *G. praemontanum* Mardal. (incl. var. *armazicum* Mardal.), *G. oshtenicum* Ehrend. & Schanzer ex Mikheev, *G. vartanii* Grossh., and *G. hyrcanicum* agg. with the microspecies *G. hyrcanicum* C. A. Mey. (= *G. grossheimii* Pobed.), *G. xylorrhizum* Boiss. & Huet, *G. czerepanovii* Pobed., *G. achurense* Grossh., *G. mite* Boiss. & Hohen., and *G. bullatum* Lipsky. Not yet included are *G. azerbayjanicum* Ehrend. & Schönb.-Tem. (published in 1991) and *G. armenum* Schanzer (published in 1997).

The present study deals in a comprehensive way with sect. *Orientigalium* in the Caucasus region. This is understood here as to include the ranges of all the Caucasian mountains within the former Soviet Union (now Georgia, Armenia, Azerbaijan, and some parts of southern Russia). In this region the section reaches the northern limits of its distribution area with the alliances of *G. incanum* Sm. and of *G. subvelutinum* (DC.) K. Koch. The former of these informal taxonomic assemblies is distributed from Greece and Crete through Anatolia to Georgia, Syria, and Lebanon; it is represented by a single uniform subspecies only in the Caucasus region (EHRENDORFER, 1951). In contrast, the *G. subvelutinum* alliance forms extremely polymorphic polyploid complexes and contains many critical species linked by transitional forms, ranging from W Turkey to N Iraq, N + W Iran, and the Caucasus region. First, EHRENDORFER (1948, 1958) suggested to consider the *G. subvelutinum* alliance as a polytypic species with a number of subspecies and related species marginal to the main centre of diversity. Such a concept, however, later on did not seem satisfactory and was rejected in favour of the recognition of numerous, more or less vicarious microspecies (EHRENDORFER & SCHÖNBECK-TEMESY, 1980, 1982; SCHÖNBECK-TEMESY 1991; EHRENDORFER & al., 2002). However, this new concept also did not solve all problems due to the very weak differences and numerous intermediates between several of the microspecies described.

Here, we attempt to clarify these problems of the taxonomic differentiation of sect. *Orientigalium* and of the relationships between its taxa in the Caucasus region by applying numerical taxonomic methods. This approach should also allow to recognize the general distribution pattern of the section in the region. Nevertheless, our results will remain preliminary, because the documentation of the different genome levels in the polyploid complexes involved is still quite insufficient.

2. Materials and methods

This survey is based partly on the plant material assembled by the first author during field work in Armenia, Georgia and Nakhichevan (1979-1982 and 1995). The collections of the herbaria ERE, LE, MHA, MO, MOSP, MW, TBI, TGM, W, and WU, and some from G, K, E, and B borrowed to WU have been considered as well. Thus, a total of about one thousand specimens have been examined, of which four hundred and three were used for the numerical study. The latter involved only members of the *G. subvelutinum* alliance.

To assess infrapopulational variability, seven to thirty-six specimens were collected in the field from each of the eighteen local populations examined. Eight collections from single localities or restricted geographical areas found in various herbaria were also considered along with the field samples to set up twenty-six Operational Taxonomic Units (OTUs) (Table 1; Figs. 1, 4, 5).

Table 1. – List of OTUs recognized for the *Galium subvelutinum* alliance in the Caucasus region. Samples from populations studied in the field are marked with asterisks.

OTU No	OTU name	Species and locality	Number of specimens
1	mite	*G. mite* (C Armenia, Aragatz, Karbi) *	12
2	achur1	*G. achurense* (Nakhichevan, Buzgow) *	26
3	azerb	*G. azerbayjanicum* (Nakhichevan, Negrom)	7
4	armen	*G. armenum* (SC Armenia, Garni) *	22
5	xylo1	*G. xylorrhizum* (N Armenia, Lusakhpur) *	30
6	xylo2	*G. xylorrhizum* (N Armenia, Shirakamut) *	23
7	xylo3	*G. xylorrhizum* (N Armenia, Nalband) *	7
8	hyrc5	*G. hyrcanicum* (Armenia, Sevan) *	36
9	hyrc3	*G. hyrcanicum* (C Armenia, Karaglukh) *	21
10	hyrc2	*G. hyrcanicum* (C Armenia, Gndevaz) *	13
11	hyrc4	*G. hyrcanicum* (CS Armenia, Khachik) *	26
12	hyrc1	*G. hyrcanicum* (Nakhichevan, Akhura) *	25
13	gross	*G. grossheimii* (NW Nakhichevan, Yayji)	9
14	bull2	*G. bullatum* (N Nakhichevan, Bichenak) *	12
15	bull1	*G. bullatum* (Nakhichevan, Shakhbuz) *	33
16	bull3	*G. bullatum* (W Nakhichevan, Badamly)	6
17	bull4	*G. hyrcanicum* (Nakhichevan, Bichenak Pass) *	7
18	achur2	*G. hyrcanicum* (SC Armenia, Arpi) *	7
19	hyrc6	*G. hyrcanicum* (E Nakhichevan, Zangezur Range) *	10
20	hyrc7	*G. hyrcanicum* (E Nakhichevan, Kalaki) *	8
21	czer	*G. czerepanovii* (SE Nakhichevan, the type collection)	11
22	osht	*G. oshtenicum* (NW Caucasus, Oshten Mt.)	9
23	praem	*G. praemontanum* (E Georgia, the type collection)	4
24	armaz	*G. praemontanum* var. *armazicum* (Georgia) = *G. xylorrhizum*	3
25	vart	*G. vartanii* (NE Azerbayjan & Daghestan)	9
26	hyrcan	*G. hyrcanicum* (Talysh Mts.)	27
Total			403

Table 2. – Characters measured on Caucasian specimens of sect. *Orientigalium*.	
1. Habit	1. dwarf caespitose habit 2. herbaceous, with thin, slightly woody stem bases 3. more or less suffrutescent
2. Brachyblasts at lower nodes	1. present 2. absent
3. Stem length	mm long
4. Stem indumentum	1. glabrous 2. shortly puberulent in nodes 3. shortly and sparsely puberulent at lower portion only 4. shortly and sparsely puberulent 5. shortly and densely puberulent 6. hirsute
5. Hair type	1. straight 2. retrorse 3. curly
6. Leaf shape	1. oblanceolate 2. linear
7. Leaf margins	1. with flat to slightly revolute margins 2. with margins strongly revolute to the midrib
8. Leaf length	mm long
9. Leaf breadth	mm wide
10. Leaf position	1. spreading, sometimes reflexed 2. reflexed
11. Leaf indumentum	1. glabrous 2. apically hairy 3. hairy along margins 4. sparsely puberulent 5. densely puberulent 6. hirsute
12. Leaves in whorls of	1. 4-6 2. 6 3. (5-)6(-7) 4. (5-)6-7(-8)
13. Inflorescence shape (at well developed generative shoots)	1. corymbiform 2. elongated but definitely corymbiform in upper part 3. narrowly, elongate, sometimes nearly cylindrical 4. narrowly pyramidal 5. broadly pyramidal 6. narrow elongate with short, only twice branched peduncles
14. Inflorescence: flower number (at well developed generative shoots)	n-flowered
15. Angle of fruiting pedicels	1. never divaricate at angles more than 90° 2. divaricate at angles more than 90°
16. Flower size	mm diam.
17. Petal appendages	1. shortly attenuate and curved inwards 2. long attenuate
18. Mericarp surface	1. smooth, with dry adherent pericarp 2. rugose, with juicy inflated pericarp
19. Mericarp color	1. dark coloured, brownish to black 2. light coloured, whitish or pinkish
20. Mericarp length	mm long

Table 3. – Data matrix of the Galium subvelutinum alliance OTU used for the cluster analysis (see Table 1). 1 - OTU Name. – 2 - Leaf length / stem length ratio. – 3 – Flowers number / stem length ratio . – 4 - Leaf breadth / leaf length ratio. – 5 – Leaf breadth. – 6 – Leaf number in a whorl. – 7 – Leaf indumentum. – 8 – Stem indumentum. – 9 - Hair type. – 10 - Flower diameter, mm. – 11 – Petal appendage shape. – 12 – Inflorescence shape. – 13 – Leaf position. – 14 – Angle of fruiting pedicels. – 15 – Flower diameter, mm. – 16 – Mericarp length, mm. – 17 – Mericarp surface & colour.

1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*
achur1	0,06	0,43	0,14	1,35	3,00	1,00	4,00	2,00	2,90	2,00	3,00	2,00	1,00	2,90	1,70	1,00
achur2	0,06	0,35	0,16	1,40	2,00	1,00	5,00	2,00	3,45	1,05	2,00	2,00	1,00	3,45	1,30	1,00
armaz	0,08	0,33	0,17	1,30	2,00	1,00	1,00	1,00	4,00	1,00	1,00	1,00	1,00	4,00	1,75	1,05
armen	0,05	0,23	0,09	1,25	2,00	1,00	2,00	1,00	3,00	1,00	4,00	1,00	1,00	3,00	2,50	2,00
azerb	0,05	0,49	0,42	2,60	2,00	1,00	3,00	1,00	2,70	1,00	3,00	1,00	2,00	2,70	1,60	1,00
bull1	0,08	0,30	0,18	1,80	2,00	2,00	5,00	1,00	3,20	1,00	1,00	1,00	1,00	3,20	3,50	2,00
bull2	0,10	0,21	0,16	1,50	2,00	2,00	4,00	1,00	3,30	1,00	1,50	1,00	1,00	3,30	3,10	2,00
bull3	0,10	0,50	0,15	1,25	2,00	1,00	5,00	1,00	4,35	1,00	1,00	1,00	1,00	4,35	2,75	2,05
bull4	0,08	0,14	0,25	2,00	2,00	2,00	4,00	1,00	4,40	1,00	1,00	1,00	1,00	4,40	1,95	1,05
czer	0,11	0,30	0,40	1,80	1,00	1,00	3,00	1,00	2,50	1,00	1,00	1,00	1,00	2,50	1,50	1,00
gross	0,08	0,29	0,45	1,90	2,00	6,00	6,00	1,00	3,00	1,00	1,00	1,00	1,00	3,00	1,75	1,05
hyrc1	0,08	0,33	0,25	1,40	2,00	1,00	4,00	1,00	3,80	1,00	2,00	1,00	1,00	3,80	1,65	1,05
hyrc2	0,06	0,22	0,22	2,00	2,00	1,00	3,00	1,00	3,00	1,00	2,00	1,00	1,00	3,00	1,80	1,00
hyrc3	0,07	0,33	0,14	1,50	2,00	1,00	4,00	1,00	2,75	1,00	2,00	1,00	1,00	2,75	1,80	1,00
hyrc4	0,08	0,33	0,24	1,50	2,00	1,00	4,00	1,00	2,50	1,00	2,00	1,00	1,00	2,50	1,60	1,00
hyrc5	0,08	0,38	0,13	1,15	2,00	1,50	4,00	1,00	3,20	1,00	2,00	1,00	1,00	3,20	1,50	1,00
hyrc6	0,08	0,25	0,24	2,00	2,00	5,50	6,00	1,00	3,00	1,00	2,00	1,00	1,00	3,00	2,10	1,00
hyrc7	0,06	0,20	0,13	1,50	2,00	1,00	3,50	1,00	2,80	1,00	2,00	1,50	1,00	2,80	1,75	1,00
hyrcan	0,07	0,27	0,21	1,40	2,00	6,00	6,00	1,00	3,50	1,00	2,00	1,00	1,00	3,50	1,70	1,00
mite	0,08	0,50	0,10	1,50	2,00	1,00	2,50	1,00	2,90	2,00	4,00	1,00	1,00	2,90	1,50	1,00
osht	0,15	0,23	0,36	1,80	2,00	1,00	2,00	1,00	3,80	1,00	1,00	1,00	1,00	3,80	1,75	1,05
praem	0,04	0,15	0,20	0,85	2,00	1,00	2,00	1,00	2,50	2,00	1,00	1,00	1,00	2,50	1,80	1,00
vart	0,15	0,30	0,33	2,00	2,00	1,00	2,00	1,00	5,50	1,00	1,00	1,00	1,00	5,50	2,00	1,00
xylo1	0,10	0,37	0,08	1,25	2,00	1,00	2,00	1,00	3,90	1,00	2,00	1,00	1,00	3,90	1,80	1,00
xylo2	0,12	0,32	0,14	1,40	2,00	1,00	2,00	1,00	4,00	1,00	2,00	1,00	1,00	4,00	1,90	1,00
xylo3	0,06	0,32	0,10	1,40	2,00	1,00	2,00	1,00	4,00	1,00	2,00	1,00	1,00	4,00	1,75	1,00

Table 4. – Specimens from sect. *Orientigalium* used for pollen diameter measurements (see Fig. 2).

Designation	***Species***	***Specimen***
achurense1	*G. achurense*	Azerbayjan, Nakhichevan ASSR, right bank of Dzhagri-chai, Buzgow, Sytin & Schanzer (MHA)
achurense2	*G. achurense*	Azerbayjan, Nakhichevan ASSR, Arpa-chai tributary, near Akhura, Sytin & Schanzer (LE)
armenum	*G. armenum*	Armenia, Abovian distr., Azat Riv. gorge upstream of Garni, N slope, , I. Schanzer (WU)
azerbayjanicum1	*G. azerbayjanicum*	Azerbayjan, Nakhichevan ASSR, Negram, Gogina (MHA)
azerbayjanicum2	*G. azerbayjanicum*	N Iran, Mt. Karnaru, Knapp (WU)
basalticum	*G. basalticum* 2n=22 (Kiehn)	Turkey: A8. Prov. Erzurum: 16-17 km SW Ovit geçidi, 18-19 km NW Ispir, Ehrendorfer et. al. 787-160A-2 (WU)
bullatum1	*G. bullatum*	Azerbayjan, Nakhichevan ASSR, Bichenak, Grossheim (LE)
bullatum2	*G. bullatum*	Azerbayjan, Nakhichevan ASSR, Badamly (LE)
bullatum3	*G. bullatum*	Azerbayjan, Nakhichevan ASSR, Bichenak Pass, Sytin & Schanzer (MHA)
czerepanovii1	*G. czerepanovii*	Azerbayjan, Nakhichevan ASSR, Ordubad distr., 1.5-2 km E of Ordubad, Egorova et al. 386 (LE)
'czerepanovii'2	*G. hyrcanicum*	'G. czerepanovii': Iran, W Azerbayjan, Maku, Rechinger no. 39207 (W)
czerepanovii1	*G. czerepanovii*	Azerbayjan, Nakhichevan ASSR, Ordubad distr., 1.5-2 km E of Ordubad, Egorova et al. 386 (LE)
hypoxylon	*G. hypoxylon* 2n=44 (Kiehn)	Turkey, Ehrendorfer no. 787-164-7 (WU)
hyrcanicum1	*G. hyrcanicum*	Azerbayjan, Talysh, Kys-jurdy, Lomakin (LE)
hyrcanicum2	*G. hyrcanicum*	Armenia, N shore of Lake Sevan, Shorzha, Sytin & Schanzer (MHA)
incanum	*G. incanum* ssp. *elatius* 2n=44 (Kiehn)	Cult. HBV G-1817. Turkey: Hatay, Amanus Gebirge bei Atik, 5 km N Belen. Ern 6917 (WU)
kurdicum	*G. kurdicum*	Iraq, Rowanduz Pass, Guest no. 2115 (K)
mite1	*G. mite* 2n=22 (Ehrendorfer, pers. comm.)	Turkey: B6, K. Maras: Göksun, Berit Da., Kuzey yamaç, Xildiz 1328 (WU)
mite2	G. mite	[Turkey]: Kagysman distr., near Novo-Nikolaevka, Woronow 12348 (LE)
nabelekii	*G. nabelekii* 2n=44 (Kiehn)	Turkey, Van, Ehrendorfer no. 787-95-16 (WU)
oshtenicum	*G. oshtenicum*	Central Caucasus: Kabardino-Balkaria, Bezengi gorge, S foot of Skalisty Range, Portenier 1915 (LE)
plurifolium	*G. plurifolium*	Iran, Khamseh, Lamond no. 1082 (W)
praemontanum	*G. praemontanum*	Georgia Orientalis, Kachetia, in viciniis opp. Tziteli-Tzkaro, Mardalejschvili (WU)
problematicum	*G. problematicum*	Iran, Tehran, Elburz, Rechinger no. 57196 (W)
pseudomegalanthum	*G. pseudomegalanthum*	Iran, Totschal, Bornmueller no. 7105 (WU)
psilophyllum1	*G. psilophyllum* 2n=44 (Kiehn)	Turkey, Ehrendorfer no. 787-131-5 (WU)
psilophyllum2	*G. psilophyllum* 2n=44 (Kiehn)	Turkey, Ehrendorfer no. 787-60-3 (WU)
vartanii	*G. vartanii*	Azerbayjan: distr. Nucha: fl. Daschagil-chai, mt. Czilim, Alexeenko 11402 (LE);
wendelboi	*G. wendelboi*	Iran, Mazanderan, Haraz valley, Wendelbo no. 294 (W)
xylorrhizum1	*G. xylorrhizum*	Armenia, Leninakan distr., between Keti & Maisian , Sytin & Schanzer (MHA)
xylorrhizum2	*G. xylorrhizum*	Armenia, Spitak distr., Shirakamut, Sytin & Schanzer (MHA)
xylorrhizum3	*G. xylorrhizum* 2n=44 (Kiehn)	Turkey, Erzurum, Ehrendorfer et al. no. 787-114-4 (WU)
xylorrhizum4	*G. xylorrhizum*	Armenia, Spitak distr., near railroad station Nalband, Sytin & Schanzer (MHA)

The group under consideration is extremely poor in qualitative morphological characters suitable for the discrimination of taxa, a fact that seems to be one of the sources for its taxonomic difficulty. Thus, only twenty characters (Table 2) most commonly used in the taxonomy of the group were measured on each of the specimens examined. These measurements were used for the key and descriptions of taxa, and partly for statistical computations and the evaluation of infrapopulational and geographic variability.

The total data matrix of four hundred and three specimens with twenty characters proved too large to be analysed as a single unit. Hence, it was necessary to analyse separately the data sets for specimens and for OTUs. The OTUs data set summarizes the specimen data for each of the twenty-six OTUs. To construct it, the median was calculated for each continuous or multistate character. This approach appeared to be useful for a preliminary assessment of relationships between the OTUs. For the analysis of both data sets several procedures of the STATISTICA for Windows programme (Release 5.0, StatSoft Inc., 1995) were used.

The OTUs data set was initially analysed using cluster analysis via the Joining (Tree Clustering) procedure. The OTUs data matrix is shown in Table 3. Three characters, stem length, leaf length, and number of flowers per inflorescence, show strong correlations over 0.6 significant at $p<0.5$. These characters were excluded from the analyses and ratios were taken instead. Euclidean distances were calculated and analysed using the weighted pair-group average linkage method (WPGMA). This method was used instead of UPGMA because the cluster sizes were suspected to be much uneven. Figure 4 illustrates the results.

The distance matrix derived via cluster analysis was further analysed using the Multidimensional Scaling (MDS) procedure in an attempt to detect meaningful underlying dimensions and to rearrange OTUs in space according to observed distances. While executing the MDS procedure the programme actually moves objects (OTUs) around in the space defined by the requested number of dimensions (we used 2 dimensions), and checks how well the distances between objects can be reproduced by the new configuration. The programme's algorithm evaluates different configurations so as to minimize the stress value defined as the sum of squared deviations of observed distances from expected distances. The results were plotted as a 2-dimensional scatterplot (Fig. 6) and compared to the initial dendrogram.

On the other hand, OTU clusters derived were evaluated by the pattern they show when being mapped on the geographical map of the region (Fig. 5).

Actual differences between clusters and between OTUs included in each cluster were evaluated via the Discriminant Analysis procedure using the initial specimen data set. This seemed to be appropriate because distances between OTUs calculated from character medians, though helpful for preliminary grouping of OTUs, doesn't reflect actual variability of these OTUs.

While performing the discriminant analysis the programme automatically determines some optimal combination of characters so that the first discriminant function provides the best overall discrimination between groups analysed, the second provides the second best, and so on. Computationally, this programme performs a canonical correlation analysis that determines the successive discriminant functions. The maximum number of functions that the programme computes is equal to the number of groups (OTUs) analysed minus one, or to the number of characters in the analysis, whichever is smaller. Discrimination between groups was visualized by plotting individual scores for the first two discriminant functions. Ellipses show confidential areas with the coefficient of 0.95.

First we tried the Discriminant Analysis with the OTUs data set to check if it can bias the results compared to those obtained with MDS (Fig. 7). The initial data were checked for normality using the Shapiro-Wilk's W-test and comparison of histograms to the normal distribution curves. It appeared that quantitative characters' distributions approach normal, while those of qualitative characters are far from that. Nevertheless, we used both types of characters for the analyses since the latter seemed to better discriminate between the OTUs. To check the results for a probable bias we independently analysed the data using the Factor Analysis procedure,

which gave very similar results. We assume that different algorithms of analysis can bias the results in different ways (DUNCAN & BAUM, 1981). Thus, the use of different methods of analysis allows the verification of the validity of the groups suggested by these analyses. The results are shown in Figures 8-13.

We used the DELTA Package (DALLWITZ, 1974, 1980; DALLWITZ & al., 1993; PARTRIDGE & al., 1993) to produce descriptions of taxa and a preliminary key which were further elaborated manually. Character weights were assessed according to standardized beta coefficients which resulted from the discriminant analysis. These coefficients for each character in each discriminant function were interpreted as a "weight" for each character: The larger the standardized coefficient, the greater is the contribution of the respective character to the discrimination between groups.

Pollen grain measurements were done under the light microscope for thirty-three herbarium specimens (including eight vouchers of karyologically studied specimens) collected from the Caucasus region and adjacent areas (Table 4). From each specimen two or three flowers were taken and boiled in water. Anthers were separated from flowers, stained with acetocarmine on a slide, and squashed. From each preparation fifty normally stained pollen grains were measured with an eye-piece micrometer under × 40 magnification. The results were statistically worked out with the STATISTICA for Windows programme. Means were calculated and plotted as a line plot (Fig. 2). As one can see from the graph the values fall within four groups corresponding to four plateaux of the line plot. Assuming that these groups may correspond to different ploidy levels we used the t-test for independent samples statistic to check the differences between these groups. The differences appeared to be significant with *p*-values less than 0.0001. Threshold values of putative di-, tetra-, and higher polyploids were calculated as medians between the group means (Fig. 3).

3. Results

3.1. Notes on morphology and habitats

All the Caucasian species of *Galium* sect. *Orientigalium* studied here inhabit rocks, stony slopes and scree at low, middle and high elevations in ± arid mountain areas, from approximately 1000 to 2500 m. Populations of these plants are usually small, restricted to separate mountains, gorges or river valleys, and are scattered through the area, being spatially isolated from each other. Sympatric occurrence of different taxa is rare and sometimes may probably lead to hybridization, e.g., between *G. hyrcanicum* and *G. achurense* in SE Armenia. No correlation between occurence of taxa and particular substrates was revealed during field and herbarium studies. E.g., *G. hyrcanicum* and *G. xylorrhizum* were found to grow on granites, quartzites, and various metamorphic rocks. *Galium mite* inhabits exclusively basaltic rocks in Aragats Mt. in Armenia, but occurs on other substrates in other parts of its wide area.

The morphological differentiation of sect. *Orientigalium* representatives is summarized in Table 2. With respect to habit, these plants range from low subshrubs to perennial herbs, reaching a height of 5 to 80 cm. Their growth and habit types are more or less dependent on habitat conditions. Plants from rock crevices usually possess a thick taproot, terminating in a polycorm with several branching woody perennial shoots, and a tuft of numerous dry annual shoots from previous years. Perennial shoots can be rather long, creeping and sometimes secondarily rooting in plants growing on scree slopes. In some taxa, as *G. mite* and its allies, such perennial woody shoots are usually quite long, thick, and ± upright, giving the plants the appearance of subshrubs. Yet, some species never possess strongly lignified stem bases, e.g., *G. vartanii*, *G. oshtenicum* or *G. praemontanum*; in *G. hyrcanicum* this character is variable. Development of numerous vegetative shoots is characteristic of a few species, e.g., in *G. oshtenicum.* This results in a caespitose habit, just as the production of many generative shoots in *G. praemontanum*. In *G. incanum* subsp. *elatius* numerous vegetative brachyblasts are formed on the nodes of the stem bases.

Stem indumentum varies significantly from densely hirsute, with hairs ca. 0.5 mm long, to shortly and sparsely puberulent with minute hairs, sometimes only on nodes, or to completely glabrous. Among Caucasian members of the *G. subvelutinum* group indumentum density decreases upwards on the stems, so that inflorescence branches are usually completely glabrous. Hairs are simple unicellular trichomes, spreading ± horizontally from the stem surface. Only in *G. achurense* they are somewhat retrorse, and more or less curly in *G. incanum*.

Leaves are sessile, oblanceolate or broad oblanceolate to oblong or linear, blunt, acute to rarely mucronate. In *G. incanum* subsp. *elatius* the leaf margins are revolute; among members of the *G. subvelutinum* group they are flat or only slightly revolute. Leaves are grouped with leaf-like stipules in pseudowhorls of 6-7, rarely only 4-6 or up to 6-9. Leaf shape, dimensions and number are to some extent species specific though considerable variation occurs in *G. hyrcanicum*. Leaf whorls are usually spreading and only occasionally more or less reflexed. Constantly reflexed leaves are very characteristic for *G. achurense* only.

Leaf indumentum is similar to that of the stem and varies from densely hirsute in some varieties of *G. hyrcanicum* to completely glabrous in *G. mite*.

Inflorescence shape and dimensions are variable but still valuable to distinguish between species groups. *G. incanum* subsp. *elatius* can be easily recognized by its relatively dense, narrow and elongate inflorescence with opposite short peduncles, branched only twice. In the species of the *G. subvelutinum* alliance inflorescences are more lax, either narrowly to broadly pyramidal, or shorter and corymbiform in their upper part. Pyramidal inflorescences are normally quite elongated and have (4)-5 and more nodes, counting from the uppermost cyme node downwards to the lowest inflorescence branch node. Corymbiform inflorescences are generally shorter and consist of 1 to 3 nodes only. In dwarf species, as *G. oshtenicum* and *G. praemontanum,* inflorescences can be reduced to small and more or less corymbiform terminal cymes. It is worth mentioning that the character of inflorescence shape refers only to mature plants with well developed flowering shoots; it is almost inapplicable when flowering shoots are poorly developed. One more valuable character is the angle at which pedicels branch at the fruiting stage. In most of the species it is usually less than 90°, but *G. azerbayjanicum* and sometimes *G. achurense* exhibit divaricate pedicels that branch at right angles and even more.

Flowers are white or sometimes pinkish, broadly crateriform to subrotate, usually about 2.5 to 4 mm in diameter, with a tube ca. 0.5 mm long to nearly absent. Unusually large corollas, 4.5 to 7 mm in diameter, are found in *G. vartanii.* Petals are apiculate to mucronate with attenuate appendages. The latter can be rather short and curved inwards to more or less long, thin, and spreading outwards. This feature, usually rather constant, sometimes may vary too, e.g., in populations of *G. hyrcanicum.*

Fruits are usually dry and consist of two one-seeded mericarps, only one of which usually develops normally. Mericarps are more or less elliptic in outline with smooth brownish to nearly black surface, 1.2-2.5 mm long, and with a closely adherent dry pericarp. In *G. bullatum* and *G. armenum* the pericarp inflates and becomes somewhat juicy, making mericarps round, rugose, enlarged up to 3-4 mm diam., and conspicuously white to pinkish in colour. This remarkable fruit character, shared by *G. bullatum* and *G. armenum,* is not unique in the genus *Galium*. In the *G. boreale-G. rubioides* group of sect. *Platygalium* it appears as a diagnostic character of *G. rubioides* L. and *G. physocarpum* Ledeb. This apomorphic feature obviously originated quite independently in these two unrelated groups of *Galium*, and constitutes a typical case of homoplasy.

3.2. Multivariate analysis

We accept as the "null hypothesis" that all investigated OTUs of the *Galium subvelutinum* alliance (Table 1) belong to a single species and then search for some underlying morpho-geographical pattern in their variation. WPGMA cluster analysis of the OTU data matrix reveals three major clusters of OTUs at the linkage distance 3.4 (Fig. 4). At the distance 3.0-2.6 the first

cluster splits into three more (sub)clusters. The second cluster also splits into two more subclusters, but since it consists of only 5 OTUs we considered it as a single cluster in further analyses. These five OTU groupings show good correspondence with their geographical distribution (Fig. 5). Cluster 5 consists of three OTUs of eastern distribution (Talysh Mts.), penetrating westward as far as Nakhichevan [with one population from W Nakhichevan described as *G. grossheimii* (gross) and another of *G. hyrcanicum* (hyrc6) from the Zangezur Range in E Nakhichevan]. This cluster 5 corresponds to *G. hyrcanicum* agg. (E).

The cluster 4 comprises four OTUs constituting the *G. mite* group: *G. achurense, G. mite*, *G. azerbayjanicum*, and *G. armenum. Galium mite* is a widely distributed species, penetrating into central Armenia from Turkey at the NE edge of its area. The others are vicarious species with much smaller geographical ranges distributed from the S foot of the Gegam Range in Armenia (*G. armenum*) to S Nakhichevan (*G. achurense*) and adjacent Iran (*G. azerbayjanicum*).

The clusters 3, 2 and 1 unite all the other OTUs distributed throughout Armenia and Nakhichevan. Cluster 2 includes OTUs with extreme N and NW distributions: *G. xylorrizum* (including its isolated population from Georgia described as *G. praemontanum* var. *armazicum*) and three morphologically and geographically distinct endemics, *G. oshtenicum* from the NW and C Caucasus, and *G. vartanii*, a geographically isolated species from the NE Caucasus. This cluster 2 corresponds to *G. xylorrhizum* agg. Cluster 1 unites only OTUs that belong to the single endemic species *G. bullatum* from central Nakhichevan. Cluster 3 links the OTUs of *G. praemontanum* known from a single locality in E Georgia and *G. hyrcanicum* agg. (W) distributed around Lake Sevan and southeastward to Nakhichevan.

As one can see from Figure 5, most of the clusters 1-5 are ± allopatric, with their geographical ranges only overlapping in E Armenia and Nakhichevan. Multidimensional scaling of the distance matrix derived from the cluster analysis enabled us to retrieve a 2-dimensional pattern of these clusters (Fig. 6). It reveals that clusters 5 [*G. hyrcanicum* agg. (E)] and 4 (*G. mite* group) are more distant from the other OTU clusters (3, 2, 1) which tend to form a more or less continuous assembly in the central part of the plot. Discriminant analysis of the same matrix reveals a nearly identical picture where the clusters are even more distant from each other (Fig. 7).

To better assess the differences between and within the five clusters of the *G. subvelutinum* alliance and their constituent OTUs, we performed discriminant analyses on the original specimen data set. As is seen from the plot in Figure 8, all the clusters except four form a continuous pattern of distribution with major overlaps. Such a pattern much differs from that found by multidimensional scaling and more resembles the results of geographical mapping of clusters. We suppose that this difference reflects variability of the OTUs which could not be assessed by comparison of medians. Thus, the links between clusters 2, 3, and 5 are of clinal nature: cluster 3 is situated between clusters 2 and 5, and that resembles the pattern of their actual geographical distribution (Fig. 5). Clusters 3 and 5 are particularly close and have completely overlapping confidential areas, constituting *G. hyrcanicum* agg., whereas cluster 2 stands more apart as *G. xylorrhizum* agg. Cluster 1 (*G. bullatum*) is closely linked to them. Cluster 4 tends to form a more clearly separated entity and corresponds to the *G. mite* group.

To control this result we analysed the same data using factor analysis and got nearly the same pattern (Fig. 9). We consider this as a good confirmation of applicability of the discriminant analyses to this study and of the fact that the difference between patterns revealed by the analyses of the two data sets reflects actual variability of populations and is not just due to any bias.

The discriminant analysis the of the *G. mite* group (Fig. 10) readily separates four species: *G. achurense*, *G. azerbayjanicum*, *G. mite*, and *G. armenum*. Major overlap of the two latter species reflects the hybrid nature of *G. armenum*, which originates from hybridization between *G. mite* and *G. bullatum* (SCHANZER, 1997). *G. mite* is a widely distributed, presumably always diploid species, penetrating into the Caucasus region as far as the S slopes of Aragats Mt. Three other species are endemics of the Araks River basin and can be regarded as marginal north-eas-

ternmost derivatives of *G. mite* (Fig. 1). According to the results of pollen measurements (Fig. 2) they appear to be partly diploid, partly tetraploid or even higher polyploid.

Exclusion of cluster 4 (*G. mite* group) from the discriminant analysis (Fig. 11) enabled us to more clearly separate *G. bullatum* (cluster 1) from the rest of the *G. hyrcanicum* group. As one can see from the plot, the clusters 3 and 5 still have nearly completely overlapping confidential areas and have to be united (*G. hyrcanicum* agg.), whereas cluster 2 (*G. xylorrizum* agg.) is somewhat more distinct. Overlaps of clusters 3, 5, and 2 again are in geographical order.

The discriminant analysis of OTUs of the *G. xylorrhizum* agg. (cluster 2) shown in Figure 12 separates three more or less distinct specific entities, probably all polyploids (Fig. 2): *G. vartanii*, *G. oshtenicum*, and *G. xylorrhizum*. It is worth mentioning that four different populations of the latter species studied (including the isolated "var. *armazicum*") are all somewhat different from each other, though with major overlaps. *G. oshtenicum* and *G. vartanii* from the Great Caucasus seem to be the close to *G. xylorrizum*, though quite separable from it.

Within *G. hyrcanicum* agg., a particular problem concerns *G. czerepanovii*, a species described from desert rocky hills in the vicinities of Ordubad in SE Nakhichevan. This species differs very weakly from Nakhichevan *G. hyrcanicum* populations, chiefly by a lower number of glabrous leaf whorl elements (4-5). As in the case of *G. xylorrhizum*, all populations of *G. hyrcanicum* in Nakhichevan differ somewhat from each other, though widely overlap in their variability range. When compared to neighbouring *G. hyrcanicum* populations (Fig. 13), *G. czerepanovii* looks at least as distinct as *G. bullatum.* Another piece of evidence supporting its recognition as a separate species was obtained from pollen grain measurements: they show that *G. czerepanovii* ranks among the diploids, whereas all other members of *G. hyrcanicum* apparently are tetraploids or higher polyploids (Fig. 2). *G. praemontanum*, an endemic from central Georgia stands much more apart from them and is probably rather distantly related to the *G. hyrcanicum* agg.

3.3. Chromosome numbers and polyploidy

A few species only of sect. *Orientigalium* have been studied so far as to their chromosome numbers, none of them from the Caucasus region. Several counts have been made by Dr. M. Kiehn (Institute of Botany and Botanical Garden, University of Vienna, Austria) from specimens collected from Turkish regions adjacent to the Caucasus. The results are still unpublished, but appear on specimen labels in the WU-Herbarium, and we are authorized to use them for this study: diploid numbers ($2n = 22$) were counted for *G. mite* and *G. basalticum*, tetraploid numbers ($2n=44$) for *G. nabelekii*, *G. psilophyllum*, *G. xylorrhizum*, *G. hypoxylon*, and *G. incanum* subsp. *elatius*. Since a correlation between ploidy level and mean diameter of pollen grains has been previously reported for the *G. incanum* alliance (EHRENDORFER, 1951), we attempted such measurements on specimens originating from twenty populations from the Caucasus and adjacent regions, using specimens with known chromosome numbers as reference points (Table 4). The results shown in Figures 2 and 3, verify the expected correlation and demonstrate that apparent di-, tetra-, and possibly hexa- or even octaploids also occur among the Caucasian populations of the *G. subvelutinum* alliance. Diploidy seems to be characteristic for *G. mite* and part of *G. azerbayijanicum* from the *G. mite* group and partly for *G. czerepanovii* from the *G. hyrcanicum* group. All the other populations can be assumed to be at least tetraploid.

3.4. Synopsis and key to the Caucasian taxa of Galium sect. Orientigalium

Galium sect. ***Orientigalium*** Ehrend. in Österr. Bot. Z. 98: 435. 1951.

= *Galium* sect. *Leiogalia* ser. *Hyrcanica* Pobed. in Schischk. & al., Fl. SSSR 23: 375. 1958 (rossice); in Novosti Sist. Vyssh. Rast. 7: 279. 1971 (latine) p.p.

= *Galium* sect. *Leptogalium* ser. *Hercynica* Pobed. in Schischk. & al., Fl. SSSR 23: 336. 1958 (rossice); in Novosti Sist. Vyssh. Rast. 7: 278. 1971 (latine) p.p.

I. *Galium subvelutinum* alliance

A. *Galium mite* group

1. *G. achurense* Grossh.
2. *G. mite* Boiss. & Hohen.
3. *G. azerbayjanicum* Ehrend. & Schönb.-Tem.
4. *G. armenum* Schanzer

B. *Galium hyrcanicum* group

5. *G. bullatum* Lipsky

Galium hyrcanicum agg.

6. *G. hyrcanicum* C. A. Mey.
7. *G. czerepanovii* Pobed.
8. *G. praemontanum* Mardal.

Galium xylorrhizum agg.

9. *G. xylorrhizum* Boiss. & Huet
10. *G. oshtenicum* Ehrend. & Schanzer ex Mikheev
11. *G. vartanii* Grossh.

II. *Galium incanum* alliance

12. *G. incanum* subsp. *elatius* (Boiss.) Ehrend.

Key

1. Stems and inflorescences with a dense, shortly appressed to curly pubescent indumentum; inflorescences relatively dense, narrowly elongate; peduncles short, usually branching only 1-2 times dichasially; leaves linear, margins revolute; numerous brachyblasts present at lower stem nodes: ***G. incanum*** alliance . . . . . .12. ***G. incanum*** subsp. ***elatius***

1a. Inflorescences ± glabrous, relatively lax, pyramidal to corymbiform; leaves oblanceolate to linear, margins hardly revolute; brachyblasts at lower system nodes absent: ***G. subvelutinum*** alliance 2

2. Inflorescences narrowly to broadly pyramidal (not corymbiform in upper part), normally with 5 and more nodes; plants often taller than 250 mm, usually ± suffruticose: ***G. mite*** group 3

2a. Inflorescences corymbiform (sometimes elongate, but still remaining corymbiform in terminal portion), normally with 1 to 3 nodes only; plants often less than 250 mm tall, mostly ± herbaceous: ***G. hyrcanicum*** group 6

3. Plants shortly retrorsely hairy at lower stem portion; leaves mostly 10-17 × 1-2 mm, in whorls of 6-7(-8), reflexed; pedicels strongly divaricate in fruit . . . . . 1. ***G. achurense***

3a. Plants ± glabrous to shortly pubescent at lower stem portion with spreading, never retrorse hairs; leaves larger, in whorls of 6, usually spreading or only slightly reflexed 4

4. Mericarps whitish or pinkish, rugose, with inflated pericarp, 2-2.8 mm diam.; leaves spreading, mostly 11-21 × 1-1.8 mm; corolla lobes broadly apiculate, with rather short inconspicuous appendages . . . . . .4. ***G. armenum***

4a. Mericarps brown to blackish, smooth, pericarp not inflated, 1.5-1.9 mm diam.; corolla lobes usually apiculate-mucronate, with elongate and conspicuous appendages 5

5. Plants suffrutescent, inflorescences broadly pyramidal, pedicels not divaricate in fruit; leaves spreading, mostly 19-29 × 1.3-1.8 mm ..... .2. ***G. mite***

5a. Plants ± suffrutescent to herbaceous; inflorescences elongate to narrowly pyramidal, pedicels divaricate in fruit; leaves often ± reflexed, 13-19 × 2-3 mm ..3. ***G. azerbayjanicum***

6. Stem bases thin, long, ± herbaceous; plants usually lower than 10 cm; inflorescences with less than 20 flowers: ***G. xylorrhizum*** agg. p.p. 7

6a. Stem bases somewhat thicker and often slightly woody; plants usually higher than 10 cm; inflorescences with more than 20 flowers 9

7. Plants caespitose; inflorescence usually reduced to less than 10 flowers on short peduncles, hardly protruding beyond upper stem leaves; flower diam. 2.5-4 mm 8

7a. Plants not caespitose; inflorescence ± well developed and protruding beyond upper stem leaves by long internodes; flower diam. 4.5-6 mm ..... .11. ***G. vartanii***

8. Plants with numerous basal vegetative shoots; generative shoots simple; corolla outside often somewhat puberulent at the base, petal appendages shortly attenuate and curved inwards ..... .10. ***G. oshtenicum***

8a. Plants without basal vegetative shoots; the numerous generative shoots branching in upper part; corolla outside glabrous, petal appendages long and thinly attenuate ..... .8. ***G. praemontanum***

9. Fruits ± spherical, deeply rugose, whitish or pinkish and with fleshy inflated pericarp when mature, 2-4 mm diam.; stems and leaves hairy ..... .5. ***G. bullatum***

9a. Fruits ± obovate, smooth, brown to black and dry when mature, 1-2 mm long; stems and leaves hairy to glabrous ..... .10

10. Stems densely to sparsely hirsute or hairy at least at lower portion; leaves ± hairy to glabrous: ***G. hyrcanicum*** agg ..... .11

10a. Stems hairy at nodes only, sometimes with scattered hairs at lower internodes; leaves always glabrous: ***G. xylorrhizum*** agg. p.p. ..... .9. ***G. xylorrhizum***

11. Leaves ± broadly oblanceolate, in whorls of 5-6, at lower nodes in whorls of 4, mostly glabrous ..... .7. ***G. czerepanovii***

11a. Leaves oblanceolate to linear, in whorls of (5-)6(-7), at lower nodes in whorls of more than 4, mostly ± hairy ..... .6. ***G. hyrcanicum***

I. *Galium subvelutinum* alliance

A. *Galium mite* group

1. *Galium achurense* Grossh. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 13: 25-26. 1950; Pobed. in Schischk. & al., Fl. SSSR 23: 363. 1958.

Plants herbaceous, with thin, ± woody stem bases. Stems (90-)176-320(-410) mm long, shortly retrorsely hairy at lower portion. Leaves in whorls of 6-8, linear to linear-oblanceolate, with flat to slightly revolute margins, (8-)10.5-17(-19) mm long, (0.9-)1-2(-3) mm wide, reflexed, glabrous. Well developed inflorescences ± elongate, not corymbiform, sometimes nearly cylindrical to narrowly or broadly pyramidal (rare), (10-)25-150(-350)-flowered. Pedicels mostly divaricate at angles of more than 90° in fruit. Flowers (2.3-)2.6-3.2(-3.8) mm diam. Petal appendages long and thinly attenuate. Mericarps smooth, with dry adherent pericarp, dark coloured, brownish to black, (1.3-)1.5-1.8(-2) mm long. Fl. VI.

Typus: AZERBAIJAN SSR, Nachichevan ASSR, Norashen distr., 1 km W of Akhura, ca. 1240 m, 19.V.1947, *Grossheim, Ilyinskaya & Kirpichnikov* (Holo-, iso-: LE!).

Specimens examined. – [**AZERBAIJAN**]: **W Nakhichevan:** Shakhbuz distr., Buzgov, Tzvelev & Czerepanov 459 (LE); Dzhagri-chai, near Buzgov, *Sytin & Schanzer* (MOSP, MHA, MW, LE, WU, W); Arpa-chai tributary, near Akhura, *Sytin & Schanzer* (MOSP, MHA, LE); Norashen distr., Kabakh-yal mt. near Arpa-chai River, *Grossheim, Ilyinskaya & Kirpichnikov* (LE); Norashen distr., N of Karabaglyar, *Tzvelev & Czerepanov 130* (LE); Nakhichevan distr., near Aznabyurt, *Grossheim, Ilyinskaya & Kirpichnikov* (LE); Arpa-chai River gorge near Yaydzhi, *Gogina & Matzenko 1261* (MHA); [**ARMENIA**]: at Nakhichevan border, near Khachik, *Sytin & Schanzer* (MOSP, MHA, LE); Yekhegnadzor distr., Elegis River gorge, between vill. Alayaz and Kavushug, *Manakyan & Czarczogljan* (ERE); Yekhegnadzor distr., near vill. Areni, *Gabrielian & Avetisian* (ERE); Mikoyan distr., Ayar gorge, *Gabrielian* (ERE).

Galium achurense is a very restricted endemic to Nakhichevan (mostly in the NW: Akhura and Dzhagri-chai River valleys) and adjacent Armenia (Fig. 1). It is probably polyploid (Fig. 2), and related to *G. azerbayjanicum* and *G. mite* (Figs. 6, 7). Morphologically, it is quite distinct and well characterized by its usually small reflexed leaves, often in whorls of 7-8, and the short retrorse indumentum on stems. Nevertheless, presumable hybrids between *G. achurense* and *G. hyrcanicum* were collected in NW Nakhichevan near Khachik village ["Armenia: at Nakhichevan border, near Khackik; *Sytin & Schanzer*" (MHA, MOSP)].

2. *Galium mite* Boiss. & Hohen. in Boiss., Diagn. Pl. Orient. 3: 37. 1843; Ehrend. & Schönb.-Tem. in Townsend & Guest, Fl. Iraq 4: 598. 1980; Ehrend. & Schönb.-Tem. in Davis, Fl. Turkey 7: 810-811. 1982.

≡ *Galium subvelutinum* subsp. *mite* (Boiss. & Hohen.) Ehrend. in Notes Roy. Bot. Gard. Edinburgh 22: 365. 1958.

Plants ± suffrutescent. Stems (230-)235-387(-460) mm long, glabrous. Leaves in whorls of 6, linear, with ± flat margins, (16-)18.8-29(-33) mm long, (1.2-)1.3-1.8(-2) mm wide, usually spreading, glabrous. Well developed inflorescences ± elongate, not corymbiform, broadly to narrowly pyra-midal, (25-)60-120(-300)-flowered. Pedicels never divaricate at angles of more than 90° in fruit. Flowers 2.9-3(-3.1) mm diam. Petal appendages long and thinly attenuate. Mericarps smooth, with dry adherent pericarp, dark coloured, brownish to black, 1.5-1.6 mm long. Fl. V-VI.

Typus: [**IRAQ**]: In monte Gara Kurdistaniae, *Kotschy 559b* (Lecto-: G!, chosen by EHRENDORFER, 1958; isolecto-: LE! sub *Kotschy 359b*); In monte Gara Kurdistaniae, *Kotschy 506a* (Syn-: G!, LE! sub *Kotschy 306a*).

Specimens examined. – [**ARMENIA**]: S of Aragats Mt., Kasakh River gorge near Karbi, *Sytin & Schanzer* (LE, MHA, MOSP, WU); S slope of Aragats Mt., near Amberd, *Akhverdov & Gokhtuni* (ERE); Paranlug gorge, *Abaran & Khotzyatovsky* (TBI); Sevan distr., near Agveran, *Mulkijanian* (ERE).

Galium mite is a species widely distributed in Turkey and W Iran, diploid (Fig. 2), and possibly ancestral to the other species of its group (Figs. 6, 7). It is penetrating into the Araks River basin and to the foothills of Aragats Mt. from the Kars highlands. Plants collected in Armenia (Kasakh River gorge) correspond well in their characters to the type of the species and the plants collected from Kars, but possess somewhat smaller fruits. In Armenia *G. mite* is at the very N limit of its distribution (Fig. 1).

3. *Galium azerbayjanicum* Ehrend. & Schönb.-Tem. in Pl. Syst. Evol. 174: 202-203, fig. 4. 1991.

– *G. hyrcanicum* auct. mult. non C. A. Mey.

– *G. mite* auct. non Boiss. & Hohen.: Mikheyev in Bot. Zhurn. 77(10): 72. 1992, p.p.

Plants herbaceous to ± suffrutescent, with thin, slightly woody stem bases. Stems 250-320(-350) mm long, shortly puberulent at lower portion, at least on nodes, with spreading hairs. Leaves in whorls of 6, linear or oblanceolate, with flat to slightly revolute margins, 13-18(-19) mm long, (1.7-)2.1-3 mm wide, mostly spreading, glabrous. Inflorescences ± elongate, not corymbiform, sometimes nearly cylindrical to narrowly or broadly pyramidal, (30-)40-110 (-300)-flowered. Pedicels in fruit divaricate at angles of more than 90°. Flowers 2.2-2.9(-3) mm

diam. Petal tips long and thinly attenuate. Mericarps smooth, with dry adherent pericarp, dark coloured, brownish to black, 1.4-1.8(-2) mm long. Fl. V.

Typus: AZERBAIJAN occid.: In saxosis calc. SE. Shahpur, versus lacum Rezaiyeh (Urmia), 1300 m, *Rechinger 41858* (Holo-: W!).

Specimens examined. – **[AZERBAIJAN]**: **Nakhichevan:** prope Negram, *Grossheim* (LE, TBI, ERE); Araks River gorge between Negrom and Darosham, *Woronow* (TBI); prope Negrom, *Prilipko & Karjagin* (LE); fl. Alyndz...inter Dzhulfa et Dzhamaldin, *Grossheim* (WU); **[SE ARMENIA]:** Ustupi, *Radde 351, 381* (LE).

Galium azerbayjanicum has been described from Iranian W Azerbaijan, and is distributed in Nakchichevan, SE Armenia and NW Iran (Fig. 1). It apparently is diploid (and tetraploid?) (Fig. 2) and exhibits relationships mainly with *G. mite*, *G. achurense* (Figs. 6, 7), and *G. problematicum* (Ehrend.) Ehrend. & Schönb.-Tem. from the Elburz Mts.in N Iran (EHRENDORFER & al., 2002).

Plants of *G. azerbayjanicum* collected from Negrom and Dorosham in Nakhichevan are almost identical to the type specimen and to those collected from Qotur valley in Iran [fl. Qotur W Khoy, *Rechinger 41699* (WU); jugo Qushchi inter Shahpur et Rezaiyeh, *Rechinger 41952* (WU)]. Since Negrom and Dorosham are situated in the Araks River valley just opposite the Qotur River mouth, it seems probable that *G. azerbayjanicum* dispersed northwards downstream the Qotur valley. One more locality of this species is situated further downstream the Araks River in the Megri Range ("Ustupi" or Hustup Mt.).

Some specimens from the Araks River valley in Nakhichevan seem to be intermediate between *G. azerbayjanicum* and *G. czerepanovii* and are probably of hybrid origin ["Nakhichevan: prope Negram, *Grossheim*" (ERE); "inter Negram et Darosham, *Grossheim*" (ERE); "prope Djamal-Edin, Mt. Dary-dag, *Schelkovnikov & Kara-Murza*" (ERE)].

4. *Galium armenum* Schanzer in Bot. Zhurn. 82(3): 126. 1997.

= *G. mite* × *G. bullatum* Schanzer in Novosti Sist. Vyssh. Rast. 26: 156. 1989.

– *G. bullatum* auct. non Lipsky.

Plant ± suffrutescent. Stems (180-)250-400(-500) mm long, glabrous or shortly puberulent at nodes, with spreading hairs. Leaves in whorls of (5-)6(-7), linear, with flat to slightly revolute margins, (10-)13.6-20.8(-24) mm long, 0.9-1.8(-2.4) mm wide, mostly spreading and glabrous. Inflorescences ± elongate, not corymbiform, broadly or narrowly pyramidal to nearly cylindrical (rare), (40-)60-90 (-130)-flowered. Pedicels in fruit never divaricate at angles of more than 90°. Flowers 2.5-3.5 mm diam. Petal tips shortly attenuate and curved upwards. Mericarps rugose, with juicy and inflated pericarp, light coloured or whitish, (1.7-)2-2.6(-3.3) mm long. Fl. IV-V.

Typus: ARMENIA, Abovian distr., Azat River gorge upstream of Garni, N slope, on talus and rock outcrops, 28.VI.1995, *Schanzer* (Holo-: LE!; iso-: ERE!, MHA!, WU!).

Specimens examined. – [**ARMENIA**]: juxta pagum Gocht kums monastery Gehard, *Fedorov* (ERE); Abovian distr., between Garni and Zovashen, right bank of Azat River, *Avetisian, Nazarova & Gandilian* (ERE); Artashat distr., Khosrov mts., *Mulkidjanian* (ERE); Ararat distr., vicinities of village Chiman, at SE foot of Ketuz mt., *Avetisian* (ERE); Erivan, Arzni, *Tamamshian* (ERE); Kotai distr., monastery Gegart, source of Azat-get Riv., *Akhverdov* (TBI); Kotai distr., between monastery Gegart and vill. Artiz, *Akhverdov* (TBI); Garni gorge in Erevan vicinities, between Gokht and Garni, *Gogina & Proskuriakova 764* (MHA); between Garni and Gokht, bank of Azat River, *Manakian* (ERE); Kotai distr., Gegart, *Akhverdov* (TBI); Mt. Eranos, *Schelkovnikov* (ERE); Mt. Eranos near vill. Getashen, *Manakian* (ERE); Vedi distr., Erakh Range, vill. Gelaisor, *Mulkijanian* (ERE); Artashat distr, Khosrov mts., *Mulkijanian* (ERE); Ararat distr., right bank of Khosrov River, between ruines of Agasi-beglu and Khosrov, *Chanjian* (ERE); prope Beiuk-Vedi, Mt. Ilanlu, *Schelkovnikov* (ERE); Vedi distr., Boz-Burun mts., *Akhverdov* (ERE); in summa Garni-Jarykh, *Tamamshian & Maleev* (ERE).

Galium armenum is probably tetraploid (Fig. 2) and endemic to SE Armenia, occurring in the Azat River valley and extending southwards into the Gegam Range (Fig. 1). It is intermediate with respect to several morphological features and distribution between diploid *G. mite* and tetraploid *G. bullatum,* and probably of hybrid origin (SCHANZER, 1997).

B. *Galium hyranicum* group

5. *Galium bullatum* Lipsky in Trudy Imp. S.-Petersburgsk. Bot. Sada 13: 300. 1894; Grossh., Fl. Kavkaza 4: 32. 1934; Grossh., Opred. Rast. Kavkaza: 252. 1949; Pobed. in Schischk. & al., Fl. SSSR 23: 352. 1958.

Plants herbaceous to somewhat suffrutescent, often with slightly woody stem bases. Stems (50-)130-250(-370) mm long, shortly puberulent at lower portion and nodes, with spreading hairs. Leaves in whorls of (5-)6-7(-8), oblanceolate to linear, with ± flat margins, (9-)12-21(-27) mm long, (1-)1.2-2(-2.9) mm wide, mostly spreading, shortly puberulent or hirsute to glabrous (rare). Well developed inflorescences definitely corymbiform, (6-)25-80(-160)-flowered. Pedicels in fruit never divaricate at angles of more than 90°. Flowers 3-4.5(-5) mm diam. Petal tips shortly attenuate and curved upwards. Mericarps globose, rugose, with juicy inflated pericarp, light coloured, whitish or pinkish, (2-)2.5-3.6(-4) mm long. Fl. V.

Typus: [**AZERBAIJAN**]: Erivan gub., Nakhichevan u., between Nakhichevan and Kazanchi, 1.VII.1893, *Lipsky* (Holo-: LE!; iso-: K, LE!).

Specimens examined. – [**AZERBAIJAN**]: **Nakhichevan**: prope Shach-buz, *Grossheim & Gurvich* (LE); near Shahbuz, *Sytin & Schanzer* (LE, MHA, MOSP, W); near Bichenak, *Sytin & Schanzer* (MHA, WU); Bichenak pass, *Sytin & Schanzer* (LE, MHA); in jugo Zangezur, prope Bitchenach, *Gavrilov* (TBI); Bitchenach, *Radde* (LE, TGM); prope Bitchenach, *Grossheim* (LE); near Bichenak, *Kutateladze & al.* (TBI); near Bichenakh, *Agababian* (ERE); Shahbuz distr., near Bichenakh, *Tzvelev & Czerepanov 218* (LE); near Kolany, *Gabrielian* (ERE); near Karababa, *Kozlovsky* (TBI); supra p. Karababa, *Fomin* (LE); upstream Termiazatiakh, *Takhtajan* (ERE); between Bartzruni & Tarmachatakh, *Khanjian* (ERE); near Aravsa, source of Alindzha River, *Mandenova* (ERE); Ordubad distr., near Nasirvaz, foot of Karadash Mt., *Oganesian* (ERE); [**ARMENIA**]: Zangezur, Sisian distr., near Aravus, Artzavan gorge, *Manakian* (ERE).

Galium bullatum is an endemic of C and N Nakhichevan, and adjacent Armenia (Fig. 1). Its occurrence in nearby NW Iran ("Persia borealis", *Szovits*, W) is doubtful and needs verification. The speccis is apparently tetraploid (Fig. 2) and relatively well separable within the *G.hyrcanicum* group. It is linked to the *G. mite* group by the also polyploid and probably hybrid *G. armenum* with which it shares the inflated, juicy mericarps (SCHANZER, 1997). Otherwise, morphological affinities are with *G. hyrcanicum* agg. (Figs. 8, 11).

Galium hyrcanicum agg.

6. *Galium hyrcanicum* C. A. Mey., Verzeichn. Pl. Cauc.: 53 (1831); Grossh., Flora Kavkaza 4: 33 (1934); Grossh., Opredelitel Rastenij Kavkaza: 252 (1949); Pobed., Fl. URSS 23: 376 (1958); Manden., Fl. Armen. 7: 93 (1980).

≡ *G. subvelutinum* subsp. *hyrcanicum* (C. A. Mey.) Ehrend. in Notes Roy. Bot. Gard. Edinburgh 22: 369. 1958.

= *G. hyrcanicum* var. *puberulum* Trautv. in Trudy Imp. S.-Petersburgsk. Bot. Sada 7: 461. 1881.

= *G. hyrcanicum* var. *glabrum* Trautv. in Trudy Imp. S.-Petersburgsk. Bot. Sada 7: 461. 1881.

= *G. grossheimii* Pobed. in Schischk. & al., Fl. SSSR 23: 720. 1958.

= *G. plurifolium* Ehrend. & Schönb.-Tem. in Pl. Syst. Evol. 174: 203. 1991.

= *G. kandevanense* Ehrend. & Schönb.-Tem. in Pl. Syst. Evol. 174: 206. 1991.

Plants ± herbaceous, often with slightly woody stem bases. Stems (20-)60-340(-380) mm long, glabrous or shortly puberulent or hirsute at lower portion and nodes, will spreading hairs. Leaves in whorls of (5-)6-7(-8), linear to oblanceolate, with flat to slightly revolute margins, (4-)6-21(-29) mm long, (0.7-) 0.9-2(-3) mm wide, spreading or ± reflexed, sparsely pubescent, hirsute or glabrous. Well developed inflorescences definitely corymbiform (to nearly pyramidal), (3-)10-110(-200)-flowered. Pedicels in fruit never divaricate at angles of more than 90°. Flowers (2-)2.5-4.4(-5.5) mm diam. Petal appendages shortly attenuate and curved upwards. Mericarps

smooth, with dry adherent pericarp, dark coloured, brownish to black, (1-)1.3-2.4(-2.7) mm long. Fl. V-VII.

Typus: [**AZERBAIJAN**, Talysh]: In rupestribus versus cacumen summum mont. prope pagum Perimbel, 7.VI.1830, no. 112, *C. A. Meyer* (Holo-: LE!; iso-: LE!, W!).

Specimens examined. – [**AZERBAIJAN**, **Nakhichevan**]: Norashen distr., Tandera mt. foothills near Arpa-chai River, 11.V.1947, *Grossheim, Ilyinskaya & Kirpichnikov* [**typus** of *G. grossheimii* (Holo-, iso-: LE!)]; Nakhichevan: inter Ordubad et fl. Arax, *Grossheim* (WU); Ordubad distr., upwards of Nyus-Nyus, source of Ordubad-chai River, *Menitzky & al. 320* (LE); Nyus-Nyus N of Ordubad, *Sytin* (LE, MOSP); Azhnodur gorge N of Ordubad, *Woronow* (TBI); Zangezur Range, Perevalnaya mt. NE of Unus, *Sytin & Schanzer* (MHA); Zangezur Range, Malashkari gorge NE of Unus, *Sytin & Schanzer* (MHA); Zangezur Range, Kalaki near Unus, *Sytin & Schanzer* (MHA); Kaputdzikh, *Skibitzky* (TBI); Norashen distr., Arpa-chai gorge near Yaydzhi, *Gogina & Matzenko 1176, 1261* (MHA); Arpa-chai tributary, near Akhura, *Sytin & Schanzer* (MOSP, MHA, LE); [**AZERBAIJAN, Talysh**]: distr. Lenkoran, circa Pirazora ditionis Zuwant, *Grossheim 971* (WU), *s.n.* (TBI); Lerik distr., near Pirasura, *Menitzky & Popova 15* (LE); Lerik distr., near Ashagy Amburdara, *Menitzky & Popova 10* (LE); Magal Zuvant, near Mistan, *Grossheim* (MHA); Sibirdu mt., *Shipchinsky 726* (MHA); Keis-jurdi, *Radde 195* (LE), *s.n.* (TBI); Kis-jurdi, *Grossheim* (LE, TBI); Kyz-jurdy, *A.L.* (LE, TBI); inter Orant et Karabagh-jurt, *Alexeenko* (LE); inter Karabagh-jurt and Mara-jurt, *Alexeenko* (LE); mt. Nashagal, 3-4 km SW Orant, *Matveeva 510* (LE); [**AZERBAIJAN, Nagornyi Karabakh**]: S Karabakh Range, Dagtumas near Dzhebrail, *Sytin* (LE); Gadrut distr., Ziarat mt., *Gogina & Proskuriakova* (MHA); Karabakh, Ziarat mt., *Akhverdov & Dolukhanov* (TBI); Shusha, *Lipsky* (LE); prope opp. Shusha, *Kolakovsky* (TBI); [**ARMENIA**]: Vardeniss distr., Lake Sevan shore near Shishkaya, *Menitzky & al.* (LE); Vardeniss distr., Shakhdagh Range, upwards of Giunei, Sarinar mt., *Menitzky & al.* (LE); N shore of Lake Sevan, between Shorzha and Artanish, *Sytin & Schanzer* (LE, MHA, MOSP, W); distr. Novo-Bajazet, prope Ozanlar, *Grossheim* (TBI); distr. Nor-Bajazet, in jugo Shach-dagh, *Zedelmejer & Geideman* (TBI); distr. Nor-Bajazet, prope Karagaply, *Zedelmejer & Geideman* (TBI); at Nakhichevan border, near Yelpin, *Sytin & Schanzer* (MHA); at Nakhichevan border, near Khachik, *Sytin & Schanzer* (MHA, MOSP); Arpa River valley, between Yekhegnadzor and Arpi, *Sytin & Schanzer* (MHA); Arpa River valley, near Gndevaz, *Sytin & Schanzer* (MHA); Dzhermuk, Arpa River gorge, *Konechnaya* (LE); Yekhegis River valley, Vardeniss Range, near Karaglukh, *Sytin & Schanzer* (MHA); near Gyadnivani, Gichi mt., Yekhegis River source, *Tamandzhian & al.* (TBI); Vayodzor Range, Darb River gorge, *Shvedchikova* (MHA, MW); Ustupi, *Radde s.n.* (LE, TBI); Hustup mt., *Popova & Handilian* (TBI); Megri distr., 8-10 km N of Nyuvadi, *Menitzky & al. 317* (LE); Megri distr., Megriget River tributary gorge upwards of Vardanadzor, *Egorova & al.* (LE); Zangezur Range, Vorotan River source, *Yelenevsky 2430* (MOSP); Zangezur Range, Gerd-chai River source, *Yelenevsky & Bylova 705, 770* (MOSP); Vank village, in Vank River gorge, *Yelenevsky* (MOSP); 10 km of Mikoian upstream Arpa River, *Yelenevsky & Yelenevskaya* (MOSP).

Galium hyrcanicum has a wide distribution in Transcaucasia and adjacent areas of Turkey and Iran (Fig. 1). It is an apparently polyploid species (Fig. 2), very polymorphic, especially with respect to its overall dimensions and indumentum. Its circumscription has been widened compared to SCHÖNBECK-TEMESY(1991) in the present and other recent treatments (EHRENDORFER & al., 2002), because populations formerly described as separate species (see synonyms) now can be shown to fall within the variation range of *G. hyrcanicum* (Figs. 8, 11). Though some differences between the E (Talysh) and W (Nakhichevan and Armenian) populations of this species do exist, it seems premature to discriminate between them as taxonomic entities.

In NW and N Iran *G. hyrcanicum* is ± vicarious with *G. subvelutinum* s.str., in E Anatolia and W Iran with *G. nabelekii* Ehrend. & Schönb.-Tem., linked to both by transitional forms (EHRENDORFER & al., 2002). Otherwise, relationships within the Caucasus region are very close to *G. czerepanovii* (see there), less to *G. xylorrhizum* agg. and to *G. bullatum* (Figs. 11, 13).

7. *Galium czerepanovii* Pobed. in Schischk. & al., Fl. SSSR 23: 720. 1958; Ehrend. & Schönb.-Tem. in Davis, Fl. Turkey 7: 815-816. 1982.

Plants herbaceous to weakly suffrutescent, with thin, slightly woody stem bases. Stems (20-)50-100(-270) mm long, shortly and sparsely pubescent at lower portion with horizontally spreading hairs. Leaves in whorls of 4-6, ± broadly oblanceolate, with ± flat margins, (4-)6-11(-14) mm long, (1-)1.5-2.3(-2.7) mm wide, mostly spreading, glabrous. Well developed inflorescences definitely corymbiform, (3-)10-60(-83)-flowered. Pedicels in fruit sometimes divaricate at angles of more than 90°. Flowers (2-)2.5-3(-3.4) mm diam. Petal appendages shortly attenuate and curved upwards. Mericarps smooth, with dry adherent pericarp, dark coloured, brownish to black, 1.3-1.6(-1.7) mm long. Fl. V-VI.

Typus: [**USSR**] Nakhichevan, distr. Ordubad in rupibus, in declivibus montanis ad orientem ab opp. Ordubad,1500 m, 6.VI.1956, *Egorova, Tzvelev & Czerepanov 148* (Holo-: LE!; iso-: LE!, WU!).

Specimens examined. – [**AZERBAIJAN**, **Nakhichevan**]: prope Negram, *Grossheim* (ERE); inter Negram et Darosham, *Grossheim* (ERE); prope Djamal-Edin, Mt. Dary-dag, *Schelkovnikov & Kara-Murza* (ERE).

Galium czerepanovii is an endemic to the Araks River valley in SE Nakhichevan, adjacent E Aanatolia and NW Persian Azerbaijan, where it occurs (always?) on limestone rocks. With the exception of its usually broader and shorter leaves in whorls of 4-5-6, its often smaller flowers and small pollen grains, suggesting at least partly diploidy (Fig. 2), it is otherwise almost identical to *G. hyrcanicum*. This makes the recognition of *G. czerepanovii* sometimes difficult. Furthermore, specimens from Negram and Dorosham possess multiflowered inflorescences with strongly divaricate pedicels, thus resembling *G. azerbayjanicum*. As the latter was collected from nearby localities, these transitional specimens may point to hybridization between the two otherwise well separated species, belonging to different groups.

8. *Galium praemontanum* Mardal. in Bot. Zhurn. 70(2): 263-265. 1985.

Plants of dwarf caespitose habit, but without basal vegetative shoorts. Generative stems 40-50 mm long, branching in the upper, with short, spreading pubescence at nodes. Leaves in whorls of 6(-7), oblanceolate, or linear, with ± flat margins, 2-4 mm long, 0.8-1 mm wide, mostly spreading, glabrous. Well developed inflorescences definitely corymbiform, 11-15-flowered. Pedicels in fruit never divaricate at angles of more than 90°. Flowers 2.5-3.5 mm diam. Petal appendages long and thinly attenuate. Mericarps smooth, with dry adherent pericarp, dark coloured, brownish to black. Fl. V.

Typus: [GEORGIA Orientalis]: Kachetia, in viciniis opp. Tziteli-Tzkaro, prope pagum Mazovka locus, "Orlinaja balka" (Artzivischevi) dictus, 750 m, 20.V.1978, *Mardalejschvili* (Holo-: TBI; iso-: LE!, WU!).

Galium praemontanum is known from the type locality only (Fig. 1). It appears relatively isolated within *G. hyrcanicum* agg. (Fig. 13).

Galium xylorrhizum agg.

9. *Galium xylorrhizum* Boiss. & Huet in Boiss., Diagn. Pl. Orient. ser. 2, 2: 115. 1856; Ehrend. & Schönb.-Tem. in Davis, Fl. Turkey 7: 816. 1982.

= *Galium praemontanum* var. *armazicum* Mardal. in Bot. Zhurn. 70(2): 263-265. 1985.

Plants herbaceous, with thin, slightly woody stem bases. Stems (50-)80-340(-410) mm long, shortly puberulent to glabrescent in lower part with spreading hairs. Leaves in whorls of (5-)6-7(-8), linear (to linear-oblanceolate), with ± flat margins, (8-)15-20(-29) mm long, (0.8-)1-1.7(-2.2) mm wide, mostly spreading, glabrous. Well developed inflorescences definitely corymbiform, (6-)15-110(-200)-flowered. Pedicels in fruit never divaricate at angles of more than 90°. Flowers (2.7-)3-4(-4.9) mm diam. Petal appendages shortly attenuate and curved upwards. Mericarps smooth, with dry adherent pericarp, dark coloured, brownish to black, 1.2-2 mm long. Fl. VI-VII.

Typus: [TURKEY]: In declivibus glareosis ad redices montis Tech Dagh Armeniae (Palandöken Da.) prope Erzeroum, VII.1853, *Huet du Pavillon* (Holo-: G).

Specimens examined. – **[ARMENIA]:** Pambak River valley, W of Kirovakan, near Shirakamut, *Sytin & Schanzer* (MHA, MW, LE, W, WU); Pambak River valley, W of Spitak, near Nalband, *Sytin & Schanzer* (MHA, MW, LE, WU); Pambak River valley, near Lusakhpyur, *Sytin & Schanzer* (MHA, MW, LE, WU); N of Leninakan, between Keti & Maisian, *Sytin & Schanzer* (MHA, MOSP, MW, LE, W, WU); N of Leninakan, Keti, *Sytin* (LE); Akhurian distr., Dzhadzhur pass, near Ahklisa, *Akhverdov* (TBI); Amasia, Akhurian River gorge, *Sytin & Schanzer* (MHA, MOSP, MW, LE, WU); Akhurian River valley upstream of Amasia, *Tzvelev & Cherepanov 491* (LE); **[GEORGIA]:** Prov. Tiflis, in vicin. Mtschet,

Armazis-chevi, *Schischkin* (TGM); in vic. Tbilissi, prope Mzcheta, in faucibus Armaz, 31.V.1981, *Mardalejschvili* [**typus** of *G. praemontanum* var. *armazicum* (Holo-: TBI; iso-: TBI, LE!, WU!)].

Galium xylorrhizum is mainly distributed from NE Turkey to SW Armenia (Fig. 1). Collections from Armaz gorge near Mzcheta in Georgia were described as *G. praemontanum* var. *armazicum*. Though this locality is disjunct from the main area of *G. xylorrhizum*, the cited specimens are nearly identical to the latter in all of their characters and do not seem to be related to *G. praemontanum*, endemic to a single locality on the S slope of the Great Caucasus Range.

10. *Galium oshtenicum* Ehrend. & Schanzer ex Mikheev in Bot. Zhurn. 77(10): 72. 1992.

– *G. vartanii* auct. non Grossh.: Schanzer in Novosti Sist. Vyssh. Rast. 26: 156. 1989, quoad pl. ex Mt. Oshten.

Plants herbaceous, of dwarf caespitose habit, with numerous basal vegetative shoots. Stems (25-)30-60(-70) mm long, shortly puberulent at nodes (rarely also on lower intrernodes), with spreading hairs. Leaves in whorls of (5-)6(-8), oblanceolate to linear, with flat to slightly revolute margins, (4-)5-8(-9) mm long, (0.7-)1.2-1.7(-2) mm wide, mostly spreading, glabrous. Well developed inflorescences definitely corymbiform, (2-)5-12(-16)-flowered. Pedicels in fruit never branched at angles of more than 90°. Flowers (3.1-)3.5-3.8(-4) mm diam. Petal appendages shortly attenuate and curved upwards. Mericarps smooth, with dry adherent pericarp, dark coloured, brownish to black. Fl. VII.

Typus: Caucasus occidentalis, mons Oshten, pedes orientalis, alt. 2500-2700 m, 14.VII.1981, Menitzky, *Popova & al. 414* (Holo-: LE!).

Specimens examined. – [**N CAUCASUS**]: Krasnodar reg., distr. Maikop, in cursu superiore fl. Belaya, mt. Oshten, *Gogina 21* (MHA, WU); Cherkessia, mt. Fisht, *Woronow & Steup* (LE); Kabardino-Balkaria, Bezengi gorge, S foot of Skalisty Range, *Portenier 1915* (LE).

Galium oshtenicum is an endemic to the NW and central parts of the Great Caucasus (Fig. 1). It is probably polyploid (Fig. 2) and most closely related to *G. xylorrhizum* and *G. vartanii* (Fig. 12).

11. *Galium vartanii* Grossh. in Trudy Geobot. Obsl. Pastb. SSR Azerbaidzhana, Ser. B, Letn. Pastb. 1: 78-79, tab. 8. 1929.

Plants herbaceous, with thin stem bases. Stem (40-)60-90(-130) mm long, with short and spreading pubescence at nodes. Leaves in whorls of (5-)6, oblanceolate or linear, with ± flat margins, (6-)8-13(-22) mm long, (0.8-)1.5-2.3(-2.5) mm wide, ± spreading, glabrous, or (rarely) shortly puberulent. Well developed inflorescenes definitely corymbiform, (5-)9-30(-43)-flowered. Pedicels in fruit branching at angles of less than 90°. Flowers (3.3-)4.5-6(-7) mm diam. Petal appendages shortly attenuate and curved upwards. Mericarps smooth, with dry adherent pericarp, dark coloured, brownish to black, 1.8-2 mm long. Fl. VII-VIII.

Typus: Transcaucasia, **[AZERBAJDZHAN]**, distr. Nucha, in pascuis Iske-Koshun et jugum Salavat, 23.VI.1928, *Jaroshenko* (Lecto-: LE!, chosen by SCHANZER, 1989); Transcaucasia, Azerbajdzhan, distr. Nucha, in pascuis Susuzdukh-Dalama, 7.VII.1928, *Jarochenko* (Syn-: LE!); Transcaucasia, Azerbajdzhan, distr. Nucha, in jugo Salavat, supra pagum Bash-Dashagyl, 18.VII.1927, *Jarochenko* (Syn-: LE!).

Specimens examined. – **[AZERBAIJAN]:** distr. Nucha: fl. Daschagil-chai, mt. Czilim, *Alexeenko 11402* (LE); fl. Daschagil-chai, Lacar Super, *Alexeenko 8451, 8454, 8456* (LE); distr. Kuba: prope pagum Adur, *Kasumov* (LE); [**DAGHESTAN**]: distr. Samur, ad fontes fl. Gedym-czai, *Alexeenko 11481* (LE).

Galium vartanii evidently is a polyploid (Fig. 2), endemic to N Azerbaijan and S Daghestan (Fig. 1). Relationships exist with *G. oshtenicum* (Fig. 12), but also probably with *G. hyrcanicum*.

II. *Galium incanum* alliance

12. *Galium incanum* subsp. ***elatius*** (Boiss.) Ehrend. in Österr. Bot. Z. 98: 454. 1951; Ehrend. & Schönb.-Tem. in Davis, Fl. Turkey 7: 818. 1982.

≡ *G. orientale* var. *elatius* Boiss., Fl. Orient. 3: 57. 1875.

= *G. grusinum* Trautv. in Trudy Imp. S.-Petersburgsk. Bot. Sada 7: 461. 1881; Grossh., Opred. Rast. Kavkaza: 252. 1949; Grossh., Fl. Kavkaza 4: 33. 1934; Pobed. in Schischk. & al., Fl. SSSR 23: 375. 1958; Mikheyev in Bot. Zhurn. 77(10): 72. 1992.

Plants herbaceous, with thin, slightly woody stem bases, or ± suffrutescent. Brachyblasts with densely imbricate leaflets at lower stem nodes well developed. Stems (70-)100-200(-300) mm long, shortly puberulent except pedicels. Leaves in whorls of 6(-7), linear 7-15(-30) mm long, 0.7-1.4(-1.6) mm wide, spreading or sometimes ± reflexed, with margins revolute to the midrib, shortly puberulent. Well developed inflorescences relatively dense, ± narrowly elongate to cylindrical (never corymbiform), 15-45-flowered, with only twice branched short peduncles. Pedicels in fruit never divaricate at angles of more than 90°. Flowers 2-4 mm diam. Petal appendages shortly attenuate and curved upwards. Mericarps smooth, with dry adherent pericarp, dark brownish to black, (1.5-)1.8-2.2 mm long. Fl. V-VI.

Typus: [**TURKEY**, A8 Gümüsane], Armenia, in collibus incultis Gumush Khane, Baibourt, *Bourgeau* (Lecto-: W!, chosen by EHRENDORFER, 1951; isolecto-: FI, P, WU!).

Specimens examined. – [**GEORGIA**]: Dzhavakhetia, Tetrobi range, *Khintibidze* (TBI); Teleti range, *Zedelmejer* (TBI); Tiflis, *Fomin* (TBI); Teleti range near Tbilisi, *Kvartzeni* (TBI); Prov. Tiflis, distr. Gori, near Borzhom, *Kozlovsky* (TBI); Prov. Tiflis, distr. Akhaltzikhe, between Ota and Tamala, *Kozlovsky* (TBI); Tiflis, Teleti forestry, *Kafiev* (TBI); Tbilisi, Kodzhori highway, *Kutateladze* (TBI); Tiflis, mons Teleti inter Krtsanisi et Chatis-teleti, *Schischkin* (TGM); Tiflis, *Zedelmejer* (TGM, LE); Tiflis, Majo 1880, *Smirnov* [**typus** of *G. grusinum* (Syn-: LE!)]; Kura valley near Aspindza, *Sytin & Schanzer* (LE, MW); Akhaltzikhe distr., Kura valley near Minadze, *Sytin & Schanzer* (LE, MHA, MW).

Several subspecies occur in this polymorphic polyploid complex, extending from Anatolia to Crete and the Balkan Peninsula, to Syria, Lebanon, and the Caucasus region (EHRENDORFER, 1951). In this region *G. incanum* is represented only by subsp. *elatius*, distributed in the mountain ranges downstream the Kura River valley, from the Kars highlands of Turkey to Tbilisi in Georgia. In this part of its area the taxon offers no taxonomical problems, being very uniform in its characters.

4. Discussion

As has already been mentioned above, all the taxa studied here consist of geographically isolated populations (Fig. 1) inhabiting rocky slopes and scree at various elevations over a vast mountain area with very diverse climates. Hence, it is not surprising that most of them differ morphologically from each other.

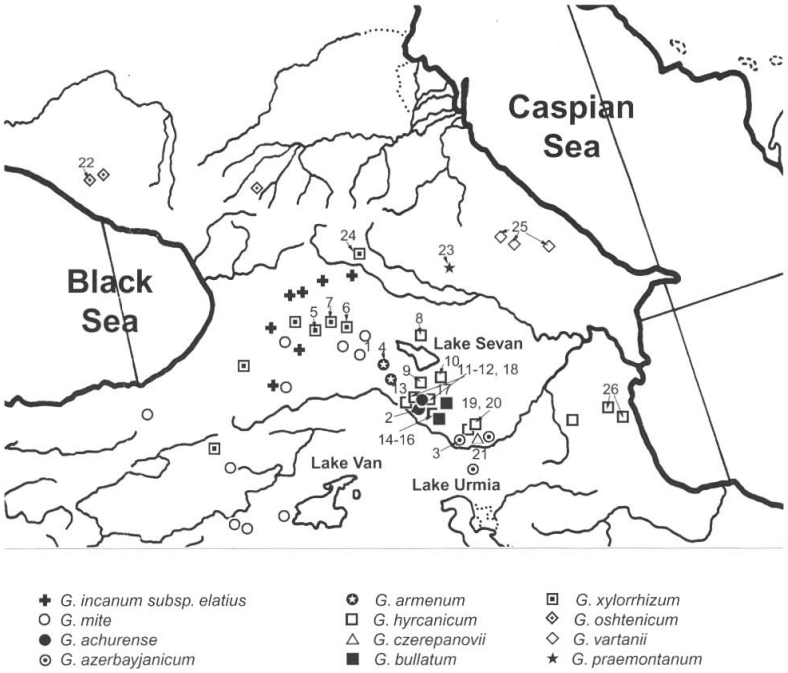
It can be supposed that ancestral groups of the *Galium subvelutinum* alliance dispersed widely into the Caucasus mountains during the Pleistocene. The climate in the region was rather mild during the glaciations and much more xeric during the interglacials (BALYAN & DUMITRASHKO, 1964). Isolation during the last glaciation cycle, one of the most powerful, can be an explanation for the origin of the probably polyploid *G. vartanii*, *G. oshtenicum*, and *G. praemontanum* (Fig. 1). These three species of *G. xylorrhizum* agg. occupy disjunct endemic areas in the Great Caucasus Range and at its southern foot, and are spatially isolated from the rest of the group. Separation is quite clear between them and from southern *G. hyrcanicum* populations, considering differential characters like dwarf growth habit, leaf shape, etc. They are probably remnants of previously widely distributed populations of the *G. subvelutinum* alliance in the Great Caucasus, which have survived in local refugia during the last Pleistocene glaciation, but have hardly dispersed into formerly glaciated areas during the Holocene. This interpretation can be also supported by the disjunct population of *G. xylorrhizum* in the Armaz gorge near Tbilisi, Georgia ("*G. praemontanum* var. *armazicum*"), a species today more widely distributed towards the SW.

In more southern parts of the area, in Armenia, Azerbaijan, and adjacent Turkey and Iran, late Pleistocene isolations never were so extensive and extinctions not so complete due to much smaller areas of glaciation. This can be the cause of the survival of some ancestral diploid populations and the much weaker differentiation between polyploid populations which were subject to numerous secondary contacts. Thus, from widely distributed variable species like *G. mite* or *G. hyrcanicum*, only few geographically or ecologically isolated populations have developed enough morphological differences to evaluate them as separate taxa. As a rule, they are endemics with small distribution areas: in the *G. mite* group *G. achurense, G. azerbayjanicum,* and *G. armenum*, in the *G. hyrcanicum* group *G. bullatum* and *G. czerepanowii*.

In cases of secondary contacts between isolated populations of both groups of the *G. subvelutinum* alliance secondary hybridization occurs now and evidently has occurred in the past. Examples for this are the cases of *G. achurense* × *G. hyrcanicum* and of *G. azerbayjanicum* × *G. czerepanovii* already mentioned. But there have been also possibilities for the hybrid origin of species. An example is the probably tetraploid *G. armenum,* endemic to the SE Armenia. Its origin from *G. mite* and *G. bullatum* as putative parents is discussed in detail in a separate paper (SCHANZER, 1997). In spite of its intermediate position between these species, it can be rather easily distinguished from both of them. It seems preferable to recognize this taxon as a separate species, since modern contacts between populations of *G. mite*, *G. bullatum* and *G. armenum* have not been found. Such contacts could have occurred in a xeric epoch of the late Pleistocene followed by further disjunction of ancestral populations during the last glaciation, when the Gegam Range to the S of Lake Sevan in SE Armenia was covered with glaciers (BALYAN & DUMITRASHKO, 1964).

In conclusion, our new data about the systematics and distribution of *Galium* sect. *Orientigalium* in the Caucasus region clearly show that growth form, habit, leaf shape, indumentum, flower and fruit characters, ploidy level etc. are extremely variable in this clade. Only the use of character combinations and biomathematical analyses reveals separation lines between taxa and correlations with the geographic pattern of distribution. Relatively few populations have developed enough individuality to qualify as separate endemic species. They are usually distributed in marginal areas of the sections total range or are restricted to some small and ± isolated mountain regions scattered throughout the areas of more widely distributed and variable ancestral species.

Fig. 1. – Distribution of twelve taxa from *Galium* sect. *Orientigalium* Ehrend. in the Caucasus region. Numbers refer to the OTUs listed in Table 1.



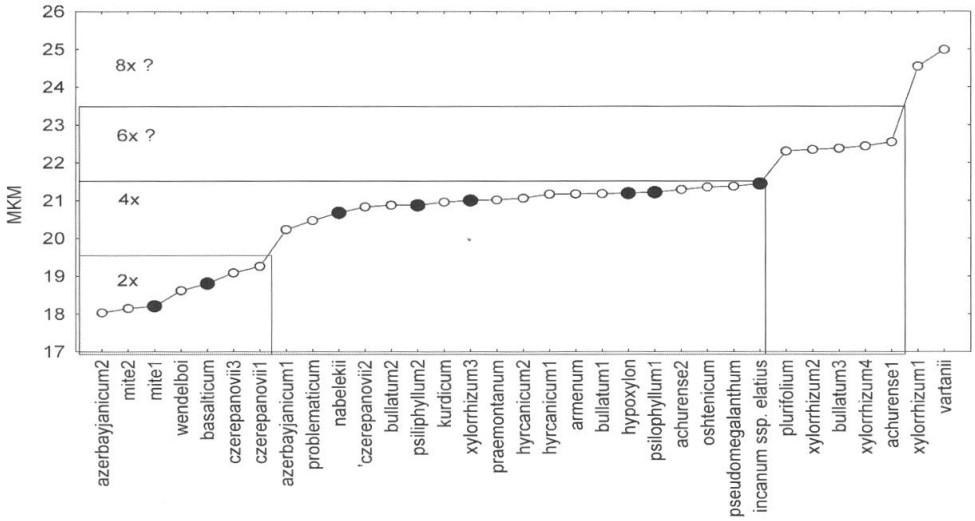
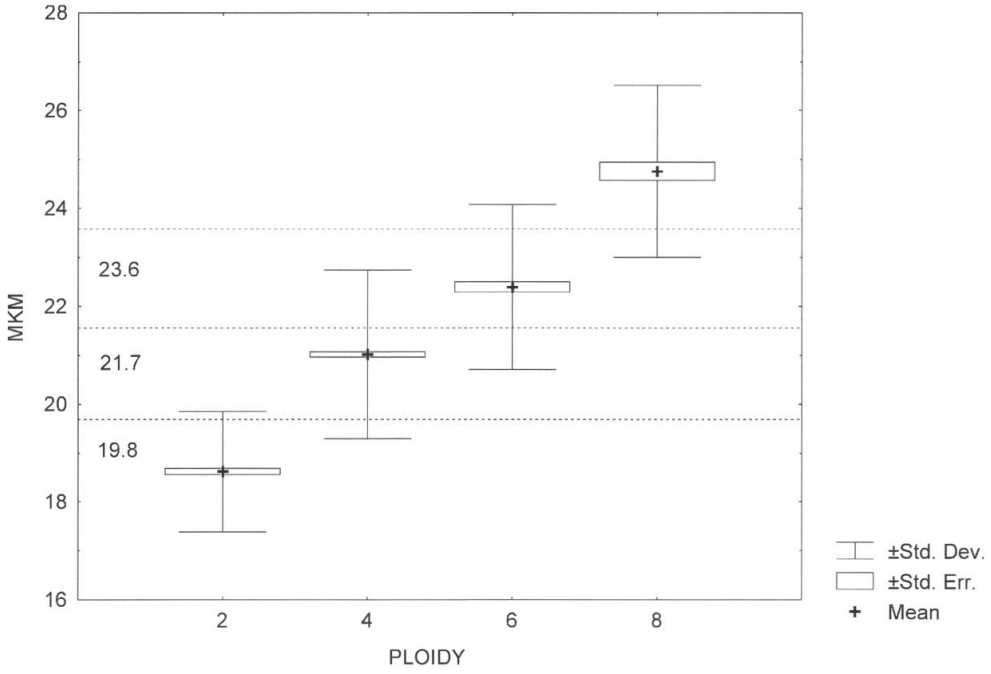


Fig. 2. – Mean pollen diameters of various taxa from *Galium* sect. *Orientigalium* Ehrend. with suggested separation lines for diploids, tetraploids, and higher polyploids. Specimens with known chromosome numbers (counts by M. Kiehn) are marked by black dots.

Fig. 3. – Means, standard deviations and standard errors for four groups of pollen grain sizes, presumably corresponding to 2*x*, 4*x*, 6*x*, and 8*x*. Threshold values for different ploidy levels calculated as medians between mean values for each group.



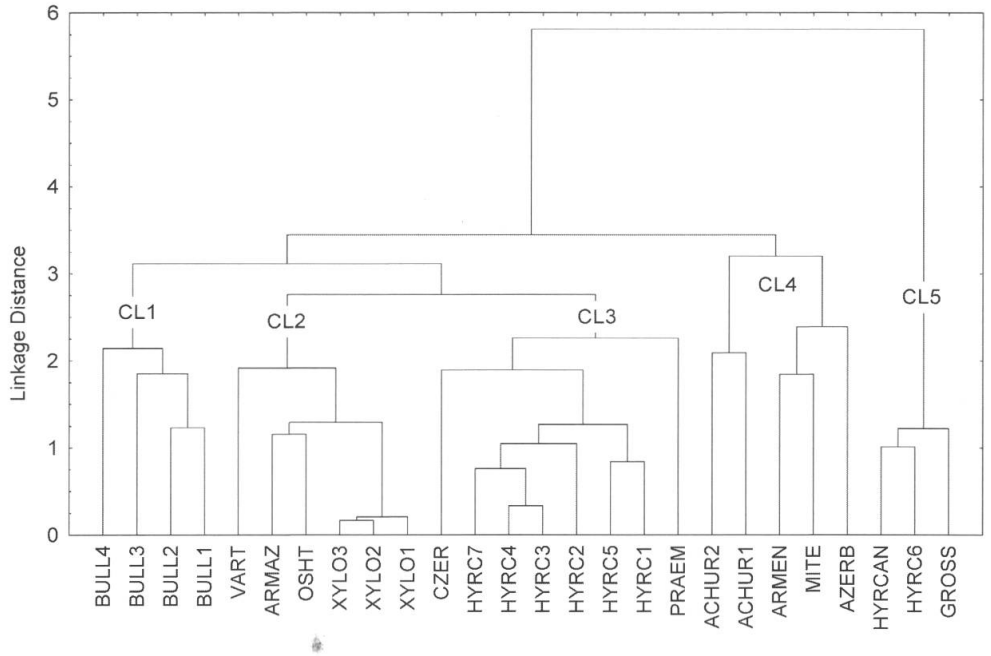
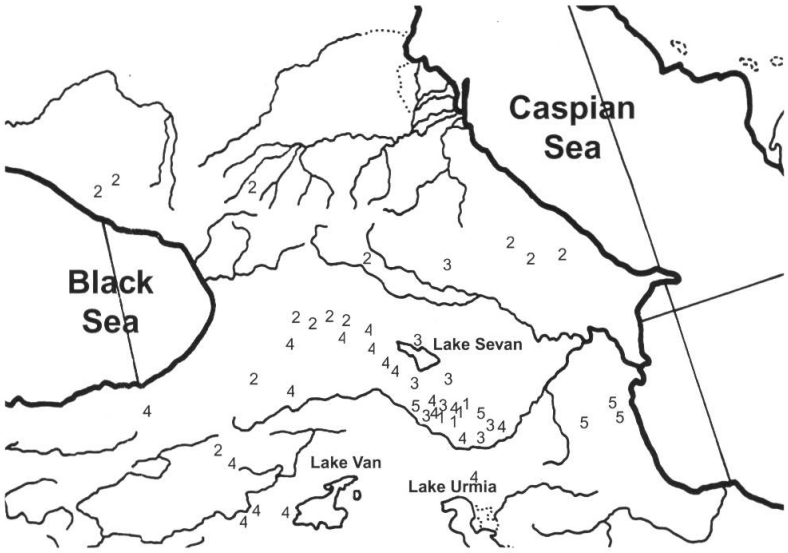


Fig. 4. – Results of a cluster analysis (WPGMA, Euclidean distances) for the taxa of the *G. subvelutinum* alliance studied. OTU names correspond to those in Table 1. The twenty-six OTUs form five clusters (CL 1-5).

Fig. 5. – Geographical distribution of the five OTU clusters of the *G. subvelutinum* alliance (see Fig. 4).



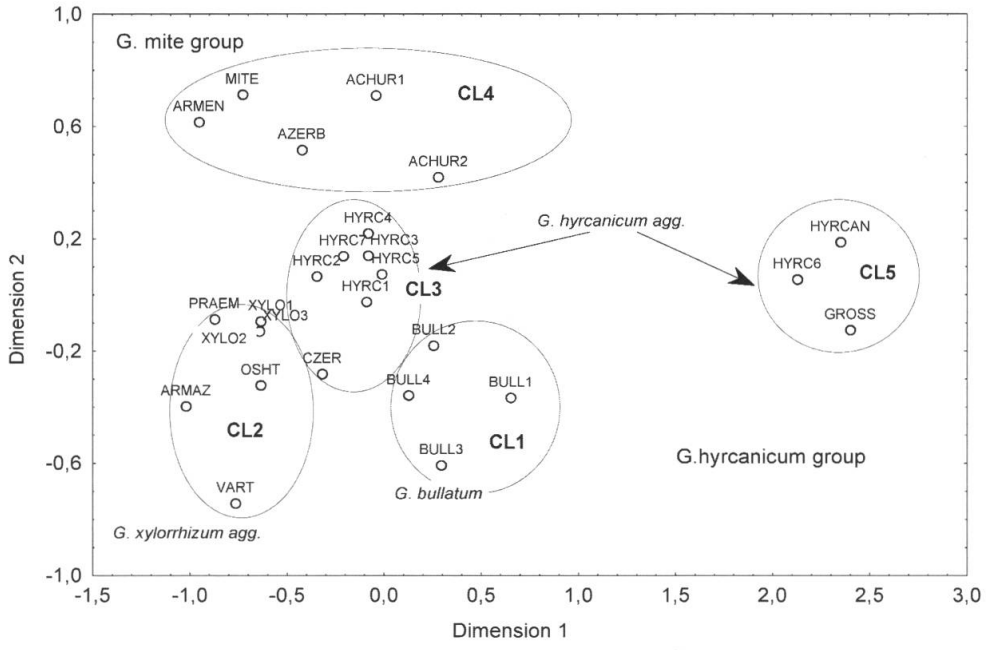
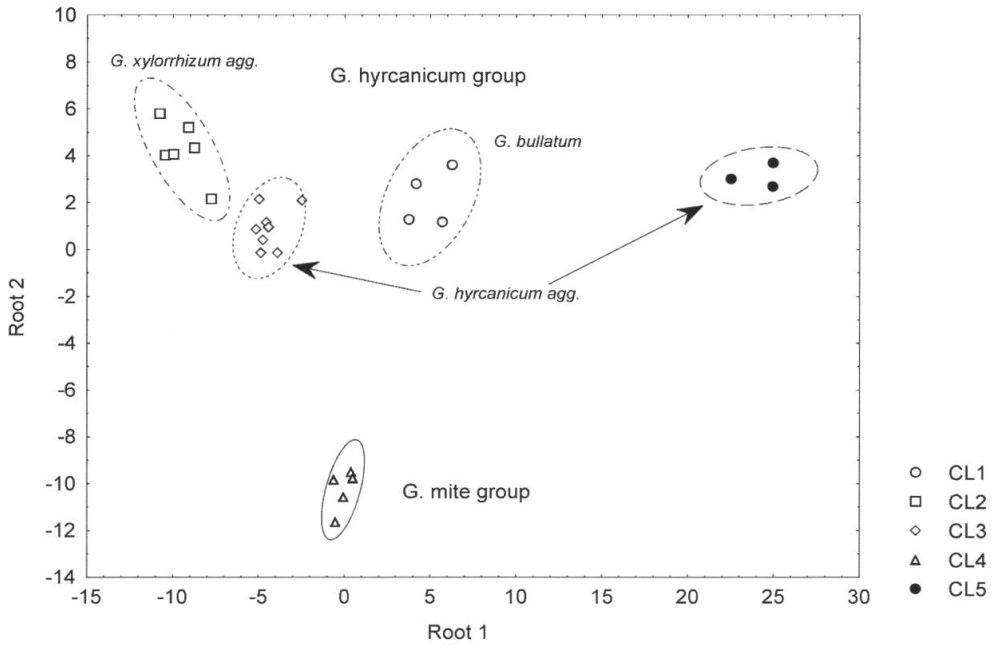


Fig. 6. – Scatterplot of multidimensional scaling for the five clusters (CL 1-5) constituting the *G. subvelutinum* alliance. Final configuration, dimension 1 vs. dimension 2 (see Fig. 4).

Fig. 7. – Scatterplot of discriminant analysis of the OTU's data set for the five clusters of the *G. subvelutinum* alliance. Canonical root 1 vs. Canonical root 2.



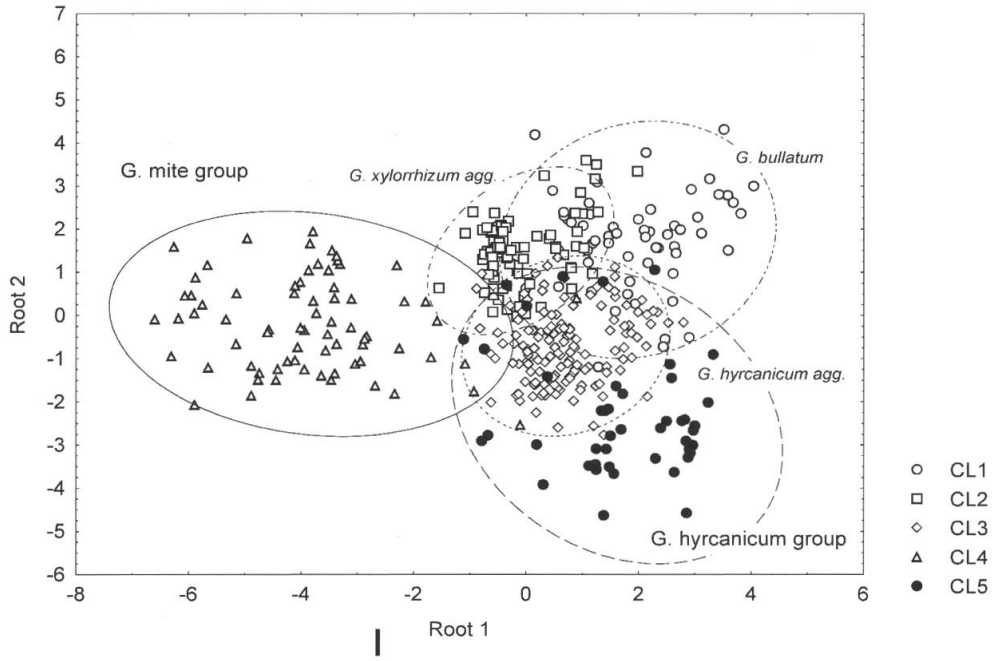
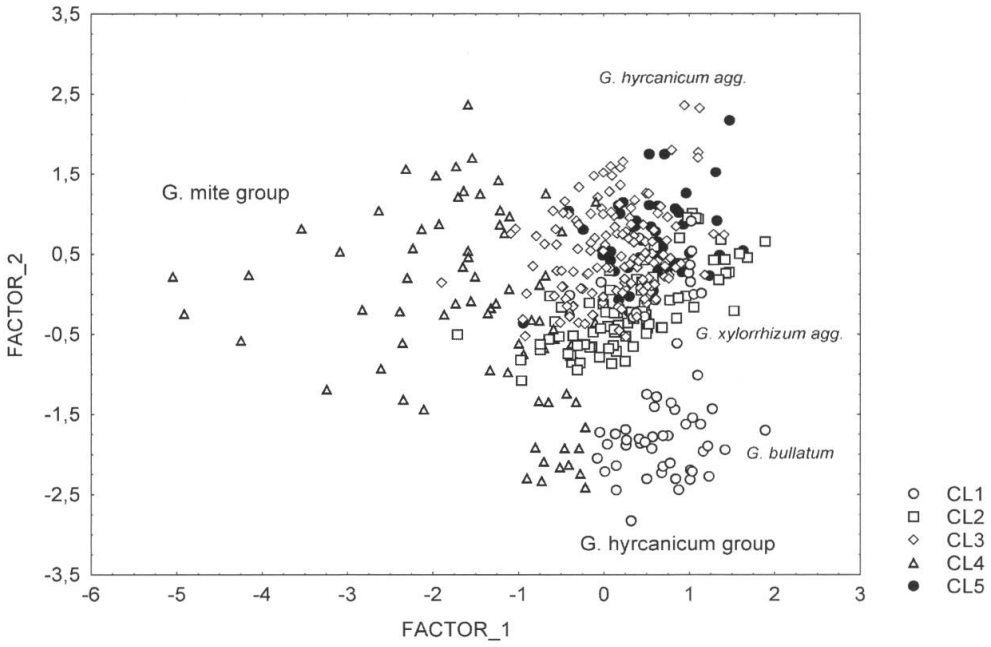


Fig. 8. – Scatterplot of discriminant analysis for the five clusters of the *G. subvelutinum* alliance. Canonical root 1 vs. Canonical root 2.

Fig. 9. – Scatterplot of factor analysis for the five clusters of the *G. subvelutinum* alliance. Factor 1 vs. Factor 2.



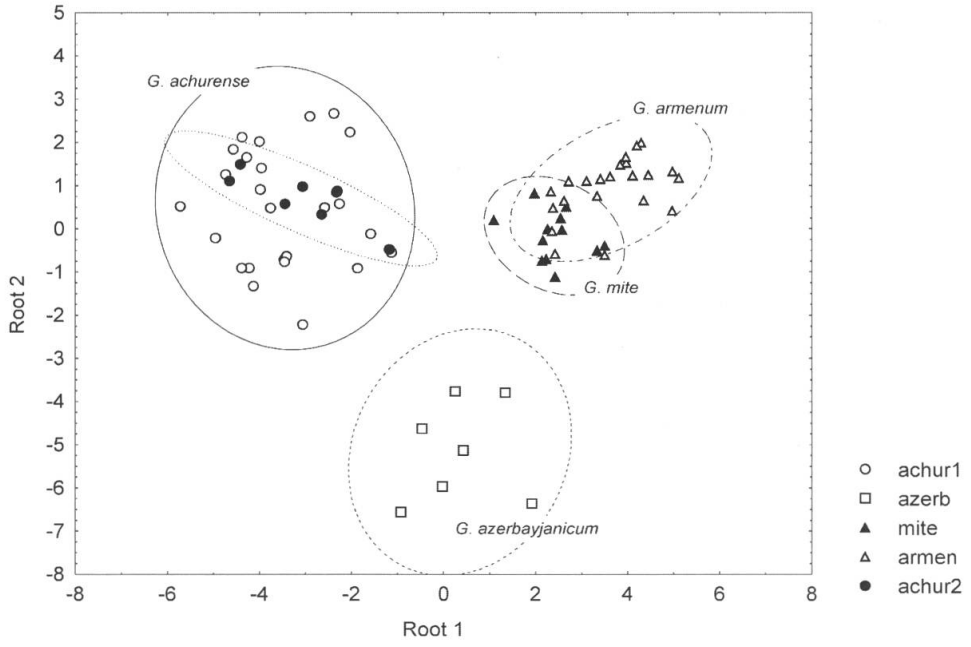
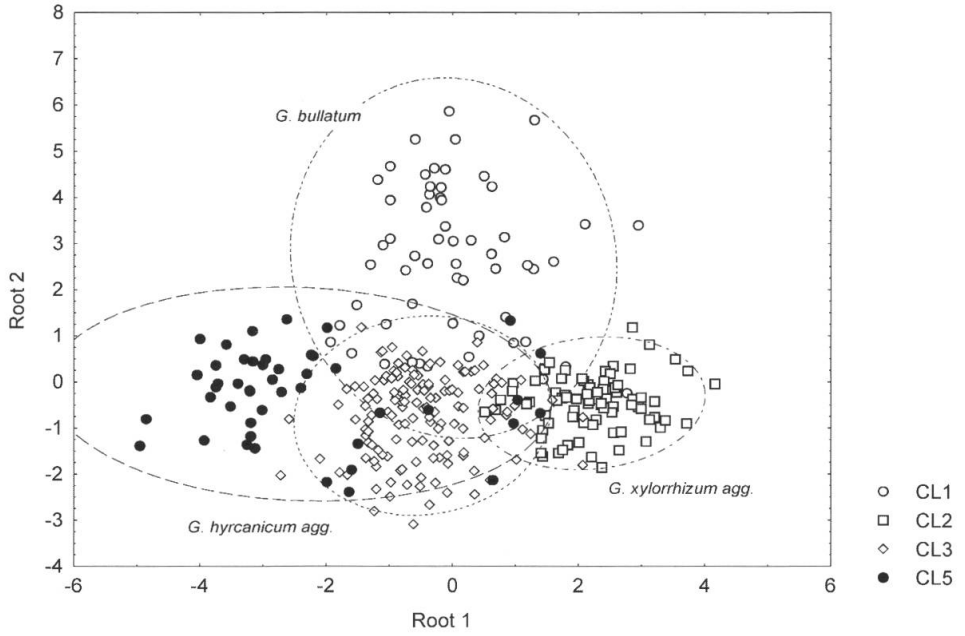


Fig. 10. – Scatterplot of discriminant analysis results for the cluster 4 (*G. mite* group). Canonical root 1 vs. Canonical root 2.

Fig. 11. – Scatterplot of discriminant analysis for the clusters 1, 2, 3, and 5 (*G. hyrcanicum* group). Canonical root 1 vs. Canonical root 2.



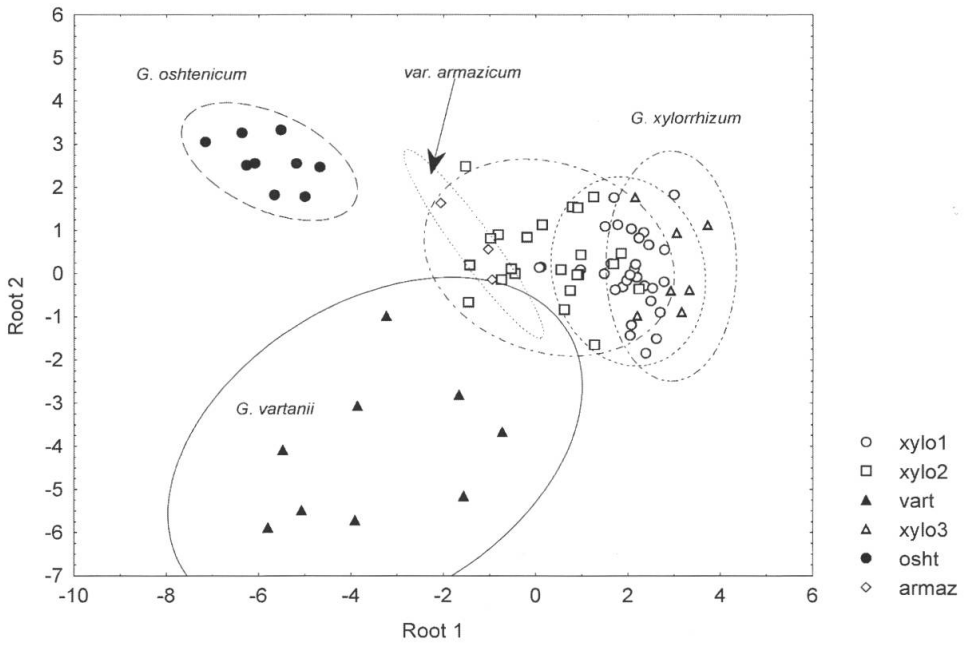
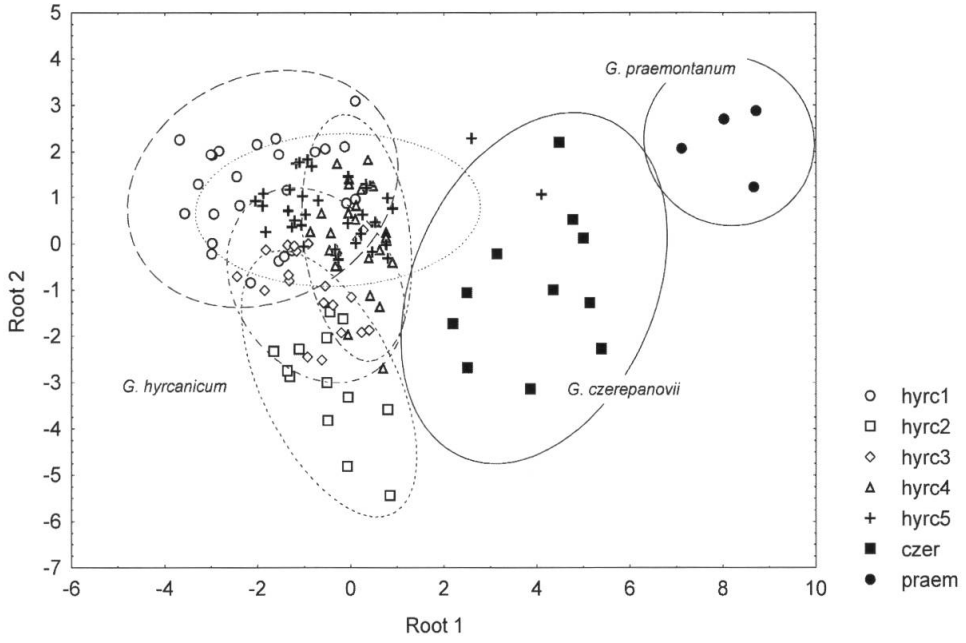


Fig. 12. – Scatterplot of discriminant analysis for cluster 3 (*G. xylorrhizum* agg.). Canonical root 1 vs. Canonical root 2.

Fig. 13. – Scatterplot of discriminant analysis for *G. hyrcanicum* agg. (W): populations from Armenia and Nakhichevan, *G. czerepanovii*, and *G. praemontanum*. Canonical root 1 vs. Canonical root 2.



ACKNOWLEDGEMENTS

The Austrian Academy of Sciences and its Commission for Interdisciplinary Ecological Studies as well as the Institute of Botany, University of Vienna, have generously supported this study. We are grateful to them as well as to the keepers of the various herbaria from which we were allowed to borrow and study specimens: B, E, ERE, G, K, LE, MHA, MO, MOSP, MW, TBI, W and WU. Furthermore, thanks are due to M. Kiehn (Vienna) who kindly gave permission to use and cite some of his chromosome counts, to K. Windsteig who helped typing the manuscript, and to an anonymous reviewer, whose valuable comments helped to improve the statistical part of the manuscript.

REFERENCES

BALYAN, S. P. & N. V. DUMITRASHKO (1964). Ancient glaciation of Armenia (in Russian). *In:* DUMITRASHKO, N. & G. TUSHINSKY (eds.), *Proceedings for the International Geophisics Year, 10. Interinstitutional conference at the Geography Department of the Moscow State University and Institute for Geography of the USSR Academy of Sciences for research of the Caucasus glaciation*: 166-183.

DALLWITZ, M. J. (1974). A flexible computer programme for generating identification keys. *Syst. Zool.* 23: 50-57.

DALLWITZ, M. J. (1980). A general system for coding taxonomic descriptions. *Taxon* 29: 41-46.

DALLWITZ, M. J., T. A. PAINE & E. J. ZURCHER (1993). *User's Guide to the DELTA System: a General System for Processing Taxonomic Descriptions*. 4th edition. 136 pp. CSIRO Division of Entomology: Canberra.

DUNCAN, T. & B. R. BAUM (1981). Numerical phenetics: its uses in botanical systematics. *Annual Review of Ecology and Systematics* 12: 387-404.

EHRENDORFER, F. (1948). Rubiaceae. *In:* RECHINGER, K. H., Ergebnisse einer botanischen Reise nach dem Iran, 1937. V. Teil. *Ann. Naturhist. Mus. Wien* 56: 212-224.

EHRENDORFER, F. (1951). Rassengliederung, Variabilitätszentren und geographische Merkmalsprogressionen als Ausdruck der raum-zeitlichen Entfaltung des Formenkreises Galium incanum s.str. *Österr. Bot. Z.* 98: 427-490.

EHRENDORFER, F. (1958). Critical notes on Turkish Rubiaceae. *Notes Roy. Bot. Gard. Edinburgh* 22: 323-401.

EHRENDORFER, F. (1971). Evolution and ecogeographical differentiation in some South-West Asiatic Rubiaceae. *In:* DAVIS, P. H. (ed.), *Plant life of South-West Asia:* 195-215. Bot. Soc. Edinburgh.

EHRENDORFER, F. (1976). Galium. *In:* TUTIN, T. G., V. H. HEYWOOD & al. (eds.), *Fl. Europaea* 4: 14-36. Cambridge.

EHRENDORFER, F. & E. SCHÖNBECK-TEMESY (1980). Rubiaceae. *In:* TOWNSEND, C. C. & E. GUEST (eds.), *Fl. Iraq* 4(1): 564-628. Baghdad.

EHRENDORFER, F. & E. SCHÖNBECK-TEMESY (1982). Galium L. *In:* DAVIS P. H. (ed.), *Fl. Turkey* 7: 767-823. Edinburgh.

EHRENDORFER, F., E. SCHÖNBECK-TEMESY & I. A. SCHANZER (2002). Galium sect. Orientigalium. *In:* RECHINGER, K. H. † & W. RECHINGER (eds.), *Fl. Iran.* 176 (in print). Salzburg.

GROSSHEIM, A. A. (1934). Rubiaceae. *Fl. Kavkaza* 4: 19-35. Tiflis.

MANDENOVA, I. P. (1972). Rubiaceae. *In:* TAKHTAJAN, A. L. & A. A. FEDOROV (eds.), *Fl. Erevana:* 205-211. Erevan.

MANDENOVA, I. P. (1980).Rubiaceae. *In:* MACHTSCHADJANA, A. L. (ed.), Rubiaceae. *Fl. Armenii* 7: 50-102. Erevan.

MANDENOVA, I. P. (1999). Rubiaceae. *In:* GAGNIZE, R. (ed.), *Fl. Georgiae,* ed. 2, 12: 290-327. Tbilisi.

MIKHEYEV, A. D. (1992). The synopsis of the family Rubiaceae of the Caucasian flora (in Russian). *Bot. Zhurn.* 77(10): 68-74.

PARTRIDGE, T. R., M. J. DALLWITZ & L. WATSON (1993). *A Primer for the DELTA System.* 3rd edition. 15 pp. (CSIRO Division of Entomology: Canberra).

POBEDIMOVA, E. G. (1958). Galium. *In:* SHISHKIN, B. K. & al. (eds.), *Fl. SSSR* 23: 287-381 (in Russian). Leningrad, Moskva [English translation (2000). *Fl. U.S.S.R.* 23: 345-459. Dehra Dun].

POBEDIMOVA, E. G. (1961). Rubiaceae. *In:* KARJAGIN, I. I. (ed.), *Fl. Azerbaijana* 8: 14-48. Baku.

SCHANZER, I. A. (1989). Notulae de generis Galium L. (Rubiaceae) speciebus Caucasicis nonnulis sectionis Orientigalium Ehrend. (in Russian). *Novosti Sist. Vyssh. Rast.* 26: 151-157.

SCHANZER, I. A. (1997). A new species of Galium sect. Orientigalium (Rubiaceae) from Armenia related to G. mite (in Russian). *Bot. Zhurn.* 82(3): 126-131.

SCHÖNBECK-TEMESY, E. (1991). New taxa of Rubiaceae-Rubieae from Iran. *Pl. Syst. Evol.* 174: 197-200.

STATSOFT, INC. (1995). STATISTICA for Windows [Computer program manual]. Tulsa, OK: StatSoft, Inc., 2300 East 14th Street, Tulsa, OK, 74104-4442, (918) 749-1119, fax: (918) 749-2217, e-mail: info@statsoftinc.com, WEB: http://www.statsoftinc.com.

Addresses of the authors: F. E.: Institute of Botany, University of Vienna, Rennweg 14, 1030 Vienna, Austria. Email: Friedrich.Ehrendorfer@univie.ac.at

I. S.: Herbarium, Main Botanical Garden, Russian Ac. Sci., 4 Botanicheskaya Str., 127276 Moscow, Russia. Email: schanzer@online.ru