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Comparative ecosystematic analysis of *Gentianaceae* in the Western Caucasus and in the Swiss Alps

Systematisch-ökologischer Vergleich von *Gentianaceae* im westlichen Kaukasus und in den Schweizer Alpen

by

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1. INTRODUCTION

The Gentian family (Gentianaceae) is an ancient plant family, numbering at present about 80 genera and more than 1000 species, widely distributed all over the Northern hemisphere. These are mainly annual and perennial herbs but in tropical and subtropical regions there are shrubs, subshrubs, lianas, trees, and small grassy saprophytes belonging to the Gentian family. Gentianaceae grow in the tundra, in steppes, in forests of different kinds and altitudes, in meadows and bogs, along the banks of water reservoirs but they appear in particularly great numbers in the mountains, in the Alpine belts where quite often they are the prevailing vegetation.

The great variety of forms and the wide ecological scope of Gentianaceae impedes the systematization. The majority of the Gentianaceae taxa belong to critical groups. The opinions as to their scope and borders are contradictory. An exception is the systematization of the Swertia genus, which based on the combination of the traditional morphological-geographical and anatomical research methods (PISYAUKOVA 1962, SHABES 1967).

The investigation of the ecotype characteristics and of the structures of coenopopulations of the critical types can help to solve moot points of taxonomy. In this connection a comparative ecosystematic analysis of the Gentian family has been carried out, based on the examination of two mountainous regions, belonging to similar belts - the Western Caucasus and the Swiss Alps.

2. MATERIAL AND METHODS

The investigated material consisted of herbarium specimens of Gentianaceae from our sample collection of the mountains of the Western Caucasus and from herbarium collections of the V.L. Komarow Botanical Institute of the Academy of Sciences of the USSR, of the Caucasian state nature sanctuary, of the Sukhumi Gardens of the Georgian Botanical Institute, of the Moscow State Institute. This analysis is based on the primary

factor data of the species habitat (warmth, water, light, chemical, and mechanical factors) listed on the sample labels and dealt with in scientific papers. For the species and groups of species which were supposed to be vicarious morphological differences were critically examined and used as the basis of their classification. The taxa are named after CHEREPANOV (1981) and HEGI (1977).

3. RESULTS AND DISCUSSION

The Caucasus is a mountainous country stretching from the northwest to the southeast between the Black Sea, the Sea of Azov and the Caspian Sea. Some of its summits are higher than Mont Blanc (4807 m) of the Alps and the highest peak of Elbrus reaches 5642 m. Some authors (e.g. DOBRYNIN 1948) draw the southern borderline between Europe and Asia along the Cumo-Manich depression. In their opinion, the whole of the Great Caucasus, the subtropical foothills of the southern macroslope excluded, should be regarded as a peculiar climatic region of Western Asia).
The analysis made by ERAMOV and PARMUSIN (1964) of the current belt system and the general composition of the vegetation in the mountains which had undergone Quarternary glaciation, enabled the authors to include the Crimea-Caucasian mountain system. At the junction of temperate and subtropical belts influenced simultaneously by the Atlantic Ocean and the continental climate of the inner parts of Eurasia the Caucasian mountains are characterized by an exceptional variety of natural conditions. With the general increase of the height of the mountains as one moves from the northwest to the southeast there is a diminution of precipitation and a strengthening of the continental climate. This is largely due to the diametrical mountain ridges stretching off the chief Caucasian Ridge to the north and south (ELENEVSKY 1939). Blocking the way for humid air masses from the west, each of these mountain ridges detains a certain quantity of moisture. The general decrease of precipitation occurs in the Causasus in the direction from the south northwards. As one moves from the moister areas towards drier areas mountainous and high-mountain landscapes give way to steppe. This general landscape reshaping is marked by many authors: the upper forest border, rises gradually, the

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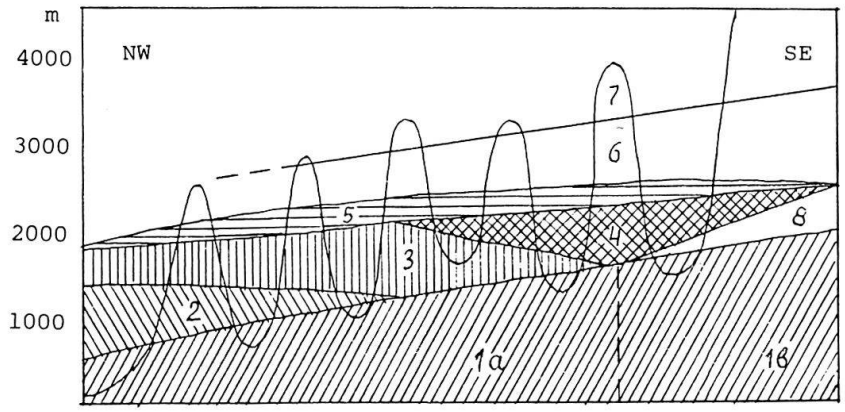

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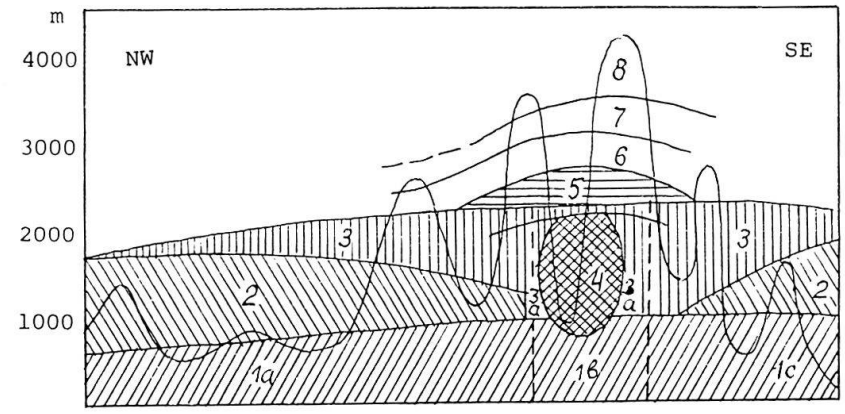

Fig. 1. Altitudinal belts in the Western Caucasus and in the Swiss Alps
Abb. 1. Höhenstufen im Westkaukasus und in den Schweizer Alpen

A. The Western Caucasus (after ELENEVSKY 1940)
1. forest steppe belt, a) the Western Caucasus, b) the Central Caucasus
2. belt of beech forests
3. belt of dark coniferous forests
4. belt of pine forests
5. subalpine belt
6. alpine belt with a subnival strip
7. nival belt
8. belt of mountainous xerophytes

B. Swiss Alps (after LANDOLT 1983)
1. belt of oak trees, a) northern Alps, b) central Alps, c) southern Alps
2. belt of beech trees
3. subalpine belt, 3a) central Alps
4. continental mountain belt
5. suprasubalpine belt
6. alpine belt
7. subnival belt
8. nival belt

forest becomes narrower and wedge-shaped, mesophyllous trees give place to xerophyllous ones; Krummholz beeches are replaced by birches; the Subalpine belt diminishes and the role of the Alpine belt grows etc. (e.g. VESELOVSKY 1927, ELENEVSKY 1939, 1940, SOCHAVA 1946, SOSNOVSKY 1947, SHIFFERS 1951, STANYUKOVICH and KRIVONOGOVA 1957). Noting the marked heterogeneity of the various parts of the Great Caucasus, TUMADJANOV (1966) has singled out the western humid region open to the Mediterranean cyclones and the region of Central and Eastern Caucasus influenced by the continental climate of Western Kazakhstan and Precaspian Plain. Characterizing changes in the vegetation of the mountains towards the inner parts of the continent, ELENEVSKY (1940) draws a diagram of the anteposterior landscape profile of the northern slope of the Western Caucasus. The profile goes through the chief Caucasian Ridge from the northwest from the Abadzesh mountains to the southeast up to the Elbrus mountain. ELENEVSKY's diagram (Fig. 1A) somewhat changed after LANDOLT (1983) to make the comparison clearer the following belts can be listed:

1) the forest-steppe belt,
2) the belt of dense beech forests, prominent in the western part of the profile and disappearing in the Small Laba river basin,
3) the belt of dark coniferous forests, where the Nordman fir, Abies nordmanniana (Stev.) Spch, is gradually replaced by spruces, Picea orientalis (L.) Link,
4) the belt of pine forests, Pinus kochiana Klotzch ex C. Koch, well marked in the Teberda river basin,
5) The subalpine belt, including small Krummholz beeches and birches (in the east), subalpine tall herbs and a rhododendron strip, Rhododendron caucasicum Pall.,
6) the alpine belt with a subnival strip,
7) the nival belts,
8) the belt of mountainous xerophytes.

By the structure of vertical belts the Western Caucasus is close to the mountainous countries of oceanic type. Its mountain belts represent, after STANYUKOVICH (1955), the Western Caucasian variant of the Coastal Atlantic or Alpine belt type widely spread in the mountains of Central Europe. Their main features in the view of STANYUKOVICH are a distribution of forests all over the mountain belts, with the exception of the high mountains, and a lack of xerophytic plants. Thus, in our opinion, the territory of the Western Caucasus stretches in the east as far as the Teberda river basin where "upland xerophytes" appear in the vegetation of the mountains for the first time.

The Alps are the most complex, high, and extensive mountain system in

Central Europe. As the Caucasus the Alps were shaped in the tertiary period and formed one whole with the Caucasus at that time. The course of further geological development resulted in their complete isolation and conditioned the origin of unique flora in each of these mountain ranges.

The Alps are divided by the diametrical valley stretching from the Lake of Constance to the Lake of Como in the high Western Alps with a characteristic topographical type and the lower Eastern Alps.

Both botanists and geographers have been looking for regions analogous to the Caucasus and the Alps. After LAVRENKO (1958) the belts of the central part of the Eastern Alps have no analogues in Europe and the belts of northern limestone Alps should be classified as "the Alpine-Carpathian variant of the Caucasian central European type of zone characteristic of the European broad-leaved province" (p. 308). The northern limestone Alps to a certain extent can be regarded as an analogue to the limestone mountains of Kolchida (SOKHADZE 1974). The major points of similarity and difference between the natural ecosystems and the belts of the Caucasus (Western and Central) and the Alps (French) are represented most convincingly by GREBENSHIKOV and OZENDA (1980). These authors have drawn a conclusion that in the high-altitude position of vegetation belts of the representative profiles under comparison there is a certain difference, which becomes greater as the belt gets higher. They have also pointed out that similar ecological environment promoted the appearance of associations of plants analogous, if not identical in structure and composition, with the chief species often being vicarious.

After GREBENSHIKOV and OZENDA (1980) the plant kingdoms of the Alps and the Caucasus should be marked by considerable similarity of genera and with great differentiation of species by a great number of vicarious types which do not upset the general physiognomical likeness.

Unfortunately they have not investigated the Swiss Alps which, in our view, are a good analogue to the Western Caucasus (Fig. 1B). It must be admitted though that the Swiss Alps on the whole are more humid than the Western Caucasus. In the foothills of the Alps there are no steppe and forest-steppe. The beech forest belt is better developed and it is lacking only in the Central Alps. The timberline in the Swiss Alps is far lower and as the snow line is higher than in the Western Caucasus the high- mountain belt is much more prominent. Nevertheless the structure of vertical belts in both mountain ranges can be compared. The upper

borders of the lower vegetation belts, the foothill belt (I) and the mountain forest belt (II) practically coincide (Table 1). The exception is the high-mountain belt (III) with its upper border higher in the Swiss Alps by 200-300 m.

Table 1. High mountain vegetation belts in the Western Caucasus and in the Swiss Alps
Tab. 1. Hochmontane Vegetationszonen im westlichen Kaukasus und in den Schweizer Alpen

NN	High altitude belts	Western Caucasus		Swiss Alps	
		Upper limit m a.s.l.	Name of belt after ELENEVSKY (1940)	Upper limit m a.s.l.	Name of belt after LANDOLT (1983)
I	Foothills	600- 800(1500)	forest steppe belt	600- 800(1000)	colline belt
II	Mountain forest				
	1. lower	1200-1400(1500)	beech forest belt	1100-1400(1700)	montane belt
	2. upper	1800-1000(2300)	coniferous forest belt	1800-2000(2100)	subalpine and continental mountain belt
III	High mountain				
	1. subalpine belt	2200-2300(2500)	subalpine belt	2000-2300(2500)	suprasubalpine belt
	2. alpine belt	2700-2900(3200)	alpine belt incl. subnival belt	2900-3100(3500)	alpine and subnivale belt

There are no papers which register full lists of Gentianaceae taxa for the Western Caucasus. After GROSSHEIM (1952) in the Caucasus the Gentian family numbers on the whole 5 genera and 30 species. For the northern macroslope of the Western Caucasus GALUSHKO (1980) lists 24 species and 7 genera. After KOLAKOVSKY (1982) there are 18 species of 4 genera in the Western Transcaucasus (the southern macroslope of the Western Caucasus).

We have ascertained that in the Western Caucasus Gentianaceae appears in 8 genera: Blackstonia Huds., Centaurium Hill., Comastoma (Wettst.) Toyokuni, Gentiana L., Gentianella Moench., Gentianopsis Ma, Lomatogonium A.Br., Swertia L. These are represented by 27 species, 9 of them (33%) are foothill species (especially of Blackstonia and Centaurium genera), 8 species (30%) prevail in the mountain-forest belt, 10 species (37%) are high-mountain species. There are 8 species (30%) endemic for the Caucasus: 4 of them are high-mountain species and 3 are mountain species. Species endemic for the Western Caucasus are: Gentiana kolakovskyi

Table 2. Habitats of Gentianaceae in the Western Caucacus and in the Swiss Alps
Tab. 2. Standorte von Gentianaceae im westlichen Kaukasus und in den Schweizer Alpen

Belt	Habitat	Species common to the Western Caucasus and the Swiss Alps	Western Caucasus		Swiss Alps	
			endemic species	wide-spread species, missing in the Swiss Alps	endemic species	wide-spread species, missing in the W Caucasus
	Genus Comastoma					
III	Moderately moist, weakly acid, mineral and humus enriched, loamy and clayey soils. Sunny spots.					C. tenellum
	Moderately moist, acid, with moderate mineral and humus content, permeable to water, sandy loamy or sandy soils. Sunny spots.		C. dechyanum		Gentianella nana	
	Genus Gentiana					
I	Moist, from weakly acid to weakly basic, clayey or peaty soils with high humus content. Sunny spots.	G. pneumonanthe				
II	Dry, basic, loamy or clayey structural soils poor in mineral content. Weakly sunny spots.	G. cruciata				
	Dry, basic, sandy loamy soils, poor in mineral content. On limestone. Bright sunny spots.					G. angustifolia G. clusii
	Moderately moist, basic, basic loamy soils. On limestone. Weakly sunny spots.		G. kolakovskyi G. paradoxa			
	Moderately moist, basic, loamy and clayey structural soils with moderate nutritive content. Weakly sunny spots.			G. schistocalyx		G. asclepiadea
	Moderately moist, basic, clayey or peaty soils with moderate mineral content. Sunny spots.					G. lutea G. utriculosa G. verna
	Moderately moist, acid, loamy soils poor in mineral content. Sunny spots.					G. kochiana G. punctata G. purpurea
	Moist, from weakly acid to weakly basic, loamy soils. Sunny spots.					G. pannonica G. rostanii
III	Dry, acid, sandy loamy soils poor in mineral content. Bright sunny spots.					G. alpina
	Dry basic mineral enriched sandy loamy soils. Sunny spots.					G. prostrata

Table 2 (continued)

Belt	Habitat	Species common to the Western Caucasus and the Swiss Alps	Western Caucasus		Swiss Alps	
			endemic species	wide-spread species, missing in the Swiss Alps	endemic species	wide-spread species, missing in the W Caucasus
	Moderately moist, weakly acid, mound and pebble soils, poor in humus and mineral content. Bright sunny spots.				G. schleicheri	
	Moderately moist, basic, sandy loamy soils poor in mineral content. Bright sunny spots.					G. orbicularis
	Moderately moist, acid, sandy loamy soils, poor in mineral content. Bright sunny spots.				G. angulosa	G. brachyphylla
	Moderately moist, from weakly acid to weakly basic, loamy and clayey soils. Bright sunny spots.		G. oschtenica	G. septemfida G. aquatica G. djimilensis		
	Moist, weakly acid, with moderate humus and mineral content, sandy, loamy soils. Sunny spots.	G. nivalis			G. bavarica	
	Genus Gentianella					
II	Moderately moist, basic clayey or peaty soils poor in mineral content. Sunny spots.				G. insubrica	G. germanica
	Dry, from weakly acid to weakly basic, loamy soils poor in mineral content. Sunny spots.	G. amarella			G. aspera	G. campestris
III	Dry, basic, loamy soils poor in mineral content. Sunny spots.				G. engadiensis	
	Dry, acid, loamy soils, poor in mineral content. Sunny spots.				G. ramosa	
	Moderately moist, basic, loamy soils poor in mineral content. Sunny spots.		G. promethea G. umbellata			
	Moderately moist, from weakly acid to weakly basic, loamy soils. Sunny spots.		G.biebersteinii			
	Genus Gentianopsis					
	Moderately moist, basic, stony, clayey or peaty soils poor in nutritive content. Weakly sunny spots.			G. blepharophora		G. ciliata
	Genus Swertia					
	Damp, basic, humus enriched clayey or peaty soils poor in mineral content. Sunny spots.		S. iberica			S. perennis

Doluch., G. oschtenica (Kusn.) Woronow, G. paradoxa Albov. All the genera of the Gentian family found in the Western Caucasus are typical for the flora of the Swiss Alps. However, Swiss botanists do not acknowledge the existence of the independent genera Comastoma and Gentianopsis. These taxa are treated within the Gentianella genus. Besides Menyanthes L. and Nymphoides Seguier, which belong to the Menyanthaceae Dumort family according to the International Botanical Nomenclature Code (1980) are also classified as Gentianaceae. As a whole in the Swiss Alps and neighbourhood (the species of the Menyanthes and Nymphoides genera excluded) 36 species of Gentianaceae are registered (BINZ 1927, HEGI 1927, 1977, THOMMEN 1951, ZOLLER et al. 1964, TUTIN 1972, LANDOLT 1977, 1983), with 5 species growing in the foothills (15%), 20 species - in the mountain forest belt (55%), 11 species - in the high-mountain belt (30%). There are 6 of these species endemic for the Alps (16%) but no species endemic for the Swiss Alps. The comparison of Gentianaceae taxa in the Western Caucasus and the Swiss Alps enabled us to point out their high generic similarity (100%). Of 63 species under comparison 14 species (22%) are found in the foothills, 28 species (44%) are mountain species and 21 species (34%) are high-mountain species. Up to now 8 species (13%) are considered to be common to the Western Caucasus and the Swiss Alps, 4 of them are foothill species (25%) of the overall number of foothill species of both mountain ranges, 3 species are mountain forest species (11% of the overall number of mountain species), and only 1 (5%) of 21 species growing in the high-mountain belt of two mountain ranges: Gentiana nivalis L. is common. Thus all above mentioned statements confirm the conclusions drawn by FYODOROVA (1952), TOLMACHEV (1974), WALTER (1986) and others concerning the autochthonous development of the Alpine flora at the level of species. The analysis and comparison of the Gentianaceae habitat in the mountains of the Western Caucasus and the Swiss Alps (Table 2) allowed the preliminary establishment of pairs of allied vicarious species. In the Comastoma genus the endemic Caucasian species C. dechyanum (Somm. et Levier) Holub and endemic species of the Alps Gentianella nana (Wulfen) Pritch. are vicarious. They grow in the high-mountain belt on the subacid, mineral and humus enriched loamy and clayey soils. In Gentiana genus two pairs of species are vicarious: 1) G. schistocalyx (C.Koch) C.Koch (Fig. 3A) and G. asclepiadea (forest belt), 2) G. angulosa Bieb. (Fig. 3B) and G. brachyphylla Vill. (high-mountain belt). G. schistocalyx and G. asclepiadea are plants with a wide eco-

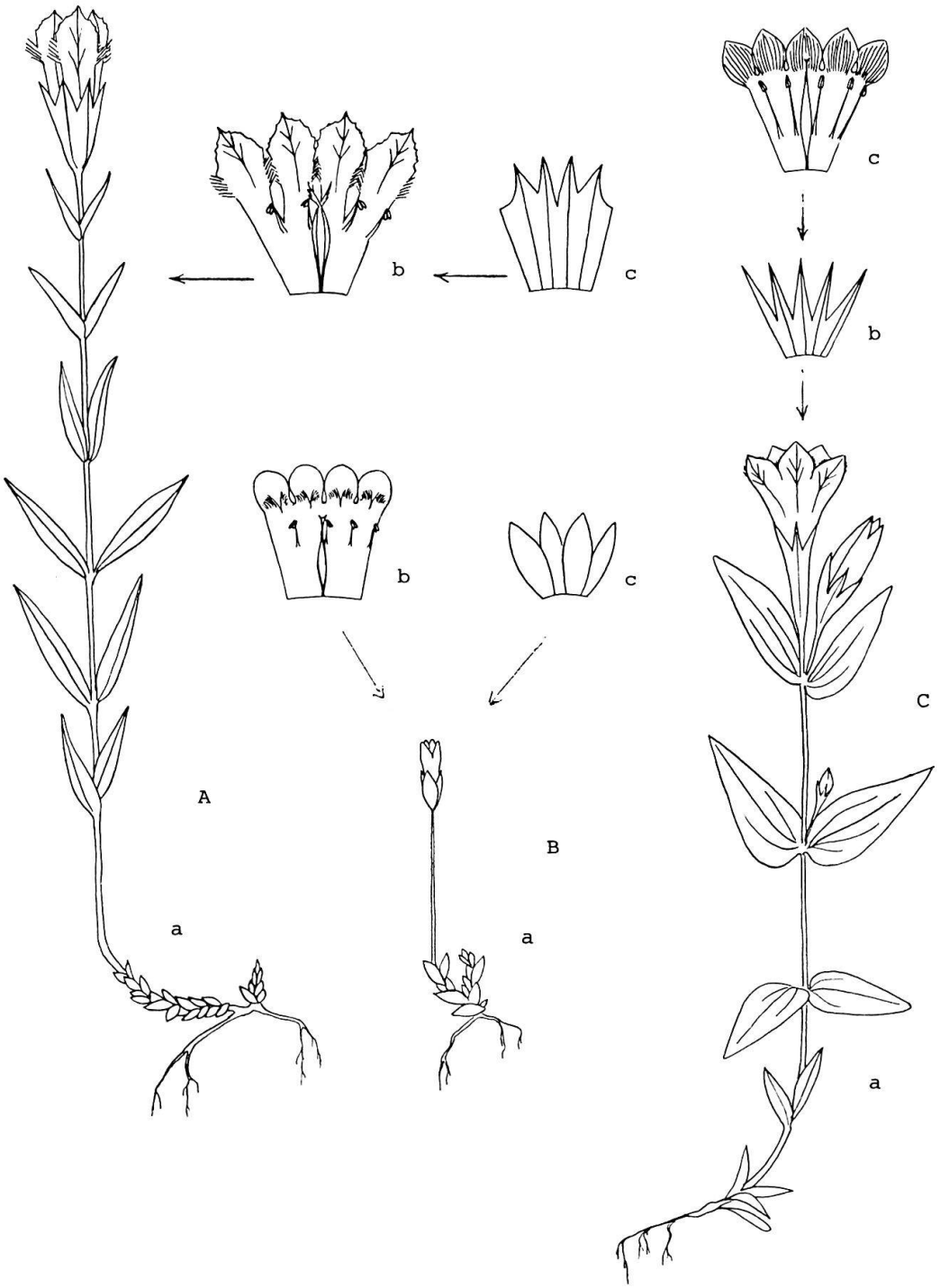

Fig. 2. Gentianopsis blepharophora (A), Comastoma dechyanum (B) and Gentianella biebersteinii (C)

a) general look, b) corolla, c) calyx; b) and c) x2

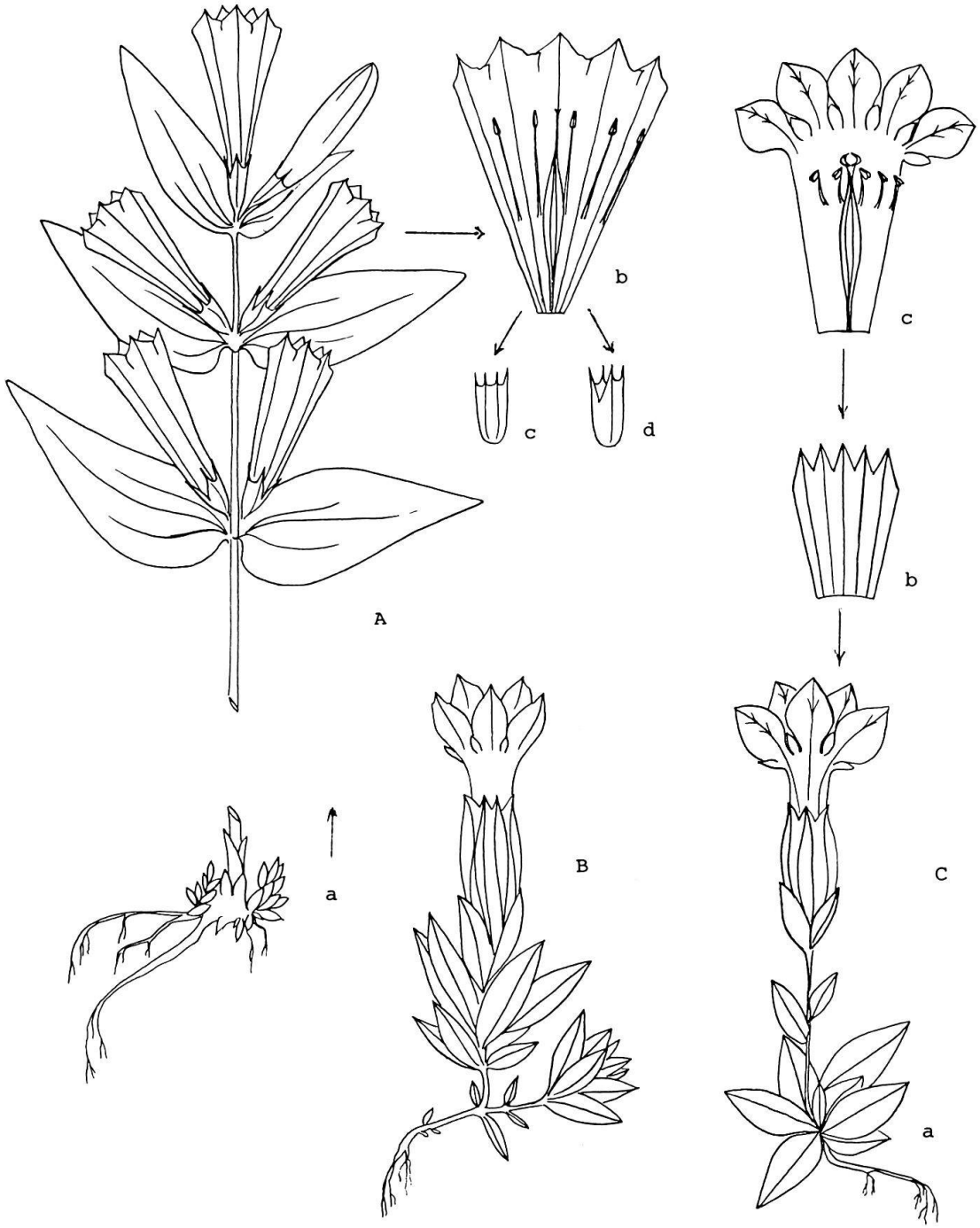

Fig. 3. Gentiana schistocalyx (A), Gentiana angulosa (B) and Gentiana oschtenica (C)

a) general look, b) corolla, c) whole calyx, d) split calyx

logical amplitude. Being mountainous species they can also often be found in the foothills and high-mountain belts. As usual their presence indicates moderate mineral humus and base content in the soil. As to the consistancy G. schistocalyx and G. asclepiadea give preference to clayey, waterproof, weakly aerated soils. These two species under close examination can be treated as one G. asclepiadea species s.l., which is characterized by a high degree of variability of such morphological features as calyx structure, the density and arrangement of leaves (KUZNETZOV 1894). The calyx features (large and split), decisive for distinguishing G. schistocalyx from G. asclepiadea, are not constant: one and the same specimen can be found with an unsplit calyx and with a calyx split to different degrees (Fig. 3A). Therefore they can hardly have a taxonomic significance for the species. The investigation of the variability of the feature against a broad ecological and geographical background will help to specify their systematic significance. The vicarious pair G. angulosa - G. brachyphylla belongs to the section Cyclostigma Griseb. and is related to G. verna L. from which it probably originates. It is found on moderately moist, waterproof, well-aerated soil poor in nutrients.

In the Gentianopsis genus G. blepharophora (Bordz.) Galushko (Fig. 2A) corresponds to G. ciliata (L.) Ma. These are species of the mountain forest belt, which can also be found in the foothills and in the high-mountain (Subalpine) belt growing on stony soils as well as on clayey and peaty soils. They are not particular about lighting and mineral content. They are most often found on limestone soils. G. blepharophora and G. ciliata species should be identical at first sight, as the examined herbarium specimens do not permit the establishment of any morphological distinctions between them. Of the genus Swertia the Caucasian endemic S. iberica Fisch. ex C.A. Mey. and S. perennis widely distributed in Central Europe can be considered geographically vicarious as far as their habitat is concerned. Both these species are found on soils rich in springs, in boggy parts of the mountain belt of the two regions under comparison. Their habitats are poor in minerals but rich in humus and consist of clayey or peaty open forestry plots and edges. The habitats of the species of Blackstonia, Centaurium and Lomatogonium have not been compared, as these genera are represented in the Western Caucasus and in the Swiss Alps only by common species.

SUMMARY

An ecological and taxonomical analysis of the Gentianaceae has given evidence that the rather high degree of similarity of natural conditions and concrete habitat factors in the related mountain systems (the Western Caucasus and the Swiss Alps) lead to parallel development of intrafamily taxa. Thereby common genera and ecologically similar groups of species are being formed. The majority of family taxa are mountain and high mountain species (76%) of the same genera. There is a considerable differentiation of species (only 13% of species are common), which is especially noticeable in the high-mountain belts. Both regions are characterized by the approximately equal degree of endemic species (11% in the Western Caucasus), geographically vicarious species are widely present. The accomplished work points out the necessity to define more precisely systematic position and limits of the genera Comastoma, Gentiana, Gentianella, Gentianopsis and the critical species Comastoma dechyanum, C. nanum, C. tenellum, Gentiana asclepiadea, G. schistocalyx, Gentianopsis blepharophora, G. ciliata and others applying ecological and phytocoenological criteria.

ZUSAMMENFASSUNG

Eine ökologisch-taxonomische Analyse der Familie der Gentianaceae im westlichen Kaukasus und in den Schweizer Alpen zeigt, dass eine relativ hohe Aehnlichkeit der natürlichen Standortsbedingungen dieser verwandten Gebirge zu einer parallelen Entwicklung der Taxa innerhalb der Familie führt. Gemeinsame Gattungen und (ökologisch sich ähnlich verhaltende) Artengruppen kommen vor. Der grösste Teil der Taxa sind Gebirgs- und Hochgebirgsarten (76%). Die meisten Arten haben sich unabhängig differenziert (nur 13% gemeinsame Arten); besonders eindrücklich ist diese Differenzierung im Hochgebirge. Beide Regionen enthalten einen ähnlichen Prozentsatz endemischer Arten (11% im westlichen Kaukasus); geographisch vikariierende Arten sind verbreitet. Die Untersuchungen zeigen, dass es notwendig ist, die systematische Stellung und Abgrenzung der folgenden Gattungen und kritischen Arten näher abzuklären: Comastoma, Gentiana, Gentianella, Gentianopsis; Comastoma dechyanum, C. nanum, C. tenellum, Gentiana asclepiadea, G. schistocalyx, Gentianopsis blepharophora, G. ciliata u.a., wobei besonders ökologische und phytocoenologische Merkmale zu beachten sind.

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