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CAN THE SECTIONAL POSITION OF *GENTIANA CACHEMIRICA* BE CLARIFIED BY A DETAILED ANALYSIS OF ITS MORPHOLOGY?

N. Davitashvili & G. Karrer

Gentiana cachemirica is a rare plant from northern Pakistan and northwestern India. The sectional position of this species has been a matter of considerable debate. Various authors have placed *Gentiana cachemirica* in one of three different sections – *Gentiana* sect. *Isomeria*, *Gentiana* sect. *Kudoa* or *Gentiana* sect. *Pneumonanthe*. The present paper assesses the taxonomic affinities of this species using a detailed study of its morphology accompanied by morphological phylogenetic and cluster analyses. Characters of the seed testa, corolla morphology and growth architecture were studied for selected species from the above-mentioned sections and closely related *Gentiana* sect. *Cruciata*. Representatives of *Gentiana* sect. *Ciminalis* were used as outgroups. Our results suggest that *G. cachemirica* belongs to *Gentiana* sect. *Pneumonanthe* and that its affinities are closer to the Western Asiatic group of this section.

Keywords. *Gentiana cachemirica*, *Gentiana septemfida*, growth architecture, *Isomeria*, *Kudoa*, Pakistan, *Pneumonanthe*, western Asia.

INTRODUCTION

Gentiana cachemirica Decne. is a rare plant from northwestern Pakistan and northwestern India. It occupies moist rocky ledges in the eastern Hindu Kush range and westernmost Himalayas (Polunin & Stainton, 1990; Omer & Qaiser, 1995b). This species was discovered by Decaisne. Hooker was not aware of Decaisne's publication and described the same species under the name *Gentiana loderi* Hook.f. Later, Clarke (1885) considered the markedly different *Gentiana stipitata* Edgew. to be conspecific with *G. cachemirica*. After almost 100 years of confusion Smith (1961) separated *Gentiana stipitata* from *G. cachemirica* and recognized *G. loderi* as a synonym of the latter.

In general, *Gentiana cachemirica* is poorly known because it has been rarely collected. This may partially account for the various conflicting sectional treatments of this species (see Table 1). Clarke (1885) included *Gentiana cachemirica* in *Gentiana* sect. *Pneumonanthe* (Gled.) Gaudin. According to his classification *Gentiana* sect. *Pneumonanthe* comprised plants 'with one or more flowers and wingless seeds'. On the basis of flower and seed morphology Kusnezow (1894) split '*Pneumonanthe*' s.l. into three sections: *Gentiana* sect. *Frigidae* Kusn., *Gentiana* sect. *Isomeria* Kusn. and *Gentiana* sect. *Pneumonanthe* s.str. *Gentiana cachemirica* (including *G. stipitata*) was

University of Natural Resources and Applied Life Sciences, Gregor-Mendel Str. 33, Vienna 1180, Austria.
E-mail for correspondence: nino.dawitaschwili@boku.ac.at

TABLE 1. Sectional treatment of *Gentiana cachemirica* by different authors. Sections in which *Gentiana cachemirica* was placed in bold; n.ac., not accepted

Clarke (1885)	Kusnezow (1894)	Smith (1961)	Ho & Liu (2001)
Pneumonanthe	*Pneumonanthe*	***Pneumonanthe***	*Pneumonanthe*
n.ac.	*Frigidae*	*Frigidae*	*Frigidae*
n.ac.	n.ac.	n.ac.	*Microsperma*
n.ac.	n.ac.	n.ac.	*Monopodiae*
n.ac.	n.ac.	n.ac.	*Phyllocalyx*
n.ac.	n.ac.	n.ac.	***Kudoa***
n.ac.	***Isomeria***	n.ac.	*Isomeria*

placed within his newly established section *Isomeria* comprising four further taxa: *Gentiana amoena* Clarke, *G. delavayi* Franch., *G. depressa* Don and *G. loderi*. This section unified Himalayan and southwestern Chinese taxa with 'indistinct corolla lobes and large symmetrical plicae' (Kusnezow, 1894). Smith (1961) showed that the differentiating characters of Kusnezow's *Gentiana* sect. *Isomeria* such as symmetrical plicae and indistinct corolla lobes also occur in other Himalayan gentians besides *Gentiana* sect. *Isomeria*. As a consequence, he rejected this section and placed *Gentiana amoena*, *G. delavayi* and *G. depressa* in *Gentiana* sect. *Frigidae*. Furthermore, he separated *Gentiana stipitata* from *G. cachemirica*, regarding the first species to be a member of *Gentiana* sect. *Frigidae*. In Smith's opinion, *Gentiana cachemirica* (including *G. loderi*) had affinities with eastern populations of *G. septemfida* Pall. and should be included in *Gentiana* sect. *Pneumonanthe*. Smith (1961) describes well the morphological peculiarities of *Gentiana stipitata* and other members of *Gentiana* sect. *Frigidae* but the paper lacks comparable information for *G. cachemirica* and, therefore, does not support the inclusion of this species in *Gentiana* sect. *Pneumonanthe* on the basis of morphology. Smith's classification of *Gentiana cachemirica* was accepted by Schiman-Czeika (1967) and Halda (1996). The recent monographers Ho & Liu (1990, 2001) ascribed much weight to growth architecture and seed morphology for the sectional classification of *Gentiana* and recognized 15 sections. In their study the representatives of *Gentiana* sect. *Pneumonanthe* are characterized by 'sympodial growth form', whereas *G. cachemirica* is a monopodial, rosulate plant. Therefore, they ignored the classification by Smith (1961) and placed *Gentiana cachemirica* in *Gentiana* sect. *Kudoa* (Masam.) Satake & Toyok. ex Toyok. This section was separated from *Gentiana* sect. *Frigidae* based on the 'monopodial branching pattern of the shoot, presence of an apical rosette, honeycomb-like seed testa structure, symmetrical plicae, and a single terminal flower' (cf. Table 2).

The conflicting ideas about the sectional position of *Gentiana cachemirica* illustrate that its morphology is not yet fully understood. As a result, the sectional placement of this species still remains unclear. A large number of molecular and morphological studies dealing with various aspects of the family *Gentianaceae* have been carried out during the last few years (e.g. Struwe & Albert, 2002; Hagen & Kadereit, 2003;

TABLE 2. Comparative morphology of *Gentiana cachemirica* and *Gentiana* sections *Isomeria*, *Kudoa* and *Pneumonanthe*, according to Ho & Liu (2001); ?, not documented or mentioned

Kudoa	*Isomeria*	*Pneumonanthe*	*Gentiana cachemirica*
Seed testa with hexagonal pits	Seed testa with simple and spongy complex hexagonal pits	Seed testa reticulate	Seed testa with hexagonal pits
Seed without wing	Seeds without wings or membranous lamellae	Seeds with various wings	Seed without wing
Plants branching monopodially	Plants branching sympodially	Plants branching sympodially	Plant branching monopodially
Corolla plicae always symmetrical	Corolla plicae symmetrical and asymmetrical	?	Corolla plicae always symmetrical
Taproot present	Taproot absent	Taproot present	Taproot present
Stolons absent	Stolons present	Stolons absent	Stolons absent

Greimler *et al.*, 2004; Chen *et al.*, 2005; Jang *et al.*, 2005; Yuan *et al.*, 2005), but the species considered for the present study have not been considered for any analysis. In the present paper we aim to elucidate various aspects of the morphology of *Gentiana cachemirica* and clarify the sectional position of this species.

We compare morphological features of *Gentiana cachemirica* and species that represent sections in which *G. cachemirica* was placed, and use cluster analysis to re-evaluate the sectional position of *G. cachemirica*. In addition, we discuss modern distribution ranges and climatic preferences of members of the sections under study.

MATERIALS AND METHODS

Selection of taxa analysed

Representatives of all three sections *Isomeria*, *Kudoa* and *Pneumonanthe* (excluding *G. asclepiadea* L.; see e.g. Löve & Löve, 1972; Mészáros, 1994; Yuan *et al.*, 1996; Karrer, 1997; Davitashvili & Karrer, 2003), in which *Gentiana cachemirica* was placed by various authors, were included in our morphological phylogenetic and cluster analyses. From *Gentiana* sect. *Pneumonanthe* taxa from Euro-Siberian, Eastern Asian and North American groups were selected (Kusnezow, 1894). In the case of *Gentiana* sect. *Isomeria*, sensu Ho & Liu (2001), we analysed most species of *Gentiana* ser. *Confertifoliae* Marquand, since its species composition corresponds to *Gentiana* sect. *Isomeria* sensu Kusnezow (1894). From *Gentiana* sect. *Kudoa* most taxa of *Gentiana* ser. *Monanthae* (Harry Sm.) T.N.Ho, and additionally one species from *Gentiana* ser. *Ornathae* Marquand, were selected. In addition, *Gentiana cruciata* L. and *G. olivieri* Griseb. (*Gentiana* sect. *Cruciata* Gaudin) were included in our analysis. This was done because representatives of *Gentiana* sect. *Cruciata* show

TABLE 3. List of species analysed and their position within the respective sections. Infrasectional groupings of *Gentiana* sections *Kudoa* and *Isomeria* according to Ho & Liu (2001), and of *Gentiana* sect. *Pneumonanthe* after Kusnezow (1894)

Section	Subsectional grouping	Species
Isomeria	*Confertifoliae*	*G. depressa*
		G. urnula
Kudoa	*Monanthae*	*G. cachemirica*
		G. stipitata
		G. szechenyii
	Ornatae	*G. veitchiorum*
Pneumonanthe	Western Asia	*G. gelida*
	Euro-Siberia	*G. pneumonanthe*
	Eastern Asia	*G. scabra*
	Western Asia	*G. septemfida*
	North American	*G. andrewsii*
		G. sceptrum
Cruciata		*G. cruciata*
		G. olivieri
Ciminalis		*G. acaulis*
		G. clusii

morphological similarities to *G. cachemirica*, and, according to previous molecular studies, have close affinities to *Gentiana* sect. *Pneumonanthe* (Yuan *et al.*, 1996). Other Asian sections – *Gentiana* sect. *Chondrophyllae* Bunge and *Gentiana* sect. *Monopodiae* (Harry Sm.) T.N.Ho – having close phylogenetic relationships to *Gentiana* sect. *Isomeria*, *Gentiana* sect. *Kudoa* and *Gentiana* sect. *Pneumonanthe* (Yuan *et al.*, 1996), as well as *Gentiana* sect. *Otophora* Kusn., were not included in the analysis as they lack morphological affinities to the species of our interest. *Gentiana acaulis* L. and *G. clusii* E.P.Perrier & Songeon from European *Gentiana* sect. *Ciminalis* (Adans.) Dumort. were selected as outgroups, since *Gentiana* sect. *Ciminalis* is sister to sections included in the analysis (Yuan *et al.*, 1996). The taxonomic position of the taxa within sectional frameworks proposed so far by different authors is presented in Table 3.

Plant material

All selected taxa were studied at the herbaria of Kew (K), Edinburgh (E), Vienna (W), and Tbilisi (TBI, TB), or were examined using living specimens from field collections. A list of selected voucher specimens examined is presented in Appendix 1.

Seeds of *Gentiana depressa*, *G. pneumonanthe*, *G. scabra* Bunge, *G. septemfida* and *G. urnula* Harry Sm. were collected from mature capsules of living plants or herbarium specimens. Seeds were put on stubs for SEM investigation. The stubs were spatter-coated with gold and examined using a scanning electron microscope (Philips XL30 ESEM). Information about seed shape and testa ornamentation of

Gentiana cachemirica and *G. stipitata* was taken from Omer & Qaiser (1995a) and Smith (1961), respectively.

Calyx and corolla drawings of *Gentiana cachemirica*, *G. pneumonanthe*, *G. septemfida*, *G. szechenyii* Kanitz and *G. veitchiorum* Hemsl. were made from prepared flowers.

All the other morphological characters were determined by the examination of macro- and micromorphological features of living and herbarium specimens.

Selection of characters for cluster analysis

Our criteria for character selection were independence of characters and stability or a high level of conservatism of character states within the species (Stuessy, 1990). We placed special emphasis on qualitative characters that were reported to have taxonomic importance (Ho & Liu, 1990, 2001):

Shoot architecture. Gentians have various growth forms that are stable within the sections. This character complex has been used by many authors for sectional delimitation in the genus *Gentiana* (Smith, 1961; Karrer, 1997; Ho & Liu, 1990, 2001; Renobales *et al.*, 1999; Davitashvili & Karrer, unpubl. data). The sections were differentiated by the type of growth form, the orientation of the belowground growth structures, the presence/absence of stolons, the branching intensity, etc.

Leaf system. Most gentians bear opposite cauline leaves, and develop rosettes. The leaves vary in the shape of the blade and in size. The rosettes vary in the presence/absence of green leaves.

Seed micromorphology. Seed morphology is one of the main characters that has been used for the sectional classification of *Gentiana* (Kusnezow, 1894; Yuan, 1993; Ho & Liu, 1990, 2001; Halda, 1996; Bouman *et al.*, 2002; Davitashvili & Karrer, unpubl. data). Seeds vary in testa cell shape, the presence/absence of wings and other characters (Bouman *et al.*, 2002; Davitashvili & Karrer, unpubl. data).

Flower morphology. The shape of the corolla is frequently used as a character for species delimitation but in some cases is also a very useful character for sectional classification (e.g. *Gentiana* sect. *Calathianae* Froel.). Similarly, variation in the margins of the plicae is traditionally used as a differential character within *Gentiana*.

Flower arrangement. Generally, gentian flowers are arranged in cymose inflorescences, but in some taxa and in some sections, for example *Gentiana* sect. *Kudoa*, the number of flowers in inflorescences is reduced to one.

Selected characters were coded as multistate characters (see Table 4).

Analysis of morphological data

The phylogenetic analysis was performed with PAUP 4.0b4a (Swofford, 1998). We conducted a maximum parsimony analysis, using a branch and bound search

TABLE 4. Morphological characters of *Gentiana cachemirica* and possible relatives coded in multistate way

No.	Characters			
1	Plants branching sympodially (0) (Fig. 1B)	monopodially (1) (Fig. 1A,C–F)		
2	Main axis orthotropic (0) (Fig. 1A,C)	plagiotropic (1) (Fig. 1B,D–F)		
3	Plants with stolons (0) (Fig. 1B)	without stolons (1) (Fig. 1A,C–F)		
4	Adult plant with primary root (0) (Fig. 1A)	without primary root (1)		
5	Apical rosette with scaly leaves (0) (Fig. 1C)	with green leaves (1) (Fig. 1A–B,D–F)		
6	Leaves ovate (0)	lanceolate (1)	spathulate (2)	
7	Testa cells isodiametric (0) (Fig. 2B,H)	oblong (1) (Fig. 2D,F)		
8	Testa cells form honeycomb-like pits (0) (Fig. 2A–B,G–H)	do not form (1) (Fig. 2C–F)		
9	Seeds with ribs (0)	without (1)		
10	Micropylar end forms collar (0)	does not form (1)		
11	Seeds compressed (0)	not compressed (1)		
12	Testa cell walls are thickened (0)	not thickened (1)		
13	Seed without wing (0)	with extended chalazal end (1) (Fig. 2C)	with side wing (2) (Fig. 2E)	with wing (3)*
14	Corolla broad funnelform to campanulate (0) (Fig. 1B,D–F)	narrow funnelform (1) (Fig. 1A)	urceolate (2)	bottle-like (3)
15	Corolla plicae symmetrical (0) (Fig. 3A,D–F)	oblique (1) (Fig. 3B–C)		
16	Corolla plicae entire (0) (Fig. 3E,F)	toothed (1) (Fig. 3B–C)	fimbriate (2) (Fig. 3A,D)	
17	Flowering shoot with only one flower (0)	with cymes (1)		

*Fig. 1 in Davitashvili & Karrer (2006).

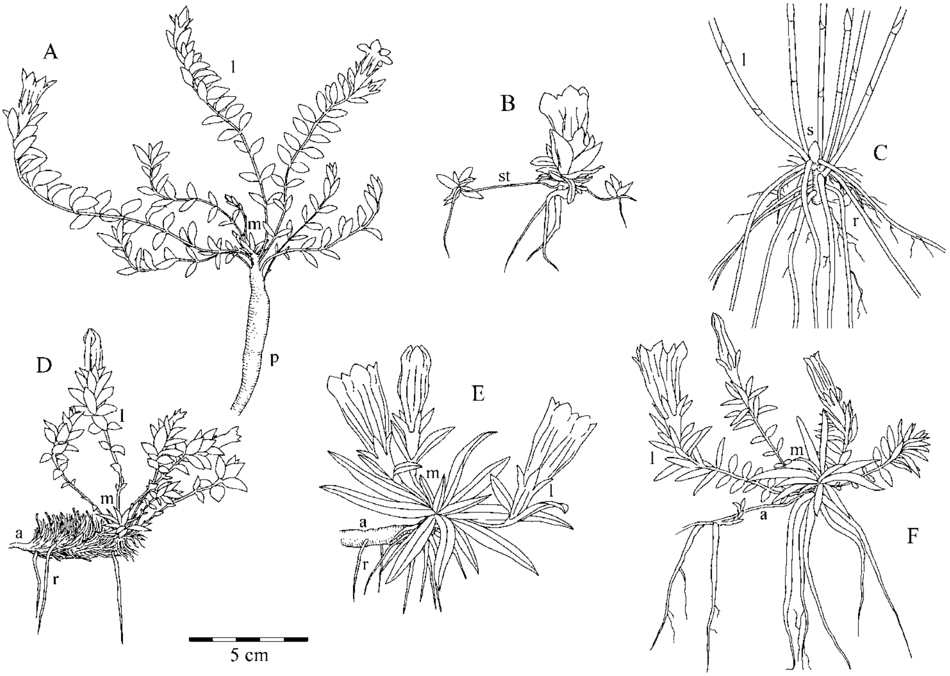

FIG. 1. Growth forms. A, *Gentiana cachemirica*. B, *G. depressa*. C, *G. scabra*. D, *G. stipitata*. E, *G. szechenyii*. F, *G. veitchiorum*. a, main axis; l, lateral short-lived flowering stem; m, monopodial rosette; p, primary root; r, adventitious root; s, monopodial rosette of scale leaves; st, stolon.

algorithm as implemented in PAUP 4.0b4a (Swofford, 1998). All characters were treated as 'unordered' and had equal weight (Fitch parsimony; Fitch, 1971). Multistate taxa were interpreted as polymorphisms. Bootstrap values were obtained based on 1000 replications. Accelerated transformation (ACCTRAN) was used for character state optimization. The character state changes were determined using the 'trace all characters' option in MacClade version 3.01 (Maddison & Maddison, 1992). For comparison, the analysis was also performed with the PAUP* 4.0b4a program using the neighbour-joining (NJ) clustering method, measuring a mean character difference as a distance measure with ties broken randomly and NJ bootstrap of 1000 replicates. The character states were recorded into a multistate matrix of 17 characters. The character matrix is presented in Appendix 2.

RESULTS

Morphology of Gentiana cachemirica

Gentiana cachemirica is clearly a perennial species. All herbarium specimens examined lacked the primary root, except one. The main axis is 5–7 mm thick.

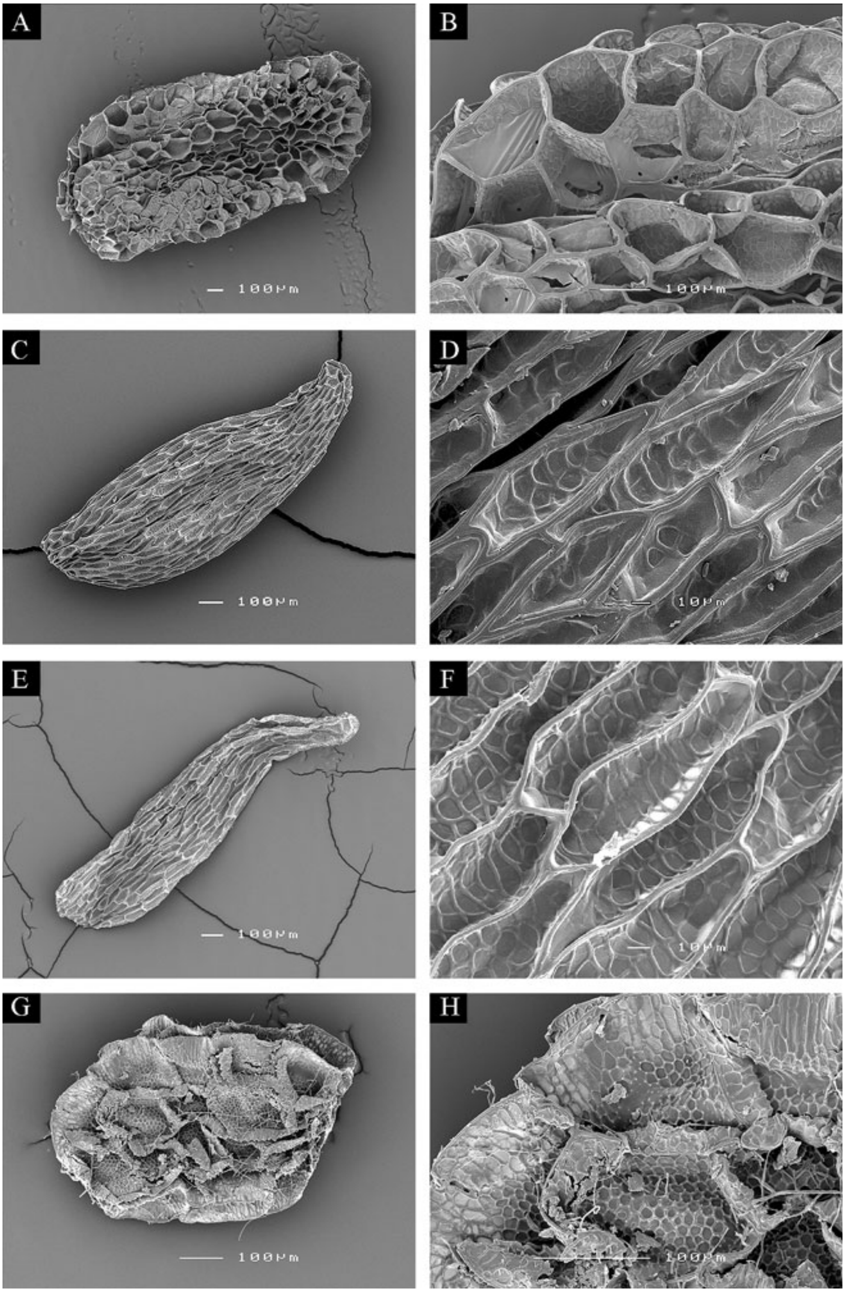

FIG. 2. Seeds and testa details of selected gentians representing the variation of characters within the compared taxa. A–B, *Gentiana depressa* (*Dickoré* (N-)812, private collection). C–D, *G. pneumonanthe* (*Davitashvili* 00-01, TBI). E–F, *G. scabra* (*T. Koyana* 833, W). G–H, *G. urnula* (*Dickoré* 6449, private collection).

It grows monopodially, due to the activity of the apical meristem, which seems to be maintained throughout the life of the plant. The withered parts of the old flowering stems, dormant buds, and adventitious roots are attached to the belowground main stem. The apical buds are covered by scale leaves, which in turn are covered by the bases of the green, oblong-lanceolate, petiolate foliage leaves that form a small, poorly developed, rosette. The flowering stems only develop from lateral buds in the leaf axils of the primary stem. They bear ovate, 3–5-veined leaves, the lowermost scale-like and the largest occurring halfway up the flowering stem. The flowers are arranged in terminal cymes, although occasionally a solitary flower may occur as well.

The seeds of *Gentiana cachemirica* are elliptic in outline, with the chalazal end extended to form a wing; the testa cells are oblong (Omer & Qaiser, 1995a).

The corolla of this species is narrowly funnelform, with distinct corolla lobes and symmetrical plicae with fimbriate margins (Fig. 3).

Phylogenetic analysis of morphological characters

All selected characters were informative for the parsimony analysis. The phylogenetic analysis of morphological characters yielded 29 best trees of 29 steps (consistency index CI = 0.8621, retention index RI = 0.9322, homoplasy index HI = 0.2069 and rescaled consistency index RC = 0.8036). One of the best trees is presented in Fig. 4A.

Gentiana cachemirica does not group with other taxa of *Gentiana* sect. *Kudoa* or *Gentiana* sect. *Isomeria*, but is arranged within *Gentiana* sect. *Pneumonanthe* and thus makes this section paraphyletic. Together with Western Asian *Gentiana septemfida*, *G. cachemirica* forms a group (bootstrap value 66%) that is characterized by the presence of ovate leaves and fimbriate plicae.

Cluster analysis of morphological characters

The result of the cluster analysis is presented in Fig. 4B. *Gentiana cachemirica* does not group together with other taxa of *Gentiana* sect. *Kudoa* or *Gentiana* sect. *Isomeria*, but is clustered (bootstrap value 74%) with *Gentiana septemfida*, the Western Asian member of *Gentiana* sect. *Pneumonanthe*.

DISCUSSION

The sectional position of *Gentiana cachemirica* has been the subject of considerable controversy. Different authors have placed the species in three different sections: *Gentiana* sect. *Isomeria*, *Gentiana* sect. *Kudoa* and *Gentiana* sect. *Pneumonanthe*. Our morphological cluster analysis contradicts the treatment of Kusnezow (1894), who included *Gentiana cachemirica* within *Gentiana* sect. *Isomeria*. This section unifies plants with sympodial branching, belowground stolons (characters 1, 3 in Fig. 4A)

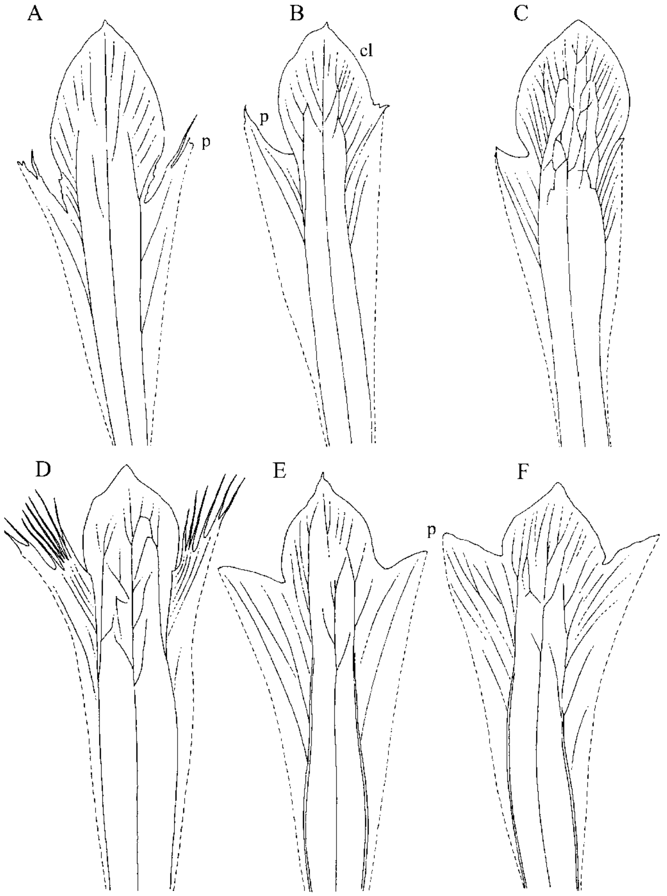

FIG. 3. Drawings of one corolla lobe with its adjacent plicae for selected gentians representing the variation of characters within the compared taxa. A, *Gentiana cachemirica* (*B.L. Burtt & M.A. Kazmi* 1244, E). B, *G. pneumonanthe* (*Davitashvili* 00-01, TBI). C, *G. scabra* (*T. Koyana* 833, W). D, *G. septemfida* (*Davitashvili* 01-01, TBI). E, *G. szechenyii* (*Chungtien-Lijiang-Dali Expedition* CLD-90 No. 757, K). F, *G. veitchiorum* (*F. Kingdon Ward* 6171, K). p, plicae; cl, corolla lobe.

and honeycomb-like seed testas, a combination of characters that differ substantially from those of *Gentiana cachemirica*.

Based on its monopodial branching Ho & Liu (2001) placed *Gentiana cachemirica* in *Gentiana* sect. *Kudoa*. Our examination shows that the branching mode of *Gentiana cachemirica*, as in *Gentiana* sect. *Kudoa*, is monopodial, but *G. cachemirica* develops an orthotropic persistent belowground shoot (character 2 in Fig. 4A), whereas representatives of *Gentiana* sect. *Kudoa* have exclusively plagiotropic belowground persistent shoots. This morphological peculiarity reflects differences in the synecology and growth architecture of *Gentiana cachemirica* as compared with

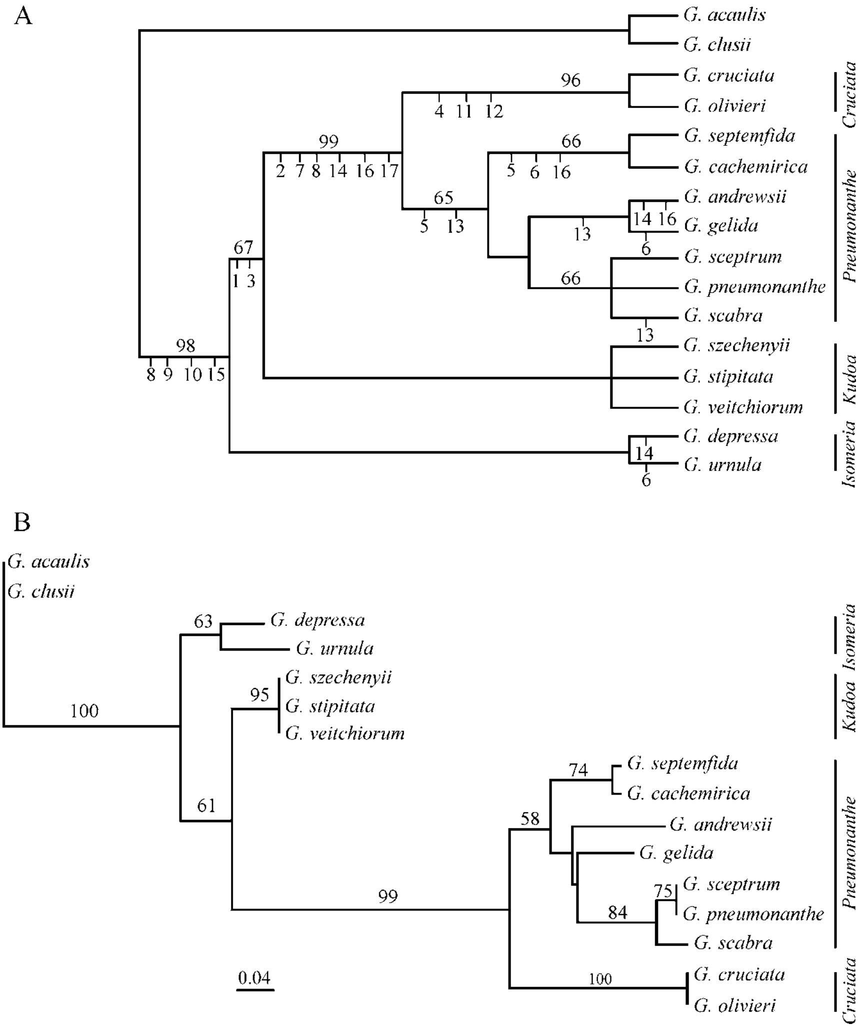

FIG. 4. Dendrograms obtained from the morphological phylogenetic and cluster analyses of *Gentiana* sections *Ciminalis*, *Cruciata*, *Isomeria*, *Kudoa* and *Pneumonanthe*. A, Parsimony analysis. B, Neighbour-joining analysis. Numbers above branches indicate bootstrap values. Numbers below branches indicate characters. The sectional affiliation is marked by vertical lines to the right of the species names following Ho & Liu (2001).

other representatives of *Gentiana* sect. *Kudoa*. The horizontal main axis of most species in *Gentiana* sect. *Kudoa* elongates during the flowering period allowing for spatial expansion, while the orthotropic belowground stem in *G. cachemirica* restricts the plant to the same microhabitats. Thus different strategies are noticeable with respect to clonal reproduction of *Gentiana cachemirica* and the other species of *Gentiana* sect. *Kudoa*. The former develops, at the most, a few daughter branches, whereas the taxa of *Gentiana* sect. *Kudoa* tend to reproduce clonally and to develop expanded clumps. Ho & Liu (2001) reported the taproot to be one of the characters of *Gentiana* sect. *Kudoa*. The primary root was found in *Gentiana cachemirica*, whereas all other representatives of *Gentiana* sect. *Kudoa* lacked the taproot. In all studied specimens the horizontal axis bore only contractile roots, whereas older parts of the horizontal main axis had died out (Fig. 1). Taking into consideration the growing strategy of taxa from this section (see description above) the statement on the presence of a primary root in *Gentiana* sect. *Kudoa* (Ho & Liu, 2001) would seem to be a misinterpretation.

Seed micromorphology (characters 7, 8 in Fig. 4A) does not support the inclusion of *Gentiana cachemirica* within *Gentiana* sect. *Kudoa* either. Omer & Qaiser (1995a) showed that *Gentiana cachemirica* has seeds with elongated testa cells and extended chalazal ends, whereas the seeds of the other taxa in *Gentiana* sect. *Kudoa* are wingless with honeycomb-like testa cells (Smith, 1961; Yuan, 1993; Bouman *et al.*, 2002; Davitashvili & Karrer, unpubl. data).

The flowering shoots of representatives of *Gentiana* sect. *Kudoa* always terminate in solitary campanulate flowers with entire plicae and produce shortened upper internodes with overlapping elliptic to linear leaves (characters 6, 14, 16, 17 in Fig. 4A). Sometimes the lower leaves wither and fall off so that only the lower internodes and upper leaves remain. In *Gentiana cachemirica* the flowering stem produces evenly distributed internodes with ovate leaves and solitary or sub-solitary narrowly funnelform flowers with fimbriate plicae.

The presence of a monopodial orthotropic main axis, the primary root (character 4 in Appendix 2), oblong seed testa cells, and a narrowly funnelform corolla, arranged in a multiflower inflorescence, makes *Gentiana cachemirica* similar to members of *Gentiana* sect. *Cruciata*. However, differences in seed micromorphology, namely the absence of thickened testa cell walls and compressed seeds (characters 11, 12 in Fig. 4A), do not affirm the inclusion of this species in *Gentiana* sect. *Cruciata*. The primary root was documented in only one specimen of *Gentiana cachemirica*. It appears that the taproot and older parts of the belowground stem die as the plant ages, though this may be an artefact of incomplete specimen sampling. Therefore further sampling is necessary to understand the development of this character in this species.

Close affinities between *Gentiana cachemirica* and the representatives of *Gentiana* sect. *Pneumonanthe* were suggested, but without clear evidence, by Smith (1961), Schiman-Czeika (1967) and Halda (1996). Our morphological phylogenetic and cluster analyses confirm the suggestions of the above-mentioned authors. Therefore, it seems reasonable to exclude *Gentiana cachemirica* from *Gentiana* sect. *Kudoa* and place this species within *Gentiana* sect. *Pneumonanthe*.

Gentiana cachemirica shares with the representatives of *Gentiana* sect. *Pneumonanthe* seeds with an extended chalazal end, but differs by the presence of a rosette with small green foliage leaves (characters 5, 13 in Fig. 4A). Most species of *Gentiana* sect. *Pneumonanthe* lack green rosette leaves, developing only transparent scale leaves on the main axis. Thus Serebryakova (1979) defined the growth mode of the section as 'non-rosulate' monopodial. However, some species seem to provide exceptions to this definition. A green-foliaged rosette is documented for a few individuals of *Gentiana septemfida* from the Dsungarian Alatau (Serebryakova, 1979) and for seedlings and juveniles in populations of *G. septemfida* from the Caucasus (unpubl. data). The North American taxon *Gentiana newberryi* A.Gray (*Gentiana* sect. *Pneumonanthe*) also bears green rosette leaves but, in contrast to *G. cachemirica*, its leaves are large and well developed. Morphologically this species is quite distinct from other representatives of *Gentiana* sect. *Pneumonanthe* and therefore its placement within this section is questionable (see also Pringle, 1977).

In general, all species of *Gentiana* sect. *Pneumonanthe* bear small green rosette leaves at least in the seedling stage or as juvenile plants, but some individuals in a few species and in most specimens of *G. cachemirica* maintain small green foliage leaves in the adult stage as well. Smith (1961) speculated about close affinities between *Gentiana cachemirica* and the eastern Caucasian populations of *G. septemfida*. The latter species is extremely variable and includes several subspecies growing in rather different habitat types, including alpine and upper forest belt pastures, and rocky crevices from 500 up to 2400 m above sea level (Dolukhanov, 1948; Grossheim, 1952, 1967; Kolakovsky, 1978; Gagnidze, 1985; Davitashvili & Karrer, 2006). Apparently the hypothesis of Smith (1961) was based on ecological and gross morphological data. Both *Gentiana cachemirica* and *G. septemfida* subsp. *lagodechiana* Kolak. grow on moist rocky ledges and are characterized by ovate leaves and fimbriate plicae (characters 6, 16 in Fig. 4A) and the present morphological and phylogenetic cluster analyses confirm his suggestion (Fig. 4).

Distribution and ecology

Distribution and ecological patterns can provide additional valuable information for plant taxonomy (Stuessy, 1990). The species of *Gentiana* sect. *Kudoa* and *Gentiana* sect. *Isomeria*, with the exception of *G. glauca* Pall., that extends to the Far East, Japan and North America, and *G. yakushimensis* Makino, an endemic species of Yakushima island, are restricted to the central and eastern parts of the Himalayas and the mountains of southeastern Asia (Toyokuni, 1960; Garg, 1987; Aitken, 1999; Ho & Pringle, 1995; Ho & Liu, 2001) (Fig. 5). Takhtajan (1986) includes this area in his 'Eastern Asiatic floristic region', characterized by heavy monsoon rainfalls that decrease rapidly in the western parts of the Himalayan chains (Bartholomew, 1988). *Gentiana* sect. *Kudoa* and *Gentiana* sect. *Isomeria* seem to have evolved along with the establishment of monsoon climates in southeastern Asia and are likely to be adapted to high amounts of summer precipitation, which are absent in the western Himalayas and the Hindu Kush mountains (Hadač, 1970; Meusel & Schubert, 1971; Haserodt, 1989; Schikoff, 1994; Peer *et al.*, 2001). This may be a reason why the floras of Pakistan and Kashmir lack any representatives of these sections.

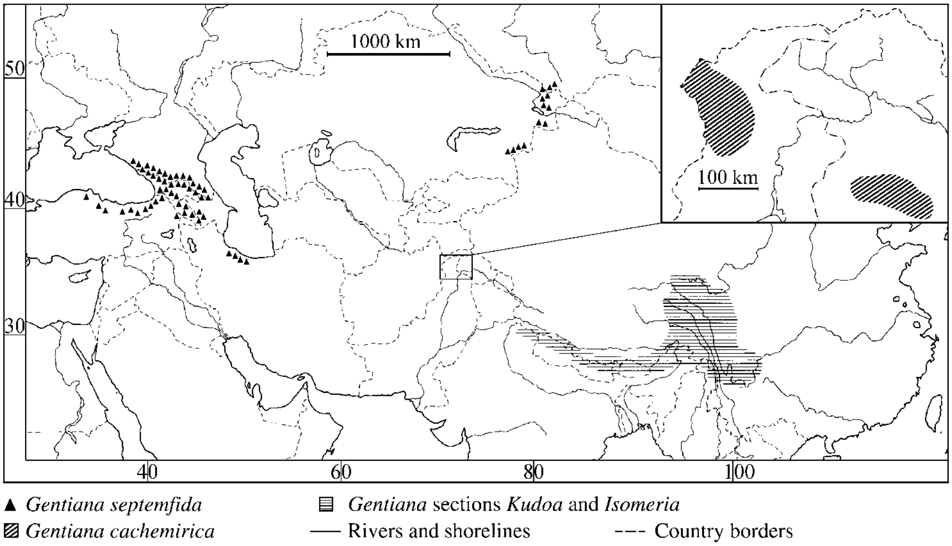

FIG. 5. Distribution of gentians in southwestern Asia.

Representatives of *Gentiana* sect. *Pneumonanthe* occur in Europe, Western Asia, Siberia, the Far East and North America between 0 and 2400 m a.s.l. and have not been recorded from the Central and Eastern Himalayas. *Gentiana cachemirica* does not grow in places of high monsoon rains, but occurs in the southern Hindu Kush and western Himalayas (Fig. 5). This species is confined to a small area belonging to the 'Irano-Turanian floristic region' where the humidity is optimal for its growth (Takhtajan, 1986). *Gentiana septemfida* appears quite near to the distributional range of *G. cachemirica*, in Caucasus, Elburz, Alatau and the Altai mountains. This scattered distribution of *Gentiana septemfida* and *G. cachemirica* suggests the possibility of a former continuous range of an ancestral species throughout Western and Central Asia (including Tien-Shan, Pamir, Hindu Kush, Elburz and Caucasus) during periods of more humid climate.

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APPENDIX 1

Selected specimens examined

Gentiana cachemirica. INDIA. Kashmir, N facing side of valley leading to Mt. Kolahoi's north glacier, on a small cliff in pockets of soil amongst the rock and hanging down, 8 viii 1983, *Chadwell et al.* 446 (E); Kashmir, 8000 ft, vi 1923, *Douie* 34 (K); in the Sind or Lidan valley? [probably Scindr valley common at Sonamany RRS], *Radcliffe* s.n. (K); Plants of N. W. Himalaya, Kashmir Amu, Lidden vy. 8500 ft, ix 1931, *R.R. Stewart* 12919 (K); W Himalaya, 14,000 ft, 14 viii 1999, *J.F. Duthie* 117 (K); Kashmir, near the Razbal Gali Pass above Lrishansar Lake, amongst rocks in crevices, 10 viii 1983, *Chadwell et al.* 441 (E); Kashmir, 11,000 ft, sub erect, growing on rocks, 26 viii 1924, *B.O. Coventry* 922 (K); Kashmir, Mt opp. Pahlgam, 10–11,000 ft, 28 viii 1945, *R.R. Stewart* 21795 (K); Kashmir, Sonamarg, rock crevices, 9000 ft, 19 viii 1922, *R.R. Stewart* 7348 (K); Kashmir, Sonamarg, rock crevices, rare, 9000 ft, 19 viii 1922, *R.R. Stewart* 7203 (K).

PAKISTAN. Chitral, x 1904, *A. Barrett* s.n. (K); Chitral, Lowani Pass, grassy slopes, *Toppin* 595 (K); Dir, Loher top, 5 x 1964, *Salin* s.n. (K); Hazara, Kagan Valley, 14,400 ft, 22 viii 1996, *J.F. Duthie* 19955 (K); Hazara, in rock crevices on open hillsides, 17 ix 1958, *B.L. Burtt & M.A. Kazmi* 1244 (E); Kupwara(?), Shönthar Valley, cliff faces, 19 viii 1935, *F. Ludlow & G. Sherriff* 1515 (E); Swat, Batain above Ushu cliffs, 9000 ft, 27 vii 1953, *R.R. Stewart & A. Rahman* 25312 (K).

Gentiana depressa. CHINA. Tibet, Taliuig, 9000 ft; x [19]24, *C.S. Cutting & A.S. Vernay* 128 (K).

INDIA. Sikkim, Alpine Sikkim, iii 1877, *Comm. Elives* s.n. (K); ibid., 15,000 ft, xi 1880, *J.S. Gamble* 9970 (K).

NEPAL. Gossain Than, 1832, *Wallich* 4387 (K); Flora of Nepal, 12,600 ft, growing in full exposure on heavily grazed land occasionally at edge of thickets of rhododendron and cotoneaster, 12 x 1970, *B. Halliwell* 64 (K); Marsyandi valley, between Pisang and Chame, on grassy scree, 2900 m a.s.l., 29 x 1969, *T. Wraber* 519 (K); Taplejung, Ghunsa, 3300 m below Ghunsa on sandy river bank, rare in this area (only specimen seen), 24 ix 1985, *Curzon* 86 (K); Marpa fields, c.4000 m, 7 ix 1973, *Grey-Wilson & Phillips* 799 (K).

Gentiana gelida. ARMENIA. Aragatson, Aparan distr., dry subalp. meadow with rocks, 2180 m, 24 viii 2005, *E. Vitek et al.* 05-1883 (W); Shirak, Amasia distr., meadow with limestone rocks, 31 viii 2005, *E. Vitek et al.* 05-2214 (W); at lake Arpilich, meadows and shore of lake, 31 viii 2005, *E. Vitek et al.* 05-2184 (W).

GEORGIA. Trialeti, surroundings of Manglisi, edge of oak forest, 1700 m, 31 viii 2001, *Davitashvili* 01-10 (TBI); Algeti reserve, meadow in oak-pine forest, 2000 m, 20 viii 2003, *Davitashvili* 03-21 (TBI); Javakheti, grazed subalpine meadow at Tabatskuri lake, 2200 m, 24 viii 2001, *Davitashvili* 01-07 (TBI).

Gentiana pneumonanthe. AUSTRIA. Nordtirol, Kreckelmoos bei Reutte, 930 m, 2 viii 1974, *Seipka* 088800 (W); Osttirol, Hohe Tauern, Schober Gruppe 9 km SW Defreggerhof, c.1220 m, Feuchtwiese, Quellmoore, 18 viii 1988, *Frendl* 015778 (W).

CZECH REPUBLIC. Bohemia australis in pascuis ad septentriones versus a vico Jindřichovice, 500 m, 3 ix 1972, *Deyl* 344 (W).

POLAND. Polonia centralis regio elata Montes, in prato solo sasulosi argilloso acido, 16 viii 1971, *H. Piękos & M. Ptak* 371 (W).

PORTUGAL. Minho, Esposende nospintialis, em terrenos múmidos, 9 ix 1964, *Bento V. Raintia* 6248 (W).

RUSSIA. Moscow, Distr. Ramenskoe, prope Kratovo, in prato, 1 viii 1976, *Proskuriakova* 81 (W); Rjasan, distr. Solotcza, prope pag Dolginino, in prato humido turfoso, 8 viii 1969, *Dovikov* 5290 (W); Smolensk, near Gnezdilovo, wet places, 1 viii 1971, *Mokarov* 6381 (W).

SLOVAKIA. In pratis siccis prope vicum Skalica, 200 m, 20 vii 1929, *Sellinger* 343 (W).

SWITZERLAND. In pratis humidis, 24 ix 1972, *Dittrich* 157 (W).

Gentiana scabra. CHINA. Kalkhügel in Kisngsu, 1933, *Wissmann* 7677 (W); Prov. Kwangtung, ad orientem urbis schnakwan, viii 1928, *Fenzel* 138 (W); W Hupeh, ix 1929, *Fenzel* 2666 (W); Kuling near Kiukiang, grassy ground on hill top, 29 ix 1929, *H. Chung* 4102 (W); Manchuria chinensis, fluvium Amur, viii 1905, *F. Karo* s.n. (W).

JAPAN. Mt. Kiyosumi, 30 x 1957, *N. Maruyama* 1616 (W); Nikko in Shimotsuko, 29 x 1953, *H. Kubota* 993 (W); Jokohama, *Wawra* 1516 (W); Moraba in Shimosa, 3 xi 1963, *T. Koyana* 833 (W); Jokohama, ix 1862, *Maximovicz* 130 (W).

KOREA. Im herbidis, x 1906, *Fauhiz* 751 (W).

RUSSIA. Primorsk, Inter Talolan et Siaololan, 11 ix 1927, *Kozlow* 14286 (W); Prov. propeurb. Voroschilov, in locus humidis, 23 ix 1905, *Palczevskyi* 3643 (W); Blagowjestschenk im Amurgebiete auf Anhöhen im Gebüsche, viii 1898, *F. Karo* 50 (W); Prov. Amur, Blogovesczensk in pratis silvaticus et substeposis, 4 ix 1904, *F. Karo* 3643 (W).

Gentiana septemfida. ARMENIA. Lori, Stepanavan distr., Pushkin pass, 2028 m, 4 ix 2005, *E. Vitek et al.* 05-2460 (W); Kotayk, Hrazdan distr., 5 km NW of Meghrazdos, 2455 m, 6 ix 2005, *E. Vitek et al.* 05-2586 (W); Shirak, Ashotsk distr., Karakhach pass, 2190 m, 1 ix 2005, *E. Vitek et al.* 05-2346 (W).

GEORGIA. Kartli, Bakuriani, Iagora meadow, wet places, 25 vii 2001, *Davitashvili* 01-01 (TBI); Tskhratskaro pass, subalpine meadow, 2400 m, 15 ix 1997, *Davitashvili* 97-12 (TBI); Kakheti, Lagodekhi reserve, clay rocks near waterfall, 800 m, 5 ix 2003, *Davitashvili* 03-25 (TBI); Lagodekhi reserve, on wet rocky crevices, 900 m, 7 ix 2003, *Davitashvili* 03-27 (TBI); Khevi, Sno valley, subalpine meadow, 2700 m, 10 viii 1993, *Davitashvili* 93-08 (TBI); Racha, Satsalike, meadow with limestone rocks, 2200 m, 9 viii 2001, *Davitashvili* 01-06 (TBI); Svaneti, grazed subalpine meadow near village Hadishi, 12 viii 1991, *Davitashvili* 91-04 (TBI); Samegrelo, Askhi Plateau, Chkhvindjula, limestone rocks, 2200 m, 25 viii 1997, *Davitashvili* 97-08 (TBI); Egrisi ridge, limestone crevices, 1700 m, 11 viii 1991, *Davitashvili* 91-03 (TBI).

IRAN. Wiese bei der Karawanenstation Pelur, 1900 m, 28 viii 1936, *A. Gilli* 1885 (W); Elburz, Gomies Notkaraj, moist mossy sloping banks by a spring, 28 viii 1966, *Southern Zagros Bot. Exp.* A53 (W); Mazanderan, in declibus borealibus jugi Kandavan, 25 viii 1948, *K.H. Rechinger* 6742 (W); Distr. Nur, Kamorband, 2400–2600 m, *K.H. Rechinger* 6395 (W); Kandavan pass, alpine meadow, moist patches, 8 ix 1977, *Breckle* 5355 (W); Ostan, deuxversants du Gol du Kuruk, au dessus de Gach-i-sar, 16 viii 1956, *F. Schmidt* 6479 (W); Tehran: Karaj valley, Assemvarak steep wet slope, 25 viii 1874, *P. Wendelbo* 14479 (W).

TURKEY. Trabson, mont. Kankanli Dağlari in vicinitate pylarum zigana, 2030–2400 m, 30 viii 1993, *V. Vaśák* 09984 (W).

Gentiana stipitata. CHINA. Sikang, between Taining (Ngata) and Taofu (Dawo) in duriprato aprico, c.3800 m, 10 ix 1934, *H. Smith* 12005 (K); Kangting (Tachienlu) distr., Cheto La, 4000–4200 m, 12 x 1934, *H. Smith* 12834 (K); Taofu (Dawo) distr., Kuku La, xii 1934, *H. Smith* 13913 (K); Taofu (Dawo) distr., Taining (Ngata) colles orient., in duriprato aprico, c.3700 m, 9 ix 1934, *H. Smith* 11970 (K); Szechuan, reg. bor-occid. Natang? alp. bor-occid. in prato aprico, c.3500 m, 17 ix 1922, *H. Smith* 4399 (K); Tibet: Tongolo (Principauté de Kiala), 1893, *J.A. Soulié* 2813 (K).

INDIA. Beautiful clumps at Noosoo Bassa, North side of Roofia Pap, 12,000 ft, *Edgeworth* 47 (K); Himalaya, c.13,000 ft, 1844, *Edgeworth* 82 (K); Flora of North Western India, ix 1983, *Duthies* 1186 (K); Tihri – Garhwal, Kidari Naula, near the summit, 7 x 1979, *J.S. Gamble* 1192 (K).

NEPAL. Midway between Jengla and Tarag, c.4700 m, 26 viii 1973, *Grey-Wilson & Phillips* 743 (K).

Gentiana szechenyii. CHINA. Western China, 13,000 ft, 9 iii year unknown, *E.H. Wilson* 4145 (K); Szechuan, reg. bor.-occid. Tsipula in rupileus calcareis, c.4700 m, 26 viii 1922, *H. Smith* 4203 (K); reg. bor.-occid. Natang alp. austr-orient in rupibus, c.4700 m, 13 ix 1922, *H. Smith* 4362 (K); on slopes of Ta-so Shen over 15,000 ft between Batang & Kanze, 1923, *Oeieira*? s.n. (K); Kansu, lower Tebbu country, on clay & conglomerate cliffs below Tsarekika, eastern Minshan, 10,000 ft, 18 ix 1926, *J.F. Rock* 14861 (K); Sikang, Kangting (Tachienlu) distr., Cheto La, in prato alpino ventoso, 4000–4200 m, 12 x 1934, *H. Smith* 12835 (K); Taofu (Dawo) distr., reg. orient., Lhamo Mondeh La, in prato alpino lapidoso, 4300–4500 m, 21 ix 1934, *H. Smith* 12358 (K); between Taining (Ngata) and Maoniu (Ndrömé), Zungkong La, Chinche Dento, in prato alpino, c.4000 m, 29 ix 1934, *H. Smith* 12539 (K).

INDIA. Yulong Shan, Gang Ho Ba Valley, 3200 m, valley floor in very open woodland in poor very fine soil, 4 x 1990, *Chungtien-Lijiang-Dali Expedition* CLD-90 No. 757 (K).

Gentiana urnula. BHUTAN. Mo Chu, S slope of Yale La, 27°47′N, 89°27′E, Dry unstable scree, Med. Ganga chung., c.4780 m, 3 x 1984, *I.W.J. Sinclair & D.G. Long* 5504 (K).

CHINA. Tibet, main Ronhbuk glacier, Moraine, 18,000 ft, 16 v 1938, *Lloyd* 21 (K); Atsa (Pass above monastery), *F. Kingdon Ward* 6149 (K); Mount Everest expedition, Rongbate valley on moraine not common also found on high ?, 17,000 ft, 26 v 1924, *R.W.G. Hingston* 379 (K); near Phari, 14,500 ft, ix 1938, *B.J. Gould* 1634 (K); Pass E. of Jira Valley, 28°14′N, 85°51′E, 5380 m, sparsely vegetated screes, 13 x 1987, *C.M.A. Roberts* 572 (K); Khambajong, ix 1903, *D. Prain* s.n. (K).

NEPAL. Sankwasabha, Barun Khola, Makalu base camp, high rocky mountain slopes, *Grey-Wilson et al.* 4302 (K); Mount Everest expedition, 17,000 ft, viii 1921, *A.F.R. Wollaston* 213 (K); Mount Everest expedition, 17,000–19,000 ft, ix 1921, *A.F.R. Wollaston* 214 (K); Mount Everest expedition, 17,000–19,000 ft, ix 1921, *A.F.R. Wollaston* 204 (K).

Gentiana veitchiorum. BHUTAN. Bapekha, 14,000 ft, 14 viii 1938, *B.J. Gould* 1543A (K).

CHINA. Tibet, Pasum Lake, abundant on alpine turf slopes around Atsa?, 11,000–12,000 ft, 19 viii 1924, *F. Kingdon Ward* 6114 (K); Gyainda, in alpine pastures, 30 viii 1924, *F. Kingdon Ward* 6171 (K); Tsarong, open marshy moorland on the Salwin-Kiu Chiang divide, 28°24′N, 98°24′E, 14–14,500 ft, x 1921, *G. Forrest* 20875 (K).

Appendix 2

Multistate character matrix used for the cluster analysis of Gentiana cachemirica *and possible relatives*

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
G. acaulis	0	1	0	1	1	1	0	1	0	0	1	1	0	0	1	0	0
G. andrewsii	1	0	1	1	0	1	1	1	1	1	1	1	3	3	0	2	1
G. cachemirica	1	0	1	0,1	1	0	1	1	1	1	1	1	1	1	0	2	1
G. clusii	0	1	0	1	1	1	0	1	0	0	1	1	0	0	1	0	0
G. cruciata	1	0	1	0	1	1	1	1	1	1	0	0	0	1	0	1	1
G. depressa	0	1	0	1	1	1	0	0	1	1	1	1	0	2	0	0	0
G. gelida	1	0	1	1	0	0	1	1	1	1	1	1	3	1	0	1	1
G. olivieri	1	0	1	0	1	1	1	1	1	1	0	0	0	1	0	1	1
G. pneumonanthe	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
G. scabra	1	0	1	1	0	1	1	1	1	1	1	1	2	1	1	1	1
G. sceptrum	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
G. septemfida	1	0	1	1	0,1	0	1	1	1	1	1	1	1	1	0	2	1
G. stipitata	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	0	0
G. szechenyii	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	0	0
G. urnula	0	1	0	1	1	2	0	0	1	1	1	1	0	0	0	0	0
G. veitchiorum	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	0	0