Botanical Journal of the Linnean Society, 2006, **152**, 169–195. With 7 figures

Taxonomy and phylogeography of *Cardamine impatiens* and *C. pectinata* (Brassicaceae)

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Received November 2005; accepted for publication March 2006

The taxonomic position of *Cardamine pectinata*, a controversial taxon treated either as infraspecific to *C. impatiens* or as a separate species, was studied. Forty-nine populations were sampled and used in multivariate morphometric and molecular (amplified fragment length polymorphism) analyses. Our results showed that *C. impatiens* and *C. pectinata* represent two well-differentiated taxa in terms of both molecular and morphological data, and should be treated as two separate species. We present the taxonomic conspectus for both species, including the list of synonyms, information on type specimens, morphological descriptions, ecological characteristics, and distribution area. Type specimens for several names are designated here. The detailed geographical distribution of *C. pectinata* is presented based on the survey and revision of herbarium material. It covers the area from the Balkans through Turkey and the Caucasus to Iran. As an introduction to the phylogeography of both species, the distribution of genetic diversity within and between the studied populations and geographical regions was assessed. In *C. pectinata*, the highest genetic diversity was observed in northern Turkey, suggesting the location of glacial refugia along the Black Sea coast. Populations in Bulgaria were less diverse, and this area has most probably been colonized postglacially. *C. impatiens*, on the other hand, did not display clear phylogeographical structure, most probably as a result of the efficient spread and mixing between different colonization routes. © 2006 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2006, **152**, 169–195.

ADDITIONAL KEYWORDS: amplified fragment length polymorphism – Balkan – Caucasus – chromosome numbers – Cruciferae – genetic diversity – glacial refugia – multivariate morphometrics – nomenclature – Turkey.

INTRODUCTION

The genus *Cardamine* L. (Brassicaceae) comprises about 200 species occurring indigenously on all continents except mainland Antarctica (Al-Shehbaz, 1988). Diploid as well as polyploid taxa up to high ploidy levels are represented (reviewed by Lihová & Marhold, 2006). Although several detailed studies have been published on polyploid complexes of *Cardamine* in Europe (*C. pratensis* group: Lövkvist, 1956; Marhold, 1994a; Urbanska *et al.*, 1997; Franzke & Hurka, 2000; Lihová, Marhold & Tribsch, 2003; Lihová, Tribsch & Stuessy, 2004b; *C. amara* group: Lövkvist, 1957; Marhold, 1992, 1995; Lihová, Marhold & Neuffer, 2000; Lihová *et al.*, 2004a; *C. raphanifolia* group: Perný *et al.*, 2005a), less attention has been paid so far to differentiation patterns in diploids. Morphometric and molecular analyses of the Balkan diploid *C. acris* have recently led to the recognition of three subspecies within this area (Perný, Tribsch & Anchev, 2005b). Variation patterns in the diploid populations of the widespread *C. amara* reflect a rather recent isolation and divergence of populations restricted to different European mountain ranges, which are now classified as subspecies (Lihová *et al.*, 2000, 2004a; Marhold, Huthmann & Hurka, 2002). On the other hand, ongoing studies on other groups of diploid taxa, the Italian–Balkan *C. maritima* (J. Kučera, J. Lihová & K. Marhold, unpubl. data) and *C. glauca* (Lakušić *et al.*, 2006), indicate much more pronounced diversification in terms of both morphology and molecular markers than revealed in the above-mentioned taxa and species groups.

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Cardamine impatiens L. is a diploid species with a wide distribution in Eurasia (Jalas & Suominen, 1994), reported as introduced also from North America (Seymour, 1969; Rollins, 1993) and southern Africa (Dreyer & Jordaan, 2000). Although several infraspecific taxa have been described in the past within this species, most of them appear currently only in synonymy. The sole exception is the taxon originally described as *C. pectinata* Pall. ex DC. by Candolle (1821: 264) based on the material collected by Pallas in Persia (today Iran). Apart from Iran (Hedge, 1968), it is also reported from the Caucasus, Turkey, and the Balkan Peninsula (Stoyanov & Stefanov, 1948; Grossgeim, 1950; Cullen, 1965; Assenov, 1970; Ketskhoveli, 1979; Kit Tan, 2002). The taxonomic status of this taxon, however, has remained controversial. It has been treated either as a separate species (by Grossgeim, 1950; Assenov, 1970; Ketskhoveli, 1979), or as a subspecies (by Stoyanov & Stefanov, 1948; Jones & Akeroyd, 1993) or variety (by Trautvetter, 1876; Zohary, Heyn & Heller, 1980) of *C. impatiens*. Cullen (1965: 443), treating this taxon at the varietal rank, argued that 'intermediates between the two varieties [var. *impatiens* and var. *pectinata*] are of frequent occurrence'. This opinion has been shared also by Kit Tan (2002: 184) and Khatri (1988), although the latter author treated *C. pectinata* at the species level. Other authors (e.g. Assenov, 1970) have no doubt that this should be a clearly separated species.

Although *C. impatiens* exhibits a wide distribution across Eurasia, the area of the present occurrence of *C. pectinata* is regarded to be restricted to the Balkan Peninsula, Turkey, Iran, and lower altitudes of the Caucasus (see references above). These areas are known to harbour considerable taxonomic and genetic diversity that can be attributed to processes associated with Pleistocene glaciations. Palaeobotanical and phylogeographical studies have shown that the southern peninsulas of Iberia, Apennines, Balkans, and the Caspian/Caucasus region served as refugia, in which many European temperate species survived unfavourable climatic conditions during the glacial periods (Hewitt, 2004). Repeated cycles of area contraction and expansion, as well as altitudinal shifts in southern mountain ranges, allowed considerable genetic diversity to be retained in these regions, in contrast with the genetic impoverishment often observed in more northern areas (Hewitt, 2002, 2004). Several continental-scale phylogeographies documenting these processes have been published in recent years, addressing mainly tree species (e.g. King & Ferris, 1998; Fineschi *et al.*, 2002; Hampe *et al.*, 2003; Heuertz *et al.*, 2004). A few phylogeographical studies also covered or at least marginally included the easternmost putative refugial areas in Turkey and the Caspian/Caucasus region (King & Ferris, 1998; Hampe *et al.*, 2003; Marcussen, 2003; Albach, Martínez-Ortega & Chase, 2004). Reconstructions of the vegetation in the last glacial maximum have documented the occurrence of broad-leaved deciduous and mixed forests in the area along the Black Sea coast of Turkey and Georgia (Adams, 1997). This region, characterized by many Tertiary and Quaternary relic species (Denk, Frotzler & Davitashvilli, 2001), may have provided favourable habitats for the survival of several temperate herbaceous species, including the *Cardamine* taxa studied here.

Two main questions are addressed in this study. First, we aimed to resolve the taxonomic position of populations assigned to *C. pectinata* in respect of the widespread *C. impatiens*. Detailed morphometric and molecular (amplified fragment length polymorphism, AFLP) analyses have been carried out, together with the survey of herbarium records from the sympatric regions. Second, as an introduction to the phylogeography of both species, the distribution of genetic diversity in the studied populations and geographical regions was assessed using AFLP data.

MATERIAL AND METHODS

Plant material

Population sampling was focused on the area with the reported occurrence of both taxa, *C. impatiens* and *C. pectinata*, i.e. the Balkan Peninsula, northern Turkey, and the Caucasus region. *C. impatiens* was also sampled from numerous populations in more distant parts of its distribution range (central and southern Europe, Japan) to cover the area without the occurrence of *C. pectinata* (Table 1, Fig. 1). For morphometric analyses, herbarium specimens of a total of 565 individuals originating from 26 populations were used (6–34 plants per population). These were collected in the sympatric area of the two taxa. Material for AFLP analyses (silica gel-dried leaves) was represented by 82 samples from 24 localities also sampled for morphometric studies, and 65 samples from an additional 23 populations collected mainly in more remote geographical areas (Table 1). For chromosome counts, seeds originating from 15 localities were used. These were either collected directly in the field or from plants collected at the localities and transplanted in the experimental field in Bratislava, Slovak Republic.

Details on the origins of the plant material are given in Table 1. Voucher specimens are deposited in the herbarium SAV.

To present a detailed view on the distribution of plants corresponding to *C. impatiens* and *C. pectinata*, especially in the area of their sympatric occurrence, herbarium material from the following herbaria was revised: B, BM, G, GH, K, KW, LE, LEU, P, PR, PRC,

Table 1. List of populations of *Cardamine impatiens* and *C. pectinata* used in karyological (2*n*), morphometric (Morph) and amplified fragment length polymorphism (AFLP) analyses (–, not used in the particular analysis). Data on chromosome numbers represent new reports. Note that chromosome numbers were counted also from two Korean populations of *C. impatiens*, not used in morphological or AFLP analyses. Voucher specimens are deposited in SAV. Collectors: *HK*, H. Kato; *HKu*, H. Kudoh; *JK*, J. Kučera; *JL*, J. Lihová; *KM*, K. Marhold; *MK*, M. Kolník; *MO*, M. Onette; *MS*, M. Slovák; *SK*, S. Kato; *SS*, S. Stoyanov; *VGO*, V. G. Onipchenko

Population code, origin and collection data	2*n*	Morph. no. ind.	AFLP no. ind.
Cardamine impatiens L.			
I-Bu-1 – Bulgaria, Plana Mts., near village Dolny Pasarel, valley of Iskar river 42°32′35″N, 23°29′02″E, 660 m, 1.vi.2003, *JK & SS*	16	30	1
I-Bu-2 – Bulgaria, Plana Mts., near lake Pasarel, under Mt. Asanitsa, 43°32′59″N, 23°28′17″E, 710 m, 1.vi.2003, *JK & SS*	–	30	3
I-Bu-3 – Bulgaria, Stara planina Mts., near village Kalofer, along the river Tundya, 42°37′31″N, 24°58′00″E, 680 m, 2.vi.2003, *JK & SS*	–	7	3
I-Bu-4 – Bulgaria, Stara planina Mts., Kalofer, Panitsite, 42°39′25″N, 24°58′51″E, 740 m, 2.vi.2003, *JK & SS*	–	24	3
I-Bu-5 – Bulgaria, Vasiliovska planina Mts., *c.* 3 km W of Bogoya (saddle), stream Kozidol, 42°51′39″N, 24°28′43″E, 910 m, 4.vi.2003, *JK & SS*	–	30	1
I-Bu-6 – Bulgaria, between Vasiliovska planina Mts. and Tetevensky Balkan Mts., *c.* 5 km S of village Ribaritsa, near spring Borisova cheshma, valley of Debelovitsa river, 42°50′54″N, 24°26′45″E, 780 m, 4.vi.2003, *JK & SS*	–	8	2
I-Bu-7 – Bulgaria, Tetevenska planina Mts., valley of Vidima river, near village Ribaritsa, 42°45′05″N, 24°54′20″E, 1010 m, 5.vi.2003, *JK & SS*	16	29	3
I-Bu-8 – Bulgaria, Tetevenska planina Mts., valley of Zavodna river, along the road from Ribaritsa to cottage Vezhen, *c.* 2 km S of Ribaritsa village, 42°48′48″N, 24°22′17″E, 760 m, 5.vi.2003, *JK & SS*	16	25	3
I-Bu-9 – Bulgaria, Tetevenska planina Mts., under the cottage Vezhen, near the tourist path from valley of Zavodna river, 42°45′35″N, 24°23′45″E, *c.* 1300 m, 5.vi.2003, *JK & SS*	16	12	3
I-Bu-10 – Bulgaria, Stara planina Mts., spring near the tourist path from Kalofer to cottage Rai, under cottage Rai, 42°37′00″N, 24°58′59″E, 2.vi. 2003, *JK & SS*	–	–	3
I-Bu-11 – Bulgaria, Zap. Rhodopi Mts., near the Yundol village, 42°06′17″N, 23°54′02″E, 1120 m, 4.vi.2004, *JK & MK*	16	–	3
I-Tu-12 – Turkey, Trabzon prov., Kalkanli Dağlari Mts., near tunnel Zigana Dag, 40°40′36″N, 39°25′56″E, 1580 m, 26.v.2004, *JK & MK*	–	–	3
I-Tu-13 – Turkey, Giresum prov., Giresum Dağlari Mts., Güdül, 40°38′43″N, 38°27′21″E, 880 m, 29.v.2004, *JK & MK*	–	–	3
I-Ge-14 – Georgia, Lesser Caucasus Mts., Bakuriani, in the forest near the WWF Education Centre, 41°45′19″N, 43°31′15″E, 2.vii.2001, *KM*	–	21	5
I-Ge-15 – Georgia, Greater Caucasus Mts., Khevi prov., N of Kazbegi, Dariali canyon, Gveleti, along the Tergi (Terek) river, near the road Tbilisi-Vladikavkaz, 42°42′21″N, 44°37′48″E, 1470 m, 7.vii.2001, *KM*	–	10	4
I-Ru-16 – Russia, Karachay-Cherkessia, Greater Caucasus Mts., Dambai, near first station of cable car, 43°16′43″N, 41°38′09″E, 1750 m, 2.viii. 2004, *JK*	–	–	3
I-Ru-17 – Russia, Karachay-Cherkessia, Greater Caucasus Mts., Teberda village, Teberdinskii zapovednik, near Teberda river, 43°26′17″N, 41°44′08″E, 1320 m, 3.viii.2004, *JK & VGO*	16	–	3
I-Ro-18 – Romania, Bucegi Mts., near the lake Lacul Bolboci, 45°21′15″N, 25°25′15″E, 1460 m, 9.vii.2003, *JK*, *MK & MO*	–	22	–
I-Ro-19 – Romania, Bucegi Mts., Cheile Zanoagei Mari canyon, 45°19′42″N, 25°25′16″E, 1320 m, 9.vii.2003, *JK*, *MK & MO*	–	6	3
I-Ro-20 – Romania, Bucegi Mts., Busteni, Gura Dihamului, valley of Valea Seaca stream, 45°26′35″N, 25°31′09″E, 990 m, 9.vii.2003, *JK*	–	8	–
I-Ro-21 – Romania, Cozia Mts., 45°18′10″N, 24°20′12″E, 720 m, 11.vii.2003, *JK & MK*	–	–	3
I-Ro-22 – Romania, Bistriţa, Arcalia, 47°04′36″N, 24°21′00″E, 21.v.2003, *MK*	–	–	2
I-Ro-23 – Romania, Turda, Cheile Thurzii, 46°33′45″N, 23°40′45″E, 7.vii.2003, *JK & MK*	–	–	1
I-Cr-24 – Croatia, Velebit Mts., Oštarje, 44°31′45″N, 15°11′16″E, 960 m, 18.vii.2003, *JK & MK*	–	–	3

Table 1. *Continued*

Population code, origin and collection data	$2n$	Morph. no. ind.	AFLP no. ind.
I-Se-25 – Serbia, Vrhpolje, 44°16′05″N, 19°26′05″E, 180 m, 22.v.2004, *JK & MK*	–	–	3
I-It-26 – Italy, Umbria prov., Terni, Marmore Waterfalls, 42°32′37″N, 12°42′58″E, 7.v.2003, *JK & MK*	–	–	5
I-It-27 – Italy, Piemont prov., W of Torino, San Francesco su Avigliana, 45°4′22″N, 7°21′37.4″E, 620 m, 14.v. 2002, *JL & KM*	–	–	2
I-It-28 – Italy, Trentino prov., Val di Breguzzo, 46°02′50″N, 10°37′25″E, 8.vi.2003, *JL, KM & MS*	–	–	3
I-Sw-29 – Switzerland, val di Poschiavo, NE of Brusio, 46°15,903N, 10°07.505E, 910 m, 9.vi.2003, *JL, KM & MS*	–	–	3
I-Sp-30 – Spain, Lérida prov., central Pyrenees, Val d'Aran, W of Vielha, Sarrat de Sepeguilha, along the road from Casau to Refugi Eth Santet, 42°42′00″N, 0°46′30″E, 1580 m, 22.vi. 2002, *JL*	–	–	2
I-Sk-31 – Slovakia, Belianske Tatry Mts., near Belianska jaskyňa cave, 49°13′37″N, 20°18′55″E, 15.viii.2003, *KM, JL & HKu*	–	–	3
I-Sk-32 – Slovakia, Slovenský kras Mts., near village Jasov, 48°40′57″N, 20°58′24″E, 27.v.2003, *MK*	–	–	3
I-Sk-33 – Slovakia, Malé Karpaty Mts., Borinka village, Medené Hámre, 48°15′14″N, 17°07′15″E, 10.v.2004, *JK*	–	–	3
I-Sk-34 – Slovakia, Muránska planina Mts., near village of Muráň, 48°43′29″N, 20°01′10″E, 18.vi.2003, MK	–	–	3
I-Ja-35 – Japan, Nagano Pref., Minami Azumi Co., Azumi village, Shimashima-dani, 36°11.797 N, 137°46.151E, 740–820 m, 18.iv.2002, *JL, KM, HK & SK*	–	–	1
I-Ja-36 – Japan, Miyazaki Pref., Higasi usuki-gun, Shiiba-son, Nakasuiryu, on route along Kiunadani Valley, 32°07′05″N, 131°09′13″E, 660 m, 14.vi.2004, *KM & HKu*	–	–	3
South Korea, Gangwon-do, Inje-gun, Buk-myeon, Mt. Myungdang, 38°10′18″N, 128°15′40″E, 400 m, vi.2005, *KM, JL, HKu et al*.	16	–	–
South Korea, Gangwon-do, Pyeongchang-gun, Yongpyeong-myeon, Nodong-ri, Mt. Gyebang, 37°42′19″N, 128°29′07″E, 840 m, 14. vi.2005, *KM, JL, HKu et al.*	16	–	–
Cardamine pectinata Pall. ex DC.			
P-Bu-1 – Bulgaria, Tetevenska planina Mts., valley of Zavodna river, 42°49′21″N, 24°22′48″E, *c*. 850 m, 5.vi.2003, *JK & SS*	16	30	3
P-Bu-2 – Bulgaria, Tetevenska planina Mts., Tsarishina nature reserve, near the cottage Vezhen, 42°46′29″N, 24°23′08″E, 1560 m, 5.vi.2003, *JK & SS*	16	30	5
P-Bu-3 – Bulgaria, Pirin Mts., valley of Demyanitsa river, near waterfall Yulenski skok, 41°46′42″N, 23°27′44″E, 1550 m, 7.vi.2003, *JK & SS*	16	34	5
P-Bu-4 – Bulgaria, Pirin Mts., near cottage Banderitsa, 41°46′07″N, 23°25′36″E, 1810 m, 9.vi.2003, *JK & SS*	–	30	3
P-Bu-5 – Bulgaria, Zap. Rhodopi Mts., Batashka planina, Batak, 41°54′20″N, 24°10′29″E, 1460 m, 3.vi.2004, *JK & MK*	–	30	1
P-Bu-6 – Bulgaria, Zap. Rhodopi Mts., Yundol, 42°06′17″N, 23°54′02″E, 1120 m, 4.vi.2004, *JK & MK*	16	13	2
P-Tu-7 – Turkey, Trabzon prov., Kalkanli Dağlari Mts., near tunnel Zigana Dag, 40°40′36″N, 39°25′56″E, 1580 m, 26.v.2004, *JK & MK*	–	25	5
P-Tu-8 – Turkey, Rize prov., Dog Karadeniz Dağlari Mts., Camlik, 40°42′36″N, 40°37′55″E, 1280 m, 28.v.2004, *JK & MK*	16	28	4
P-Tu-9 – Turkey, Rize prov., Dog Karadeniz Dağlari Mts., Ikizdere–Cimil, 40°46′08″N, 40°34′08″E, 510 m, 28.v.2004, *JK & MK*	16	29	5
P-Tu-10 – Turkey, Giresum prov., Giresum Dağlari Mts., Kümbet, 40°33′37″N, 38°24′32″E, 1510 m, 29.v.2004, *JK & MK*	–	29	3
P-Tu-11 – Turkey, Artvin prov., Balikli Dağlari Mts., Hopa–Scuruca Geç., 41°23′46″N, 41°31′55″N, 690 m, 30.v.2004, *JK & MK*	–	7	5
P-Tu-12 – Turkey, Kastamonu prov., Ilgaz Dağlari Mts., 41°04′09″N, 33°44′53″E, 1860 m, 2.vi.2004, *JK & MK*	16	–	4
P-Ge-13 – Georgia, Lesser Caucasus Mts., Bakuriani, in the forest near the WWF Education Centre, 41°45′19″N, 43°31′15″E, 2.vii.2001, *KM*	–	18	7

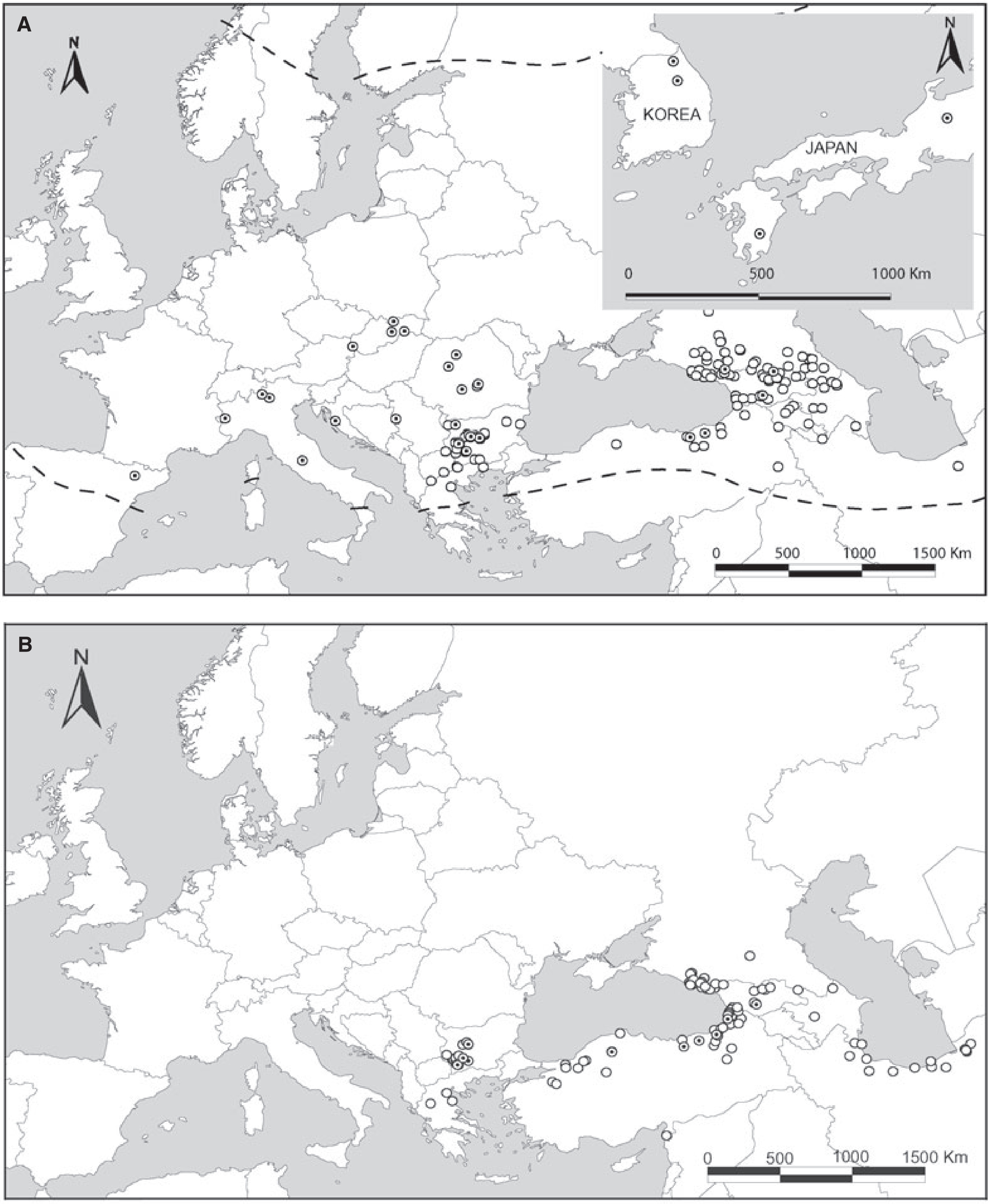

Figure 1. Distribution map of *Cardamine impatiens* (A) and *C. pectinata* (B), showing our collection sites (circles with dots) and herbarium records (empty circles; 165 records of *C. impatiens* and 163 records of *C. pectinata* from 15 herbaria). Total distribution range of *C. impatiens* is indicated by dashed lines and extends further to Asia; herbarium records shown are only from the area of sympatry with *C. pectinata*. Herbarium records of *C. pectinata* marked on the map represent the whole distribution range of this taxon.

SAV, SO, SOM, W, WU (herbarium acronyms follow Holmgren, Holmgren & Barnett, 1990).

KARYOLOGICAL ANALYSES

Chromosome numbers were determined from mitotic metaphases of cells from root tips taken from germinating seeds. The root tips were pretreated with 0.002 M hydroxyquinoline for 5 h. They were fixed in a freshly prepared mixture of concentrated ethanol and acetic acid (1 : 1) and hydrolysed in a mixture of concentrated hydrochloric acid and ethanol (1 : 1) for 1–2 min. Squashes were made in a drop of 45% acetic acid under a cellophane square (Murín, 1960), and stained in a 10% solution of Giemsa stock solution in Sörensen phosphate buffer for 1 h.

MORPHOMETRIC ANALYSES

Nine quantitative vegetative characters and five floral characters were measured on the collected plants and three ratio characters were derived (see Table 2). The characters included in the morphometric analysis corresponded to those usually used for the delimitation of *C. pectinata* and its discrimination from *C. impatiens* (Stoyanov & Stefanov, 1948; Cullen, 1965; Khatri, 1988; Jones & Akeroyd, 1993), as well as others that appeared to be variable in the populations sampled in the field. Floral characters were measured on one randomly selected flower per plant. Fresh floral parts were attached to adhesive tape, dried, and scanned on a Microtek ScanMaker 9800XL. Maximum values for each floral character were measured and recorded in the computer program CARNOY (Schols *et al.*, 2002).

We performed both hierarchical and nonhierarchical multivariate morphometric evaluation of the measured data. Hierarchical UPGMA (unweighted pair-group method using arithmetic averages) (Everitt, 1986) cluster analysis was based on populations characterized by average values of the measured characters. The characters in the primary matrix were standardized by zero mean and unit standard deviation, and a Euclidean coefficient was used to compute the secondary distance matrix. Principal component analysis (PCA) (Sneath & Sokal, 1973; Krzanowski, 1990), based on individual plants and the correlation matrix between the characters, was performed to reduce the multidimensionality of the original character space and to display the variation pattern along the first three components extracting most of the variation. To test the results from the cluster analysis based on populations, canonical discriminant analysis (CDA) and classificatory discriminant analysis (nonparametric classificatory discriminant analysis) (Klecka, 1980) based on individual plants were computed. Two groups resolved by UPGMA (see ‘Results’) and corresponding to *C. impatiens* and *C. pectinata* were defined. In CDA, a discriminant function was derived to maximize between-group variation, and a histogram showing the extent of group separation was produced. To

Table 2. Eigenvectors of principal component analysis (Prin 1, Prin 2, and Prin 3) based on individuals of *Cardamine impatiens* and *C. pectinata*, expressing correlation of the examined characters with the principal components (see Fig. 3); total canonical structure (Can 1; correlation coefficients of the characters and canonical axis) of canonical discriminant analysis based on individuals of *C. impatiens* and *C. pectinata* (see Fig. 4)

Morphological character	Prin 1	Prin 2	Prin 3	Can 1
Length of sepals (mm)	0.728	0.255	–0.146	0.668
Width of sepals (mm)	0.538	0.211	–0.165	0.435
Length of petals (mm)	0.911	0.016	–0.151	0.900
Width of petals (mm)	0.904	0.118	–0.063	0.876
Length of filaments (mm)	0.736	–0.038	–0.321	0.674
Height of stem from base to the lowest peduncle of flower or fruit (cm)	–0.732	0.365	–0.305	–0.713
Number of stems (except the main stem)	0.240	0.085	–0.222	0.234
Number of lateral inflorescences	–0.269	0.385	–0.566	–0.189
Number of stem leaves	–0.864	0.162	–0.310	–0.877
Number of leaflets of the middle stem leaf	–0.856	0.103	–0.309	–0.881
Length of terminal leaflet of the middle stem leaf (LTL) (cm)	0.186	0.892	0.211	0.281
Width of terminal leaflet of the middle stem leaf (WTL) (cm)	0.276	0.871	0.116	0.335
Ratio LTL/WTL	–0.418	0.443	0.545	–0.390
Length of lowermost lateral leaflet of the middle stem leaf (LLL) (cm)	–0.016	0.935	–0.140	0.052
Width of lowermost lateral leaflet of the middle stem leaf (WLL) (cm)	0.216	0.887	–0.018	0.265
Ratio LLL/WLL	–0.678	0.310	0.391	–0.666
Ratio LTL/LLL	0.320	–0.008	0.609	0.363

reveal the correlations of characters with the canonical axis, the total canonical structure was computed. The classificatory discriminant analysis was used to assess the percentage of plants correctly assigned to the predetermined groups. The cross-validation procedure was used, in which the classification criterion is based on $N - 1$ individuals, and then applied for the individual left out.

In addition, mean values, standard deviations, and percentiles were computed for all characters (exploratory data analysis). Cluster analysis was performed using SYN-TAX 2000 (Podani, 2001). For other analyses, the SAS statistical package (SAS Institute, 2000) was used.

AFLP FINGERPRINTING

Genomic DNA was extracted from silica gel-dried leaves using a modified cetyltrimethylammonium bromide (CTAB) procedure (Doyle & Doyle, 1987) according to Schönswetter *et al*. (2002). The quality of the isolated genomic DNA was checked on agarose gels, and the amount of DNA was estimated photometrically (UV-160A, Shimadzu). The AFLP procedure (Vos *et al*., 1995) followed the general protocol (Applied Biosystems, 1996) with minor modifications (see Schönswetter *et al*., 2004). The genomic DNA was restricted with *Mse*I and *Eco*RI restriction endonucleases, and two double-stranded adaptors were ligated at 37 °C for 2 h. The product was diluted in $TE_{0.1}$ buffer (10 mM Tris, 0.1 mM EDTA). Amplifications were performed in two steps using a GeneAmp PCR System 9700 thermal cycler (Applied Biosystems). Preselective amplification using two primers with 1-base pair (bp) extensions at the 3′ end was performed with the following cycle profile: initial hold at 72 °C for 2 min; 20 cycles at 94 °C for 1 s, 56 °C for 30 s, and 72 °C for 2 min; last hold at 60 °C for 30 min and cooling to 4 °C. The products of preselective amplifications were checked on agarose gels and diluted in $TE_{0.1}$ buffer. Three primer combinations giving clear and reproducible bands, applied in previous *Cardamine* studies (see, for example, Lihová *et al*., 2004b), were used for selective amplifications: *Eco*RI-AAG-(HEX), *Eco*RI-ATC-(6-FAM), *Eco*RI-AGC-(NED), *Mse*I-CTG, *Mse*I-CAG, and *Mse*I-CTG (VBC Genomics, Vienna, Austria). The polymerase chain reaction (PCR) cycle profile was as follows: initial cycle at 94 °C for 2 min, 65 °C for 30 s, and 72 °C for 2 min; eight cycles at 94 °C for 1 s, 64 °C for 30 s (decreasing by 1 °C in each cycle from 64 °C to 57 °C), and 72 °C for 2 min; 23 cycles at 94 °C for 1 s, 56 °C for 30 s, and 72 °C for 2 min; and the last hold at 60 °C for 30 min and cooling to 4 °C. The AFLP fragments were loaded onto 4.5% polyacrylamide gels with an internal size standard GeneScan 500 ROX (Applied Biosystems), and electrophoresed on an automated sequencer (ABI 377). Raw data were analysed by GeneScan (Applied Biosystems) and then by GenoGrapher program (version 1.6.0, ©Montana State University, 1999; http://hordeum.msu.montana.edu/genographer/). The presence or absence of AFLP fragments was scored for each sample (only well-scorable and unambiguous fragments were analysed) and transferred into a binary matrix.

AFLP DATA ANALYSES

Genetic variation was analysed from both a taxonomic and phylogeographical perspective.

1. First, principal coordinate analysis (PCoA) and neighbour-joining (NJ) analysis were performed on the entire dataset of 147 samples to obtain the general view on the AFLP variation pattern, particularly to address the genetic differentiation between populations morphologically assigned to *C. impatiens* and *C. pectinata*. For PCoA, the secondary matrix was computed using Jaccard's coefficient, and the analysis was performed by SYN-TAX 2000 (Podani, 2001). NJ analysis was carried out using Nei & Li's (1979) genetic distance in the PAUP* program (version 4.0b10; Swofford, 2003), with the bootstrap option of 5000 replicates. Three accessions of *C. lazica* Boiss. were used to root the tree.
2. To document the genetic divergence between the two taxa, we additionally calculated the total number of fragments per taxon, the number of polymorphic fragments, the number of private fixed fragments (those restricted to the taxon and present in all of its individuals), and the number of private fragments (those restricted to the taxon but not necessarily present in all of its individuals).
3. The geographical structure of genetic variation was explored by analyses of molecular variance (AMOVAs) using ARLEQUIN (version 2.000; Schneider, Roessli & Excoffier, 2000). The original binary matrix was divided into two matrices of *C. impatiens* and *C. pectinata*, respectively, and the AMOVAs were run separately for each of these two taxa. Euclidean distances were computed between all pairs of AFLP phenotypes to produce distance matrices. Total genetic variation was partitioned into the following hierarchical levels: between individuals within populations, between populations, and between regions. Different groupings of populations were tested following those suggested by PCoA and NJ analysis, or by phytogeographical areas. One thousand permutations were run to obtain test statistics.
4. Finally, to estimate the genetic diversity within populations and geographical regions, the following diversity measures were calculated using POP-

GENE 1.32 (Yeh *et al.*, 1997): the total number of AFLP fragments in a population/region (f_{pop}), the mean number of AFLP fragments per individual in a population (f_{ind}), the number and percentage of polymorphic fragments ($\%P_{\mathrm{pop}}$), the number of rare (f_{r}; fragments present in less than 10% of the investigated individuals belonging to the taxon), private (f_{pr}), and private fixed ($f_{\mathrm{pr\text{-}f}}$) fragments, and Shannon's diversity index $H_{\mathrm{Sh}} = -\Sigma(p_i \ln p_i)$, where p_i is the relative frequency of the ith fragment (Legendre & Legendre, 1998). As the numbers of individuals per population analysed for AFLPs were not equal, but ranged from one to nine individuals, these diversity measures were calculated on reduced datasets that included three (the most common number) or, exceptionally, two individuals (in cases in which only two individuals were sampled) per population. From populations in which more individuals were sampled, three individuals were randomly selected.

RESULTS

CHROMOSOME NUMBERS

Chromosome numbers were counted in eight populations of *C. impatiens* and seven populations of *C. pectinata*. The diploid chromosome number $2n = 16$ was determined in all cases (Table 1).

MORPHOMETRIC ANALYSES

UPGMA cluster analysis based on 17 morphological characters resulted in a dendrogram with two main clusters corresponding to populations traditionally understood as *C. impatiens* and *C. pectinata*, respectively (Fig. 2). Further clustering in *C. pectinata* reflected the geographical origin of the analysed populations (Balkan and Turkey/Caucasus region), whereas clustering within *C. impatiens* did not show any pattern. The ordination diagram of PCA based on individual plants (Fig. 3) showed two compact groupings separated along the first axis, in accordance with the results of cluster analyses. Only a minute overlap represented by few plants was present. The following characters were strongly correlated with the first component axis (in descending order): length of petals, width of petals, number of stem leaves, number of leaflets of the middle stem leaf, length of filaments, height of stem, and length of sepals (Table 2). No further groupings were apparent along the second or third axes, although there was some variation within both groups, especially in *C. impatiens*.

The histogram of CDA (Fig. 4), based on individual plants and two groups as defined by cluster analysis, showed a clear separation between the populations corresponding to *C. impatiens* and *C. pectinata*. The characters highly correlated with the canonical axis were the same as revealed in PCA (Table 2). It is

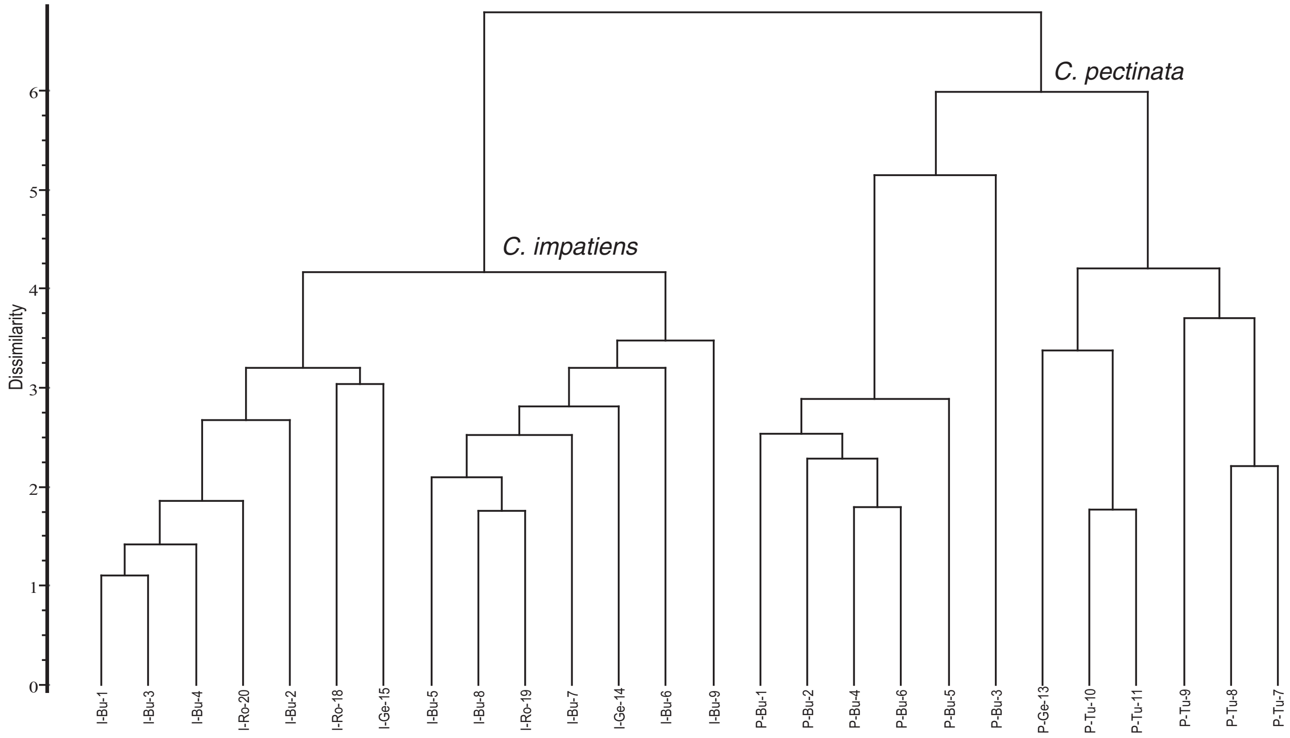

Figure 2. Cluster analysis (unweighted pair-group method using arithmetic averages, UPGMA) of populations of *Cardamine impatiens* (I) and *C. pectinata* (P) based on 17 morphological characters.

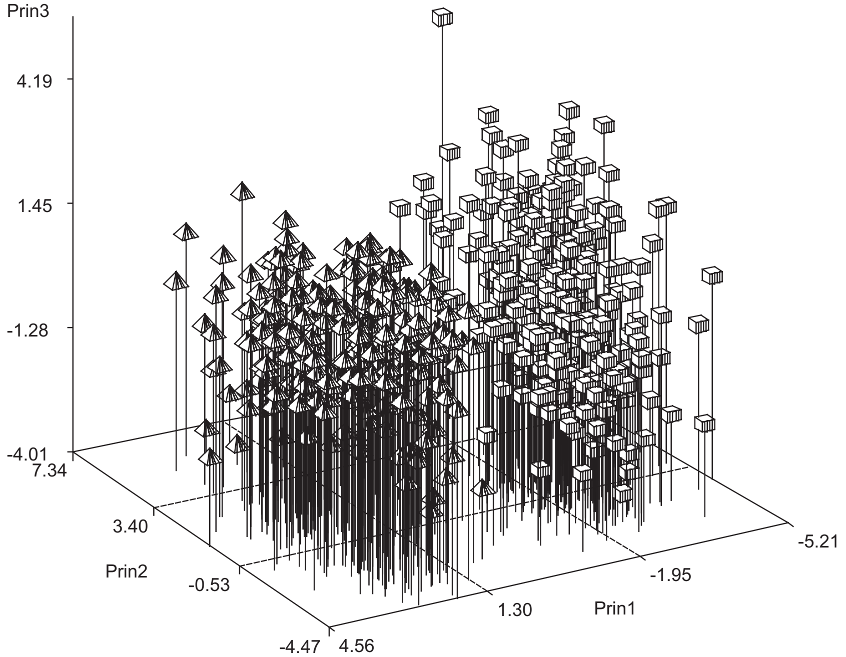

Figure 3. Principal component analysis of individuals of *Cardamine impatiens* (cubes) and *C. pectinata* (pyramids) based on 17 morphological characters (see Table 2). The first three axes explain 35.57, 23.29, and 10.18% of the total variation, respectively.

apparent that there are no (or only very few) plant individuals that can be considered as morphologically intermediate between *C. impatiens* and *C. pectinata*. Accordingly, in the classificatory discriminant analysis, percentages of correctly classified individuals were 100%, without any misclassified individuals.

The results of exploratory data analysis of *C. impatiens* and *C. pectinata* (Fig. 5) showed that these two taxa differed in several characters, with an overlap only in extreme values of a few individuals. Again, the length of petals, width of petals, number of stem leaves, number of leaflets of the middle stem leaf, length of filaments, height of stem, length of sepals, and the ratio LLL/WLL (length of lowermost lateral leaflet of the middle stem leaf/width of lowermost lateral leaflet of the middle stem leaf) were the characters best differentiating between these two taxa.

AFLP ANALYSES

PCoA based on AFLP data resulted in two groupings placed on opposite sides of the first axis (figure not shown), corresponding to *C. impatiens* and *C. pectinata,* respectively. The pronounced genetic differentiation was also apparent from the NJ tree, where two main clusters of *C. impatiens* and *C. pectinata* with high bootstrap values were resolved (Fig. 6). Of the 214 fragments scored in 147 individuals (excluding *C. lazica* used to root the tree), 198 (93%) were polymorphic. In *C. impatiens*, 153 fragments were resolved: 130 (85%) were polymorphic, 88 were private, and seven were private fixed. In *C. pectinata*, 119 fragments were found: 95 (80%) were polymorphic, 53 were private, and eight were private fixed.

Apart from the clear taxonomic structure, resolving *C. impatiens* and *C. pectinata* as two genetically differentiated entities, the NJ tree suggested further geographical patterns within both taxa. Two main clusters in *C. pectinata* corresponded to populations from: (1) the Balkan Peninsula and western and central Turkey; and (2) eastern Turkey and the Caucasus; however, the clusters received very low bootstrap support. Within both clusters, further clustering again reflected the geographical origin of the accessions. Similarly, three main clusters were apparent within *C. impatiens*: (1) Japan; (2) eastern group of Turkey and Caucasus; and (3) western group of the Balkan Peninsula and other parts of Europe (Fig. 6).

Several three-level AMOVAs were performed to assess partitioning of the overall genetic variation and to test the suggested geographical structure within AFLP data (Table 3). Two to five geographical groupings were suggested for both taxa to compare the between-region variance. In *C. impatiens*, about 20–26% of the total variation was accounted for by variation within populations, and 30–38% by variation between populations. By partitioning populations into

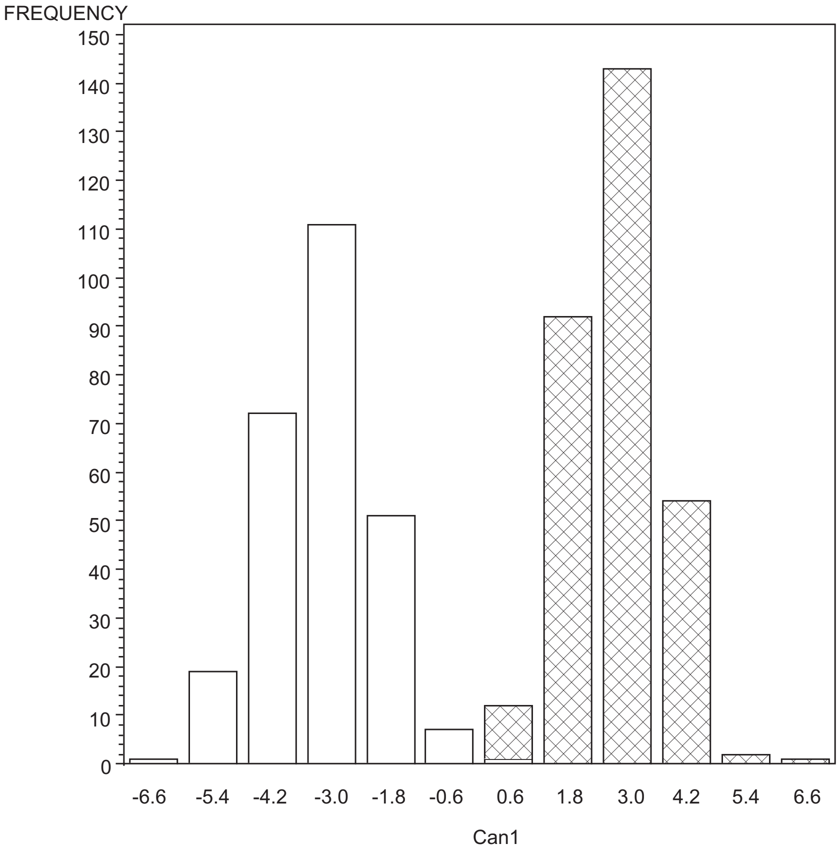

Figure 4. Canonical discriminant analysis of individuals of *Cardamine impatiens* (white) and *C. pectinata* (cross-hatched) based on 17 morphological characters (see Table 2).

two main geographical groups, the western and eastern groups (Japanese accessions were excluded from AMOVA), almost 50% of the overall genetic variation was attributed to the differentiation between these two areas. By partitioning the populations into smaller groups, the geographical resolution was always weaker (Table 3). In *C. pectinata*, the highest between-region differentiation was achieved when considering three geographical groups (Balkan Peninsula, central Turkey, eastern Turkey together with the Caucasus), representing almost 61% of the total variation. This value decreased slightly (to 58%) when two groups were considered: eastern Turkey together with the Caucasus as one group and the remaining populations as the second group (Table 3).

Table 4 presents genetic diversity estimates for the analysed populations and geographical regions, which are also shown in Figure 7. In most cases, the number of individuals analysed was the same as the number of detected AFLP phenotypes. Only in a single population of *C. impatiens* (I-Ge-15, Georgia, Gveleti) did all three individuals share the same AFLP phenotype. In *C. pectinata*, two pairs of individuals sharing the same AFLP phenotype were found. In *C. impatiens*, several populations with high levels of genetic diversity (reflected by the high percentage of polymorphic fragments, number of rare and private fragments, and higher H_{Sh} values) were identified, which were concentrated to the western part of the studied area (western Carpathians, regions south of the Alps). A few populations with higher genetic variation or with several private AFLP fragments were also found scattered in Bulgaria, Romania, and the Caucasus. In *C. pectinata*, the eastern populations (located along the Black Sea coast in northern Turkey and the Caucasus) displayed high genetic diversity, with several private fragments, in contrast with Bulgarian populations with reduced genetic variation. In populations of the latter region, however, a few private fragments were also present.

DISCUSSION

TAXONOMIC POSITION OF *C. PECTINATA* AND ITS MORPHOLOGICAL AND MOLECULAR DIFFERENTIATION

Different taxonomic treatments can be found in the literature with regard to the recognition and taxonomic status of the taxon originally described as

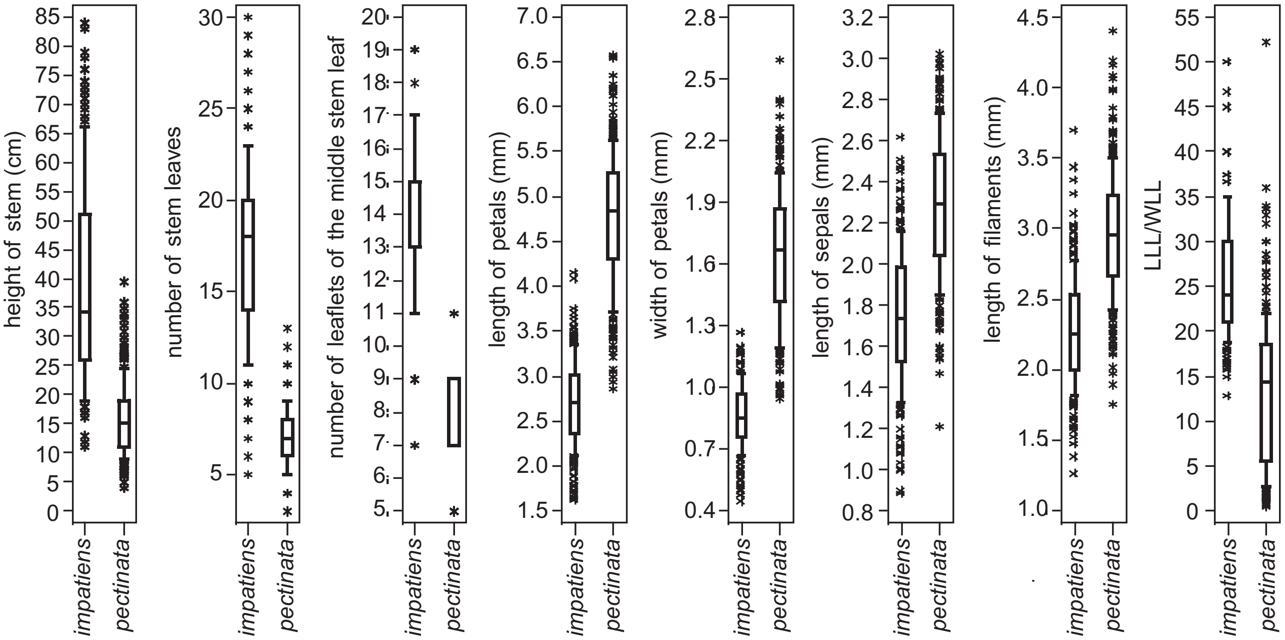

Figure 5. Variation of selected morphological characters of *Cardamine impatiens* and *C. pectinata*. Rectangles define 25th and 75th percentiles, horizontal lines show median, whiskers are from 10th to 90th percentiles, and asterisks show extreme values. LLL/WLL, length of lowermost lateral leaflet of the middle stem leaf/width of lowermost lateral leaflet of the middle stem leaf.

C. pectinata (Assenov, 1970; Khatri, 1988; Kit Tan, 2002). Several authors did not accept it as a separate species, but placed it within *C. impatiens* (Stoyanov & Stefanov, 1948; Zohary *et al.*, 1980; Jones & Akeroyd, 1993). Although morphological differences between these two taxa have been reported, the existence of morphological intermediates has also been assumed (Cullen, 1965; Kit Tan, 2002). According to *Flora Europaea* (Jones & Akeroyd, 1993) and national floras from the relevant areas (e.g. Stoyanov & Stefanov, 1948; Grossgeim, 1950; Cullen, 1965; Assenov, 1970; Kit Tan, 2002), several morphological characters, such as the height of plants, number of leaflets of the stem leaves, shape of the leaflets, length of the petals, branching of the stem, width of the siliquae, length of the style, and the position of the siliquae in the inflorescence, can distinguish between *C. impatiens* and *C. pectinata* (often treated as a subspecies or variety within the former). Until our study, however, no detailed morphological investigation has been performed. Our results, based on a large amount of plant material, showed two morphologically clearly differentiated entities, corresponding to *C. impatiens* and *C. pectinata*. We have not recorded any morphologically intermediate or uncertain populations, which cannot be classified reliably. This was confirmed at the level of individual plants and also from localities in which both taxa grew in close proximity. Morphological characters, which were resolved in our analyses as diagnostic, mostly corresponded to those reported by the authors of several taxonomic treatments (for references, see above). Fruit characters were not included in our detailed morphometric evaluation, as the population samples were collected at flowering time. Nevertheless, we studied numerous fruiting specimens in herbaria. *C. pectinata* typically possesses secund siliquae, and the resulting fruiting inflorescence shape can be considered as a character distinguishing it from *C. impatiens*; however, exceptions occur. In addition to the traditionally reported differentiating characters, our study showed differences in the length of the sepals, width of the petals, and length of the filaments. The extreme values of the discriminating characters may overlap in some cases (see Fig. 5), but, by using a combination of a few characters, it is always possible to identify *C. impatiens* or *C. pectinata* without doubt.

In populations of both *C. impatiens* and *C. pectinata*, plants with hairy siliquae are seldom found. In the past, they were classified either as a separate species, *C. dasycarpa* M. Bieb., or as varieties of either *C. impatiens* (var. *eriocarpa* DC.) or *C. pectinata* (var. *trichocarpa* N. Busch). Following the lectotypification in the present paper, *C. dasycarpa* is a synonym of *C. impatiens*, and two other names fall into the synonymy of *C. pectinata*. The character 'hairness of siliquae' apparently has no taxonomic value. In addition, apetalous plants very often occur in populations of *C. impatiens*. They were named by Gilibert (1782) as *C. apetala*; however, this name is currently treated as

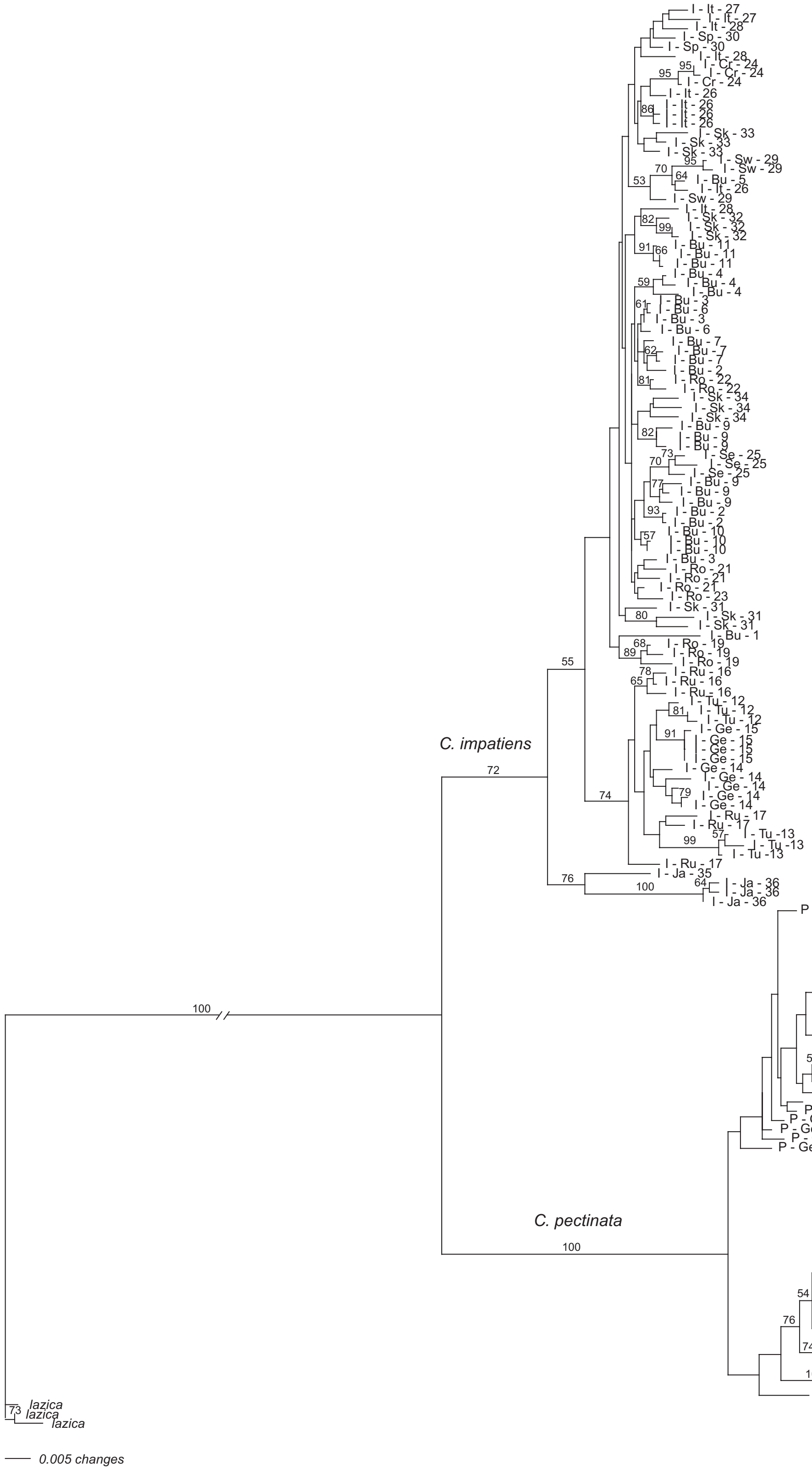

Figure 6. Neighbour-joining tree of amplified fragment length polymorphism (AFLP) data including 95 accessions of *Cardamine impatiens* and 52 accessions of *C. pectinata*. For explanation of the accession labels, see Table 1. Bootstrap values are shown above the branches. *Cardamine lazica* was used to root the tree.

Table 3. Analysis of molecular variance (AMOVA) of amplified fragment length polymorphism (AFLP) data performed with different geographical groupings within both *Cardamine impatiens* (A–D) and *C. pectinata* (E–H). C: Partitioning of populations in the Caucasus and eastern Turkey follows the pattern resolved by the neighbour-joining tree: E Turkey, Caucasus (1) represents populations I-Tu-13, I-Ru-16, -17; E Turkey, Caucasus (2) represents populations I-Tu-12, I-Ge-14, -15. Values discussed in the text are marked in bold

Grouping	Source of variation	d.f.	Sum of squares	Variance components	% of total variance
Cardamine impatiens					
A. [Turkey, Caucasus],[Europe]	Between groups	1	243.88	7.05	**49.32**†
	Between populations	27	436.25	4.43	30.99†
	Within populations	59	166.08	2.81	19.69†
B.[Turkey,Caucasus],[Carpathians],[Balkan], [western Europe]	Between groups	3	306.53	4.03	37.02†
	Between populations	25	373.60	4.04	37.11†
	Within populations	59	166.08	2.81	25.87†
C. [E Turkey, Caucasus (1)],[E Turkey, Caucasus (2)], [Carpathians],[Balkan],[western Europe]	Between groups	4	339.28	4.16	38.55†
	Between populations	24	340.85	3.82	35.37†
	Within populations	59	166.08	2.81	26.08†
D. [Caucasus],[Turkey],[Carpathians],[Balkan], [western Europe]	Between groups	4	322.43	3.90	36.28†
	Between populations	24	357.69	4.04	37.55†
	Within populations	59	166.08	2.81	26.17†
Cardamine pectinata					
E. [Turkey, Caucasus],[Bulgaria]	Between groups	1	167.99	6.48	51.09*
	Between populations	10	164.60	3.20	25.24†
	Within populations	18	117.18	3.00	23.67†
F. [E Turkey, Caucasus],[central Turkey],[Bulgaria]	Between groups	2	234.22	7.62	**60.92**†
	Between populations	9	98.37	1.88	15.06†
	Within populations	39	117.18	3.00	24.02†
G. [E Turkey, Caucasus],[central Turkey,Bulgaria]	Between groups	1	202.25	7.38	**57.72***
	Between populations	10	130.33	2.40	18.79†
	Within populations	39	117.18	3.00	23.49†
H. [Caucasus],[Turkey],[Bulgaria]	Between groups	2	194.62	5.09	45.38*
	Between populations	9	137.96	3.12	27.83†
	Within populations	39	117.18	3.00	26.79†

d.f., degrees of freedom.
*$P < 0.01$.
†$P < 0.001$.

invalid (see 'Taxonomic conspectus'). Moench (1794) apparently intended to publish the name *C. apetala* again for apetalous plants of *C. impatiens*, but the only original element connected with this name, an illustration in *Flora Danica* (Müller, 1777: table 735), depicts undoubtedly *C. flexuosa* With. This variation has no taxonomic value.

From our AFLP data, *C. impatiens* and *C. pectinata* are also genetically well differentiated. The large number of private AFLP fragments, as well as the overall variation pattern illustrated by PCoA and the NJ tree, show pronounced genetic differentiation between these two taxa. These results are in clear accordance with morphometric data, and provide convincing evidence that *C. impatiens* and *C. pectinata* should be treated as two different species. We did not find any signs of interspecific gene flow; no intermediate AFLP phenotypes were seen on the ordination diagram of PCoA and no morphological intermediates were observed. Our recent study on phylogenetic relationships between European *Cardamine* diploid taxa using DNA sequence data from three different markers (ITS nrDNA, *trnL-trnF* of cpDNA, and nuclear single-copy *CHS* gene) also included a few accessions of *C. impatiens* and *C. pectinata*. They were resolved as two closely related sister taxa, forming a well-supported and distinct lineage amongst the other analysed taxa (Lihová, Shimizu & Marhold, 2006).

Thirty original chromosome number records of $2n = 2x = 16$ have been published for *C. impatiens* across its distribution range (for details, see Karyological database of the genus *Cardamine*: http://147.213.100.117/cardamine/index.php; Kučera, Valko & Marhold, 2005). This is, in agreement with our

Table 4. Distribution of amplified fragment length polymorphism (AFLP) fragments and genetic diversity measures for the populations and regions analysed (see also Fig. 7). The population codes follow Table 1

Region	Pop.	N	f_{pop}	f_{ind}	$\%P_{\mathrm{pop}}$	f_{r}	f_{pr}	$f_{\mathrm{pr\text{-}f}}$	H_{Sh}
Cardamine impatiens									
Turkey			87		25 (16.56%)				0.104
	I-Tu-12	3	76	73	7 (2.65%)	3	–	–	0.030
	I-Tu-13	3	76	74	5 (3.31%)	8	4	4	0.021
Caucasus			92		34 (22.52%)				0.113
	I-Ge-14	3	75	72	4 (2.65%)	3	–	–	0.017
	I-Ge-15	3	74	74	0	3	1	1	0
	I-Ru-16	3	75	72	7 (4.64%)	3	–	–	0.030
	I-Ru-17	3	82	74	18 (11.92%)	6	1	–	**0.076**
Balkan			96		44 (29.14%)				0.115
	I-Bu-2	3	74	68	10 (6.62%)	3	–	–	***0.042***
	I-Bu-3	3	72	70	6 (3.97%)	1	1	–	0.025
	I-Bu-4	3	72	67	8 (5.3%)	2	1	–	0.034
	I-Bu-7	3	72	69	5 (3.31%)	1	–	–	0.021
	I-Bu-8	3	70	67	7 (4.64%)	2	1	–	0.029
	I-Bu-9	3	76	73	5 (3.31%)	3	–	–	0.021
	I-Bu-10	3	70	68	3 (1.99%)	0	–	–	0.013
	I-Bu-6	2	72	71	3 (1.99%)	2	–	–	0.014
	I-Bu-11	3	68	67	2 (1.32%)	0	–	–	0.008
	I-Cr-24	3	69	67	4 (2.65%)	2	–	–	0.017
	I-Se-25	3	73	69	9 (5.96%)	2	1	1	0.038
E, S Carpathians			82		27 (17.88%)				0.098
	I-Ro-19	3	71	67	9 (5.96%)	2	–	–	0.038
	I-Ro-21	3	74	69	10 (6.62%)	2	–	–	***0.042***
	I-Ro-22	2	72	71	3 (1.99%)	2	2	–	0.014
W Carpathians			97		42 (27.81%)				0.133
	I-Sk-31	3	88	75	23 (15.23%)	9	4	–	**0.097**
	I-Sk-32	3	68	66	5 (3.31%)	2	1	–	0.021
	I-Sk-33	3	75	69	11 (7.28%)	2	–	–	***0.046***
	I-Sk-34	3	77	70	13 (8.61%)	2	–	–	**0.055**
W Europe			105		37 (24.50%)				0.125
	I-Sw-29	3	82	75	13 (8.61%)	4	3	2	**0.055**
	I-It-28	3	77	68	17 (11.26%)	4	–	–	**0.072**
	I-It-27	2	76	72	8 (5.3%)	4	–	–	0.037
	I-It-26	3	72	71	2 (1.32%)	2	–	–	0.008
	I-Sp-30	2	73	70	6 (3.97%)	3	–	–	0.028
Cardamine pectinata									
Caucasus & Turkey			107		67 (57.26%)				0.216
	P-Ge-13	3	67	62	10 (8.55%)	4	3	–	**0.054**
	P-Tu-11	3	65	62	7 (5.98%)	3	2	–	0.037
	P-Tu-8	3	64	63	3 (2.56%)	1	–	–	0.016
	P-Tu-9	3	70	66	8 (6.84%)	2	–	–	***0.043***
	P-Tu-7	3	78	65	24 (20.51%)	9	5	–	**0.128**
	P-Tu-10	3	71	63	16 (13.68%)	7	6	–	**0.086**
	P-Tu-12	3	77	70	12 (10.26%)	6	5	2	**0.064**
Bulgaria			79		16 (13.68%)				0.050
	P-Bu-1	3	73	69	8 (6.84%)	1	1	–	***0.043***
	P-Bu-2	3	70	68	4 (3.42%)	0	–	–	0.021
	P-Bu-3	3	71	68	5 (4.27%)	2	1	–	0.027
	P-Bu-4	3	74	69	9 (7.69%)	5	4	–	***0.048***
	P-Bu-6	3	69	68	2 (1.71%)	1	–	–	0.012

Pop., population code; N, number of investigated individuals (reduced dataset with two to three individuals per population, see 'Material and methods'); f_{pop}, total number of fragments in a population/region; f_{ind}, mean number of fragments per individual in a given population; $\%P_{\mathrm{pop}}$, number and percentage of polymorphic fragments in a population/region; f_{r}, number of rare fragments (present in less than 10% of individuals); f_{pr}, number of private fragments; $f_{\mathrm{pr\text{-}f}}$, number of private fixed fragments; H_{Sh}, Shannon's diversity index for a population/region. Three classes of H_{Sh} values were established to discuss the diversity patterns: high values are in bold, medium values are in bold italic, and low values are in normal type.

Figure 7. Sample sites of *Cardamine impatiens* (A) and *C. pectinata* (B) included in our amplified fragment length polymorphism (AFLP) study. Population codes follow Table 1. Intrapopulational genetic diversity, as assessed by Shannon's diversity index (H_{Sh}), is indicated by different circle sizes (small circle, low H_{Sh}; medium circle, medium H_{Sh}; large circle, high H_{Sh}; see Table 4). The number of private AFLP fragments is shown by '+'. Arrows delimit geographical groups that show the most pronounced genetic differentiation (analysis of molecular variance, AMOVA; see Table 3, values in bold). In *C. pectinata*, two almost equal partitionings are indicated.

results, the only reliably documented chromosome number for this species. Three authors have also published the tetraploid level for *C. impatiens*. The tetraploid record by Hindáková (in Májovský *et al*., 1974), published from Slovakia, refers in fact to *C. flexuosa* (based on the revision of the voucher specimen; Marhold, 1994b). We have not been able to trace the voucher specimens of the tetraploid chromosome numbers published by Gohil, Ashruf & Raina (1981) and Jee, Dhar & Kachroo (1983) from the area of Kashmir. Therefore, we cannot consider these data as reliable. These records may well refer to another taxon. In the account of the Cruciferae of Continental North America (Rollins, 1993), the tetraploid number was reported, but without the indication of any particular locality, and thus this record cannot be considered as reliable. For *C. pectinata*, the only chromosome number record was published from Bulgaria (Anchev & Goranova, 1999), which is in accordance with our results, confirming the diploid level from seven populations (Table 1).

GEOGRAPHICAL DISTRIBUTION AND ECOLOGY OF *C. PECTINATA*

Based on the revision of herbarium specimens deposited in relevant herbaria, we present the distribution area of *C. pectinata* (Fig. 1, Appendix). It covers mountain ranges in the Balkan Peninsula (Bulgaria, Greece), northern Turkey, the Caucasus region, and northern Iran. There is one herbarium record originating from a locality in southern Turkey near the border with Syria, which is distant from any other reports from northern Turkey (see Fig. 1, Appendix). The specimen was collected in 1913 by M. Haradjian in the Amanus Mountains (Nur Dağlari) that belonged at that time to Syria, nowadays to the province of Hatay in Turkey. It was identified by Rechinger as *C. impatiens*, but morphologically it undoubtedly corresponds to *C. pectinata*. As a result of the large geographical disjunction and only a single record from that area, we may consider this record as doubtful. However, M. Haradjian is known by his collections from Syria and Cyprus (Lanjouw & Stafleu, 1957), and we are not aware of any of his collections from the known distribution area of *C. pectinata*. Therefore, it seems that the localization of the origin of this specimen is correct, and extends the known distribution area of *C. pectinata* to the area of southern Turkey.

From the consultation of numerous floras from the relevant area, a similar ecology has been reported for *C. impatiens* and *C. pectinata*. Both species usually grow on moist sites in shady forests; however, differences reported between *C. impatiens* and *C. pectinata* in terms of altitudinal range and forest types are controversial. Our field observations, on the other hand, indicate a clear and consistent pattern in terms of ecological differentiation. *C. pectinata* occurs in coniferous or mixed (*Abies–Fagus*) forests; we have not found any locality in an entirely deciduous forest. The altitudinal range was recorded to be 690–1860 m, with a single locality at 505 m, where only a few plants were observed, apparently originating from a population growing at higher elevation. *C. impatiens*, on the other hand, occurs either in lowland deciduous forests or in mixed (*Abies–Fagus*) forests, but has not been observed in an entirely coniferous forest. It is usually observed at lower altitudes from 180 to 1750 m; populations in the upper altitudinal range occur only in the Caucasus Mountains with surrounding peaks reaching 5000 m. Both species can meet in mixed forests, and, indeed, we have observed three localities in which they are found in close vicinity (populations I-Bu-11 and P-Bu-6; I-Tu-12 and P-Tu-7; I-Ge-14 and P-Ge-13; Table 1). Even in these cases, however, they showed microspatial separation, indicating differences in their ecological preferences.

PHYLOGEOGRAPHICAL HYPOTHESES

Different distribution areas occupied by *C. impatiens* and *C. pectinata*, and the concentration of *C. pectinata* populations in assumed glacial refugia (Hewitt, 2004), led us to explore the phylogeographical patterns within these species. AMOVA and the assessment of genetic diversity have been applied to reveal the geographical partitioning of genetic variation, to identify the genetically most diverse populations (potential refugial populations serving as source populations for postglacial colonization), and to track postglacial migrations. In *C. pectinata*, strong genetic differentiation was observed between the populations from eastern Turkey/Caucasus, central Turkey, and Bulgaria (see Fig. 7), indicating long-term isolation and restriction of gene flow between these three regions. Populations from mountain ranges along northern Turkey (P-Tu-12, -10, -7) and a population from the Lesser Caucasus (P-Ge-13) displayed the highest H_{Sh} values, accounting for both the number of AFLP fragments and their frequency. The same populations also harboured most private fragments. These genetic patterns are in clear accordance with the assumed location of glacial refugia along the Black Sea coast, as shown by several authors (e.g. Hampe *et al.*, 2003; Marcussen, 2003; Krebs *et al.*, 2004). Survival of populations within this area and altitudinal shifts during glacials and interglacials may have enabled them to retain considerable genetic variation and accumulate private fragments (see Petit *et al.*, 2003). *C. pectinata* currently grows at higher altitudes within this area; thus, during colder periods, it may have found suitable habitats in the same or neighbouring areas at lower altitudes. Indeed, palaeoclimatological and palynological data (Adams, 1997) suggest that such suitable habitats were available within this area. The mountainous distribution of *C. pectinata* also explains the strong geographical differentiation revealed by AMOVA. Gene flow between the populations occupying different mountain ranges is more restricted than if the species was continuously distributed. The three genetically differentiated regions (Fig. 7) coincide well with the current distribution pattern, showing distributional gaps in the lowlands separating these regions (the area of north-west Turkey west of Istanbul, and central Turkey; Fig. 1). Bulgarian populations located at the western distribution border of this species, on the other hand, were revealed as less diverse, but still harboured private fragments not present in the populations from Turkey and the Caucasus. This indicates that the mountainous area of Bulgaria has been colonized postglacially, but probably not from the refugia in Turkey. According to the reconstruction of the vegetation composition in the Balkans during the last glacial maximum, there have been areas with a continuous presence of both coniferous and deciduous tree species (Willis, 1994). A high diversity of tree species has been documented, e.g. in Ioannina (north-west Greece). *C. pectinata* may have survived the unfavourable climatic conditions in such refugial populations. Unfortunately, we have not sampled populations from Greece that may have served as source populations for those in more northern areas of Bulgaria. To obtain more detailed insights into the phylogeography of this species, more individuals per population, larger sampling within the analysed regions, and sampling in areas not covered here (Greece, northern Iran, the Greater Caucasus) are needed.

The distribution range of *C. pectinata* is intriguing, because, in contrast with the widespread *C. impatiens*, it is much smaller and restricted to refugial areas and adjacent regions, but still within the range of the latter. Considering their sister relationships, we can assume two speciation scenarios from their common ancestor. Allopatric speciation may have occurred preglacially near the current distribution of *C. pectinata*, and the current sympatry may have originated as a result of their secondary contact. Alternatively, sympatric speciation may have occurred, but, in this case, strong genetic barriers must have been generated that have prevented gene flow. Detailed genetic and genomic studies may reveal the mechanisms of their reproductive isolation. Self-pollination has been reported for *C. impatiens* (Kimata, 1983), but assuming from the rather high intrapopulation variation, outcrossing should also occur.

Cardamine impatiens, in contrast with *C. pectinata*, exhibits only a weak phylogeographical structure within the studied area. AMOVA reveals the east–west differentiation (see Fig. 7), but less pronounced than in *C. pectinata*, and further genetic differentiation within these two areas is not supported. Populations harbouring the highest genetic diversity are scattered across the investigated area. They are present mainly in the previously glaciated areas or in their vicinity, where they may have only hardly survived during the glacials (the Greater Caucasus Mountains, the Alps, and the Carpathians). Therefore, we can hypothesize that the high genetic diversity revealed in these regions has been generated through the contact between colonization routes from different refugia, as found in many other species (Petit *et al*., 2003). Alternatively, the efficient spread and mixing between different colonization routes may have completely blurred any phylogeographical pattern that may have resulted from postglacial migrations.

TAXONOMIC CONSPECTUS OF *C. IMPATIENS* AND *C. PECTINATA*

CARDAMINE IMPATIENS L., *SP. PL.*: 655, 1753.

Ind. loc.: 'Habitat in Europae nemoribus ad radices montium.'
Lectotype: LINN, no. 835.9 (Jafri, 1973: 169).
≡ *Ghinia impatiens* (L.) Bubani, *Fl. Pyren*. 3: 160, 1901.

= *C. brachycarpa* Opiz, *Naturalientausch* 11: 411, 1826.
Ind. loc.: 'In monte wysoká hora ad Karlstein. C, her. boëmiae.'
Type: Not designated.

= *C. impatiens* f. *apetala* O. E. Schulz, *Bot. Jahrb. Syst*. 32: 455, 1903.
Ind. loc.: 'China centralis: prov. Szech'uan pr. Nanch'uan leg. v. Rosthorn 1891 n. 2049, leg. idem n. 2048 (H. B); prov. Hupeh leg. A. Henry 1885–88 n. 7855 (H. B., H. C); in m. Tientai leg. E. Faber 1889 (H. B). Japonia: leg. Rein (H. B).'
Type: Not designated.

= *C. dasycarpa* M. Bieb., *Fl. Taur.-Cauc*. 3: 437, 1819.
Ind. loc.: 'Habitat in Iberiâ occidentali.'
Lectotype (designated here): ex herb. Steveni, 1809 (LE).
≡ *C. impatiens* 'proles' *dasycarpa* (M. Bieb.) O. E. Schulz, *Bot. Jahrb. Syst*. 32: 457, 1903.
≡ *C. impatiens* var. *dasycarpa* (M. Bieb.) T. Y. Cheo & R. C. Fang, *Bull. Bot. Lab. N.-E. Forest. Inst., Harbin* 6: 21, 1980.

= *C. impatiens* 'proles' *elongata* O. E. Schulz, *Bot. Jahrb. Syst*. 32: 459, 1903.
Ind. loc.: 'Asia: Affghanistan leg. Griffith ante 1861 n. 1358 (H. B., H. C., H. V), pr. Otipore leg. idem (H. Boiss.); Tibet leg. Hügel n. 185 (H. V); Himalaya bor.-occid. 1670–3340 m leg. T. Thomson (H. B., H. C., H. V), pr. Abetamorsch leg. Stolitzka 2000–2340 m (H. V), Kashmir 2670–3000 m leg. J. F. Duthie 1892 (H. B), Garhwal in Nila Valley pr. Phuláldaru 3340–3370 m leg. idem 1883 n. 916 (H. B. Boiss.), pr. Sing-jari, 3000 m, legg. R. Strachey et J. E. Winterbottom n. 3, pr. Rogila 3370 m legg. iidem n. 10, Kumaon pr. Dewali, 2830 m legg. iidem n. 9 (H. C., H. P. Ac.), Sikkim 2000–3340 m leg. J. D. Hooker (H. B., H. Boiss., H. C., H. V); Mandschuria austr.-litoralis ad Olga Bai leg. F. Schmidt 1861 (H. P. Ac.).'
Lectotype (designated here): Garhwál, Sing-jari, 9000 feet, s.a., leg. R. Strachey et J. E. Winterbottom n. 3 (GH).

= *C. impatiens* var. *pilosa* O. E. Schulz, *Bot. Jahrb. Syst*. 32: 459, 1903.
Ind. loc.: 'Turkestania in distr. Akdishan et Namangan leg. D. Litwinow 1899, pr. Wernij leg. F. Killomann 1888 (H. P. Ac.); Altai leg. Ledebour (H. P); China: prov. Schensi sept. in m. Hua-tzo-pin leg. Gius. Giraldi 1894 (H. Biondi n. 443 in H. B), prov Szech'uan leg. v. Rosthorn 1891 n. 2054 (H. B).'
Lectotype (designated here): Turkestania, distr. Akdishan, fl. Kara-Lesigur, 30.v.1899, leg. D. Litvinow (LE).

= *C. impatiens* var. *angustifolia* O. E. Schulz, *Bot. Jahrb. Syst*. 32: 459, 1903.

Ind. loc.: 'Caucasus centralis ad fl. Aragwa leg. Lagowski (H. P).'
Holotype: Am Aragwa, leg. Dr Lagowski (LE).

= *C. impatiens* var. *obtusifolia* Knaf, *Flora* 19: 294, 1864.
Ind. loc.: 'Bei Hallstadt in Oberösterreich.'
Type: Not designated.
≡ *C. impatiens* f. *obtusifolia* (Knaf) Markgr., in Hegi *Ill. Fl. Mitteleurop*. ed. 2, 4(1): 205, 1958.

= *C. impatiens* var. *microphylla* O. E. Schulz, *Bot. Jahrb. Syst*. 32: 460, 1903.
Ind. loc.: 'Ins. Sachalin leg. F. Schmidt 1860 (H. P).'
Holotype: Insula Sachalin, zaliv Estaing, 1860, F. Schmidt (LE).

= *C. impatiens* var. *acutifolia* Knaf, *Flora* 19: 294, 1846.
Ind. loc.: Not stated.
Type: Not designated.

= *C. impatiens* f. *macropetala* (Boiss.) O. E. Schulz, *Bot. Jahrb. Syst*. 32: 459, 1903.
≡ *C. impatiens* γ *macropetala* Boiss., *Fl. Orient*. 31, 1888.
Ind. loc.: 'Hab. secus torrentes vallis subalpinae Djimil Ponti Lazici 6000' (Bal.).'
Holotype: Bords des torrents de la vallée sous-alpine de Djimil (Lazistan), vers 2000 métre d'altitude, Juillet-Août 1866, leg. Balansa (G).

= *C. impatiens* var. *minima* Schur, *Verh. Naturf. Vereins Brünn* 15: 77, 1876.
Ind. loc.: 'Auf buschigen Abhängen am Wege nach Jundorf unweit der neuen Welt bei Brünn, mit *Linaria arvensis,* Juni 1871; Auch in Siebenbürgen, 1850.'
Type: Not designated.

– *C. apetala* Gilib, *Fl. Lith*. 1: 42, 1782, nom. inval. (opera uttique opressa).
– *C. impatiens* var. *communis* N. Busch, *Fl. Sib. i Dal. Vostoka* 2: 243, 1915, nom. inval. (Art. 24.3).

Excluded name: C. apetala Moench, *Meth. Plantas Horti Bot. et Agri Marburgensis* 259, 1794.
Ind. loc.: 'h. frequens am Rhinberg prope Caldern.'
Lectotype (designated here): Müller, *Fl. Dan*. 5/13, 1777: table 735.
= *C. flexuosa* With.

Description: Biennial or, rarely, annual herb. Height of stem from base to the lowest peduncle of flower or fruit (15–) 18–75 (–85) cm. Stem erect, sometimes flexuous, simple or very rarely branched, glabrous. Rosette leaves shrivelled by anthesis, pinnate, sparsely hairy, with four to eight pairs of petiolulate, circular-ovate, lobate, or sometimes pinnatipartite leaflets. Cauline leaves (7–) 9–25 (–28), auriculate, pinnate, or sometimes pinnatisect above, with (7–) 9–17 (–19) denticulate to lobed or pinnatipartite leaflets. Terminal leaflets (0.7–) 0.9–2.8 (–3.3) × (0.2–) 0.3–1.2 (–1.5) cm, petiolulate or sessile, lanceolate to ovate lanceolate. Lateral leaflets (0.5–) 0.7–2.3 (–2.6) × (0.18–) 0.2–1.0 (–1.4) cm, petiolulate or sessile, lanceolate to ovate. Inflorescence racemose with 0–14 (–17) lateral inflorescences. Sepals oblong (1.0–) 1.2–2.3 (–2.5) × (0.3–) 0.5–0.8 (–0.9) mm, margin membranous; petals (1.7–) 1.9–3.5 (–3.7) × (0.5–) 0.6–1.1 (–1.3) mm, white, oblanceolate, apex rounded. Stamens 6, anthers green–yellow, filaments (1.5–) 1.7–2.9 (–3.4) mm long; stigma not conspicuous. Pedicels and siliquae patent or erect-patent.

Chromosome number: $2n = 2x = 16$.

Ecology: Moist sites in shady forests, lowland deciduous forests, or mixed forests up to 2400 m (Caucasus).

Distribution area: Eurasia, introduced to North America and southern Africa.

C. PECTINATA PALL. EX DC., *SYST. NAT*. 2: 264, 1821.

Ind. loc.: 'Hab. In Persiâ *Pallas* (v. s. sp. in h. Lamb.).'
Lectotype (designated here): E Persia, Herb. Pallas (BM).
≡ *C. impatiens* ssp. *pectinata* (Pall. ex DC.) Stoj. & Stef., *Fl. Bãlg*., ed. 3: 503, 1948.
≡ *C. impatiens* var. *pectinata* (Pall. ex DC.) Trautv., *Trudy Imp. S.-Peterburgsk. Bot. Sada* 4 (1): 105, 1876.

= *C. impatiens* var. *eriocarpa* DC., *Syst. Nat*. 2: 262, 1821.
Ind. loc.: 'in Iberiâ occidentali.'
Holotype: Imeretia, parte var. impatientes Iberiae, m.[isit] Steven 1820 (G-DC).

= *C. oxycarpa* Boiss., *Ann. Sci. Nat. (Paris)*, ser. 2, 17: 56, 1842.
Ind. loc.: 'N. 113, Alpes Laristan; 4119, Zarinkou.'
Lectotype (designated here): Mt. Zarinkou, Aucher-Eloy-Herbier d'Orient, no. 4119 (G).

= *C. pectinata* var. *trichocarpa* N. Busch, *Fl. Caucasica Critica* 3: 340, 1904–10.
Ind. loc.: 'Hab. in umbrosis silvaticis et ad rivulos regionis subalpinae Caucasi occidentalis et Transcaucasiae occidentalis., Exsicc. Aucher-Eloy, Herbier d'Orient, no. 4119; B. Balansa, Plantes d'Orient (1866), no. 1361.'

Lectotype (designated here): Mt. Zarinkou, Aucher-Eloy-Herbier d'Orient, no. 4119 (G).

= *C. lucorum* Boiss. & Huet, *Fl. Orient*. 1: 161, 1867.
Ind. loc.: 'Boiss. et A. Huet in pl. Arm. Exs. 1853.'
Lectotype (designated here): Armenia in umbrosis supra Keuprubachu, inter Trapezuntem et Baibout, 5500–6000 p.s.m., Maio 1853, A. Huet du Pavillon, Plantae Orientales exsiccatae (G).

= *C. pectinata* var. *adzharica* Albov, *Prodr. Fl. Colchic*. 19, 1895.
Ind. loc.: 'Adzharia, Yaïla Medzybna prope pagum Akria, 1500–2000 m (N. A. 1893, n. 80).'
Lectotype (designated here): Spusk' s' yaily Medzybny k' sel. Akria, 1500–2000 m, 10 juin 1893, N. Alboff, Plantes d'Adjarie no. 80 (G).

= *C. parviflora* f. *latifolia* O. E. Schulz, *Bot. Jahrb. Syst*. 32: 484 (1903).
Ind. loc.: 'ad mare Caspium, pr. Lenkoran, leg. C. A. Meyer 1829 (H. Boiss, H.P.Ac.).'
Lectotype (designated here): ad m. Caspium, 1829, C. A. Meyer, Enum Cauc. no. 1594 (G).

Description: Biennial or, rarely, annual herb. Height of stem from base to the lowest peduncle of flower or fruit (6–) 7–27 (–35) cm. Stem erect, flexuous, often branched from the base or simple, glabrous. Rosette leaves shrivelled by anthesis, pinnate, sparsely hairy, with two to four pairs of petiolulate, circular-ovate, lobate, or sometimes pinnatipartite leaflets. Cauline leaves (3–) 4–10 (–11), auriculate, pinnate, or sometimes pinnatisect above, with 5–9 (–11) denticulate to lobed or pinnatipartite leaflets. Terminal leaflets (0.7–) 0.9–3.7 (–4.8) × (0.2–) 0.3–1.6 (–1.8) cm, longer than lateral leaflets, petiolulate or sessile, lanceolate. Lateral leaflets (0.5–) 0.6–2.4 (–2.8) × 0.2–1.3 (–1.5) cm, petiolulate or sessile, lanceolate to ovate. Inflorescence racemose with 0–8 (–9) lateral inflorescences. Sepals oblong (1.6–) 1.8–2.8 (–3.0) × (0.5–) 0.6–1.0 (–1.1) mm, margin membranous; petals (3.1–) 3.4–5.8 (–6.4) × (1.0–) 1.1–2.2 (–2.4) mm, white, oblanceolate, apex rounded. Stamens 6, anthers green–yellow, filaments (2.0–) 2.3–3.6 (–4.1) mm long; stigma not conspicuous. Pedicels erect-patent and siliquae expanded and often secund.

Chromosome number: $2n = 2x = 16$.

Ecology: Moist sites in shady forests, mixed or coniferous forests from 50 to 3000 m (Iran).

Distribution area: Mountain ranges in the Balkan Peninsula (Bulgaria, Greece), northern Turkey, the Caucasus region, and northern Iran. A single record from the Hatay province in southern Turkey.

ACKNOWLEDGEMENTS

We would like to thank our colleagues from Bulgaria: M. Anchev, S. Stoyanov; Turkey: S. Hayirlioğlu-Ayaz, M. Keleş; Russia: D. Geltman, V. G. Onipchenko and Slovakia: M. Kolník for their help and accompanying during the fieldworks, curators of herbaria given in the Material and Methods section for allowing us to study herbarium specimens, and finally K. Tremetsberger, Vienna, Austria, for the help in molecular laboratory. This study was suported by the Scientific Grant Agency of the Ministry of Education of the Slovak Republic and the Slovak Academy of Sciences, VEGA, Bratislava (grant no. 3042), by the Research and Development Support Agency (grant no. APVT-51-026404), and by the Ministry of Education, Youth and Sports of the Czech Republic (grant no. 0021620828).

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APPENDIX

Survey of herbarium specimens of *C. impatiens* (from the area of sympatry with *C. pectinata*) and *C. pectinata* (reflecting the whole distribution area of this species) from herbaria B, BM, G, K, KW, LE, LEU, P, PR, PRC, SAV, SO, SOM, W, WU.

CARDAMINE IMPATIENS L.

BULGARIA. STARA PLANINA: in silvaticis m. Ruj, non procul pagum Odorovci, 16.vi.1903, *Iv. K. Urumov* (SOM 32080); Odorovci, *Iv. K. Urumov* (PRC); prope Teteveni, 6.vi.1910, *Iv. K. Urumov* (SOM 32048); in silvaticis ad pagum Gložene, distr. Pleven, 14.vi.1910, *Iv. K. Urumov* (SOM 32049); bei Trojan, 1900, *Iv. K. Urumov* (PRC); Trojan Balkan, 1899, *Iv. K. Urumov* (PRC); Trojan Balkan, 22.vii.1898, *Iv. K. Urumov* (WU); Gabrovo, dolina r. Panicharka u Khadisi Tsoneva mosta sredi skal, 29.v.1930, *A. Yurkovskii* (SOM 32036); Gabrovo, po kamenisti mesta v dolinata na r. Panicharka krai Khadzhi Tsoneviya most, 29.v.1930, *A. Yurkovskii* (SO 83221); Petkovo Niva, Gabrovo, 25.iv.1897, *Iv. Neuchev* (SOM 32073); in saxosis et pratis mt. Balkan central, ad riv. Star ad v. Gabrovo, 450 m, 3.v.1907, *B. Davidov* (SOM 32062); in saxosis et pratis mt. Balkan central, ad riv. Star ad v. Gabrovo, 400 m, 2.vi.1907, *B. Davidov* (SOM 32067); Koškov, pg. Šumla, 19.v.1891, *K. Polák* (PRC); Chernomorsko kraibrezhie, reservat 'Kamchiya' do Lesinski azmak, 9.v.1996, *D. Stoyanov & D. Ivanov* (SO 98398). VITOSHA: Ad Bojana prope Sofia, 17.v.1910, *Iv. K. Urumov* (SOM 32055, 32052; SO 83220); Vitosha, po ptya Kopitoto-Molina skala, 25.v.1964, *B. Kitanov* (SO 28210); in Mt. Vitoša, 1889, *Škorpil* (PRC). LOZENSKA PLANINA: Lozenska planina, in declivibus umbrosis infer frutices supra pagum Dolni Losen, distr. Sofia, 7.vi.1978, *N. Vihodcevski* (SOM 139181). PLANA: In saxosis humidis mt. Plana ad faucem rivi Iskar, 750 m, 3.v.1910, *B. Davidov* (SOM 32066). OSOGOVSKA PLANINA: In uliginosis umbrosis ad p. Skakavica, distr. Kjustendil, 1902, *Iv. K. Urumov* (SOM 32057, 32054). BELASITSA PLANINA: Belasitsa planina, po ptya za vrkh Tumba (portala s. Skrt), 24.v.1998, *S. Kostaninova* (SO 99754); Belasitsa, iz vlazhnite dolove nad s. Kolarovo, 19.v.1999, *P. Zhelev & G. Gogushev* (SOM 154937). RILA: in silvaticis humidis mt. Manastirska Rila ad coenobium Rila, 1200 m, 21.v.1912, *B. Davidov* (SOM 32065); Rila pl., pod Musala do r. Bistritsa, viii.1897, *V. Stribrni* (SO 28202); Rila planina, in silvis *Piceae excelsae* umbrosis inter Saparevo et Skakavica, 1120 m, 31.vii.1923, *A. Novák 225* (PRC); Skakavica planina, 10.vii.1902, *Iv. K. Urumov* (PR); in silvaticis saxosis mt. Malka Rila, Šišman vrch versus rivi Iskar, 1150 m, 27.v.1911, *B. Davidov* (SOM 32070). RODOPI: Ad Jundola m. Rhodope, 1912, *Iv. K. Urumov* (SOM 32046); Sredni Rodopi, Trigradsko zhdrelo, pokrai ptya pod peschlivi kamenisti mesta, 15.vi.1986, *M. Anchev* (SOM 145068); M. Rhodope, in valle fl. Černa supra Rajkovo, 11.viii.1961, *G. Zochev* (SO 28209).

GREECE. NORTH-EAST: Nom. Pellis, Ep. Almopias, Mt. Tzena, N of the village of Notia, by a forest road, 1600–1750 m, 41°09′N, 22°11′E, 30.v.1999, *Strid et al. 49012* (G). NORTH CENTRAL: NW Macedonia, Pisoderion, damp shady place in ravine near the Hagia Trias Monastery, 4000 ft, 28.vi.1932, *A. H. G. Alston & N. Y. Sandwith 1037* (K); Flora of Thrace, Xanthia-Shanin Road., 600 ft, 23.v.1933, *H. G. Tedd* (K). EAST CENTRAL: Olymp, Eichenwäldern im Enipcostal, 1400–1600 m, vii.1938, *E. Behr* (W 21519).

TURKEY. A5 KASTAMONU: Prov. Kastamonu, Ilgaz Dağ, 5000 ft, 9.vi.1954, *Cullen 1963* (K). A7 GIRESUN: Prov. Giresun, Tamdere, Yavuzkemal, near Karinca, by roadside, 1500 m, 13.viii.1952, *Davis et al. 20710* (BM, W 8710, K). A7 TRABZON: Maçka, Hamsiköy, Zigana dağ., Bachufer, 1400 m, 18.vii.1958, *A. Huber-Morath 14788* (G). A7 GÜMÜSHANE: Armenia Turcica, Szanschak Gümüschkhane, Kurzul, im dumetis, 6.vi.1894, *C. Haussknecht 5754*, Iter Orientale 1894 (PRC, PR, G). A8 RHIZE: Prov. Rize, Ikizdere-Carankaya yayla, 1000 m, 25.viii.1952, *Davis 20886 & Dodds* (BM); Bords des torrents de la vallée sous-alpine de Djimil (Lazistan) vers 2000 meters d'altitude, 1866, *B. Balansa* (PRC, K, G). A8 ARTVIN: Prov. Coruh (Artvin), Kardevan dag (Yalnizçan-Dağlari), near Kütül yayla, 2200 m, 28.vi.1957, *Davis 30240 & Hedge* (K, G); idem, 2100 m, 18.vi.1957, *Davis 30203 & Hedge* (K). B9 SATAK: Prov Van, distr. Satak, Kavuçsahap Dag, 6500 ft, 22.vii.1954, *Davis 23011 & O. Polunin* (BM, K).

RUSSIA. KRASNODARSKII KRAI: Caucasus occidentalis, distr. Lazarevskoe, in valle fluminis Shakhe infra vicum Solokhaul, 300 m, 26.vi.1979, *V. Vašák* (W 05699); Chernomor. okr., Sochi, 28.v.1895, *W. Lipsky* (LE); Caucasus occidentalis, distr. Sochi, in valle augusta rivi Agva ad cataractus 'Orekhovye vodopady' dicta, *c.* 300 m, 11.vi.1978, *V. Vašák & A. Vězda* (W 05697); Caucasus occidentalis, distr. Khosta, reservatum naturale 'Sanshitovaya rosca', 100–130 m, 16.vi.1978, *V. Vašák & A. Vězda* (W 05698); Zapadnii Kavkaz, Krasnaya polyana, g. Achishkho, bukovyi les, 5.vii.1988, [sine coll.] (LE); Zapadne Zakavkaz'e, g. Achishkho, JZ sklon, 1850 m, bukovyi les, 3.vii.1979, *I. A. Sakhalova & A. A. Pautov* (LEU); Chernomorskaya g., Krasnaya Polyana, Yu. sklon Achishkho, 30.vi.1915, *A. Abletsov* (LE); Krasnodarskii krai, Labinskii r-n., okr. st. Khodz', 26.v.1989, *Dolmatova et al.* (LE); Severnii Kavkaz, Krasnodarskii krai, Mostovskoi r-n, pos. Psebai, okolo sel. Nikitovka, pravyi bereg r. Malaya Laba, 27.vii.1990, *Yu. Menitskii et al.* (LE); Severo-Zapadnii Kavkaz, vodorazdel r. Bol'shaya Laba, 23.vii.1930, *A. I. Leskov* (LE). ADYGEA: Severnii

Kavkaz, okr. Maikopa, 10.vi.1923, *N. L. Pastuchov* (LE). KARACHAY-CHERKESSIA: Severnii Kavkaz, Stavropol'skii krai, okr. sel. Leso-Kefar' 16 km v verkh po tech. r. Kefar', pravyi bereg, 10.viii.1989, *Yu. Menitskii et al*. (LE); Teberdinskii zapovednik, pos. Dombai, les, 15.ix.1977, *A. O. Malunaev 77-931* (LE); Teberda, 4300 ft, 13.vi.1904, *I. Ya. Akinfieva* (LE); r. Teberda, 22.vii.1939, *V. L. Komarov & I. V. Komarova* (LE); Teberda, 1939, *V. L. Komarov & I. V. Komarova* (LE); Kuban prov., levyi bereg reky Teberdy, 4200 ft, 13–16.vi.1908, *N. Busch* (LE); Kuban prov., Teberda, 4200 ft, 14.vi.1907, *E. A. Endaurova* (LE); Karachay Khumarinskii okrug, lugovina po r. Teberde mezhdu Mikoyan-Shakharom i aulom Senty, 13.vii.1928, *K. I. Marusyak* (LE); Karachevo-Cherkesskaya avtonomnaya oblast', Stavropolskii krai, Dombai, oddelenie Teberdinskogo zapovednika, 7.ix.1974, *M. Kotov* (KW); Stavropol'skii krai, Karachaevo-Cherkesskaya AO, 6–10 km k vostoku ot Ust-Dzheguty, dolinnyi les po r. Dzhegonas, 18.vi.1988, *Geltman et al*. (LE); Kuban, obl. Batalyatinsk, 2.vi.1892, *W. Lipsky* (LE); Karachaevo-Cherkesskaya AO, 7 km k vostoku ot s. Cherkeska, mezhdu s. Markoli i Nizhnaya Mara, 9.vii.1989, *Geltman et al*. (LE). KABARDINO-BALKARIYA: Kavkaz, Kabardino-Balkarskii zapovednik, Tserek Balkarskii verkhoviya, r. Kara-su, 10.vii.1963, *Tikhonova* (LE); Terskaya obl., sel. Nal'chik, 2.v.1970, *V. Pal'tseva* (LE); Kab.-Balk. ASSR, Golubye ozera, lug na pravom beregu r. Cherek, u 1-ogo ozera, 9.vi.1964, *E. Dobynina* (LEU). NORTH OSSETIYA: Severnaya Ossetiya, teritoriya Severo-Osetinskogo zapovednika, verkhov'ya r. Mamison-don, ushchel'e Zemagon, 29.viii.1989, *Yu. Menitskii et al*. (LE); Caucasus, Ossetia, districtus Alagir, 320–330 m, 20.v.1861, *Ruprecht* (LE); Caucasus, Ossetia, pr. Alagir, 14.iv.1899, *Marcowitsch* (LE); Severo-Osetinskii gos. zapovednik i ego okhrannaya zona, Tseiskoe lesnichestvo, levyi bereg reky Tseidon, nizhe turbazy Tsei, 8.vii.1987, *B. P. Serov & I. V. Sokolova* (LE); Kavkaz, Ossetia, Vladivkavkaz, near Lisaya mt., 14.vi.1900, *G. A. Levitskii* (KW). STAVROPOL'SKII KRAI: Flora Stauropolensis, 21.vi.1881, *A. Normann* (LE); Stavropol, 1889, *A. Normann* (LE); Stavropol'skaya vozvyshennost', shirokolistvennye lesa po vos. sklonam g. Strizhament k severu od st. Novo-Ekaterinovskaya, 24.vi.1988, *Geltman et al*. (LE); Kavkaz, Zheleznovodsk, v.1887, *I. Akinfiev* (LE); Terskaya oblast', Zheleznovodsk (u vershiny g. Zheleznaya), v lesu u dorogy, ne chasto, 24.vi.1906, *P. Tischevsky* (KW); Prov. Terek., distr. Pyatigorsk, gora Beshtau, 17.vii.1913, *A. Gordiagin* (LE). CHECHENIYA: Checheno-Ingushetiya SSR, Sovetskii raion, dolina reky Chanty-Argun, okr. sel. Itum-Kale, na beregu ruch'ya, 26.vi.1967, *V. M. Prima* (LE); Checheno-Ingushetiya SSR, Groznenskii raion, okr. stanitsy Petropavlovskaya, opushka lesa, 14.vi.1967, *V. M. Prima* (LE). DAGESTAN: Dagestan, subalpinskii poyas', mezhdu Kodorskim perevalom i s. Khupro, 17.vii.1904, *N. Busch* (LE); Daghestan, subalpiiskii poyas' mezhdu s. Bezhita i perevalom Michishl', 12.vii.1904, *N. Busch* (LE); Tsyarashinskii rn., dolina Avarskno Keieu mezhdu s. Sovetskoe i Tsyarasha v. 7 km yuzhne Kosob-orta (1400–1500 m), vlazhnoi galernik, 19.vii.1961, *N. N. Tsvelev et al*. (LE); Dagestanskaya ASSR, raion Gumbetovskii, mezhdu sel. Burtunai i perevalom k sel. Danukh, bukovyi les po sklonu k rechke, 17.6.1961, *N. N. Tsvelev et al*. (LE); Dagestanskaya ASSR, raion Gumbetovskii, mezhdu sel. Burtunai i perevalom k sel. Danukh, zasurennii lug, 17.vi.1961, *N. N. Tsvelev et al*. (LE); Prov. Dagestan, distr. Dargi, pr. Murguk, 2700 ft, in humidis ad rivulum, 7.vii.1898, *Th. Alexeenko* (LE); Prov. Dagestan, distr. Temir-Chan-Schura [Buinaksk], in declivitate boreali m. Madygir-tau, supra Erpeli, ad rivulum, 4100 ft, 29.vi.1898, *Th. Alexeenko* (LE); Prov. Dagestan, Temir-Chan-Schura [Buinaksk], T. Ch. Schura Erpeli, 1700–1800 ft, 19.vii.1897, *Th. Alexeenko* (LE); Dagestan, Gunibskii okrug, verkhoviya Kara-Lagur, 2400 m, 25.viii.1928, leg. *A. Poretskii* (LE); Dagestanskaya ASSR, Buinakskii raion, vost. sklon Gimrinskogo khr., sel. Verkhni Kazanishi, 7.vi.1961, *N. N. Tsvelev et al*. (LE); Prov. Dagestan, distr. Samur, loco Zassyl-dere, inter Lutszek et Kina, in *Pinetis*, 6000–6600 ft, 9.viii.1898, *Th. Alexeenko* (LE); Dagestanskaya ASSR, Akushinskii raion, mezhdu sel. Garshina i Akusha, dolina r. Akusha, 9.vii.1961, *N. N. Tsvelev et al*. (LE); Dagestanskaya ASSR, Rutul'skii r-n., sel. Khmot mezhdu s. Akhty i s. Rutul Ushcheloe, pravogo pritoka r. Samur, 27.vi.1961, *N. N. Tsvelev et al*. (LE).

GEORGIA. ABKHAZIA: Abkhazskaya ASSR, Gogrskii izvestnyakovyi massiv, yuzhnii makrosklon khr. Berchil', bas. r. Sandripsh, okr. p. Gyuzlya, 12 km k SV OT g. Gagra, 27.vi.1989, *Geltman et al*. (LE); Abkhaziya, verkhnaya chast' levogo borta r. Bzib', gora Adats, 25.viii.1933, *Yu. R. Roskov* (LE); Abkhazskaya ASSR, Gruzinskaya SSR, 25 km above Ritsa, lake Ritsa on acid rock at lumber camp in mixed coniferous/deciduous forest, Lashipse-Bzib valley, 24.vi.1971, *C. R. Frazer-Jenkins 2756* (BM); Caucasus occidentalis, distr. Gudauta, in vicinitate lacus Rica, 1000–1300 m, 21.vi.1977, *V. Vašák* (W); Caucasus occidentalis, distr. Gudauta, in vicinitate lacus Mzymt et angustiarum Acetuki, 1700–2300 m, 16.vi.1971, *V. Vašák* Iter Caucasicum 1971 (PR); Caucasus occidentalis: Georgia: distr. Sukhumi, vicinitas Latior pagi Pskhu, loco Sanchava dicto, secum rivum Akhei, 700–800 m, 5.viii.1983, *V. Vašák* (W); Caucasus occidentalis, distr. Gulripsch, in vicinate pagi Sakeni, 1000–1100 m, 12.vi.1971, *V. Vašák* Iter Caucasicum 1971 (PR). AJARIA: Batumskaya obl., Adzhariya, bl. st. Nonus'-ogly, 1300 m, 25.vi.1913, *D. Litvinov'* (LE). GURIA:

Caucasus occidentalis, distr. Chokhatauri, vicinitas pagi Bakhmaro, montes Meskhadski khrebet, in declivibus septentrionalibus montis Sakornia, 2000–2400 m, 20.vii.1980, *V. Vašák* (W 05702). SAMTSKHE: Adugenskii r-n., okr. Abastunani, 9.viii.1977, *Yu. Menitskii* (LE); pr. Borshom, vi, *G. Radde 134* (LE); Borshom, vii.1865, *G. Radde* (LE); Borshom, 1884, *G. Radde* (LE); Bakuriani, 20.vi.1913, *I. Novopokrovskii* (LE); prope Bakuriani, vi.1881, *A. I. Brotherus & V. F. Brotherus* (LE, BM); Prov. Kartli (K'artli, Kartli), Trialetisches Gebirge (T'rialet'is k'edi, Trialetis kedi), Nordhang des Berges Kokhta gora (Kochta gora), *c.* 2 km ö. Bakuriani, 1800–1900 m, 43°32′E, 41°45′N, 15.vii.1997, *M. Staudinger* (W 01005); Gruz. SSR, Borzhomskii r-n, okr. sel. Tsikhirzhvari, 1800 m, bukovyi les, 27.vi.1980, *T. Popova et al*. (LE); prope urb. Tambow, in silva umbrosa subhumida, 5.vi.1902 fl., 22.vi.1902 fr., *I. Schirajevski* (LEU, KW). KARTLI: Kavkaz, Tiflis, 27.v.1865, *E. Overin* (LE); Caucasus centralis ad fl. Aragwa, *Lagowski* (LE); Kudarskii raion, al'piiskii lug na perevale Dzedo, 1950 m, 8.viii.1928, *E. Busch & N. Busch* (LE); pod perevalom Vanuri-ztseg, pastbishche Erdusta, 2200 m, 8.vii.1930, *E. & N. Busch* (LE); Bass. Maloi Liakhvy, Shuatskhuri, g. Nekh, 18.vii.1933, *E. Busch & N. Busch* (LE); Shuatskhuri, senokosnii subal'piiskii lug na g. Nekh, 2200 m, 9.vii.1930, *E. Busch & N. Busch* (LE); Shuatskhuri, bukovyi les na urochishche Galergevden, na levom borte ushchel'ya r. Bestauty-don, 2000 m, 7.vii.1930, *E. Busch & N. Busch* (LE); Verkhne Kabustinskoe ushchel'e, 7.viii.1929, *E. Busch & N. Busch* (LE); Ermani, Zaleznik r. Verkhnii Ermani, 21.vii.1937, *I. I. Abramov* (W 3341); Yugo-Osetinskii gorno-lugovoi statsionar, mestnost' Ermani, 24.vii.1938, *B. A. Shtakel'berg* (LEU); Yugo-Osetinskii gorno-lugovoi statsionar, mestnost' Ermani, 15.viii.1938, *G. P. Kvaratskheliya* (LEU); Yugo-Osetinskii gorno-lugovoi statsionar, mestnost' Ermani, levyi bort Sredne Ermanskogo ushchel'ya, v bereznyake, 10.vii.1938, *I. I. Abramov* (LE); subal'piiskii senokosnii lug levogo borta Verkhnego Ermanskogo ushchel'ya, 2550 m, 18.viii.1929, *E. Busch & N. Busch* (LE); Chaparukhskoe ushchel'e, les na urochishche Zandzhiket bliz L'bira, 1900 m, 10.viii.1930, *E. Busch & N. Busch* (LE); Kudarskii raion, gora Nasty-tsup (Mikhal-Gabyr), les, 2000 m, viii.1928, *E. Busch & N. Busch* (LE). MTIULETI: In Pasanaur, 550 m, 26.v.1861, *E. Overin* (LE); U perevala Gudaur', 17.vii.1893, *W. Lipsky* (LE). KHEVSURETI: Khevsuria, subalp. lugy mezhdu uroch. Mirgva guba i s. Bats'aligo, 6.vii.1903, *N. Busch* (LE). KAKHETI: Sabuck, 23.v.1820, [sine coll.] (LE); Kakheti, Grosser Kaukazus (Kavkasionis kedi), naturreservat Lagodekhi (Lagodekhis nakrzsali), schluchtartiger Abschnitt bis zum Wasserfall, 550–900 m, 46°18′12″E, 41°52′33″N, 19.v.2001, *G. M. Schneeweis & A. Tribsch* (W 10200).

ARMENIA. TAVUSH: Idzsevanskii r-n., Azartsii i s. Tekhut, 1300 m, 7.vi.1973, [sine coll.] (BM); Tavush province, Ijevan distr., *c.* 6 km N of Dilijan, E of Aghartsin monastery, 1460 m, 44°50′E, 40°46′N, *Fagus orientalis* and *Quercus macranthera* forest with small meadows and rocks in between, 13.vi.2002, *Fayvush et al. Optima Iter XI/0371* (SAV); Transcaucasia, Armenia borealis, distr. Idzhevan, prope p. Idzhevan, in declivibus monti Gatsha, 10.vi.1937, *C. Gurvitsch* (LE). GEGHARKUNIK: Kotayk province, Hrazdan distr., valley of river Marmarik, *c.* 18 km NW of Hrazdan, *c.* 1 km NW of village Artavaz, 1940 m, 44°33′E, 40°38′N, dry to semihumid meadows, tragacanth community with *Astragalus microcephalus*, 17.vi.2002, *Fayvush et al. Optima Iter XI/0839* (SAV). VAYOTS DZOR: Vayotsdzor province, Vajk distr., *c.* 2 km NE of Jermuk, 2115 m, 45°42′E, 39°51′N, forest with *Quercus macranthera* and meadows, 25.vi.2002, *Fayvush et al. Optima Iter XI/2023* (SAV). SYUNIK: Megrinskii r-n., gradsko-dubskoi les vyshe pos. Vardanidzor, 6.vii.1956, *T. V. Egorova et al*. (LE).

AZERBAIDZHAN. XANLAR: Khanlarskii r-n., OKREST. s. Zurnabad, 17.vi.1988, *G. Z. Davi'yan* (LE); Talüsch, 1836, *D. Kavelin* (LE). ZAQATALA: distr. Zakataly, prope pag. Dzhory, 25.v.1936, *T. Heideman & H. Kadinov* (BM); Flora Caucasi, Gub. Elisabethpol, Dis. Nucha, ad fl. Jatuch-czai (Bum-czai), ad ripam 6900 ft, 23.vii.1899, *Th. Alexeenko* (LE). QUBA: Flora Caucasi, Gub. Baku, Dis. Kuba [Quba], ad pag. Chinalug [Xinaliq] (Ketisch, Lechin) SW versus Madzigerdrich, in angustiis, 6900 ft, 22.viii.1900, *Th. Alexeenko* (LE); Transcaucasia, Aserbaidzhan, Kubatenskii r-n., selo Laza, les, 18.vii.1973, *Gatinov* (LE). LENKORAN: Lenkoranskaya expeditsiya, mezhdu s. Lekin i s. Ofanz, 8.vii.1931, *N. Shiiinskii 648* (LE).

IRAN. MAZANDARAN: Mazanderan, Sang-Deh, 30 km SE Polé-Séfid in Rocky mt., 2500–3000 m, 11.vii.1974, *Renz* (W 6842); Mazanderan, Nezva Kuh area, between Orim and Taru, in the forest, 35°59′N, 53°11′E, 2000 m, 6.vii.1959, *P. Wendelbo* (W 14903).

CARDAMINE PECTINATA PALL. EX DC.

BULGARIA. STARA PLANINA: prope Teteveni, 11.v.1910, *Iv. K. Urumov* [orig. det. as *C. graeca*] (SOM 32060); Etropole, s.d., *Iv. K. Urumov* (PRC). KONIAVSKA PLANINA: Koniavska planina, po vlazhni mesta v dol. severo ot Mrzen-Malinazha, 21.vii.1957, *D. Jordanov & As. Janev* (SO 94144). RILA: Rila pl., iz elovite gori pokrai r. Blagoevgradska Bistritsa, 25.vi.1955, *Iv. Penev* (SO 28204); Zap. Rila, iz bukovite gory po severniya sklon v mestnosta 'Dobro pole', 28.vi.1955, *I. Penev* (SO 28206); Rila, rezervat 'Parangalitsa' vlazhni senchesti mesta, yugozapadnii sklon, nad r. Khaidushka, 29.vi.1975, *N. Andreev* (SOM 132165);

Zapadna Rila, Partizanska polyana, 21.vi.1957, *Iv. Bondev* (SOM 109126); Rila pl., nad monastira, s. d., *N. Arnaudov* (SO 28205); Rila, iz gorata v raiona na 'Partizanska polyana' iztochno ot Rilski monastir, 17.vi.1966, *N. Vihodcevsky* (SO 28207); Wald zwischen Borowetz und Bistritza, 13.vi.1964, *W. Hempel* (B); Rila, vlazhni mesta iz iglolistnata gora nad Borovets, 29.vi.1972, *N. Vihodcevsky* (SO 30020); in silvis umbrosis m. Rila, 1909, *Iv. K. Urumov* (SOM 32079); in silvis umbrosis mt. Tsarska Rila, Sokolets, 1300 m alt., 30.v.1910, *B. Davidov* (SOM 32064); in silvaticis humidis mt. Zarska Rila, Zarska Bistriza, 1350 m alt., 5.vi.1911, *B. Davidov* (SOM 32043, SOM 32047, SO 83223); in umbris silvarum M. Rila, viii.1889, *Velenovský* (PRC); in Mont. Rila, v.1894, *Stříbrný* (PRC). Pirin: Pirin, rezervat 'Baiovi dupki' vlazhni senchesti mesta v sobchestva na biala mura, 20.vi.1977, *N. Andreev* (SOM 135641); Montes Pirin (centralis), ad oppidum Bansko, vallis Banderica, *c*. 1900 m, solo calcareo, vii.1936, *I. Klášterský & M. Deyl* (PR).

GREECE. Southern Pindos: Epirus, prov. Ioannina, distr. Metsovo, in latere boreali montis Kira ad austro-occidentem pagi Milea (secum viam ad Metsovo ducentem), 1500 m, 15.viii.1974, *A. Charpin et al*. (G 106058). East Central: Im m. Olympo Thessaliae fagetis supra valle Stravits, 1700–1900 m, 23.vii.1937, *N. Stoyanov & D. Jordanov* (SOM 32037); in *Pineti* umbrosis m. Olympi Thesaliae, 25.v.1851, *de Heldreich* (WU, G); Thesalien: Ossa-Gebirge, SE Olymp, 1200 m, 22°42′E, 39°50′N, 20.v.1989, *H. Malicky* (W); in silvis fagetum, supra Mon. AG. Dimitrios, prope pagum Csaigesi Ossa Mt. (Thess.), 26.vii.1936, *O. Grebenchikov* (K).

TURKEY. A2 Bursa: Bursa, Mezit Deresi, 23.vi.1976, *Y. Akunza, Quézel 6143* (G); Prov. Kütahaya (Bursa), Tavşauli to Inegol, 30 miles from Tavsauli, 1200–1400 m, 23.vi.1962, *Dudley* (W3496). A3-A4 Bolu: Bolu, Auşar Ormani, umgebung von Auşar Yaylasi & Sultanköy Yaylasi, *c.* 1500 m, 20.v.1970, *I. Bozakman & K. Fitz 642* (W 13892); Woods above Abant Gölü, 15.vii.1940, *B. V. D. Post* (G); Seben dag, bei Bolu, *Abies bornmulleriana* wald, 12.v.1955, *H. Walter et al. 4556* (B); Prov. Bolu, Karadere to Yedigöl, bare banks in forest, 650 m, 18.vii.1962, *Davis et al. 37689* (K); Prov. Bolu, distr. Ala Dağ., 800 m, 13.viii.1960, *Khan et al. 554* (K). A5 Kastamonu: Prov. Kastamonu, Ilgaz Dag, 5000 ft, 9.vi.1954, *Davis 21725* (BM); Prov. Kastamonu, distr. Kastamonu, Ilgaz-Dağlari, road Kastamonu Ilgaz, *Abies* forest, 14.viii.1960, *Khan et al. 615* (K); Kastamonu (Paphlagonien), Ilgaz–Kastamonu, Ilgaz Dag, *Abietum* 2 km nördlich der Passhöhe, 1700 m, 21.vi.1955, *A. Huber-Morath 13762* (G). A5 Sinop: distr. Ayancik, Cangal Dag ab Ayancik, 1100 m, 1.vii.1958, *A. Huber-Morath 14787* (G). A7 Giresun: 25 km S of Giresum, 500 m, 7.vii.1969, *F. Sorger* (W 8277). A7 Trabzon: Trabzon, 3 km S of Hamsiköy (*c*. 45 km SSW of Trabzon), mixed forest of *Picea* and *Fagus*, with shrub layer of mainly *Carpinus*, *Corylus*, *Alnus*, *Sambucus*, *Ribes*, and *Rhododendron*, humid loamy soil, *c*. 1900 m, v–vi.1959, *Hennipman et al. 1867* (K, B); Trabzon, on slopes in woodland ascending to Sumela Monastery, *c*. 53 km S of Trabzon, 1180 m, 8.v.1988, *C. C. Townsend 88/83* (K); Prov. Trabzon, Soganli Pass, growing with roots in running water very bushy, 7000 ft, 17.viii.1962, *P. Furse 3985* (K); Prov. Trabzon, Soganli Pass, 5000 ft, 16.viii.1962, *P. Furse 3948*, *3966* (K); Trabzon, Bayburt, of 2 km N pass, 2300 m, 14.vii.1984, *M. Nydegger 19166* (G 488601); in umbrosis supra Keuprubacku, inter Trapezuntem [Trabzon] et Baibout [Baiburt], 5500–6000 m, v.1853, *Huet du Pavillon*, Plantae Orientales exsiccae (K). A8 Rhize: Prov. Rize, Ikizdere-Carankaya yayla, 1000 m, 25.viii.1952, *Davis 20886 & Dodds* (K); Región montagnese du Lazistan prés de Djimil, 1800 m, 19.vii.1866, *B. Balansa* (P, G); Eviron de Rhizé, bouddes chemins humides, alt. 400 m (Lazistan), vi.1866, *R. du Parquet* (BM); Environs de Behizé (Lazistan), sur les salus ombragés des chemins creux, 27.v.1866, *B. Balansa* (K, PRC, G); in alpibus Lazistani, *A. Eloy 113* (K); Rize, 100 ft, 22.iv.1959, *K. M. Guichard TUR/24/59* (K); Senyuva, Strasserand, 14.iv.1969, *Steiner* (W 04033); Rize, SE oberhalb Ayder Ilica, 16–18 km SE Çamlihemşim, 1400–1500 m, 8.ix.1980, *F. Sorger* (W 8278). A8 Artvin: Artvin, by roadside flush 5 km S of side turning to Demirkent, Çoruh valley, 50 km S of Artvin, 10.ix.1970, *C. R. Fraser-Jenkins 2390* (BM); Prov. Çoruh (Artvin), mountain above Artvin, wet places in *Picea* forest by stream, 1800 m, 19.vi.1957, *Davis 29775 & Hedge* (K, W 8708); Prov. Çoruh (Artvin), mountains above Artvin, 1800 m, 19.vi.1957, *Davis 29775 & Hedge* (BM); Prov. Artvin (A9), Yalniczam Gebirge bei Karaköy, östlich von Savsat, 1900 m, im Felsgeröll eines Blockstromes in der oberen *Abies–Picea*-Nadelwaldstufe, 5.viii.1981, *Raus 4771* (B); 20 km E Savsat, wald 2000 m, 4.viii.1981, *Raus* (W8276); Artvin A9, Yalniczam Silsilesi, 8 km SE of Şavşat, *c.* 1750 m, 10.vii.1967, *Albury et al*. 3144 (K); Prov. Çoruh (Artvin), Kordevan dag (Yalnizçan–Daglari) near Kütül yayla, 2100 m, *Picea* forest, 18.vi.1957, *Davis & Hedge 30203* (BM). A8 Erzurum: Erzeroum (Erzurum), M. Zorab (Zohrab) [s.d., s. coll.] (K). B1 Balikesir: Anatolien, Çatal dag, bei Balikesir, 18.vi.1955, *H. Walter et E. Walter 661* (B). C6 Hatay: Plantae Syrae Borealis, Montes Amanus, vallés, 800–3000 ft, 1913, *M. Haridjian 4670* (G).

RUSSIA. Krasnodarskii krai: Caucasus occidentalis: distr Adler (Sochi), in faucibus fluminis Psakho, infra vicum Kamenka, 200–300 m, 21.vi.1979, *V. Vašák* (G 2169346); Caucasus occidentalis: Colchis: distr. Sochi, in vicinitate pagi Izmailovka, in valle fluminis Macesta, 200–400 m, 4.vii.1984, *V. Vašák* (W); Caucasus occidentalis: distr. Sochi, in vicinitate pagi Macesta, ad ripam sinistram rivuli Macesta, 50–200 m, 7.vi.1978, *V. Vašák* (G 269343); Flora Caucasica, Zap. Zakavkaz'e, Khosta zapovednik, 18.vi.1962, *N. Spasskaya* (LEU), *L. K. Aleksandrova* (LEU); Zap. Zakavkaz'e, Krasnodarskii krai, Khostinskii zapovednik, syrie tenistye mesta, 27.vi.1958, *K. K. Smirnova* (LEU); Caucasus occidentalis: distr. Sochi, in faucibus rivi Agua (flumen Sochi 15 km ab ostio), 100–150 m, 17.vi.1979, *V. Vašák* (W); Caucasus occidentalis, distr. Sochi, in valle augusta rivi Agva ad cataractus 'Orekhovye vodopady' dicta, *c*. 300 m, 11.vi.1978, *V. Vašák & A. Vězda* (G 269344); Yuzhnaya chast Chernomorskogo okruga mezhdu Adlerom i Tuanse, 25.viii.1929, *S. Ya. Sokolov* (LE); Krasnaya polyana, p. Pudzik, 6.vii.1936, *N. Busch* (LEU); Zapadne Zakavkaz'e, gora Achishkho, 1200 m, bukovyi les, 3.vii.1979, *T. Onipko et al*. *238* (LEU); Chernomorskaya Gub., Achishkho, 19.vii.1907, *A. N. Kiritschenko* (LE); Zapadnoe Zakavkaz'e, Krasnaya polyana, gora Achishkho, sklon yuzhnoi ekspozitsii, poyas bukovogo lesa, 4.vii.1985, *I. V. Seferova* (LE); Zapadne Zakavkaz'e, Yugo-zap. sklon g. Achishkho, bukovyi les, 1800 m, 3.vii.1979, *L. I. Kurlakova* (LE); Chernomorskii okrug, Kr. Polyana, yuzhni sklon g. Achishkho, 1500 m, 12.vi.1930, *Yu. P. Byallovich* (LE); Chernomorg. okr., Krasnaya Polyana, 3.viii.1895 (LE); Cherkesia, Chernomorskii okr., g. Achishkho, 9.vi.1929, *W. Steup* (LE); Chernomorskaya gub., Achishkho, 19.vii.1907, *A. N. Kiritschenko* (LE); Caucasus occidentalis: distr. Adler, in vicinitate pagi Krasnaya Polyana, vallis flumionis Mzymta, 900–1000 m, 15.vi.1976, *V. Vašák* (G 314654). ADYGEA: Zapadnii Kavkaz, levyi bereg reky Belaya mezhdu sel. Hamishki i Tuzerini, *Carpineto-Rhododendretum*, 500 m, 5.vii.1951, *Ig. V. Vasiliev* (LE); Kavkazskii zapovednik, Maikopskii raion, Tuzerini, dolina reky Belaya, 3.vii.1935, *Ig. V. Vasiliev* (LE); Zapadnii Kavkaz, v 34 km ot Dakhovskoi (stanitsy) po levomu beregu reky Beloi, suchoi kamenisty sklon s dubravoi, 500 m, 5.vii.1951, *Ig. V. Vasiliev* (LE); Severo-Zapadnii Kavkaz, vodorazdel r. Belaya Laba, 16.vii.1930, *A. I. Leskov* (LE). KARACHAY-CHERKESSIA: Kavkaz, Kubansk, obl. Teberda, 4200 ft, 1.v.1905, *D. Lumeinov* (LE); Stavropol'skii krai, Pregradnenskii r-n., pravyi bort ushch. r. Bol'shaya Laba, v okr. p. Zagedan (40 km k yu. ot p. Kurdzhinovo), 6.vii.1989, *Dolmatova et al*. (LE).

GEORGIA. ABKHAZIA: Abkhaziya, okresnosti ozera Ritsa, 22.v.1959, *S. Lipschitz* (LE); Abkhazskaya ASR, Ritse-Abkharskii zapovednik, u ozera Ritsa, na bregu, 950 m, 14.v.1955, *M. Kotov* (KW); Zap. Zakavkaz'e, Abkhazskaya ASSR, elovo-pichtovyi les, SV sklon, v 10 km ot ozera Ritsa, 1100 m, 2.vi.1963, *N. G. Averyanova* (LEU); Caucasus occidentalis, distr. Gagra, apud 'Goluboe ozero' in vicinitate rivi Bzyb, 150 m, 15.vi.1971, *V. Vašák*, Iter Caucasicum 1971 (PR); Zap. Zakavkaz'e, Avadkharskii zapovednik, doroga na Avadkharu, 12.vi.1957, *A. Bobrov* (LEU); Zap. Zakavkaz'e, Abkhazskaya ASSR, r. Avadkhara, 1900 m, severnii sklon, v tenistom i vlazhnom meste, 28.vi.1964, *Belozub et al*. (LEU); Caucasus occidentalis, distr. Gudauta, prope rivulum Avatchara, 1700–2100 m, 15.vi.1971, *V. Vašák,* Iter Caucasicum 1971 (PR, G); Caucasus occidentalis, distr. Gudauta, in vicinate lacus Mzymt et angustiorum Acetuki, 1700–2300 m, 16.vi.1971, *V. Vašák*, Iter Caucasicum 1971 (PR); Abkhazskaya SSR, Sukhumskii r-n., ot Pskhu k Anchkho, 12.vii.1980, *T. Popova et al*. (LE); Caucasus ocidentalis: distr. Sukhumi, in faucibus fluminis Vostochnaya Gumista, prope pagum Kaman, 250 m, 23.vi.1977, *V. Vašák* (G 289300); Caucasus occidentalis: distr. Sukhumi, vicinitas pagi Akhalsheni, in valle fluminis Zapadnaya Gumista, 400–700 m, 13.vii.1980, *V. Vašák* (W); Caucasus occidentalis, distr. Sukhumi, in declivibus apud rivum Gumista, 10–150 m, 13.vi.1971, *V. Vašák* Iter Caucasicum 1971 (PR); Abkhazskaya ASSR, Gul'ripshskii r-n, okresnosti s. Amtkel, dolina r. Kholodnoi, v 6 km k SSV ot Tsebel'dy, 25.vi.1989, *A. Dolmatova et al*. (LE); Caucasus occidentalis, distr. Gulripsh, in vicinitate pagi Sakeni, 1000–1100 m, 12.vi.1971, *V. Vašák*, Iter Caucasicum 1971 (PR); Caucasus occidentalis, distr. Gulripsh, in declivibus montis Lachult, in vicinitate pagi Sakeni, 1300–2000 m, 10.vi.1971, *V. Vašák* Iter Caucasicum 1971 (PR). AJARIA: Prov. Batum, ad rupes humidas prope fort Goniiskii, 1902, *Alexeenko & Woronow* (LE); Prov. Batum, in silvis ad rupes littoralis prope fort Goniiskii, 100–300 ft, 30.v.1902, *Alexeenko & Woronow* (LE); Batumskii botanicheskii sad, pri vkhode s Zel. mysa, vmeste s *Trachystemon* i *Petasites*, 28.viii.1987, *A. Dmitrieva* (LE); Batumskii botanicheskii sad, 2.ii.1962, *A. Dmitrieva* (LE), idem, 27.v.1962, *A. Dmitrieva* (LE), idem, 16.iv.1973, *A. Dmitrieva* (LE); idem, 19.viii.1980, *A. Dmitrieva* (LE), idem, 12.ii.1939, *Popov* (LE), Chernomorskaya Gub., Sukhumskii okrug', Batumskaya oblast', vershina Aibgi, 1911, *I. V. Palibin & N. I. Vorobev* (LE); Kavkaz, Batumsk. obl., i u. okr. Batuma, na Zelenom' mysu, okrainy smeshan., bukovogo lesa, 12.vi.1916, *P. N. Krylov & E. I. Shteinberg* (LE); okr. Batuma, Zelenii mys, listennyi les, bliz botanicheskogo sada, 4.vii.1917, *B. Shishkin* (LE); Flora Caucasica, Chakva, 3.iv.1896, *B. Levandowski* (LE); Batumi, po r. Chakve, na skalakh, 21.iv.1950, *M. G. Popov & K. D. Stepanova* (LE); Adzhariya, okr. sela Khulo, 13.ix.1939, *A. Dmitrieva* (LE). GURIA: Makharadzevskii r-n., doroga Chokhatauri-Kobuleti, 22.iv.1987, *V. Nikitin et al*. (LE); Zakavkazie, Guriya, Kutaisskaya gub., Ozurgetskii u., vi–vii.1914, *E. I. Kikodse* (LE); Caucasus occidentalis, distr. Chokhatauri, vicinitas pagi Bakhmaro, montes Meskhadski khrebet, in declivibus septentrionalibus montis Sakornia, 2000–2400 m, 20.vii.1980, *V. Vašák* (B); Caucasus occidentalis, distr. Chokhatauri, ad orientem versus pagi Bakhmaro, montes Meskhetski khrebet, in declivibus montis Mzis amosulis gori, 2000–2300 m, 23.vii.1979, *V. Vašák & G. Esrandzhia*, Iter Caucasicum secundum 1979 (W). SAMTSKHE: Transcaucasia, montes Ssuremenses, praedium Rikoti [above Borjomi], 3900 ft, 21.vi.1902, *R. Regel* (LEU); Georgia, inter Bakuriani et Tanbiszchuni, vi.1881, *A. I. Brotherus & V. F. Brotherus* (LE); Bakuriani, Zagveri, vi.1881, *A. I. Brotherus & V. F. Brotherus* (BM). KARTLI: les bliz Dzhalabet, uroch. Khusar, 1300 m, 27.viii.1928, *E. Busch & N. Busch* (LE); Shuatskhuri, ushchel'e r. Potnisa, bukovyi les, 5.vii.1930, *E. Busch & N. Busch* (LE); Bass. Maloi Liakhvy Shuatskhuri, Ikata, bukovyi les, 23.vii.1933, *E. & N. Bush* (LE); verkhov'ya Kuptinskogo ushchel'ya, zarosl. *Rhododendron caucasicum* na g. Dzirisa, 2100 m, 8.viii.1930, *E. & N. Bush* (LE); Chaparukhskoe ushchel'e, les Skatykom-kad, 1900 m, 20.vii.1930, *E. Bush & N. Bush* (LE); okr. s. Fatkudzhin, 1250 m, 27.viii.1928, *E. Bush & N. Bush* (K). KAKHETI: Kakheti, Groser Kaukazus, Natureserve Lagodekhi, Schluchtartiger, Abschnitt bis zum Wasserfall, 550–900 m, 46°18′12″E, 41°52′33″N, 19.v.2001, *G. M. Schneeweiss & A. Tribsch* (WU).

AZERBAIDZHAN. QUBA: Florae Trascaucasiae, Gila, vii.1873, *N. Sredinsky* (LE). LENKORAN: Gub. Baku, Talysch, in silvis umbrosis inter Sijon et Tazdy-Pok, 3300–4100 ft, 3.viii.1897, *Th. Alexeenko* (LE); Transcaucasia, Azerbajdzhan, prov. Baku, distr. Lenkoran, inter m. Naduz-galasi et p. Kagoj, 14.vii.1929, *L. Prilipko* (LE). ASTARA: Azerb. SSR, Lenkoran, okr. Astara, r. Ismi-su (Usmi-su), 20.vii.1975, *Yu. Menitskii & T. Popova* (LE).

IRAN. GILAN: Guilan, vi.1936, *N. Lindsay 1063* (BM); Qulan, *N. Lindsay 870* (BM); Gilan, m. Talyschgebirge, *P. Buhse* (K); Prov. Gilan, in silvis supra Asalem (Navrud) ad viam versus Khalkhal (Herowabad) ducentem, 200–800 m, 15.v.1971, *K. H. Rechinger* (W 11854, 11855). MAZANDARAN: Mazandaran: in montis silvaticis 10 km merid. Ab oppido Behsharh, 23.vi.1977, *J. Soják* (SAV); Dimalu, Mazenderan, in dense shade, 23.vii.1940, *W. Koelz* (W 6671); Sargan, Bandar Gaz, v.1968, *Sharif* (W 6978); Mazandaran, Kiasak, Pete forest, 1250–1600 m, 10.vii.1974, *Rense* (W 6836); S of Chalus, Caspian rain forest, 500 ft, 27.vi.1962, *P. Furse 2885* (K); Elburz in foothills near Chalus, 1500 ft, 17.iii.1962, *P. Furse* (K); Mazanderan, im Elbursgebirge bei Weyser, östlich des Chalus-Tales, 1150 m, 31.vii–6.viii.1968, *E. Steiner & H. M. Steiner* (W 2471); Mazanderan, S of Amol, *c.* 60 m, 11.vi.1966, *J. C. Archibald 2295* (K); Lajim forest, Manzanderan, 3000 ft, 20.v.1955, *H. F. Mooney 6633* (W 17400); Lajim forest, Mazanderan, under shady moist calcareous clay bank in beech forest, 3000 ft, 20.v.1955, *H. F. Mooney* (K); Ladjim, Aghamashad (Fagetum), 800 m, 30.iv.1965, *Tregubov* (W 1844); Ostan 2, entre Khozlok et Gurgan, forêt humide, 300–1600 m, 6–7.vi.1956, *F. Schmidt 6022* (W24346, G); Sargan, Naharkhorran, 21.iv.1974, *Riedl & Ershad* (W 21444); in montis Astrabadensis prope Siaret, iv–v.1858, [without *leg.*] (K, G); Prov. Gorgan (Asterabad), in silvis prope Sharbat inter Gorgan et Ziarat, s/d, *Gauba* (W 6823).