

Paeonia (Paeoniaceae) in the Caucasus

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The taxonomy of the genus *Paeonia* in the Caucasus has been controversial, with recognized species varying in number from one to 13. The taxonomic history of *Paeonia* in this area is reviewed (including an analysis of the characters used by previous authors) based on extensive field observations, population sampling and critical examination of a large number of herbarium specimens. The results show that *Paeonia* may be divided into three groups. The *P. intermedia* group is known from only a single population. In the *P. tenuifolia* group, all the characters used for distinguishing the three previously recognized species were found to be polymorphic. In the *P. daurica* group, petal colour, shape and size of leaflets, and indumentum of leaflets and carpels were used to distinguish nine species, but these characters were found to be polymorphic or continuous in variation, and thus can only be used for infraspecific classification. Thus, three species are recognized: *P. intermedia*, *P. tenuifolia* and *P. daurica*. The last species is further divided into five subspecies: ssp. *coriifolia*, *wittmanniana*, *mlokosewitschii*, *macrophylla* and *tomentosa* **stat. nov.** © 2003 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2003, 143, 135–150.

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INTRODUCTION

The taxonomy of the genus *Paeonia* in the Caucasus Mountains has been controversial, with the number of recognized species varying from one (Albow, 1895), three (Huth, 1892), four (Ruprecht, 1869; Busch, 1901), five (Lomakin, 1897), six (Grossgeim, 1930, 1950; Stern, 1946), seven (Lipsky, 1899) and nine (Schipcinsky, 1937), to as many as 13 (Kemularia-Nathadze, 1961). An up-to-date taxonomic treatment is urgently required, based on a deeper understanding of the biology of *Paeonia* in this region, particularly of the variation of characters and their taxonomic value. We recently undertook an expedition to the Caucasus, where we conducted extensive field observations and population sampling. In addition, we critically examined a large number of herbarium specimens from the Komarov Institute of Botany, Russian Academy of Sciences (LE), National Institute of Botany, Georgian Academy of Sciences (TBI), and National Institute of Botany, Azerbaijan Academy of Sciences (BAK). Fol-

lowing a careful study of morphological characters, we present a taxonomic revision.

REVIEW OF TAXONOMIC HISTORY

Paeonia in the Caucasus was first recorded by Ledebour (1842), who identified three species: *P. corallina* (= *P. mascula*) (Georgia), *P. tenuifolia* (Armenia), and *P. hybrida* (near Stavropol, Russia; misidentification of *P. tenuifolia*).

Lindley (1846) described a yellow flowered *Paeonia* species as new – *P. wittmanniana* Hartwiss ex Lindley – based on material from Abchasia in Georgia, sent by C. M. Worontzoff. Two years later Steven (1848) described as new a *Paeonia* species with yellow petals under the same specific name, *P. wittmanniana* Steven, based on material from Atskhu, Meskheta, Georgia. These taxa are similar, although the former has tomentose carpels, while the latter, according to the prologues, has glabrous ones. Kemularia-Nathadze (1961) gave the latter a new specific name, *P. steveniana* Kem.-Nath.

Boissier (1867) enumerated three species with short descriptions: *P. corallina* and *P. corallina* var. *triter-*

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nata, *P. wittmanniana* Steven, and *P. tenuifolia*. He pointed out that the leaf of *P. wittmanniana* was similar to that of *P. corallina*, but differed in having yellow flowers and glabrous carpels.

Ruprecht (1869) recognized four species: *P. triternata* (with a new form, f. *coriifolia*), *P. wittmanniana*, *P. tenuifolia*, and a new species, *P. biebersteiniana*, based on material from Stavropol in Russia.

Huth (1892) distinguished three, based on whether leaflets were entire or lobate and petals yellow or red: *P. corallina* var. *typica*, *P. tenuifolia* and *P. wittmanniana*.

Albow (1895) did not consider colour to be of value for distinguishing species. Thus, *P. wittmanniana* was reduced for the first time to a variety of *P. corallina*, i.e. *P. corallina* var. *wittmanniana*, under which he described a new form, f. *macrophylla*, based on specimens from Adjara, Georgia.

Lomakin (1897) recognized five species. In addition to enumerating *P. tenuifolia* and *P. corallina*, he described a new species, *P. mlokosewitschii* Lomakin from Lagodekhi in east Georgia, which has yellow flowers, leaflets obovate, rarely oblong, and short-puberulous beneath, and tomentose carpels. He also described a new variety, *P. wittmanniana* var. *tomentosa* Lomakin, from the Talysh Mountains, Azerbaijan, with tomentose carpels, and raised Albow's form, *P. corallina* var. *wittmanniana* f. *macrophylla*, to specific rank, *P. macrophylla* (Albow) Lomakin.

Lipsky (1899) enumerated seven, following Lomakin's taxonomy but separating *P. triternata* from *P. corallina* and *P. biebersteiniana* from *P. tenuifolia*.

Busch (1901) adopted a new classification, recognizing four, based on petal colour and leaf shape and division: *P. corallina* ssp. *triternata* (Pall.) Boiss., *P. corallina* ssp. *triternata* var. *coriifolia* (Rupr.) N. Busch, *P. tenuifolia*, *P. tenuifolia* var. *biebersteiniana* (Rupr.) N. Busch, *P. wittmanniana* f. *macrophylla* (Albow) N. Busch, *P. wittmanniana* ssp. *tomentosa* (Lomakin) Lomakin, and *P. mlokosewitschii* Lomakin.

Grossgeim (1930) recognized six, based on petal colour, shape and division of leaflets, and indumentum of leaflets and carpels: *P. tenuifolia*, *P. corallina* (var. *caucasica* Schipchinsky and var. *coriifolia* (Rupr.) Grossgeim), *P. mlokosewitschii*, *P. wittmanniana*, *P. wittmanniana* var. *macrophylla* (Albow) N. Busch, *P. tomentosa* (Lomakin) N. Busch ex Grossgeim and *P. abchasica* Misch. ex Grossgeim.

Schipczinsky (1937) recognized nine, placed in three series: (1) series Obovatae Kom. which was described as having leaf lobes (or leaflets) entire, more or less orbicular or ovate, rarely acuminate, with one species in the Caucasus, *P. mlokosewitschii* Lomakin; (2) series Corallinae Kom. with leaf lobes entire, rather wide, acuminate, including *P. triternata* Pall.,

P. caucasica N. Schipcz., *P. wittmanniana* Hartwiss ex Lindl., *P. macrophylla* (Albow) Lomakin, *P. tomentosa* (Lomakin) N. Busch, and *P. abchasica* Misch. ex Grossg., distinguished by petal colour, indumentum of carpels, and size and indumentum of leaflets; (3) series Fissae Kom. with leaves biternate, triternate or pinnate, and multifid with narrow segments, including two species – *P. tenuifolia* and *P. biebersteiniana* – distinguished by width and indumentum of leaf segments.

Stern (1946) recognized six, assigning them to two subsections in section *Paenonia*: (1) subsect. *Dissectifoliae* with two species, *P. tenuifolia* and *P. anomala* var. *intermedia* (*P. biebersteiniana*); (2) subsect. *Foliolatae* with four species, *P. daurica*, *P. mascula*, *P. mlokosewitschii*, and *P. wittmanniana* (with four varieties), distinguished by petal colour, shape of leaflets, and indumentum of leaflets and carpels.

Grossgeim (1950) also recognized six, although these differed from those in his 1930 classification: *P. biebersteiniana* was treated as a species, not as a variety; *P. corallina* was divided into two species, *P. daurica* (= *P. mascula*; *P. corallina*) and *P. kavachensis* (*P. caucasica*); *P. tomentosa* was reduced to a synonym of *P. mlokosewitschii*; and *P. abchasica* was treated as a synonym of *P. wittmanniana*.

Ketzchoweli (1959) described two new species: *P. majko* and *P. carthalinica*. The former was based on material from Igoeti, Kartli, Georgia and belongs to the *P. intermedia* group. The type of *P. carthalinica* was from the same locality and was said to be very closely related to *P. tenuifolia*, differing from it in having broader leaf segments and greyish pubescence on ovaries and fruits.

The most radical treatment was that of Kemularia-Nathadze (1961), who described the species in the Caucasus and also erected a taxonomy for the rest of the genus. She divided the genus into five sections according to habit, petal colour and texture, margin and division of leaflets. It was further divided into 18 series. For peonies in the Caucasus, she recognized 13 species in five series of three sections. The previously described species were all accepted by her except for *P. abchasica*. In addition she described two new species: *P. ruprechtiana* and *P. steveniana*. She believed that *P. carthalinica* might be identical to *P. tenuifolia*. She frequently used slight differences in colour of leaves and hairs on leaves or carpels (e.g. leaves green vs. dull-green; glaucescent on both sides vs. green on both sides or blue-greyish on the lower side; ovaries and fruits red-tomentose vs. yellowish or whitish-greyish tomentose). Her work will be discussed further in 'Observations and Discussion'.

It is thus clear that the taxonomic history has been varied and controversial. At one extreme, Albow (1895)

recognized only one species, *P. corallina*, while at the other Kemularia-Nathadze (1961) accepted all the described species, except for *P. abchasica*, and described two new ones. Huth (1892), Busch (1901) and Lomakin (1897) held an intermediate position, recognizing three, four and five species, respectively. In addition to using petal colour, division of leaves, shape and size of leaflets, and indumentum of leaflets and carpels to delimit species, Kemularia-Nathadze (1961) also used slight differences in texture and colour of leaflets, colour of hairs on carpels and so forth.

Our purpose in this paper is to address the following questions: Which characters are truly diagnostic? Is petal colour, for example, really so useful that it can be used for distinguishing species, groups of species or even sections? How many species are there in the Cau-

casus? Our conclusions are based on critical examination of variations in morphological characters and evaluation of their taxonomic value.

MATERIAL AND METHODS

We travelled to the Caucasus, touring the relevant areas in Georgia, Azerbaijan, and Russia. We visited the type localities of all the taxa described from the region except for *P. wittmanniana*. All morphological characters were examined critically and their variation documented. Thirteen populations were sampled in the field, and vouchers are deposited in the herbaria A, CAS, K, MO, PE and US. The populations studied included herbarium specimens listed in Table 1. In addition, individuals of *P. wittmanniana* (type locality,

Table 1. Populations of *Paeonia* sampled in fieldwork in 1999

Population	Locality	Community	Herbaria	Taxon
H99028	Georgia: Kartli, Igoeti, 630 m	Sandstones, S. slope, sparse bushes and grasses	A, CAS, K, MO, PE, US	<i>P. tenuifolia</i>
H99029	as above	Sandstones, deciduous forest gentle NW slope, thick soil	A, CAS, K, MO, PE, US	<i>P. caucasica</i> (= <i>P. daurica</i> ssp. <i>coriifolia</i>)
H99033	as above	as above	PE	The type locality of <i>P. majko</i> (= <i>P. intermedia</i>)
H99035	Georgia: Lagodekhi, 1040 m	S. slope, deciduous forest	A, K, MO, PE, US	The type locality of both <i>P. mlokosewitschii</i> and <i>P. lagodekhiana</i> (= <i>P. daurica</i> ssp. <i>mlokosewitschii</i>)
H99039	Georgia: Borjomi, National Park, 870 m	Volcanic rock, N. slope, mixed conifer and deciduous broad-leaved forest	MO, PE	The type locality of <i>P. ruprechtiana</i> (= <i>P. triternata</i> f. <i>coriifolia</i> = <i>P. daurica</i> ssp. <i>coriifolia</i>)
H99043	Georgia: Kartli, Mukhrani, near Village Dampalo, 760 m	S. slope, river terrace, sparse bushes and young trees	A, CAS, K, MO, PE, US	The type locality of <i>P. carthalinica</i> (= <i>P. tenuifolia</i>)
H99046	Azerbaijan: Lerik, Orand, Zubu, (Mt. Talysh.), 1170 m	Sandstones, pasture with bushes and young trees	as above	The type locality of <i>P. tomentosa</i> (= <i>P. daurica</i> ssp. <i>tomentosa</i>)
H99052	Russia: Stavropol, 630 m	Gentle S. slope, sloping meadows,	as above	The type locality of <i>P. biebersteiniana</i> (= <i>P. tenuifolia</i>), and <i>P. tenuifolia</i>
H99053	as above	500 m away from H99052	as above	as above
H99059	Russia: Krasnodar, E of Klyuch, 400 m	Sandstone, S. and N. slope, deciduous forest	as above	<i>P. caucasica</i> (= <i>P. daurica</i> ssp. <i>coriifolia</i>)
H99060	Georgia: Borjomi, Bakuriani, 1700	Volcanic rocks, N. slope, pure <i>Fagus</i> forest	as above	The type locality of <i>P. steveniana</i> (= <i>P. daurica</i> ssp. <i>macrophylla</i>)
H99062	as above	Volcanic rock, S. slope, <i>Picea orientalis</i> forest and glade	MO, PE	ditto
H99065	Georgia: Adjaria, Machuhtseti, 1160 m	NE. slope, <i>Fagus</i> forest	A, CAS, K, MO, PE, US	The type locality of <i>P. macrophylla</i> (= <i>P. daurica</i> ssp. <i>macrophylla</i>)

Abchasia) now in the Tbilisi Botanical Garden and of *P. daurica* (type locality, Tauria) in the Five-Mountains Eco-Botanical Station in Pyatigorsk, Russia, were vouchered by herbarium specimens H99025, H99068 and H99056.

More than 400 herbarium specimens from the Komarov Institute of Botany, Russian Academy of Sciences (LE), National Institute of Botany, Georgian Academy of Sciences (TBI), National Institute of Botany, Azerbaijan Academy of Sciences (BAK), and Batumi Botanical Garden, Georgian Academy of Sciences (BATU), were critically examined and the variation of morphological characters analysed.

OBSERVATIONS AND DISCUSSION

According to our observations in the field and in the herbaria, with reference to previous classifications (Ketzchoweli, 1959; Kemularia-Nathadze, 1961), *Paeonia* in the Caucasus may be classified clearly into three major groups as follows:

- 1 Roots fusiformly thickened; leaflets/segments of lower leaves more than 70 in number, narrow-lanceolate to filiform, less than 1.5 cm wide.
 - 2 Leaflets/segments of lower leaves with segments less than 100 in number, narrow-lanceolate 1, *Intermedia* group.
 - 2 Leaflets/segments of lower leaves more than 130 in number, linear to filiform 2, *Tenuifolia* group.
- 1 Roots carrot-shaped; leaflets of lower leaves mostly 9, rarely 10–19; leaflets ovate, oblong or obovate, over 3 cm wide 3, *Daurica* group.

GROUP 1: *INTERMEDIA*

This group was discovered by Ketzchoweli (1959) near the village of Igoeti, Kartli district, Georgia and described as a new species, *P. majko*. It had a single small population (voucher H99033). We found this population in a deciduous forest of *Quercus*, *Carpinus*, *Cornus*, *Acer* and *Crataegus* with thick soil. We saw only five individuals (the flowers had already been plucked by someone). Luckily, in a private garden in Tbilisi City we encountered one flowering individual, introduced from the type locality. With permission, we collected one stem with a flower (H99034). The plant had fusiform-thickened roots, ternate leaves with 78–91 leaflets/segments that were 4–10 mm wide and glabrous on both sides, red flowers with two bracts, three sepals, five petals, and two tomentose carpels.

These morphological characters show no significant differences from those of *P. intermedia*, which is distributed in Central Asia from the Altai Mountains to Uzbekistan. Therefore, Group 1 is probably most appropriately named *P. intermedia*.

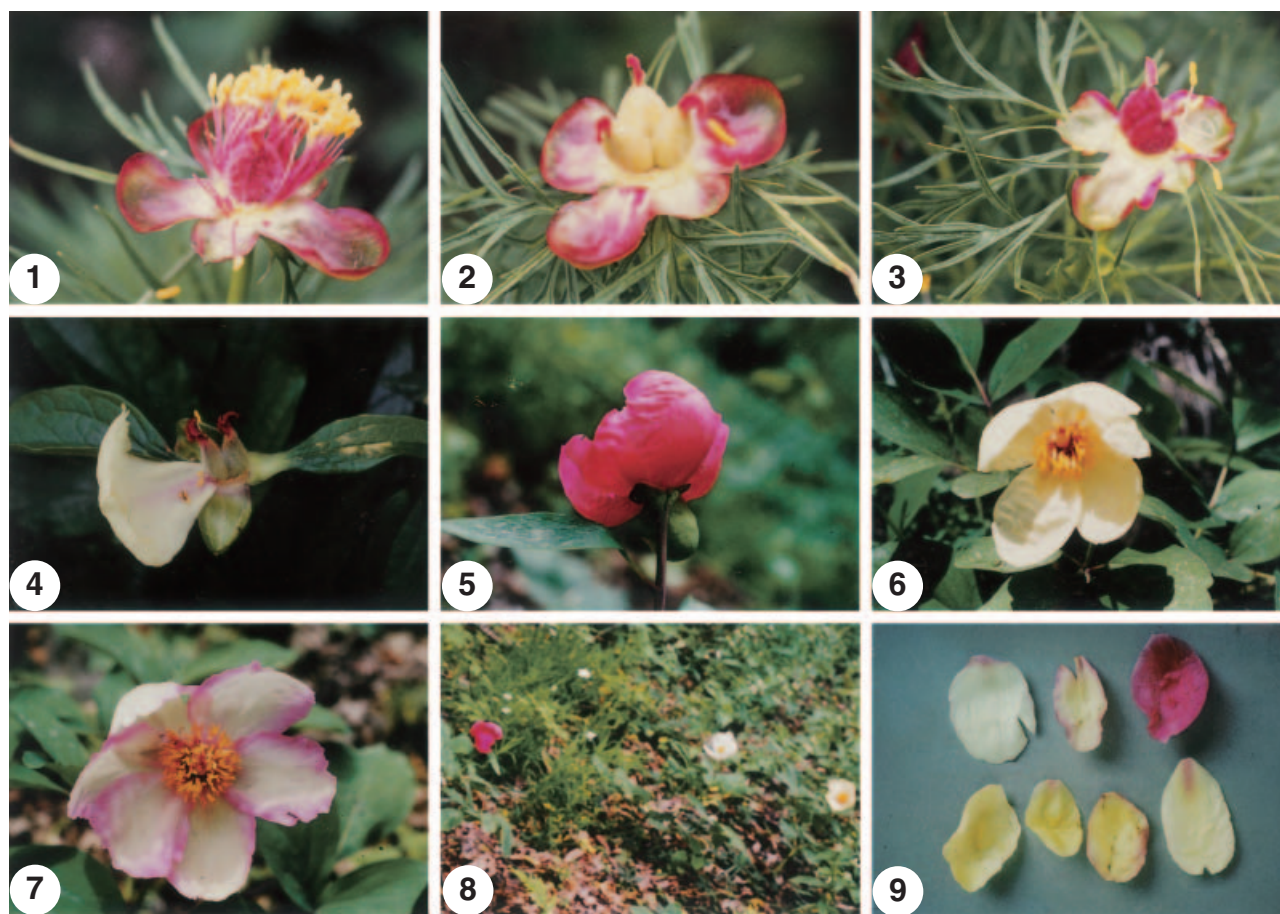
GROUP 2: *TENUIFOLIA*

This group includes *P. tenuifolia* L., *P. biebersteiniana* Rupr. and *P. carthalinica* N. Ketzch. The first was described from Ukraine, the second from Stavropol in north Caucasus (Russia), and the third from Kartli, Georgia. The treatment of *P. biebersteiniana* has been controversial. Huth (1892) reduced it to a synonym of *P. tenuifolia*; Lomakin (1897) did not recognize it as a species; Busch (1901) and Grossgeim (1930) treated it as a variety of *P. tenuifolia*; Lipsky (1899), Schipczinsky (1937), Grossgeim (1950) and Kemularia-Nathadze (1961) recognized its specific status. Stern (1946) stated that “this description (by Grossgeim, 1930) seems to fit *P. anomala* var. *intermedia*”, but added “this name must remain in doubt” because he was unable to examine specimens from the Stavropol region. *P. biebersteiniana* was said by Schipczinsky (1937) to have leaf segments 3–10 mm wide and hispid along veins above, whereas *P. tenuifolia* had leaf segments 1–2 mm wide and glabrous above.

We visited Temnolesskaya, south of Stavropol, Russia, the type locality of *P. biebersteiniana*. We found a huge population there stretching over hundreds of metres on sloping meadows. Two population samples were taken at an interval of about 500 m (H99052 and H99053). All plants possessed fusiform roots, biternate leaves with 134–340 segments and red flowers, but varied in colour of filaments, colour and number of carpels, and width of leaf segments. Filament colour varied widely from yellowish white, pink below and red above, to totally red; carpels were one, two or three in number, all tomentose, with hair colour green or red (Figs 1–3); the width of leaf segments varied from 1.2 to 4.3 mm. Sixty-seven herbarium specimens in LE from the Ukraine and north Caucasus were measured; *P. biebersteiniana* varies from 0.5 to 6.0 mm.

It is of particular interest that an individual specimen collected from Crimea (near Malbai) by N. Busch in 1905 (N. Busch, s. n. LE!) has three shoots which differ widely in width of leaf segments: 1.5 mm, 3.5 mm and 5.5 mm, respectively. A similar phenomenon was also observed during our expedition (H99028, H99053) and in cultivated individuals in the Tbilisi Botanical garden. The leaves are mostly glabrous, very rarely with white bristles along veins above; only six of the 82 specimens were found to have bristles and their leaf segments are 0.6–3.6 mm wide. Therefore, the presence of bristles along veins on the upper side of leaf segments is not correlated with wide leaf segments. It suggests that *P. biebersteiniana* is at one extreme in the continuum of variation of leaf segment width in *P. tenuifolia*.

Paeonia carthalinica N. Ketzch. was distinguished by Kemularia-Nathadze (1961) from *P. tenuifolia* (broader leaf segments and greyish pubescence on



Figures 1–9. Variation in colour of floral parts of *Paeonia* in the Caucasus. Figs 1–3. *P. tenuifolia* group, from the population H99043. Fig. 1. Purple sepals, filaments and carpels. Fig. 2. Purple sepals and yellowish green carpels. Fig. 3. Green sepals, purple at the periphery, yellow filaments and purple carpels. Figs 4–9. *P. daurica* group. Fig. 4. From H99025 '*P. wittmanniana*' cultivated in the Tbilisi Botanical Garden, showing a yellow petal with a pink spot at the base. Figs 5–9. From H99035. Fig. 5. Red flower. Fig. 6. Pale yellow flower. Fig. 7. White petals with pink periphery. Fig. 8. Red-flowered and yellow-flowered individuals growing side by side. Fig. 9. Various colours of petals within the population (see Table 1 for further information).

ovaries), and from *P. biebersteiniana* (green, not greyish, leaves that are glabrous without bristles along veins on the upper side as in *P. biebersteiniana*). We sampled two populations in Kartli region, Georgia, the type locality: H99028 near Igoeti and H99043 near Dampalo. A form with wide leaf segments was found in population H99028 and variable colouring of hairs on carpels was discovered in H99043: yellowish green, pink, red and purple-red. As we have mentioned above, in *P. tenuifolia* (including *P. biebersteiniana*) leaf segments are usually entirely glabrous above, only occasionally with bristles along the veins. Some individuals in H99028 and H99043 were found to be covered with white bristles along veins. Slight differences in leaf colour, greyish or green, occur frequently within natural populations. We see no basis on which to recognize *P. carthalinica* as an independent species,

and recognize only one species, *P. tenuifolia*, with *P. biebersteiniana* and *P. carthalinica* both reduced to synonyms.

GROUP 3: DAURICA

This is the group with the most controversial taxonomy; the number of recognized species varies from one (Albow, 1895), two (Huth, 1892), three (Busch, 1901), four (Stern, 1946; Grossgeim, 1950); five (Lipsky, 1899; Grossgeim, 1930), seven (Schipczinsky, 1937) to nine (Kemularia-Nathadze, 1961). For this group (or complex), eight populations (Table 1) were sampled from the south-east (the Talysh Mountains in S. Azerbaijan) to the north-west (Krasnodar in Russia) of the region in addition to vouchering individuals of *P. wittmanniana* in the Tbilisi and Bakuriani Botani-

cal Gardens introduced directly from the type locality. More than 300 herbarium specimens were critically examined. The morphological characters used for distinguishing species in this complex are analysed in the present work.

This complex has several characters in common: roots very slightly carrot-thickened, but not fusiform-thickened; leaves mostly biternate with nine leaflets, very occasionally triternate with up to 19 leaflets, or some of the nine leaflets bifid; flowers solitary, with 0–2 bracts, 2–3 sepals, 5–8 petals, and numerous filaments. The complex varies in petal colour, shape and size of leaflets and indumentums on leaflets and carpels, characters which were used particularly by Schipczinsky (1937) and Kemularia-Nathadze (1961) in their classifications. We have paid particular attention to these characters.

Petal colour

All the previous taxonomists except for Albow (1895) divided this complex into two major groups using this character: yellow or red (or white). Kemularia-Nathadze (1961) went even further, and established sect. *Flavonia* Kem.-Nath., based solely on yellow flowers, disregarding significant differences among its members, e.g. in habit (herb or shrub) and other characters (e.g. flowers solitary or in an inflorescence). Thus she placed *P. delavayi* Franch. (red flowers) and *P. lutea* Delavay ex Franch. (yellow flowers) into two separate sections, sect. *Paeon* and sect. *Flavonia*. When we examined the *P. delavayi* complex (incl. *P. lutea*) we conducted extensive observations in its distribution range and found that colour variation of petals within and between populations was a common phenomenon. In Zhongdian County, Yunnan Province, we found two populations where petal colour was extremely variable: white, pale yellow, yellow, yellow with a red spot at the base, orange, rose, red, purple red, and dark purple (Hong, Pan & Yu, 1998). *P. lutea*, which was described as a new species based on yellow flowers, has naturally been merged into *P. delavayi* (Hong *et al.*, 1998).

This was not an isolated case. *P. obovata* Maxim. has red petals, while *P. japonica* was established as a species based on white petals. Within the group petals vary in colour from white, white with pink periphery, rose to red; sometimes red and white coexist within a population. Thus *P. japonica* has been treated as a synonym of *P. obovata* (Hong *et al.* 2001). The same phenomenon was also observed in wild populations of *P. lactiflora* which has different petal colour forms: white, white with red periphery, pale rose, rose and red. As a result, Kemularia-Nathadze (1961) placed distinctly different species within the same section, e.g. *P. delavayi* and *P. obovata*, in sect. *Paeon*. Although they both have red petals, they are different

in a number of diagnostic characters: woody, leaflets segmented, inflorescences a cyme in the former vs. herbaceous, leaflets entire, flowers solitary and terminal in the latter. Her classification, based on overemphasis on a single character, ignoring all others, with little attention paid to colour variation of petals, was clearly artificial.

In our investigation, we observed that petal colour did in fact characterize some populations. For example, in populations H99029, H99039 (Kartli, Georgia) and H99059 (Krasnodar, Russia) all flowers observed were red; in H99065 (Adjara, Georgia) they were yellowish white. In H99046 (Talysh Mountains, Azerbaijan) petals were mostly totally pale yellow, although a few individuals had petals which were reddish at the base. H99060 and H99062 (Bakuriani above Borjomi, Georgia), were described as having yellow petals by Kemularia-Nathadze (1961), but some individuals had petals which were red at the base or pink at the periphery. Flowers of *P. wittmanniana* were previously described as yellow by all the previous authors; however, one individual (Tbilisi Botanical Garden, from Abchasia, type locality) showed a red spot at the base (Fig. 4). Therefore, there was no distinct demarcation line in this complex. Furthermore, in H99035 (Lagodekhi, type locality of both *P. mlokosewitschii* (yellow flowers) and *P. lagodechiana* (pink flowers)), we found all the colours mentioned above: white, pale yellow, yellow, pink, red and purple-red, or yellow but with red or pink periphery or a red spot at the base (Figs 5–9), the same situation as in *P. delavayi* (Hong *et al.*, 1998). This is another typical example of polymorphism in petal colour. Clearly, it cannot be used as a diagnostic character for distinguishing species; unfortunately the previous authors did so, with Kemularia-Nathadze (1961) even using it to separate sections.

Leaflet shape

This was used by Schipczinsky (1937) and Kemularia-Nathadze (1961) for distinguishing *P. mlokosewitschii* from the other species and *P. macrophylla* from *P. steveniana* in the complex. As shown in Figure 10, variations in shape are quite distinct. For example, H99035 (*P. mlokosewitschii*) mostly had leaflets obovate with rounded but mucronate apex, while H99025 and H99063 (*P. wittmanniana*) had leaflets ovate with acuminate or acute apex. However, nearly continuous gradation exists between the extremes. From Figure 10, it is clear that it, like colour, cannot be used as a diagnostic character.

Leaflet size

On the basis of larger leaflets, *P. macrophylla* was established first as a form of *P. corallina* var. *wittmanniana* by Albow (1895), then as an independent spe-

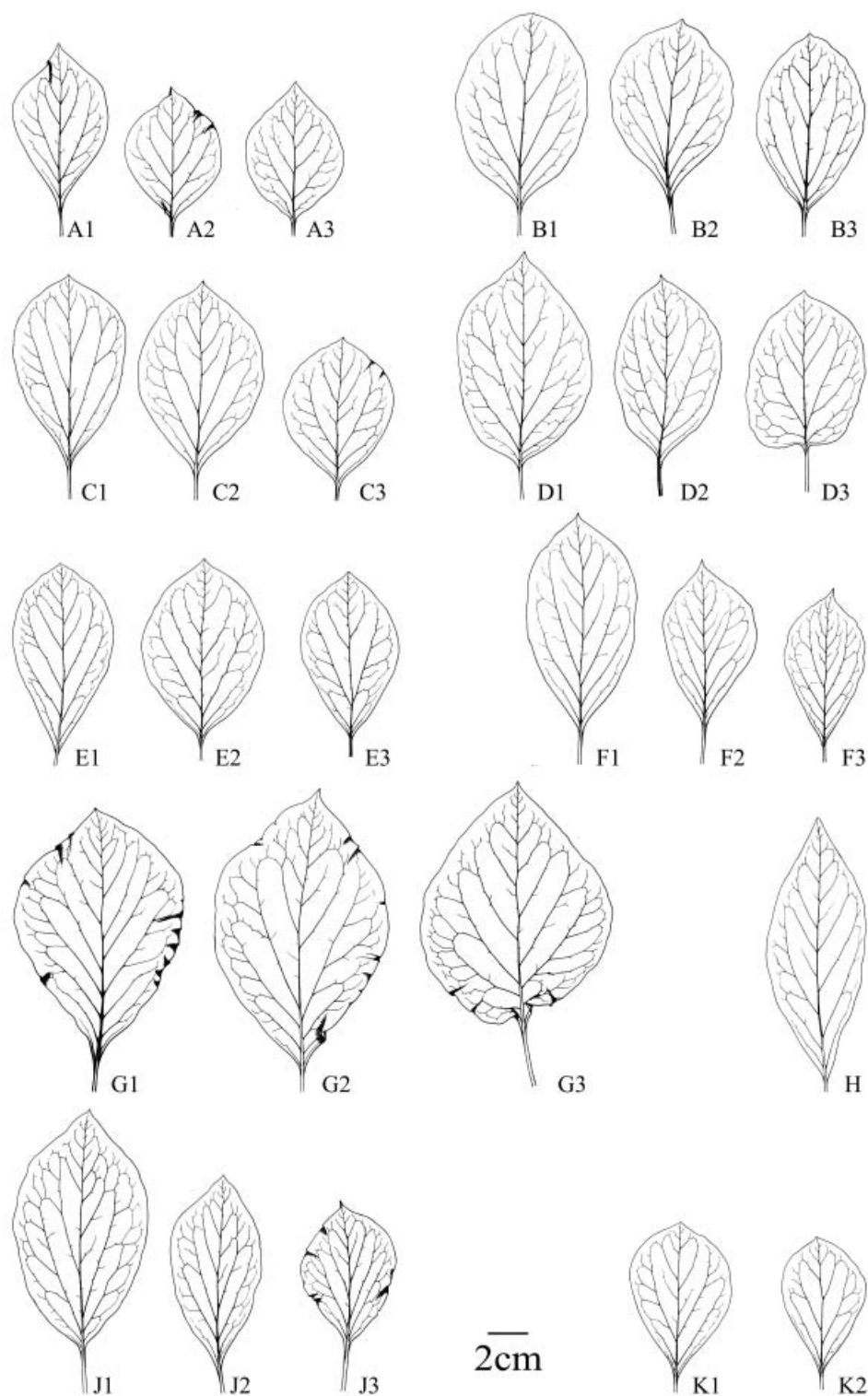


Figure 10. The variation of terminal leaflets in shape and size within and between populations of the *Paeonia daurica* complex in the Caucasus. A1–3. H99029. B1–3. H99035. C1–3. H99039. D1–3. H99046. E1–3. H99059. F1–3. H99060. G1–3. H99065. H. H99068. K1, 2. H99069 (see Table 1 for details of the populations).

cies by Lomakin (1897), and recognized as such by Lipsky (1899), Schipczinsky (1937) and Kemularia-Nathadze (1961). The leaflets in H99065 sampled by us at its type locality were generally larger than those in the other populations. However, our statistical sampling shows that the variation among the populations is continuous (Fig. 11). Discontinuity in size exists neither between H99065 (*P. macrophylla*) and the other populations, nor between the populations with yellow flowers (H99046, H99060 and H99065) and those with red flowers (H99029, H99039 and H99059). We consider that although the difference between the smallest leaflets in H99029 and the largest ones in H99065 is remarkable, and leaflet size may characterize some races, it is not distinct enough for distinguishing species in the complex.

Leaf indumentum

Paeonia tomentosa was described first as a variety of *P. wittmanniana* by Lomakin (1897), then raised to subspecific rank by Busch (1901) and finally to specific

rank by Busch (1919) because leaflets were densely covered with appressed hairs and thus greyish on the lower surface. Our survey of eight populations and some cultivated individuals of *P. wittmanniana* in the botanical gardens at Tbilisi and Bakuriani showed that there was no population where all individuals were glabrous on the lower surface of leaflets. To show the variation within and between populations we divided density of indumentum into six grades with 0 glabrous, 1–4 intermediate and 5 nearly tomentose. In this complex three types of hairs were found; villose and pilose hairs were often mixed though their frequencies were different, while puberulous hairs were found only in H99035. The results of our survey are presented in Table 2. Here, it is clear that there is no distinct demarcation in indumentum between the populations, although quantitative differences exist between them; an exception occurs in H99035 where only one type of hairs (puberulous) was found. However, leaf indumentum cannot be considered as a sufficiently good character for distinguishing species, because among eight individuals sampled from H99035 two are totally glabrous, one nearly glabrous and the rest five vary from sparsely to rather densely hairy.

Carpels

The number of carpels was discovered to vary greatly from one to five in the complex, and such variation could be found even within populations (e.g. H99029). Fortunately, no taxonomist has ever used this character. Carpels usually changed their colour from yellow when still covered by petals and stamens to green

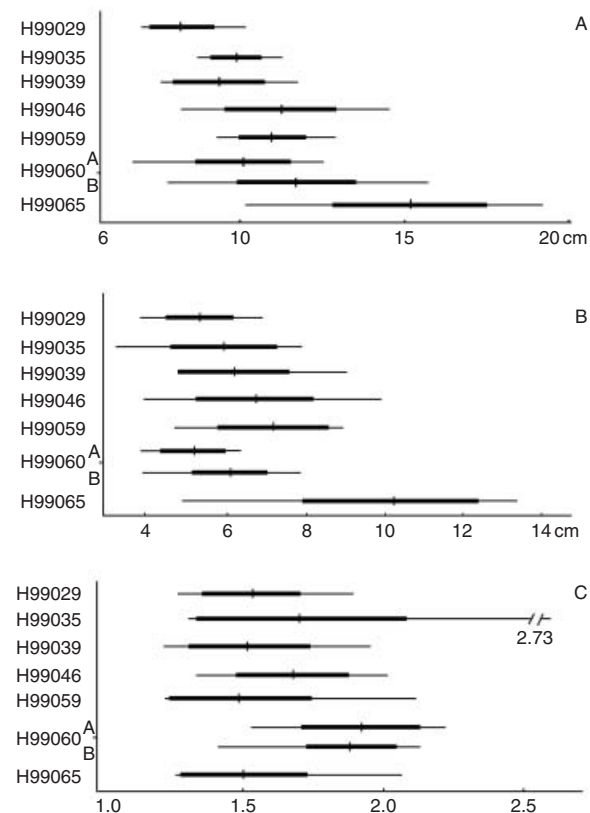


Figure 11. Standard deviation showing the variation of leaflets in shape and size within and between populations of the *Paeonia daurica* complex in the Caucasus. ($n = 8-12$, $1n =$ mean of 3 leaflets). (A) length, (B) width and (C) length/width of leaflets (see Table 1 for details of the populations).

Table 2. The density and type of indumentum on the lower surface of leaflets within the *Paeonia daurica* complex in the Caucasus (for explanation see 'Leaf Indumentum' in the text). * See Table 1 for further information. † Two individuals of '*P. wittmanniana*' in the Tbilisi Botanical Garden introduced from Abchasia, the type locality of *P. wittmanniana*

Population*	Density of indumentum	Type of indumentum		
		villose	pilose	puberulous
H99029	0–2	+	+	+
H99035	0–3			
H99039	0–2	+	+	
H99046	3–4	+		
H99059	0–2	+	+	
H99060	3–4	+		
H99062	3	+	+	
H99065	2–4	+	+	
H99025†	2			

when exposed gradually. Therefore, young follicles were nearly always green if not entirely covered with hairs. The indumentum of carpels characterizes populations to some extent. For example, all the individuals observed at higher altitudes (above 1100 m) in Borjomi and Adjara (Georgia: H99060, H99062, H99065) had glabrous carpels, while those at lower altitudes (with red flowers, H99029, H99039 and H99059) were found to have tomentose carpels. In H99046 all carpels observed were sparsely to densely tomentose. Among 33 herbarium specimens from north-west Georgia (Abchasia and adjacent regions) that we examined in LE and TBI, 16 have glabrous, 15 yellow-brown tomentose, and two [(Dolmatova *et al.* 935 (LE) and Komarov, s. n. (LE)] very sparsely villose carpels. The indumentum of carpels may therefore be considered as a character appropriate for infraspecific classification but not for specific recognition.

Hairs on carpels were usually yellow or yellow-brownish, but we found that an individual in Tbilisi (*P. wittmanniana*) had carpels covered with yellow hairs below and pinkish above when anthesis was just over (May 1) (Fig. 4). Three weeks later they were totally covered with yellow hairs. Thus, slight differences in colour of hairs and leaves (also in the *P. tenuifolia* group) cannot be used as characters for distinguishing species or even infraspecific taxa.

From our observations in the field and statistics based on both population sampling and a large amount of herbarium specimens (Figs 1–11, Table 2) it is clear that there are no morphological characters distinct enough for distinguishing species in the complex, although petal colour, leaflet shape and size, and indumentum of leaflets and carpels characterize some races, e.g. 'macrophylla' in south-west Georgia, 'tomentosa' in southern Azerbaijan, 'wittmanniana' in Abchasia and adjacent areas, and 'mlokosewitschii' in east Georgia and adjacent areas in Russia and Azerbaijan. It is therefore relatively reasonable to treat the complex as a single species, and to divide it into five subspecies.

TAXONOMIC TREATMENT

KEY TO SPECIES OF *PAEONIA* IN CAUCASUS

- 1 Lower leaves divided into >70 segments; segments <1.5 cm wide; roots tuberous.
 - 2 Lower leaves with <100 segments; segments 4–10 mm wide.....1. *P. intermedia*
 - 2 Lower leaves biternate, with >130 segments; segments 0.5–6.0 mm wide.....2. *P. tenuifolia*
 - 1 Lower leaves usually with 9, rarely up to 19 leaflets (or segments), leaflets or segments over 3.5 cm wide; roots slightly carrot-like but attenuate downwards.....3. *P. daurica*
1. *Paeonia intermedia* C. A. Meyer in Ledebour, Fl. Alt. 2: 277, 1830. TYPE: The Altai Mountains, s. coll., s. n. (Holotype, K!).
- Paeonia majko* N. Ketzchoveli in Notul. Syst. ac Geograph. Inst. Bot. Tiphlis. Fasc. 21: 17. 1959; Kemularia-Nathadze in Trud Tbilisi Bot. Inst. 21: 27, 1961. syn. nov. TYPE: Georgia, Kartli, Igoeti village, 15.v.1958. N. Ketzchoveli, s. n. (Holotype, TBI!).
- Notes.* A perennial with roots fusiformly thickened; leaves ternate, segments 78–91 in number, 4–10 mm wide, glabrous on both sides; bracts 2; sepals 3; petals 5, red; carpels 2, pink-tomentose.
- Examination of a large number of herbarium specimens from Central Asia of *P. intermedia* at LE and PE shows that leaves are also ternate, with 35–65 segments, 3–11 mm wide, glabrous on both sides, rarely with bristles along veins on the upper side.
- We have not discovered any reliable differences in morphology between the Caucasian population and those in Central Asia. Therefore, it is reasonable to identify the Caucasian population as *P. intermedia* and to reduce *P. majko* to a synonym.
- Paeonia intermedia* is found in Xinjiang (China), Kazakhstan, Kirghizstan, Tadzhikistan, and Uzbekistan, where it grows usually in sunny spots among bushes and grasses at altitudes below 3000 m. It is possible that there is only a single population (in a forest with only five individuals) in the Caucasus.
- Additional specimens examined.* GEORGIA, Kartli: Igoeti, 630 m alt., in deciduous forest, 2.v.1999, D. Y. Hong and S. L. Zhou H99033 (PE); the same locality, 15.v.1958, Ketzchoveli, s. n. (TBI); the same locality, 4.v.1959, Ketzchoveli, s. n. (TBI); the same locality, 3.iv.1960, Sanadze *et al.* s. n. (TBI); the same locality, 5.v.1964, Ketzchoveli, s. n. (TBI).
2. *Paeonia tenuifolia* Linnaeus, SP. Pl. ed. 2. 748. 1762; Ledebour, Fl. Ross. 1: 73. 1842; Boissier, Fl. Orient. 1: 98. 1867; Ruprecht, Fl. Caucas. Mem. Acad. Imper. Sci. St.-Petersb. Ser. 7. 15(2): 47. 1869; Huth in Engl. Bot. Jahrb. 14: 271. 1892; Lipsky, in Trud Tiflis Bot. Sada (Fl. Caucas. and Suppl.). 4: 213. 1899, et Fl. Caucas. 2: 91. 1930; Schipczinsky in Komarov: Fl. USSR, 7: 29. 1937; Stern, Study Gen. Paeonia, 110, 1946; Grossgeim, Fl. Caucas. 4: 13. 1950; Kemularia-Nathadze in Trud Tbilisi Bot. Inst. 21: 29. 1961. TYPE: Ukraine, not designated.
- Paeonia biebersteiniana* Ruprecht in Mem. Acad. Imper. Sci. St.-Petersb. Ser. 7. 15(2) (Fl. Caucas.): 47. 1869; Lipsky in Trud Tiflis Bot. Sada (Fl. Caucas. and Suppl.) 4: 214. 1899; Schipczinsky in Komarov(ed.), Fl. USSR, 7: 29. 1937; Grossgeim, Fl. Caucas. 4: 13. 1950;

Kemularia-Nathadze in Trud Tbilisi Bot. Inst. 21: 31. 1961.

Paeonia tenuifolia var. *biebersteiniana* (Rupr.) Busch, Fl. Caucas. Crit. 3(3): 9 et 224. 1901; Grossgeim, Fl. Caucas. 2: 91. 1930. TYPE: Russia, near Stavropol, M. Bieberstein, s. n. (LE!)

Paeonia carthalinica N. Ketzchoweli in Notul. Syst. ac Geogr. Inst. Bot. Tbil., 21: 18. 1958; Kemularia-Nathadze in Trud Tbilisi Bot. Inst. 21: 30, 1961, syn. nov. TYPE: Georgia, Kartli, Tindznisi village, 10.v.1958, N. Ketzchoweli, s. n. (Holotype, TBI!).

Notes. Perennials with roots consistently fusiform-thickened. Leaves biternate, leaflets fine-segmented, with >130 segments, segments varying from 0.5 to 6 mm in width, glabrous on both sides, rarely with sparse bristles along veins on the upper surface. Flowers consistently red; bracts and sepals green, green but purple-red at periphery to totally purple-red; filaments entirely yellowish white, pink below but yellowish white above to entirely purple-red; carpels 1–3, consistently tomentose, hairs green, yellow to totally purple; stigmata red.

Our observations show that this species varies greatly in width of segments and colour of filaments and carpels, but all these characters are polymorphic, even within populations.

The species is distributed in Bulgaria, Yugoslavia, Romania, south-west Russia and Ukraine. Within the Caucasus, it is mainly found in the northern part of the region; Azerbaijan and Georgia each have only one locality. It grows in meadows, sparse bushes and sparse woods. It is confined to below 800 m, and flowers from late April to early June, $2n = 10$ (Punina, 1987, 1989).

Additional specimens examined. AZERBAIJAN, Southern Karabakh: Zangelan, Kegnja-Pirtshevan, 26.v.1937, Grossgeim, s. n. (BAK) et 30.v.1937. Grossgeim, s. n. (BAK); Zangelan, near Pirchevan, 400 m, 7.v.1948, Grossgeim *et al.* s. n. (LE); Zangelan, Pirchevan, 7.v.1948, Vasiliev, s. n. (LE). GEORGIA, Kartli: between Igoeti and Lamiskana, v.1958, Ketzchoweli, s. n. (isotype of *P. carthalinica*, LE!); near Igoeti, 2.v.1985, Punina, s. n. (LE); the same locality, 630 m alt., 2.v.1999, D. Y. Hong and S. L. Zhou H99028 (A, CAS, K, MO, PE, US); Mukhrani, near village Dampalo, 760 m alt., S. slope, on terrace, 5.v.1999, D. Y. Hong and S. L. Zhou H99043 (A, CAS, K, MO, PE, US). RUSSIA, Checheno-Ingushetia: Terski Mountain Range, near Goragorski, 21.v.1974, Magulaev, s. n. (LE); Krasnodar, Markotkh Mountain Range, near Kabardinka, 09.vi.1989, Dolmatova *et al.*, 1877 (LE); the same locality, 10.vi.1989. Dolmatova *et al.*, 1997

(LE); at Station Tonnelnaya on the mountain pass from Krasnodar to Anapa, 2.vi.1952, Fedorov, s. n. (LE); Kuban: Gustie Hutora, 16.vi.1926. Schifffers 342a (LE); Mt. Shize, 21.iv.1907. Busch and Klopotov, s. n. (LE); Novorossiisk: Markotkh Mountain Range, 10.v.1921, Leonova 459 (LE); Stavropol: 1867. Tzeker 56 (LE), 1867. Recuer. s. n. (LE); near Stavropol, 8.v.1972, Mordak and Zakhariyeva 1048(LE); slope to Rybnoie Lake, 10.viii.1949. Vasilchenko 476a (LE); the same locality, vii.1949, Vasilchenko 417 (LE); Rybnoie Lake, 28.v.1892. Lipsky, s. n. (LE); Prikalausskie Heights, 4–6 km NW of Kruglolesskoye, 27.vi.1988. Geltman *et al.* 1772 (LE); Stavropol Height, Mt. Strizhament, 700–800 m alt., 21.vi.1988, Geltman 1476 (LE); Temnolesskaya, 44°52'N, 42°10'E, 630 m, 15.v.1999, D. Y. Hong and S. L. Zhou H99052 (A, CAS, K, MO, PE, US) and H99053 (A, CAS, K, MO, PE, US); Pyatigorsk: 1910. Pastukhori, s. n. (LE); Terskaya: near Essentuki, 20.vi.1912. Stuchenberg 15(LE); the same locality, 19.v.1960. Andreev, s. n. (LE); Usiskaya, Kubinskaya Stanitsa. 1889. Gagman, s. n. (LE); Caucasus, no exact locality, Schnader, s. n. (LE); Ledebour, s. n. (LE); Fischer, s. n. (LE).

3. *Paeonia daurica* Andrews, Bot. Rep. 7: t. 486, 1807; Stern, Study Gen. *Paeonia*, 70, 1946; Grossgeim, Fl. Caucas. 4: 12. 1950. TYPE: Andrews' tab. cited.

Paeonia corallina auct. non Retzius: Ledebour, Fl. Ross. 1: 73, 1842; Bossier, Fl. Orient. 1: 97. 1867; Huth in Engl. Bot. Jahrb. 14: 267. 1892, p. p.; Albow, Prodr. Fl. Colchic. 14. 1895; Busch, Fl. Caucas. Crit. 3(3): 10. 1901; Grossgeim, Fl. Caucas. 2: 91. 1930.

Paeonia triternata Pallas *ex* DC., Prodr. 1: 65. 1824; Ruprecht in Mem. Acad. Imper. Sci. St.-Petersb. Ser. 7. 15 (2) (Fl. Caucas.): 47. 1869; Lipsky in Trud Tifis Bot. Sada (Fl. Caucas. and Suppl.) 4: 213. 1899. TYPE: Crimea, Pallas, s. n. (Holotype BM!).

Notes. As pointed out in 'Observations and Discussion', the *P. daurica* complex in the Caucasus has notable polymorphism, and no distinct differences have been found between the populations. It is thus considered that the group has differentiated only at the stage of geographical races, and is better treated as a single species with five subspecies.

Perennials. Roots carrot-like, attenuate downwards. Lower leaves usually biternate with nine leaflets, occasionally triternate, with up to 19 leaflets; leaflets entire or sometimes bifid, obovate, oblong, wide-elliptic, sometimes undulate, apex round, mucronate, acute or shortly acuminate, glabrous above, glabrous or sparsely to densely villose or pilose, or sparsely to rather densely puberulous beneath, 4.8–11.5 × 8.1–

17.1 cm. Flowers solitary and terminal; bracts 0–2; sepals 2–3, green; petals 5–8, white, pale yellow, yellow, yellow with a red spot at base or with red periphery, rose, red, or purple-red; filaments purple; carpels 1–5, glabrous or sparsely to densely tomentose; styles nearly absent.

The distribution pattern of the five subspecies is as follows: *ssp. coriifolia* is found below 1000 m in the western part of the Caucasus (including the Transcaucasus), while the other four occur at subalpine and alpine zones at altitudes of (800) 1000–2300 m. They are vertically vicarious with *ssp. coriifolia*, but allopatric with *ssp. wittmanniana* in the north-west, *ssp. mlokosewitschii* in the north-east, *ssp. tomentosa* in the south-east, and *ssp. macrophylla* in the south-west.

KEY TO SUBSPECIES OF *P. DAURICA*

- 1 Leaflets puberulous on the lower surface or glabrous; obovate; apex rounded or obtuse, often with a short mucro
.....*ssp. mlokosewitschii* (Lomakin) D. Y. Hong
- 1 Leaflets villose and (or) pilose on lower surface or glabrous; oblong or elliptic-oblong; apex rounded, acute to acuminate.
 - 2 Petals red; leaflets glabrous on both sides or sparsely villose on lower side
.....*ssp. coriifolia* (Rupr.) D. Y. Hong
 - 2 Petals yellow or yellowish white, but sometimes red at periphery or with a red spot at base: leaflets always villose or pilose.
 - 3 Carpels and follicles tomentose.
 - 4 Leaflets mostly densely villose or pilose and thus greyish on lower side
..... *ssp. tomentosa* (Lomakin)
D. Y. Hong
 - 4 Leaflets usually sparsely villose
..... *ssp. wittmanniana*
(Hartwiss ex Lindley) D. Y. Hong
 - 3 Carpels and follicles glabrous or nearly glabrous
 - 5 Leaflets mostly densely villose or pilose and thus greyish on lower surface*ssp. macrophylla*
(Albow) D. Y. Hong
 - 5 Leaflets usually sparsely villose
.....*ssp. wittmanniana*
(Hartwiss ex Lindley)
D. Y. Hong

Paeonia daurica *ssp. coriifolia* (Ruprecht) D. Y. Hong, **stat. nov.** ≡ *Paeonia triternata* f. *coriifolia* Ruprecht, in Mem. Acad. Imper. Sci. St.-Petersb. ser. 7. 15(2): 46. 1869. *P. corallina* *ssp. triternata* var. *coriifolia* (Rupr.) Busch, Fl. Caucas. Crit. 3(3): 12, 1901. *P. caucasica* var. *coriifolia* (Rupr.) Schipczinsky in

Komarov (ed.): Fl. USSR, 7: 29. 1937. *P. kavachensis* var. *coriifolia* (Rupr.) Grossgeim, Fl. Caucas. 4: 12. 1950. TYPE: Georgia: Borjomi, not designated.

Paeonia corallina var. *caucasica* Schipczinsky in Notul. Syst. Herb. Hort. Bot. Petrop. 2: 45. 1921; Grossgeim, Fl. Caucas. 2: 91. 1930. *P. caucasica* (Schipczinsky) Schipczinsky in Komarov (ed.): Fl. USSR, 7: 28. Plate 3, 1. 1937; Kemularia-Nathadze in Trud Tbilisi Bot. Inst. 21: 23, 1961. TYPE: the Caucasus, Schipczinsky in Komarov (ed.): Fl. USSR, 7: 1937, the plate cited.

Paeonia ruprechtiana Kemularia-Nathadze in Trud Tbilisi Bot. Inst. 21: 22, 1961. TYPE: Georgia, Imeretia, Schorapan, near village Parckhali, 1916, 04, 18. Buachidze, s. n. (Holotype, TBI !)

Paeonia kavachensis auct. non Aznavour (in Magyar Bot. Lapok, 16: 7. 1917): Grossgeim, Fl. Caucas. 4: 12. 1950.

Paeonia triternata auct. non Pall. ex DC: Ruprecht, in Mem. Acad. Imper. Sci. St. Petersburg. ser. 7. 15(2) (Fl. Caucas.): 44. 1869; Lipsky in Trud Tiflis Bot. Sada, 4 (Fl. Caucas. and Suppl.): 213. 1899; Schipczinsky in Komarov (ed.): Fl. USSR. 7: 28, 1937; Kemularia-Nathadze in Trud Tbilisi Bot. Inst. 21: 26, 1961.

Notes: This subspecies is found at altitudes below 1000 m in western and north-western Caucasus and grows in deciduous forests dominated by *Quercus*, *Fagus*, *Ulmus*, *Acer* and *Fraxinus* or in mixed deciduous broad-leaved and conifer forests dominated by *Picea*, *Fagus* and *Quercus*. It is found on a wide range of sandstone, limestone and volcanic rocks, $2n = 10$ (Punina, 1987, 1989). It differs from the other subspecies in having red petals and glabrous or sparsely villose leaflets.

Additional specimens examined. GEORGIA, Abkhazia: Sukhumi, near Jurjevskoje, 31.iii.1912. Woronow, s. n. (LE); Sukhumi, near Yurievka, iv.1900, Woronow, s. n. (LE); Sukhumi, Tsebelda, Mt. Akhupach, iv.1904, O. Woronow, s. n. (LE); Ritza region, near Avadhary, 8.v.1973. Maximova 133 (LE). Batumi: Artvin distr., Ardanuch, Mt. Vartskhet, mixed forest, 26.v.1914, Turkevich 456 (LE); Artvin distr., Talovara, above Bugaret, 28.iv.1912. Andronoki, s. n. (LE); Borjomi: National Park, 41°50'N, 43°22'E, north slope, 870 m alt., 4.v.1999. D. Y. Hong and S. L. Zhou H99039 (MO, PE); Gombori; Ujarma village, 12.v.1964. Ketzchoweli et al. s. n. (TBI); Imereti: Marilisi-Didvake, 25.iii.1965. Tshikvaidze, s. n. (TBI); Ladogani, 30.v.1928. Kemularia-Nathadze, s. n. (TBI); Tkibuli, near Akhal-sopeli village, Mt. Tsintskala, 4.v.1948. Kuzhazheladze, s. n.

(TBI); Kahetia: Chalaubani, v.1984. Mikheev, s. n. (LE); Kartli: Igoeti, 630 m alt., 2.v.1999. D. Y. Hong and S. L. Zhou H99028 (A, CAS, K, MO, PE, US); the same locality, iv.1959. Ketzchoweli, s. n. (TBI) et 6.v.1959. Ketzchoweli, s. n. (TBI); Tbilisi, near ruins of Gudareha near Bely Klush, 17.v.1908, Florensky, s. n. (LE); Tbilisi, Saguramo, 24.v.1960. Mordak 486 (LE); Ratscha-Letskhumi: Alpana, Mt. Koitschu, 12.iv.1932. Kemularia-Nathadze, s. n. (TBI); between Mekvena and Alpana, 23.iii.1966. Kemularia-Nathadze, s. n. (TBI); Tsagerski, Rioni valley, 19.iv.1987. Nikitia *et al.* s. n. (LE); Thrialeti: near Manglisi, 1100 m alt., 23.v.1965, Abaschidze, s. n. (LE). RUSSIA, Caucasus Nature Reserve: Near Krasnaya Poliana, 20.v.1981, Lebedeva, s. n. (LE); path to Belorechensky Mt. Pass, 10.vi.1973. Sergienko, s. n. (LE); the same locality, limestone, 20.vi.1983, Sergienko, s. n. (LE); Guzerkilo, 19.vii.1928. Leskov 203 (LE); Krasnodar: Abtal, 5.iv.1987. Morda and Dorofeev 2273/191 (LE); Anapa, 25.v.1958. Kotov and Omelchuk, s. n. (LE); Mostovskiy, near Psebai, 28.vii.1990. Menitsky *et al.* 15 (LE); Dante's Gorge, Goriachy Kluch, 6.v.1969. Maximova, s. n. (LE); Gelendzhik, Mikhailowsky Mountain Pass, 3.viii.1990. Menitsky *et al.* 22 (LE); Kuban: between Ahota and Veliaminovskiy Mountain Pass, 25.iv.1907, Busch and Klotow, s. n. (LE); Holodny, Erin, near Goriachy Kluch, 11.v.1907. Busch and Klotow, s. n. (LE); Maykop, road to Tuapse, iv.1911. Shestounow 1275 (LE); near Neberdzhavskaya, 16.iv.1907. Busch and Klotow s. n. (LE); near Erivanskaya, Mt. Shize, 21.iv.1907. Busch et Klotow, s. n. (LE); N. Caucasus: upper reaches of Pshish River, near Goishkh, 12.viii.1946. Gavrilovich, s. n. (LE); upper reaches of Psheha River, Tubinsky Mt. 700 m alt. 1.viii.1946. Chernovol, s. n. (LE); upper reaches of Pshiskha River, near Tuby, 500 m alt., 1.viii.1946. Sochava, s. n. (LE); Novorossisk: no exact locality, 22.v.1889. Lypsky, s. n. (LE); South Novorossisk, iv.1897. Akinfiyev, s. n. (LE); Sochi: Dagomys, 21.vii.1937. Vekilunov 32(LE); Krasnaya Poliana, Mt. Aibga, 900–1000 m alt. 11.v.1930. Muhin 10(LE); Sochi, 19.iv.1930. Uhanov, s. n. (LE); Hosta, 15.iv.1930. Uhanov, s. n. (LE); in Agur River Valley, 9.iv.1924. Shteip, s. n. (LE); Krasnaya Polyana, 30.iii.1987, Mordak and Dorofeev, 2183/102 (LE); Stavropol: Korachaevo-Cherkesskaya Autonomous Land, W. end of Mt. Pastbishny, 17.vi.1988. Geltman *et al.* 1211 (LE); Tuapse: Kuibyshevka, 15.vi.1986. Chernovol, s. n. (LE); the same locality, 25.vi.1986. Chernovol, s. n. (LE).

Paeonia daurica* ssp. *mlokosewitschii (Lomakin) D. Y. Hong, **stat. nov.** = *Paeonia mlokosewitschii* Lomakin in Trud Tiflis Bot. Sada 2: 282, 1897; Lipsky in Trud Tiflis Bot. Seda 4 (Fl. Caucas. and Suppl.): 213. 1899; Busch, Fl. Caucas. Crit. 3(3): 14. 1901; Grossgeim, Fl. Cauc., 2: 91. 1930 et Fl. Caucas. 4: 13.

1950; Schipczinsky in Komarov (ed.), Fl. USSR, 7: 26, 1937; Stern, Study Gen. Paeonia, 54, 1946; Kemularia-Nathadze in Trud Tbilisi Bot. Inst. 21: 20. 1961. TYPE: Georgia, Kachetia, near Lagodekhi, 99.iv.1901, Mlokosewitsch 57 (Holotype TBI!; isotype, LE!)

Paeonia lagodechiana Kemularia-Nathadze in Trud Tbilisi Bot. Inst. 21: 25. 1961. TYPE: Georgia: Kachetia, Lagodekhi, Ninigora, 10.v.1953. Kasarova et Doluchanov, s. n. (Holotype, TBI!)

Notes: The types of *P. mlokosewitschii* and *P. lagodechiana* both came from the same population, which we visited and observed during our expedition. As we mentioned in 'Observation and discussion', this population was extremely polymorphic in petal colour and indumentum of leaflets (Figs 5–9, Table 2).

Among the five subspecies of *P. daurica*, ssp. *mlokosewitschii* is relatively distinct; its leaflets are usually obovate with rounded but mucronate apex, mostly sparsely or rather densely puberulous, but sometimes glabrous. The subspecies is found so far only in eastern Georgia, north-western Azerbaijan and the adjacent region of Russia. It grows in deciduous forests dominated by *Fagus*, *Quercus*, *Ulmus*, *Castanea* and *Acer*, $2n = 10$ (Punina, 1987, 1989).

Additional specimens examined. AZERBAIJAN, Zakataly: in forests, 9.v.1963. Zansheb, s. n. (BAK). GEORGIA, Kachetia: Lagodekhi, Mt. Kudigora, 960 m, 29.v.1954. Doluhanov, s. n. (TBI); Lagodekhi, 5.v.1939. Kemularia-Nathadze, s. n. (TBI); 12.v.1939. Kemularia-Nathadze, s. n. (TBI); 6.v.1958. Kemularia-Nathadze, s. n. (TBI); the same locality, in forests, 13.v.1939. Kapeller, s. n. (TBI); the same locality, 41°51'N, 46°15'E, 1040 m, 3.v.1999. D. Y. Hong and S. L. Zhou H99035 (A, CAS, K, MO, PE, US); Kiziki: Shiraki, Kvemo Kedi, along the Alazan River, 25.iv.1985. Punina, s. n. (LE); Shiraki, introduced to Tbilisi Bot. Gard. 11.v.1976. Kemularia-Nathadze, s. n. (TBI). RUSSIA, Dagestan: upper part of the Stvarskoe-koisu River, near village Takhoti, 28.vi.1948. Doluhanov, s. n. (TBI); Caucasus Nature Reserve: the upper reaches of Shahe River, Belorechensky Mountain Pass, 23.v.1923. Malysheva and Solodko, s. n. (LE).

Paeonia daurica* ssp. *wittmanniana (Hartwiss ex Lindley) D. Y. Hong, **stat. nov.** = *Paeonia wittmanniana* Hartwiss ex Lindley in Bot. Reg. 32: t 9. 1846; Ruprecht in Mem. Acad. Imper. Sci. St-Petersb. ser. 7. 15(2) (Fl. Caucas.): 46. 1869; Huth in Engl. Bot. Jahrb. 14: 266. 1892; Schipczinsky in Komarov (ed.) Fl. USSR. 7: 29. 1937; Stern, Study Gen. Paeonia, 56. 1946; Grossgeim, Fl. Caucas. 4: 12. 1950; Kemularia-Nathadze in Trud Tbilisi Bot. Inst. 21: 17. 1961. TYPE: Abchasia, Lindley's tab. cited.

Paeonia abchasica Miscz. ex Grossgeim, Fl. Caucas. 2: 92. 1930; Schipczinsky in Komarov (ed.): Fl. USSR, 7: 33. 1937. TYPE: Abchasia, not designated.

Notes: This subspecies is found in north-western Georgia (Abchasia, Imereti, Megrelia, Ratsha-Letskhumu and Svaneti) and the adjacent region of Russia (upper reaches of the Mzymta River). It grows in deciduous forests and alpine or subalpine meadows at altitudes of 1000–2300 m. All the available records of herbarium specimens show that it is confined to the limestone areas.

Although we were unable to visit localities of this subspecies due to security considerations, a large number of herbarium specimens and live individuals in the Tbilisi and Bakuriani Botanical Gardens in Georgia show that leaflets in this subspecies vary from glabrous to sparsely villose and/or pilose (Table 2), carpels from one to three in number and from glabrous and sparsely villose to tomentose, and petals from yellow to yellow with a pink spot at the base. The entity is not sufficiently distinct to allow recognition specific status.

This subspecies was reported to be a tetraploid with the chromosome number $2n = 20$ (Punina, 1987, 1989).

Additional specimens examined. GEORGIA, Abchasia: Gagra, near Guzlia, Mt. Berchil, limestone, 28.vi.1989. Geltman *et al.* 3109 (LE); Gagra, Dzhovihahu Mountain Range, 16.iv.1913. Sakharov 957 (LE); Gagra, path to Ritsa Lake, Gegi River, 17.v.1940. Komarov, s. n. (LE); Himtsa, 19.v.1928. Zakharova 958c (LE); Sukhumi Region, Mt. Ahupach, Tsebelda, iv.1904. O. Woronowa, s. n. (LE, G); Tsebelda (Zebelda), 16.v.1904. G. Woronow, s. n. (LE, G); between Tsebelda and Amtkal, 21.iv.1947. Yabrova, s. n. (LE); Tschernomore, 08.v.1923. Steup, s. n. (LE); Mt. Bzipi, 800 m alt., 13.vii.1958. Sochadze, s. n. (TBI); Mt. Bzipi, near Ritsa, 22.v.1948. Purtskvanidze, s. n. (TBI); Predbzybsky Mountain Range, alpine meadows, 1800 m alt., 30.vi.1936. Paniutin 958a (LE); Bzybsky Mountain Range, Mt. Pshechishho, 1700–1750 m alt., 1.viii.1930. Petiaev, s. n. (LE); Bzybsky Mountain Range, Mt. Khou, Vall. Heczigware, 1850 m, 2.x.1893, N. Albow 430 (G); the same locality, 1800 m, 3.x.1893. N. Albow 289 (G); east end of Bzybsky Mountain Range, Abats, 1800–1900 m alt., 20.viii.1990. Dolmatova *et al.* 935 (LE); Mt. Mamdzyshkha, alpine pasture, 1900 m alt., 8.vii. 1905. G. Woronow 191 (LE, G); Mt. Dzyshra, subalpine meadows, 21.vii.1929. Al. and An. Fedorov, s. n. (LE); Mt. Massivum, limestone, 20.vi.1980. Davlianidze and Kapanadze 1434 (TBI); upper reaches of Kodor River, near Sakeni, 2.vii.1964. Mordak, s. n. (LE); Joe kbara, 20.vii.1945. Kemularia-Nathadze, s. n. (TBI); 10.v.1902. G. Woronow, s. n. (LE); Borjomi: Bakuriani, the Botanical Garden, introduced, 19.v.1999. D. Y. Hong and S. L. Zhou H99063

(PE); Imereti: Kutais, Mt. Vakerali, 20.vii.1929. Kemularia-Nathadze, s. n. (TBI); upper part of Kvirila, NW of Perevi, 31.vii.1955. Dolukhanov and Kazarova, s. n. (TBI); Megrelia: Ohalkui, 2.vii.1958. Sochadze, s. n. (TBI); the same locality, 1500 m alt., 30.vi.1958. Sochadze, s. n. (TBI); the same locality, 1300 m alt., 6.vii.1958. Sochadze, s. n. (TBI); Siniagvar, 1600 m alt., 18.v.1937. Zaharova, s. n. (LE); Mt. Ohachkuie, limestone, 1600–1800 m alt., 27.viii.1987. Adzinba and Chitanova, s. n. (LE); Mt. Dzhwari, 2000 m, 25.viii.1893. N. Albow 607 (G); no exact locality, 2000 m alt., 25.vii.1956. E. and M. Sochadze, s. n. (TBI); Ratsha-Letskhumu: Mt. Massivum, limestone, 1700 m alt., 18.vii.1980. Davlianidze 1460 (TBI); Mt. Hvamli, 840 m alt., 4.ix.1925. Meffert, s. n. (LE); the same locality, 18.vii.1980. Gviniashvili, s. n. (LE); near Tsageri, top of Kulus, ix.1927. Meffert, s. n. (LE); Mt. Khvamli, 11.vi.1958, Kemularia-Nathadze *et al.* s. n. (TBI); the same locality, 1400 m alt., 6.vii.1957. Sochadze, s. n. (TBI); the same locality, 1600 m alt., 6.viii.1955. Sochadze, s. n. (TBI); Shkmeri, Kvagakhetkia, 1700 m alt., 23.viii.1968. s. coll., s. n. (TBI); the Shovi River, 17.vi.1965. Gagnidze *et al.* s. n. (TBI); Svaneti: Tsana, 1700–1800 m alt., 21.vii.1978. Mukhaniani *et al.* s. n. (TBI); Mt. Koruldani, 5.v.1964. Serdjukov, s. n. (TBI); near Kakhura, Goldashi, 2300 m alt., 12.vii.1979. Mukhaniani *et al.* s. n. (TBI); Tbilisi: Tbilisi Botanical Garden, introduced from Tsebelda, Abchasia, 3.v.1923. A. Woronowa, s. n. (LE); the same garden, introduced from Abchasia, 1.v.1999. D. Y. Hong and S. L. Zhou H99025 (PE) et 23.v.1999. D. Y. Hong and S. L. Zhou H99068 (PE). RUSSIA, Caucasus Nature Reserve: right bank of Mzymta River, Ahtsu Gorge, 29.iv.1989. Lebedeva, s. n. (LE); upper reaches of the Mzymta River, Sochi region, 23.ix. 1984. Solodko, s. n. (LE).

Paeonia daurica ssp. *macrophylla* (Albow) D. Y. Hong. **stat. nov.** = *Paeonia corallina* var. *wittmanniana* f. *macrophylla* Albow, Prodr. Fl. Colchicae. 15. 1895. *Paeonia macrophylla* (Albow) Lomakin in Trud Tiflis Bot. Sada, 2: 282, 1897; Lipsky in Trud Tiflis Bot. Sada (Fl. Caucas. and Suppl.) 4: 213. 1899; Schipczinsky in Komarov (ed.): Fl. USSR. 7: 32. 1937; Kemularia-Nathadze in Trud Tbilisi Bot. Inst. 21: 14. 1961. *P. wittmanniana* f. *macrophylla* (Albow) Busch, Fl. Caucas. Crit. 3(3): 13. 1901. *P. wittmanniana* var. *macrophylla* (Albow) Busch ex. Grossgeim, Fl. Caucas. 2: 91. 1930; Stern, Study Gen. Paeonia, 61. 1946. TYPE: Georgia, Adjara, Mt. Chakvis-Mta, above village Agara, 800–1000 m, 14.vii.1893. N. Albow 157 (Lectoholotype, here designated, G!, paratypes K!, G!)

Paeonia wittmanniana Steven in Bull. Soc. Nat. Moss. 21(3): 275. 1848; Boissier, Fl. Orient. 1: 97. 1867;

Lipsky in Trud Tiflis Bot. Sada, 4(Fl. Caucas. and Suppl.): 213. 1899, p. p. excl. var. *Paeonia corallina* var. *wittmanniana* (Steven) Albow in Prodr. Fl. Colch. 14. 1895. p. p. excl. form. TYPE: Georgia, Meskheta, between Akhaltsikhe and Kartalinia, near Atskhur.v.1842. Wittman, not designated.

Paeonia steveniana Kemularia-Nathadze in Trud Tbilisi Bot. Inst. 21: 15. 1961. TYPE: The same as that of Steven's *wittmanniana*.

Paeonia wittmanniana var. *nudicarpa* Schipczinsky in Not. Syst. Herb. Hort. Bot. Petrop. 2: 44, 1921; Stern. Study Gen. Paeonia, 59, 1946; Grossgeim, Fl. Caucas., 4: 12, 1950. TYPE: the same as Steven's.

Notes. This subspecies was established as a new taxon by Albow (1895) and raised to specific rank by Lomakin (1897) on the basis of larger leaflets. The entity is characterized by larger leaflets and glabrous carpels. However, glabrous carpels also occur in the subspecies *wittmanniana* and Figure 10 shows that the larger leaflets are only part of the continuous variation of leaflets in size in the complex. We have not found any other character which distinguishes it from the others.

The subspecies is confined to the high mountainous area in south-western Georgia (Adjara, Guria, south Imereti, south-west Kartli and Meskheta) and in north-eastern Turkey at altitudes from (800) 1200 to 2200 m. It grows in deciduous forests or mixed conifer and deciduous broad-leaved forests and also in glades, with no specific soil preference. This subspecies is a tetraploid with the chromosome number $2n = 20$ (Punina, 1987, 1989).

Additional specimens examined. GEORGIA, Adjara: Mt. Czakwis-Mta, supra pagum Agara, 14.vii.1893. N. Albow 156 (paratype, G!) and 161 (paratype, K!); Machuhtseti, 1160 m alt., , *Fagus* forest, 21.v.1999. D. Y. Hong and S. L. Zhou H99065 (A, CAS, K, MO, PE, US); Lodidziri, 6.viii.1910. Yu. Woronow and Popov 1205 (LE); Kobuleti, Dibvoke, 1200 m alt., 21.v.1962. Dmitrieva, s. n. (LE); Beschumi, 2025 m alt., Davitadze, s. n. (BATU); Machuntseti village, 1200 m alt., Davitadze, s. n. (BATU); Adjaro-Guria Gorge, Nagvarevis-Khevi to Pass Gomis-Mta, 2100 m alt., Dolukhanov and Kazarova, s. n. (TBI); Akho-Iaila, near Xalebashvili, subalpine zone, 8.viii.1939. Kvaratskhelia, s. n. (TBI); Akhaltsikhe: between Batumi and Akhaltsikhe, in forest, 23.vi.1890. S. Sommier and E. Levier, s. n. (G); Adjaro-Imeretinsky Mountain Range, Oshora, 15.vii.1926. Meffert 956(LE); Borjomi: Bakuriani, 12.vi.1934. Massagetov, s. n. (LE); Bakuriani 1700–1800 m alt., 25.vii.1984. Punina, s. n. (LE); the same locality, 29.v.1957. Harkevich, s. n. (LE);

Bakuriani, between Andeziti and Sakotschavi, 9.vii.1957. Tschaidze, s. n. (LE); Bakuriani, near the botanical garden, 25.vii.1960. Kemularia-Nathadze, s. n. (TBI); in forest, 15.v.1917. Sosnowsky, s. n. (TBI); Baniskhevi, 24.v.1920. Kozlowsky, s. n. (TBI); Sakotschavi, near Bakuriani, 08. 1935. Barnabishvili, s. n. (TBI); near the Kvabiskhevi River, 10 km from Kvabiskhevi, 3.vi.1964. s. coll., s. n. (TBI); Bakuriani, 1700 m alt., north slope, volcanic rock, 19.v.1999. D. Y. Hong and S. L. Zhou H99060 (A, CAS, K, MO, PE, US) et south slope, 1850 m alt., 19.v.1999. D. Y. Hong and S. L. Zhou H99062 (MO, PE); Emereti: Lukhunis-Tskali, c. 1250 m alt., iii.08. 1958. Dolukhanov, s. n. (TBI); Ermani: Delavars, 5.vii.1937. Busch s. n. (LE); Delavars, between Nizhny Ermani and Shavloho, 1850–2200 m alt., 24.viii.1929. Busch, s. n. (LE); Ahubat, 24.vi.1940. Sharova, s. n. (LE); Ahubat, between Ermani and Edis, 2000 m alt., 24.vi.1936. Busch, s. n. (LE); Edis, 29.vi.1938. Abramov, s. n. (LE); Hodzhehor, 19.viii.1930. Busch, s. n. (LE); Guria: Mt. Somlia, 8–10 km from Bahmaro, c. 2200 m alt., 2.ix.1980. Zaikonnikova, s. n. (LE); Adjaro-Imeretinsky Mountain Range, Mt. Gurusky, alpine pastures, Zortis-Keli, 3.vii.1914. Kikodze s. n. (LE); the same locality, near Bahmaro, 6.vii.1914. Kikodze, s. n. (LE); the same range, the gorge of Gedis-Dere River, 22. xii. 1921. Meffert, 957(LE); Mt. Bakhmaro-Zotiskheli, 1800–2000 m, 15.vi.1893. N. Albow 229 (G), 252 (G), 255 (G), 318 (G). TURKEY, A8 Rize, Ikidere, above Mesekey village, 1850 m, 15.ix.1993. M. Pitman and A. Wickham Turx 253 (K); Rize, Gamhhemsin, Yukari Amlakit Yaylasi., 2300 m, 25.vi.1981. A. Guler 3842 (E); Rize, S. Andesen, Bez Chamlihemshin, elenit-Alm, 2200 m, 28.vi.1971. E. and H. M. Steiner 98 (W); A9, Artvin, Yalniczam Silsilesi, 10 km ESE of Savsat, 2000–2400 m, 10.vii.1967. Albury, Cheese and Watson 3160 (K).

Paeonia daurica* ssp. *tomentosa (Lomakin) D. Y. Hong, **stat. nov.** \equiv *Paeonia wittmanniana* Stev. var. *tomentosa* Lomakin in Trud Tiflis Bot. Sada, 2: 283. 1897; Lipsky in Trud Tiflis Bot. Sada, 4(Fl. Caucas. and Suppl.); 213. 1899; *P. wittmanniana* ssp. *tomentosa* (Lomakin) Busch, Fl. Caucas. Crit. 3(3): 14. 1901. *P. tomentosa* (Lomakin) Busch in Fomin and Voron., Opred. Rast. Kavkaza; Kryma, 7. 1919; Grossgeim, Fl. Caucas., 2: 91. 1930; Stapf in Bot. Mag. t. 9249. 1931; Schipczinsky in Komarov (ed.): Fl. USSR, 7: 32. 1937; Stern, Study Gen. Paeonia, 56. 1946, pro syn.; Kemularia-Nathadze in Trud Tbilisi Bot. Inst., 21: 19. 1961. TYPE: Azerbaijan, the Talysch Mountains, Mt. Nudus-Galasi, c. 1800 m alt., 17.vi.1894. Lomakin (Holotype TBI!)

P. mlokosewitschii auct. non Lomakin: Grossgeim, Fl. Caucas., 4: 14. 1950. p. p., excl. specim. Lagodechi.

P. corallina var. *triternata* Boissier, Fl. Orient. 1: 97. 1867. p. p. quoad specim. Talysh.

Notes. The subspecies is characterized by leaflets nearly always densely covered with villose and/or pilose hairs on the lower surface, petals pale yellow but reddish at the base of a small proportion of individuals, and carpels mostly densely, rarely sparsely, tomentose. It mostly resembles ssp. *wittmanniana*, but differs from it in having leaflets mostly densely villose or pilose on the lower surface and carpels more or less tomentose. In contrast, ssp. *wittmanniana* possesses leaflets mostly sparsely villose or pilose and carpels often glabrous. The two subspecies are geographically isolated by a long distance.

Paeonia daurica ssp. *tomentosa* is found in the Talysh Mountains of Azerbaijan in the Caucasus and in northern Iran. It grows in deciduous forests with soil derived from sandstone at altitudes from 1100 to 1800 m. We also found this subspecies growing on a pasture with scattered trees or shrubs. Punina (1987, 1989) reported that the subspecies had the chromosome number $2n = 20$, and thus it is a tetraploid.

Additional specimens examined. AZERBAIJAN, Lerik: Orand, 21.viii.1938. Rzazade, s. n. (BAK); Orand, 3.vii.1962. Akundov, s. n. (BAK); Orand, 1500 m, 08.vii.1931. Schipchinsky 652(BAK); Orand, Zubu, 38°46'N, 48°25'E, 1170 m, 9.v.1999. D. Y. Hong and S. L. Zhou H99046 (A, CAS, K, MO, PE, US); between Orand and Schinabad, 13.v.1946. Grossgeim, s. n. (BAK); from Orand to Schinabad, 14.vi.1979. Menitsky and Popova, 14(LE); Orandskoye Gorge, 5.v.1960. Gusev 109 (LE); near Schinabad, 11.v.1946. Grossgeim, s. n. (BAK); between Schinabad and Lenkoran, 5.v.1960. Achundov and Sulejmanov, s. n. (BAK); between Schinabad and Lulekeran, 5.v.1960. Mordak 251 (LE); near Lerik, 24.vii.1963. Bobrov and Tzvelev 893 (LE); near Lerik, 14.v.1935. Grossgeim, s. n. (BAK, LE); the same locality, 4.v.1946. Irinskai and Kirpichnikov, s. n. (LE); Lerik, 28.vii.1975. Menitsky and Popova (LE); between Lerik and Lulia-Keran, 9.vii.1968. Kuzmina and Trukhakeva, s. n. (LE); between Lerik and Buzagar, 1700 m, 3.vii.1931. Schipczinsky 513(LE); Lenkoran: between Alasapin and Nadusgalasi, 12.vii.1929. Prilipko, s. n. (BAK); Lenkoran, in forest, v.1838. Hohenacker, s. n. (BM, E, G, K); IRAN, Prov. Mazandaran, Chalus valley, above Siah Bisheh, 2200 m, 23.v.1974. Wendelbo and Shirdelpur 11668 (E); Prov. Astrabad, Siaret, iv.1858. Bunge, s. n. (K); the same locality, v.1858. Bunge, s. n. (K); Elburz Mountains, 1800 m, 1907. R. B. Woosnaw (BM).

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