

Paeonia daurica Andrews or *P. mascula* ssp. *triternata* (Pall. ex DC.) Stearn & P. H. Davis (Paeoniaceae)?

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The peony in the Crimea of Ukraine and its allied populations have been variously taxonomically treated, as *Paeonia daurica* Andrews or *P. mascula* ssp. *triternata* (Pall. ex DC.) Stearn & P. H. Davis. Supported by the National Geographical Society, we have conducted extensive field observations and population sampling of this group in Turkey. In addition, relevant herbarium specimens from the herbaria B, BEO, BM, BUCA, E, G, GZU, K, P, SA, SOM, UPA, and WU were critically examined. Principal coordinate analysis was performed using MVSP-Version 3.13b analysis software. As a result, *P. daurica* was shown to be clearly differentiated from *P. mascula* in the number of leaflets/segments of the lower leaves and the shape of the terminal leaflets. *P. daurica* is diploid, except for three local tetraploids in the Caucasus, whereas *P. mascula* is consistently tetraploid. The two units were not found growing together, even in southern Turkey, where they are sympatric. *P. daurica* is considered to be a good species, which ranges from Croatia to Iran through Turkey and the Caucasus, and comprises six subspecies. © 2007 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2007, 154, 1–11.

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INTRODUCTION

Paeonia daurica was described by Andrews in 1807 (Andrews, 1807) from Tauria (Ukraine: Crimea) ('Dauria' is a spelling error for Tauria). According to the plate in Andrews (1807), it was characterized by undulate and nearly orbicular leaflets. This peony was earlier named *P. triternata* by Pallas in 1792, but without a description. Sims (1812) was the first botanist to recognize *P. daurica*. Anderson (1818) recognized *P. daurica* and treated *P. triternata* as its synonym in his monographic work on *Paeonia*. In the same year, de Candolle (1818) also recognized *P. daurica*, while treating *P. triternata* as a synonym; however, 6 years later, he described *P. triternata*, based on a specimen from Tauria, and treated *P. daurica* as its synonym (de Candolle, 1824). It was de Candolle who made the name *P. triternata* valid. Thus, the peony from Tauria then had two names, *P. daurica* Andrews (1807) and *P. triternata* Pall. ex DC. (1824). Later, botanists fol-

lowed de Candolle (1824), recognizing *P. triternata* at specific rank (Ledebour, 1842; Ruprecht, 1869; Lynch, 1890; Schipczinsky, 1921, 1937; Stebbins, 1939), but more botanists used '*triternata*' for this unit at different infraspecific ranks. Boissier (1867) was the first plant taxonomist to treat the unit as a variety, *P. corallina* (= *P. mascula*) β *triternata* (Pall. ex DC.) Boiss. The treatment was followed by Gürke (1903) and Ascherson & Graebner (1923). According to Gürke (1903), the peony was distributed from the Transcaucasus to Corsica. Fiori (1898) made nearly the same treatment for this peony, *P. officinalis* ssp. *corallina* var. *triternata*. Slightly different from Boissier (1867), Rouy & Foucaud (1893) treated it as a form, *P. corallina* f. *triternata* (Pall. ex DC.) Rouy & Foucaud, whereas Busch (1901) raised the taxonomic rank of the peony from varietal to subspecific level, *P. corallina* ssp. *triternata* (Pall. ex DC.) Busch. Huth (1891) proposed, surprisingly, a superfluous name for the unit, *P. corallina* var. *pallasii* Huth. Stern (1943) used the name *P. daurica*, and indicated that the name *P. triternata* was given by Pallas in 1795, but

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was never described by him. Later, Stern (1946: 71) stated that *P. triternata* Pall. was a *nomen nudum*, which meant that *P. triternata* Pall. ex DC. was a superfluous name. For many years after Stern (1946), all authors recognized this peony as an independent species. Most taxonomists used the name *P. daurica* (Grossheim, 1950; Cullen & Heywood, 1964; Davis & Cullen, 1965), whereas Nyárády (1953) and Kemularia-Nathadze (1961) still used the superfluous name *P. triternata* Pall. ex DC. It was Stearn & Davis (1984) who accepted Boissier's viewpoint (Boissier, 1867), treating the peony as an infraspecific taxon of *P. mascula* (= *P. corallina*), *P. mascula* ssp. *triternata* (Pall. ex DC.) Stearn & P. H. Davis. This treatment was accepted by Akeroyd (1993) and Phitos (2002), but not by Krupkina (1996), who still kept it at specific rank, *P. daurica*.

Stearn & Davis (1984: 18) stated that: 'Some morphological overlap between subsp. *triternata* and subsp. *mascula* in Anatolia has led us to give it subspecific rank here. Possibly the Greek material is best designated as "*triternata*-approaching"' This statement means that they made this treatment with some reservation, and that Anatolia is a key region for clarifying the relationship between *triternata* and *mascula*.

The above review on the history of taxonomic treatments indicates that there is still controversy with regard to the treatment of the peony in the Crimea and its related populations as a species separate from *P. mascula* or as a subspecies in *P. mascula*. To answer this question, i.e. to reveal the relationship between *P. daurica* and *P. mascula*, we conducted extensive fieldwork in Turkey, examined a large number of herbarium specimens, and undertook the subsequent statistics, with the results presented here.

We did not include the population samples from the Caucasus and the Talish Mountains in the analysis for three reasons. First, as stated in the 'Results and discussion' section and in Hong & Zhou (2003), the five subspecies of *P. daurica* which occur there are distinct from *P. mascula*. Second, the samples were sent as exsiccatae to the herbaria A, CAS, K, MO, PE, and US immediately after the preparation of the article (Hong & Zhou, 2003). Third, it was the report of 'some morphological overlap between the two units in Anatolia' that led Stearn & Davis (1984: 18) to give *triternata* subspecific rank, and so we focused our investigations on this group in Turkey.

MATERIAL AND METHODS

Supported by the National Geographical Society (NGS), the authors conducted extensive field observations in Turkey in 2002. Five populations of the *P. mascula*/*P. daurica* group were sampled: *H02211*,

H02212, *H02213*, *H02215*, and *H02221* (Table 1). In these populations, three individuals were dug up to observe their roots, three more individuals were collected leaving the underground parts *in situ* and intact, and, in addition, one of the lower leaves of each of four individuals was taken.

We critically examined all the exsiccatae of the *P. mascula*/*P. daurica* group from the following herbaria: B, BEO, BM, BUCA, E, G, GZU, K, P, Dr W. Sauer's Private Herbarium at Tübingen, Germany (SA), SOM, UPA, and WU.

For both herbarium specimens and our own collections, morphological characters were documented. *P. daurica* was considered to be characterized by undulate leaves, obovate leaflets with rounded apices, nine leaflets, and a chromosome number of $2n = 10$ (Davis & Cullen, 1965). According to our observations on a large number of specimens in the field and in herbaria, the undulate feature is not reliable as a diagnostic character, as it varies even within populations and occurs more frequently in the Crimean populations than in the populations in southern Turkey and Serbia. As we do not have much information on chromosomes in this group, it was not used in the statistics because of the lack of individual information. We found that the number of leaflets/segments of the lower leaves was rather stable and was a good diagnostic character. Therefore, five characters were used and coded for the statistical analysis (Table 2).

A data matrix was constructed using the five characters and with each individual as an operational taxonomic unit (OTU) (Table 1). The materials of *P. daurica* were grouped into four regional units: UDT for the peony from the Crimea, Ukraine; TD1 and TD2 for those from Turkey; and BDY for that from the Balkans. According to the recent taxonomy (Akeroyd, 1993; Özhatay & Özhatay, 1995), *P. mascula* includes five subspecies: ssp. *mascula* from northern Spain to Asia Minor via France, Italy, and Greece; ssp. *russoi* in Sicily and Calabria of Italy; ssp. *hellenica* in the Aegean; ssp. *bodurii* confined to Çanakkale Province, Turkey; and ssp. *arietina* from Italy to Turkey via the Balkans. *P. mascula* ssp. *arietina* (G. Anderson) Cullen & Heywood (= *P. arietina* G. Anderson) has been found to always have tuberous roots (vs. carrot-shaped in the *P. mascula* group), and villose stems, petioles, and sepals, and thus is morphologically distinct from the group under study (D.-Y. Hong, X.-Q. Wang, D.-M. Zhang & S. T. Koruklu, unpubl. data). On molecular trees of internal transcribed spacer (ITS) sequences and *matK*, *P. arietina* is separate and only distantly related to the *P. mascula* group (Sang, Crawford & Stuessy, 1995, 1997). Thus, *P. mascula* ssp. *mascula* from France (FMM) and Turkey (TM1, TM2), where it was sympatric with *P. daurica* (TD1, TD2), and *P. bodurii* (TMB) were included in the present analysis.

Table 1. Data matrix for Gower principal coordinate analysis, and the origin of the materials used in the statistics and their vouchers

Coding number	Locality	Voucher	Taxon	Number of leaflets/ segments of lower leaves	Length of terminal leaflets	Length/ width of terminal leaflets	Widest point*	Shape of apex of terminal leaflets†
FMM-1	France: Cote d'Or	<i>P. A. Genty, s. n. (P)</i>	<i>P. mascula</i> ssp. <i>mascula</i>	15	8.6	1.79	0.39	6
FMM-2	France: Cote d'Or	<i>s. coll. s. n. (P)</i>	<i>P. mascula</i> ssp. <i>mascula</i>	10	10.2	1.59	0.45	5
FMM-3	France: Cote d'Or	<i>G. Legrand, s. n. (P)</i>	<i>P. mascula</i> ssp. <i>mascula</i>	13	9.8	1.78	0.48	5
FMM-4	France: Cote d'Or	<i>Vergues, s. n. (P)</i>	<i>P. mascula</i> ssp. <i>mascula</i>	12	12.2	1.97	0.41	5
FMM-5	France: Envirov de Bloir	<i>Boreau, s. n. (P)</i>	<i>P. mascula</i> ssp. <i>mascula</i>	13	9	1.84	0.38	5
FMM-6	France: Loir et Cher	<i>A. Sejourne s. n. (P)</i>	<i>P. mascula</i> ssp. <i>mascula</i>	13	9	1.96	0.45	6
TM1-1	Turkey: Antalya, Gebiz	<i>P. H. Davis 15711 (K)</i>	<i>P. mascula</i> ssp. <i>mascula</i>	14	9.5	1.38	0.48	5
TM1-2	Turkey: Bitlis	<i>P. H. Davis 46082 (K)</i>	<i>P. mascula</i> ssp. <i>mascula</i>	13	7.7	1.38	0.46	4
TM1-3	Turkey: Ismir	<i>P. H. Davis 41775 (K)</i>	<i>P. mascula</i> ssp. <i>mascula</i>	22	13	1.59	0.46	5
TM1-4	Turkey: Bitlis	<i>McNeill 621 (K)</i>	<i>P. mascula</i> ssp. <i>mascula</i>	14	9.5	1.9	0.47	6
TM1-5	Turkey: Hatay	<i>Davis & Hedge 21159 (K)</i>	<i>P. mascula</i> ssp. <i>mascula</i>	17	9.5	2.11	0.43	6
TM1-6	Turkey: Adana, Bahee	<i>Davis & Hedge 26879 (BM)</i>	<i>P. mascula</i> ssp. <i>mascula</i>	14	12	1.33	0.48	3
TM1-7	Iraq: MAM, Sarsang	<i>E. Chapman 26370 (K)</i>	<i>P. mascula</i> ssp. <i>mascula</i>	12	12.2	1.85	0.5	5
TM1-8	Iraq: MAM, Sarsang	<i>R. Wheeler Haines W. 959 (K)</i>	<i>P. mascula</i> ssp. <i>mascula</i>	18	11.2	2	0.49	6
TM2-1	Turkey: Hatay, Senkoy	<i>Hong et al. H02211 (PE)</i>	<i>P. mascula</i> ssp. <i>mascula</i>	11	9.4	1.91	0.47	5
TM2-2	Turkey: Hatay, Senkoy	<i>Hong et al. H02211 (MO)</i>	<i>P. mascula</i> ssp. <i>mascula</i>	12	17	1.95	0.41	5
TM2-3	Turkey: Hatay, Senkoy	<i>Hong et al. H02211 (K)</i>	<i>P. mascula</i> ssp. <i>mascula</i>	15	12	1.76	0.51	6
TM2-4	Turkey: Hatay, Belen	<i>Hong et al. H02212 (PE)</i>	<i>P. mascula</i> ssp. <i>mascula</i>	11	9.9	1.83	0.47	5
TMB-1	Turkey: Çanakkale, Camyayla	<i>Hong et al. H02203 (A)</i>	<i>P. mascula</i> ssp. <i>bodurii</i>	9	12.7	1.46	0.4	6
TMB-2	Turkey: Çanakkale, Camyayla	<i>Hong et al. H02203 (CAS)</i>	<i>P. mascula</i> ssp. <i>bodurii</i>	9	13.8	1.89	0.42	5
TMB-3	Turkey: Çanakkale, Camyayla	<i>Hong et al. H02203 (K)</i>	<i>P. mascula</i> ssp. <i>bodurii</i>	10	14.8	1.76	0.39	6
TMB-4	Turkey: Çanakkale, Camyayla	<i>Hong et al. H02203 (MO)</i>	<i>P. mascula</i> ssp. <i>bodurii</i>	10	16.7	1.88	0.47	6
TMB-5	Turkey: Çanakkale, Camyayla	<i>Hong et al. H02203 (PE)</i>	<i>P. mascula</i> ssp. <i>bodurii</i>	11	14.5	2.01	0.41	6
TMB-6	Turkey: Çanakkale, Camyayla	<i>Hong et al. H02203 (UPA)</i>	<i>P. mascula</i> ssp. <i>bodurii</i>	10	14.5	1.76	0.38	6
TMB-7	Turkey: Çanakkale, Camyayla	<i>Hong et al. H02203 (PE)</i>	<i>P. mascula</i> ssp. <i>bodurii</i>	11	12.5	1.74	0.43	6
TMB-8	Turkey: Çanakkale, Camyayla	<i>Hong et al. H02203 (PE)</i>	<i>P. mascula</i> ssp. <i>bodurii</i>	11	14.5	1.91	0.43	6
TMB-9	Turkey: Çanakkale, Camyayla	<i>Hong et al. H02203 (PE)</i>	<i>P. mascula</i> ssp. <i>bodurii</i>	9	13.5	2.18	0.44	6
BDY-1	Serbia: Kosovo	<i>S. Matvejev, s. n. (BEO)</i>	<i>P. daurica</i> (= <i>P. mascula</i> ssp. <i>triternata</i>)	9	7.1	1.69	0.36	3
BDY-2	Serbia: Kosovo	<i>H. Oehm, s. n. (BEO)</i>	<i>P. daurica</i>	9	9.5	1.3	0.37	3
BDY-3	Serbia: Kosovo	<i>Diklic & Nikolic, s. n. (BEO)</i>	<i>P. daurica</i>	9	15.2	1.19	0.45	4

Table 1. Continued

Coding number	Locality	Voucher	Taxon	Number of leaflets/ segments of lower leaves	Length of terminal leaflets	Length/ width of terminal leaflets	Widest point*	Shape of apex of terminal leaflets†
BDY-4	Serbia: Kosovo	<i>B. Panjkovic, s. n.</i>	<i>P. daurica</i>	9	12.2	1.56	0.31	2
BDY-5	Bosnia: Mt. Jamnica	<i>K. Maly, s. n. (K)</i>	<i>P. daurica</i>	10	9.7	1.29	0.43	3
UDT-1	Ukraine: Simferopol	<i>A. Gallier 526 (P)</i>	<i>P. daurica</i>	9	6.7	1.34	0.38	3
UDT-2	Ukraine: Simferopol	<i>A. Gallier 526 (P)</i>	<i>P. daurica</i>	9	6.5	1.34	0.38	3
UDT-3	Ukraine: Simferopol	<i>A. Gallier 526 (K)</i>	<i>P. daurica</i>	9	6.5	1.16	0.39	3
UDT-4	Ukraine: Crimea	<i>H. D. Bunge, s. n. (P)</i>	<i>P. daurica</i>	9	9.5	1.16	0.26	1
UDT-5	Ukraine: Crimea	<i>W. Besser, s. n. (K)</i>	<i>P. daurica</i>	9	5.5	1.1	0.4	1
UDT-6	Ukraine: Crimea, Yalta	<i>Davis 33375 (K)</i>	<i>P. daurica</i>	9	7.2	1.18	0.33	2
TD1-1	Turkey: Hatay, Mt. Amanos	<i>Hong et al. H 02213 (PE)</i>	<i>P. daurica</i>	9	8.1	1.65	0.35	4
TD1-2	Turkey: Hatay, Mt. Amanos	<i>Hong et al. H 02213 (MO)</i>	<i>P. daurica</i>	8	8.5	1.57	0.33	2
TD1-3	Turkey: Hatay, Mt. Amanos	<i>Hong et al. H02215 (A)</i>	<i>P. daurica</i>	9	11.2	1.7	0.4	4
TD1-4	Turkey: Hatay, Mt. Amanos	<i>Hong et al. H02215 (CAS)</i>	<i>P. daurica</i>	9	10.8	1.74	0.31	4
TD1-5	Turkey: Hatay, Mt. Amanos	<i>Hong et al. H02215 (K)</i>	<i>P. daurica</i>	9	11.1	1.82	0.29	4
TD1-6	Turkey: Hatay, Mt. Amanos	<i>Hong et al. H02215 (MO)</i>	<i>P. daurica</i>	10	10.5	1.62	0.39	4
TD1-7	Turkey: Hatay, Mt. Amanos	<i>Hong et al. H02215 (PE)</i>	<i>P. daurica</i>	9	8.5	1.73	0.33	4
TD1-8	Turkey: Hatay, Mt. Amanos	<i>Hong et al. H02215 (UPA)</i>	<i>P. daurica</i>	9	11.1	1.8	0.39	4
TD1-9	Turkey: Hatay, Mt. Amanos	<i>Hong et al. H02215 (PE)</i>	<i>P. daurica</i>	9	11.3	1.64	0.43	4
TD1-10	Turkey: Hatay, Mt. Amanos	<i>Hong et al. H02215 (PE)</i>	<i>P. daurica</i>	9	10.2	1.44	0.42	4
TD1-11	Turkey: Hatay, Mt. Amanos	<i>Hong et al. H02215 (PE)</i>	<i>P. daurica</i>	9	9.2	1.46	0.43	4
TD2-1	Turkey: Samsun, Havza	<i>Hong et al. H02221 (A)</i>	<i>P. daurica</i>	10	8	1.6	0.38	4
TD2-2	Turkey: Samsun, Havza	<i>Hong et al. H02221 (CAS)</i>	<i>P. daurica</i>	10	8.9	1.25	0.37	2
TD2-3	Turkey: Samsun, Havza	<i>Hong et al. H02221 (K)</i>	<i>P. daurica</i>	9	8.5	1.23	0.38	2
TD2-4	Turkey: Samsun, Havza	<i>Hong et al. H02221 (MO)</i>	<i>P. daurica</i>	9	9.3	1.01	0.34	2
TD2-5	Turkey: Samsun, Havza	<i>Hong et al. H02221 (PE)</i>	<i>P. daurica</i>	9	9.4	1.19	0.45	4
TD2-6	Turkey: Samsun, Havza	<i>Hong et al. H02221 (UPA)</i>	<i>P. daurica</i>	9	7.5	1.7	0.36	4
TD2-7	Turkey: Samsun, Havza	<i>Hong et al. H02221 (PE)</i>	<i>P. daurica</i>	9	9.3	1.45	0.42	4
TD2-8	Turkey: Samsun, Havza	<i>Hong et al. H02221(PE)</i>	<i>P. daurica</i>	9	10.1	1.38	0.42	4
TD2-9	Turkey: Samsun, Havza	<i>Hong et al. H02221 (PE)</i>	<i>P. daurica</i>	10	9.3	1.55	0.43	4
TD2-10	Turkey: Samsun, Havza	<i>Hong et al. H02221 (PE)</i>	<i>P. daurica</i>	11	9.3	1.58	0.44	4

*See Table 2 for explanation.

†See Figure 1 and Table 2 for explanation.

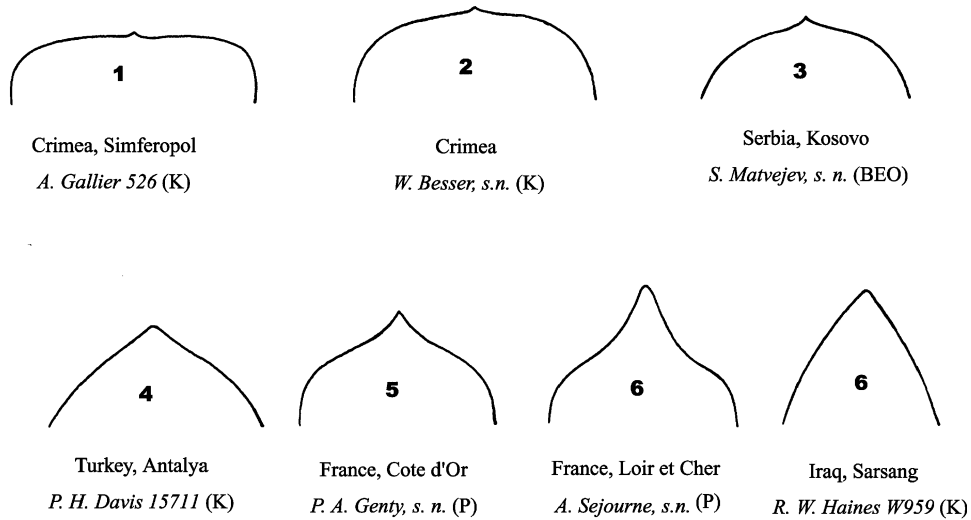


Figure 1. The apex of terminal leaflets of the *Paeonia daurica*/*P. mascula* group, illustrated to explain the character coding in Table 2.

Table 2. Characters and coding (in parentheses) used in the statistical analysis of the relationship between *Paeonia mascula* and *P. daurica*

1	Number of leaflets/segments of lower leaves
2	Length of the terminal leaflets
3	Length/width of the terminal leaflets
4	Position of the widest part of the terminal leaflets (distance from the top to the widest part/total length)
5	Shape of apex of the terminal leaflet: * emarginate to truncate (1); broad-rounded, with or without a minute mucro (2); rounded, with or without a minute mucro (3); obtuse-subacute (4); rounded-cuspidate (5); cuspidate or acute (6)

*See Figure 1 for further explanation.

The Gower general similarity coefficient for mixed data sets was used in the analysis. Principal coordinate analysis was conducted using MVSP-Version 3.13b analysis software.

RESULTS AND DISCUSSION

MORPHOLOGICAL DIFFERENTIATION

As shown in Table 1, the number of leaflets/segments of the lower leaves was mostly nine, rarely ten, and very occasionally 11 in *P. daurica*, whereas, in *P. mascula*, it ranged from 11 to 22, rarely ten, and very occasionally nine. This character was rather stable, with little variation within populations. In the population *H02215* (Mt. Amanos, Hatay, Turkey), for example, we observed an additional 25 individuals, which all had nine leaflets/segments. On the mountain, there were hundreds of *P. daurica* individuals from 1300 to 1550 m, but very few had more than nine leaflets/segments. The length of the terminal leaflets varied from 55 to 152 mm, with a standard deviation of 92 ± 19 mm in *P. daurica*, and from 77 to 167 mm,

with a standard deviation of 118 ± 25 mm in *P. mascula*; the length to width ratio ranged from 1.01 to 1.82, with a standard deviation of 1.45 ± 0.23 in *P. daurica*, and from 1.33 to 2.18, with a standard deviation of 1.79 ± 0.22 in *P. mascula*. The apex of the terminal leaflets was mostly truncate, broad-rounded, or rounded in *P. daurica*, whereas it was mostly acute, cuspidate, or rounded-cuspidate in *P. mascula*. The widest point of the terminal leaflets was also different in the two forms. Although the point was above the middle in both forms, it was much above the middle, approximately in between the top and the middle, in *P. daurica*, but just above the middle in *P. mascula*. Thus, the terminal leaflets were broad-obovate or nearly orbicular in *P. daurica*, but obovate, oblong, or ovate in *P. mascula*. As indicated in Figure 2, *P. daurica* was clearly differentiated from *P. mascula* in morphology.

Paeonia daurica (= *P. triternata* Pall. ex DC.) had been recognized with specific status by most taxonomists before Stearn & Davis (1984) (Schipczinsky, 1921, 1937; Stebbins, 1939; Stern, 1943, 1946; Cullen & Heywood, 1964; Davis & Cullen, 1965). Stearn &

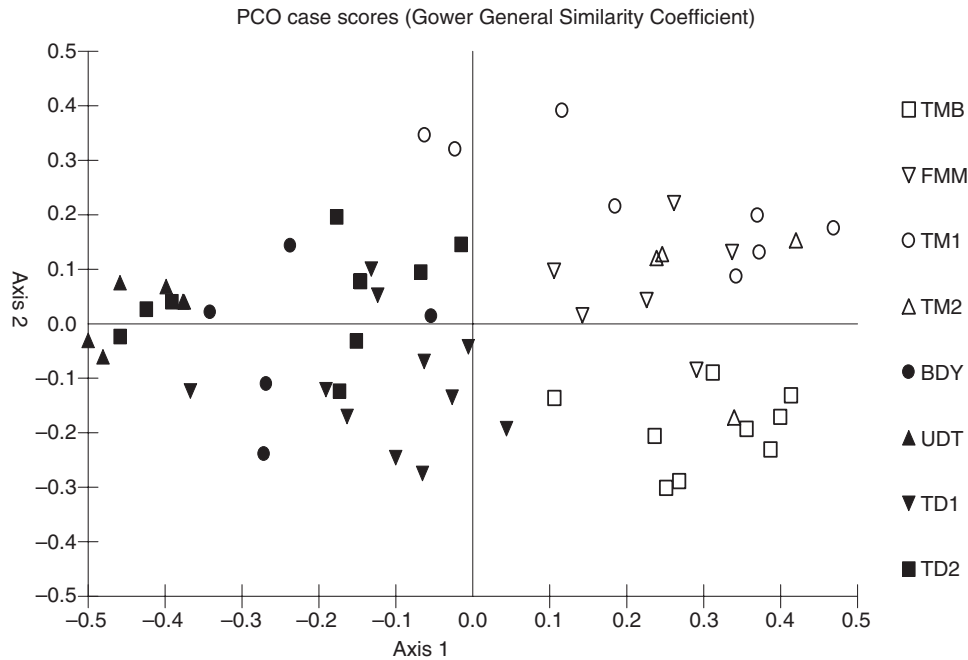


Figure 2. Gower general similarity coefficients, showing a clear morphological differentiation between *Paeonia daurica* (BDY, from Bosnia and Serbia; UDT, from Ukraine: Crimea; TD1, from Turkey: Hatay; TD2, from Turkey: Samsun) and *P. mascula* (TMB, from Turkey: Çanakkale; FMM, from France; TM1, from Turkey and Iraq; TM2, from Turkey: Hatay). PCO, principal coordinate.

Davis (1984) treated *P. daurica* with subspecific status in *P. mascula*, but they stated (Stearn & Davis, 1984: 108): 'These characters (leaflets obovate, concave upper surface, undulate margin and rounded to truncate apex) may appear individually but apparently not all together within *mascula* populations outside the Crimea and the status of such plants, which are covered by the above description, is doubtful. They have more acute leaflets than ssp. *triternata* sensu stricto.'; and 'A variant of *P. mascula* occurring in Romania with typical *mascula* but approaching *triternata* in its obtuse or subacute leaflets was named *P. corallina* var. *triternatiformis*... Population studies are needed to clarify the status of taxa within this *mascula* complex.' From these statements, it is clear that they also emphasized the shape of leaflets, but not the number of leaflets/segments of the lower leaves, to distinguish these two units.

Although the shape of the leaflets is a valuable character for distinguishing between *triternata* and *mascula*, it is secondarily important because it shows some overlap between the two units, as stated by Stearn & Davis (1984). The most distinct character for the differentiation between these two units, however, is the number of leaflets/segments of the lower leaves. Unfortunately, this character was neglected by the previous authors and also by Stearn & Davis (1984). This is possibly because they failed to conduct exten-

sive field observations, and most exsiccatae lacked lower leaves, which made the previous authors unable to use this character. Our extensive population observations in the Caucasus, Turkey, Spain, France, Italy, and Greece showed that no more than 5% of individuals had lower leaves with more than nine leaflets/segments in *P. daurica* (Stearn & Davis' *triternata*), whereas more than 94% of individuals had lower leaves with ten or more leaflets/segments in *P. mascula* (Stearn & Davis' *mascula*). Even more important is that the number of leaflets/segments of the lower leaves is correlated with the shape of the leaflets: in *P. daurica*, the lower leaves usually have nine leaflets/segments and the leaflets are usually obovate or orbicular, and truncate, obtuse, or rarely acute at the apex; in *P. mascula*, the lower leaves usually have 10–22 leaflets/segments and the leaflets are usually obovate or elliptic-obovate, and short-acuminate or acute at the apex. Furthermore, these differences between the two units are correlated with the number of chromosomes (diploid or tetraploid). Tetraploids ($2n = 20$) occur in three subspecies of *P. daurica* in the Caucasus and the Talish Mountains, but are isolated in alpine or subalpine regions. Although these three subspecies of *P. daurica* are not clearly differentiated from *P. mascula* by the shape of entire leaflets and of the terminal part of the leaflets, they are readily distinguished by other characters in addition

to the number of leaflets/segments of the lower leaves. In *P. daurica* ssp. *macrophylla*, the carpels are glabrous and the petals are yellow or yellowish white; in ssp. *tomentosa*, the leaves are densely villose beneath and the petals are yellow; in ssp. *wittmanniana*, the carpels are glabrous, sparsely hairy to tomentose and the petals are yellow or yellow with a red spot at the base (Hong & Zhou, 2003).

Paeonia daurica and *P. mascula* overlap geographically by a large area. In our expedition to Turkey, particularly in Hatay Province, they were found to be morphologically distinct, and not intermingled with each other. No hybrids were found there. Based on the results mentioned above, it would be rational to treat *P. daurica* (= *P. mascula* ssp. *triternata*) as a species separate from *P. mascula*.

Stearn & Davis (1984: 108) stated that the two units geographically overlapped in the eastern Aegean islands (Lesvos and Samos). A critical examination of all the specimens of this group from the regions mentioned above was made at the herbaria ATH, E, G, LD, and UPA. It was found that the specimens from Lesvos and Samos, including *E. Stamatiadou 2666* (ATH), determined by P. H. Davis as *P. mascula* ssp. *triternata*, all belong to *P. mascula* ssp. *mascula*, and thus

no subspecies *triternata* was present on these two islands.

CHROMOSOMAL DIFFERENTIATION

The chromosome reports so far available are summarized in Table 3, from which it is clear that *P. mascula* is always tetraploid, whereas *P. daurica* is diploid, except for the three subspecies at the alpine or subalpine regions in the Caucasus and the Talish Mountains. It should be mentioned that *P. daurica* and *P. mascula* ssp. *mascula* both occur in southern Turkey, e.g. in Hatay (Table 3), but are distinct with regard to both morphology and ploidy level (diploid vs. tetraploid).

TAXONOMIC TREATMENT

Owing to the clear morphological differentiation and ploidy differentiation between *P. daurica* and *P. mascula*, as shown in Figure 2 and Table 3, we consider it unjustifiable to treat *P. daurica* as a subspecies of *P. mascula*, i.e. *P. mascula* ssp. *triternata* (Pall. ex DC.) Stearn & P. H. Davis.

Table 3. Chromosomal reports of *Paeonia daurica*/*P. mascula*

Taxon	Locality	Chromosome number	Reference
<i>P. daurica</i>	Bulgaria	2n = 10	Koeva & Sarkova (1997)†
	Greece: Drama	2n = 10	Tzanoudakis & Arampatzis (1998)
	Macedonia	2n = 10	Sopova (1971)
	Turkey: Hatay, Mt. Amanos	2n = 10	D.-Y. Hong <i>et al.</i> , unpubl. data
	Turkey: Samsun	2n = 10	cf. Davis & Cullen (1965)
	Ukraine: Crimea	2n = 10	cf. Tzanoudakis & Arampatzis (1998)
	Ukraine: Crimea	2n = 10	Barber (1941)
	Cultivated	2n = 10	Langlet (1927)
<i>P. mascula</i> * ssp. <i>mascula</i>	Greece: Boeotia	2n = 20	Tzanoudakis (1977)
	Greece: Samos	2n = 20	Tzanoudakis (1977)
	Italy	2n = 20	Bernardo <i>et al.</i> (1995)
	Turkey: Hatay	2n = 20	D.-Y. Hong <i>et al.</i> , unpubl. data
<i>P. mascula</i> ssp. <i>bodurii</i>	Turkey: Canakkale	2n = 20	Özhatay & Özhatay (1995)
	Turkey: Canakkale	2n = 20	D.-Y. Hong <i>et al.</i> , unpubl. data
<i>P. mascula</i> ssp. <i>hellenica</i>	Greece: Andros	2n = 20	Tzanoudakis (1977)
	Greece: Euboea	2n = 20	Tzanoudakis (1977)
	Greece: Icaria	2n = 20	Tzanoudakis (1977)
<i>P. mascula</i> ssp. <i>russoi</i>	Sicily: <i>sine loc.</i>	2n = 20	Raimondo, Rossitt & Ottonello (1983)
	Sicily: Mt. Carbonara	2n = 20	D.-Y. Hong <i>et al.</i> , unpubl. data

*According to the senior author of the present article (D.-Y. Hong *et al.*, unpubl. data), *P. mascula* ssp. *arietina* is a distinct species (see explanation in 'Material and methods' section); 'ssp. *russoi*' in Corsica, Sardinia, and the Ionian Islands of Greece belongs to another species, *P. corsica* Sieber ex Tausch. (Hong & Wang, 2006).

†These two authors misused the name *P. mascula*, because the specimens from Bulgaria all belong to *P. daurica*.

KEY TO *P. DAURICA/P. MASCULA*

- 1a. Leaflets/segments of lower leaves 9, rarely 10, very occasionally 11; terminal leaflets usually broad-obovate or nearly orbicular, with length/width 1.2–1.7, apex mostly truncate, broad-rounded, or rounded, and the widest point in between the middle and top; chromosome number $2n = 10$ ***P. daurica***
- 1b. Leaflets/segments of lower leaves 11–22, rarely 10, very occasionally 9; terminal leaflets obovate, oblong, or ovate, with length/width 1.6–2.0, apex mostly acute, rounded-cuspidate or cuspidate, and the widest point just above the middle; chromosome number $2n = 20$ ***P. mascula***

Paeonia daurica Andrews, *Bot. Rep.* 7, t. 486 (1807); Sims, *Bot. Mag. t.* 1441 (1812); Anderson, *Trans. Linn. Soc. London*, 12: 270 (1818); De Candolle, *Syst. nat.* 1: 391 (1818); Stern, *J. Roy. Hort. Soc. London*, 68: 126 (1943); Stern, *Stud. Gen. Paeonia*: 70 (1946); Cullen & Heywood, *Fl. Europ.* 1: 244 (1964); Davis & Cullen, *Fl. Turkey*, 1: 205 (1965); Hong & Zhou, *Bot. J. Linn. Soc.* 143: 144 (2003). Type: Tab. in Andrews *Bot. Rep.* 7, t. 486 (1807)

Paeonia triternata Pall. ex DC., *Prodr.* 1: 65 (1824); Pall., *Nov. Acta Petrop.* 10: 312 (1792) & *Tabl. Taur.*: 52 (1795), *nom. nud.*

= *Paeonia corallina* var. *triternata* (Pall. ex DC.) Boiss., *Fl. orient.* 1: 97 (1867).

= *Paeonia mascula* var. *triternata* (Pall. ex DC.) Gürke in Richter (ed.), *Pl. eur.* 2: 400 (1903).

= *Paeonia corallina* f. *triternata* (Pall. ex DC.) Roy & Foucaud, *Fl. France*, 1: 144 (1893).

= *Paeonia corallina* ssp. *triternata* (Pall. ex DC.) Busch in Kusnezow, Busch & Fomin (eds), *Fl. Cauc. Crit.* 3(3): 10 & 224 (1901).

= *Paeonia officinalis* ssp. *corallina* var. *triternata* (Pall. ex DC.) Fiori in Fiori & Paoletti (eds), *Fl. Analit. Ital.* 1(2): 527 1898, *p.p.*

= *Paeonia mascula* ssp. *triternata* (Pall. ex DC.) Stearn & P.H. Davis, *Peonies of Greece*: 107, figs 33,34 (1984). Type: Ukraine, Crimea, *P. S. Pallas*, *s. n.* (lectotype here designated: BM!).

Paeonia corallina var. *pallasii* Huth, *Engl. Bot. Jahrb.* 14: 267 (1891).

Type: Andrews, *Bot. Rep.* t. 486 (1807)!

Paeonia corallina var. *triternatiformis* Nyár. in Săvulescu (ed.), *Fl. Reip. Pop. Român.*, 2: 403, 675, pl. 63, fig. 2 (1953).

Type: Nyárády's fig. cited above.

Although Huth (1891) used the name var. *pallasii*, he did not give a description or cite an exsiccata; instead, he cited Andrews' tab.

Paeonia daurica Andrews is widely distributed from Croatia and Bosnia in the west to Iran in the east through Turkey and the Caucasus. As the five subspecies of *P. daurica* in the Caucasus and the Talish Mountains have been treated and described in detail by Hong & Zhou (2003), we deal here only with the populations west of the Caucasus, which belong to the typical subspecies, *Paeonia daurica* ssp. *daurica*.

Paeonia daurica Andrews ssp. *daurica* (Fig. 3)

Lower leaves biternate, leaflets rarely segmented; leaflets/segments nine, rarely ten, very occasionally 11, obovate or orbicular, truncate, rounded, or obtuse, rarely acute at the apex, glabrous to sparsely villose beneath; flowers red or pink; carpels always tomentose. Chromosome number $2n = 10$.

The typical subspecies is distributed in Bosnia, Croatia, Serbia, Macedonia, Romania, Bulgaria, Ukraine (Crimea), Greece (Drama), Turkey, and Lebanon. It grows in woods at 350–1550 m.

Additional specimens examined: BOSNIA: Mt. Jamnica, near Vardiste, 860–1000 m, 30.v.1911, *K. Maly s. n.* (K).

BULGARIA: Turnovo, 1904, *I. K. Urumov s. n.* (SOM); Vratsa, vi.1898, *s. coll.*, *s. n.* (SOM).

CROATIA: Dobrovnik (Ragusa): Mt. Dalmatia, *Adamovic s. n.* (WU).

GREECE: Drama Prov. (Macedonia): Mt. Menikion, c. 10 km from Panorama, 1050 m, 41°15'N, 23°44'E, 27.v.1996, *T. Arampatzis & K. Vidakis s. n.* (UPA).

LEBANON: *sine loc.*, 31.v.1879, *E. Peyron 544* (G).

MACEDONIA: Demir Kapija, 9.vi.1925, *P. Černjavski s. n.* (BEO).

ROMANIA: Buzau: Gura, Savatii, 350 m, 17.viii.1948, *C. Dobrescu s. n.* (BUCA); *loc. eodem*, 400 m, 5.v.1948, *C. Dobrescu s. n.* (BUCA); Nisicov Valley, Cheia, Tisau County, 14.iv.1959, *G. Dihoru s. n.* (BUCA); Mt. Ciolanu, 2.v.1966, *R. Wallfisch s. n.* (BUCA); Mehedinti, Virciorova, 18.v.1966, *N. Roma s. n.* (BUCA); *loc. eodem* 350 m, 9.viii.1948, *E. Topa s. n.* (BUCA).

SERBIA: Kosovo: Kosovska, Mitrovica, 28.v.1949, *S. Matvejev s. n.* (BEO); between Kosovo and Albania, Mt. Koritnik, v.1937, *H. Oehm s. n.* (BEO); between Kosovo and Albania, Pastrik, 500–1500 m, 26.vii.1979, *N. Diklić & V. Nikolić s. n.* (BEO); Srbija, Belevik, Istok, 14.vi.1997, *B. Panjković s. n.* (Institute for Nature Protection, Novi Sad).

TURKEY: Adaba: Dumani, Mt. Haruniye, 1300 m, 19.iv.1957, *Davis & Hedge D26879* (ANK); Antalya: 1000 m, 25.viii.1941, *P. H. Davis 14287*(K); Hatay: Mt. Amanos, above Topaktas, 1290 m, 18.v.2002, *D. Y. Hong, D. Y. Zhang, X. Q. Wang & S. T. Koruklu H02213* (MO, PE); *loc. eodem*, 1380–1540 m, 18.v.2002, *D. Y.*

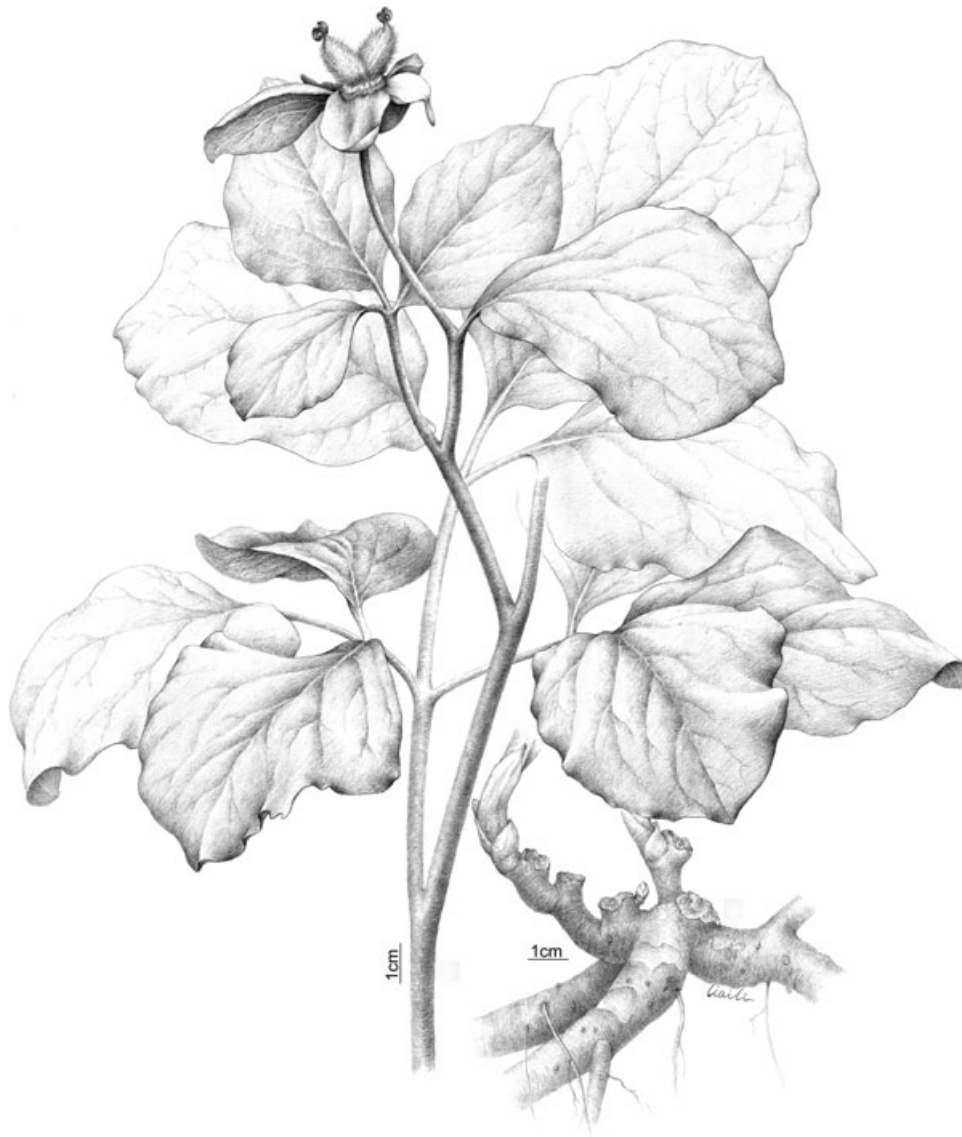


Figure 3. *Paeonia daurica* Andrews ssp. *daurica*, based on the population H02215 from Mt. Amanos, Hatay, Turkey, drawn by Miss LI Ai-Li.

Hong, D. Y. Zhang, X. Q. Wang & S. T. Koruklu H02215 (A, CAS, K, MO, PE, UPA); Belen, Suguk Oluk, 1200 m, 24.iv.1957, *Davis & Hedge D 27104* (ANK); Dörtyol, Kuzuculu to Bulke, 1000 m, 4.v.1965, *M. J. E. Coode & B. M. G. Jones 443* (E); Isparta: Egirdir Lake, Yaka Village, 1300–2100 m, *Pinus nigra-Juniperus excelsa* forest, 19.v.1973, *H. Pesman & A. M. G. 3467* (ANK); Samsun: Havza, Taskaraca-Oren Village, 880–920 m, 21.v.2002, *D. Y. Hong, D. Y. Zhang, X. Q. Wang & S. T. Koruklu H02221* (A, CAS, K, MO, PE, UPA); Samsun, Burial Mound, 800 m, 10.v.1963, *C. Tobey 101* (E); Samsun, Ladik, Kara Dağ, 1150–1200 m, oak scrubs, 8.v.1965, *C. Tobey 944* (E); Gümüşhane: Kalkanli, Zigana, 19.v.1972, *H. J. Leep s. n.* (SA); Asia Minor, *sine loc.* *Aucher-Eloy 4019* (BM, G).

UKRAINE: Crimea: Simferopol, near Neusatz, in woods, 7.v.1900, *A. Gallier 526* (BM, E, G, K, P, WU); Baidar, in woods, 1899, *M. Wetzchky s. n.* (G); near Stavri-Kaja, 26.iv.1913, *J. Wankow s. n.* (K); Jalta, in woods, 18.v.1910, *J. Wankow s. n.* (B); Jalta, 1350 m, 3.vi.1959, *Davis 33373* (E, G, K, LE); *loc. eodem*, pine woods, 4.vii.1946, *Kutova s. n.* (LE); Jalta, Mt. Laila, 700–800 m, 27.iv.1979, *S. Husak s. n.* (GZU); *loc. eodem*, 1.v.1905, *N. A. Busch s. n.* (LE); Jalta Region, near Baidarskie verota in *Fagus* forest, 22.v.1922, *S. Ganeshin s. n.* (LE); Aluschda, Walder des Tschatyr-Dagh, 18.vi.1895, *A. Gallier s. n.* (WU); *sine loc.* *W. Besser s. n.* (G, K); *sine loc.* *H. D. Bunge s. n.* (P); *sine loc.* vii.1885, *Jelenetzky s. n.* (G); *sine loc.* 11.vi.1893, *O. & B. Fedtschenko s. n.* (G); *sine loc.* v.1828, *Govet s.*

n. (G); Bakhchisarai, 500–700 m, 30.vii.1977, V. Vašák *s. n.* (W); Sevastopol, 500 m, 12.v.1991, V. Vašák *s. n.* (W); Mt. Bedenekir, forest glade, 16.v.1898, K. Golde *s. n.* (LE); Pendike, 28.v.1898, K. Golde *s. n.* (LE); above Uchan-Su, 15.v.1896, K. Golde *s. n.* (LE); Last Valley, 4.v.1905, N. A. Busch *s. n.* (LE); between Otus and Koktebek, 10.v.1905, N. A. Busch *s. n.* (LE); Karadak, *Quercus* forest, 2–7.viii.1968, T. Hort, A. Bobrov & V. Siplivinsky *s. n.* (LE); Grushevaja Poljana Nature Reserve, in forest, 25.v.1929, S. Stankov & A. Pegova *s. n.* (LE).

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