The taxonomic status of peonies (*Paeonia* L.) of Emilian Apennines (Northern Italy)

PAOLO PUPILLO
Emeritus professor, Dipartimento di Farmacia e Biotecnologie, Università di Bologna, Italy – Email: paolo.pupillo@unibo.it

GIANCARLO MARCONI
Unione Bolognese Naturalisti, Bologna, Italy – E-mail: gianmarc48@gmail.com

Abstract

Peonies have been the subject of much interest since antiquity for their beauty and medicinal uses. Peonies growing on Emilian Apennines from Bologna to Parma (Emilia-Romagna Region) have been known for centuries, but their taxonomic treatment has been controversial with attributions to different species (*Paeonia officinalis*, *P. peregrina*) and subspecies. In this work we review their properties, which are distinct from *P. officinalis* and consistent with assignment to *P. arietina*, an eastern species. Recent genetic data suggest that *P. arietina* is partially ancestral to *P. officinalis* and cannot be considered as a subspecies of the latter (*P. officinalis* subsp. *arietina* N.G. Passal.), as currently accepted. Therefore, the Emilian peony populations albeit genetically unknown should be designated as *P. arietina*.
Abbreviations: EAPs, Emilian Apennine peonies; PAPs, Pre-Alpine peonies.

Keywords. Italian flora; peony; *Paeonia*; *Paeonia arietina*; *Paeonia officinalis.*

Riassunto

Status tassonomico delle peonie (Paeonia L.) dell'Appennino emiliano (Italia settentrionale)
Le peonie sono state oggetto fin dall'antichità di notevole interesse per la loro bellezza e per gli usi medicinali. Le peonie che crescono sull'Appennino emiliano fra Bologna e Parma (Regione Emilia-Romagna) sono note da secoli, ma il loro trattamento a livello tassonomico è stato controverso con attribuzioni a specie (*Paeonia officinalis*, *P. peregrina, P. arietina*) e sottospecie diverse. In questo lavoro noi esaminiamo le loro caratteristiche, che sono distinte da quelle di *P. officinalis* e conformi all'assegnazione a *P. arietina*, una specie orientale. Studi genetici recenti indicano come *P. arietina* sia in parte ancestrale a *P. officinalis* e non si possa considerare una sottospecie di quest'ultima (*P. officinalis* subsp. *arietina* N.G. Passal.), com'è attualmente accettato. Pertanto le popolazioni emiliane di peonia per quanto geneticamente sconosciute devono essere designate come *P. arietina*.
Abbreviazioni: EAPs, Peonie dell'Appennino Emiliano; PAPs, Peonie Pre-Alpine.

Parole chiave: Flora, Italia, *Paeonia, Paeonia arietina, Paeonia officinalis.*

Introduction

Since antiquity, peonies were the subject of keen interest thanks to their reputed medicinal qualities. The very name *Paeonia officinalis* refers to their curative properties, of "roots" in particular, which were believed to heal from madness (Pseudo-Apuleius, *De virtutibus herbarum*) and epilepsy (Floridus Macer, *De viribus herbarum*); Italian 16th century herbalists Andrea Mattioli and Castore Durante praised the special effectiveness of minced peony root in small bags hung to a child's neck. Other indications were agains asthma and gout thanks to the seeds (Gesner's fig. 1), that had to be ingested by night to prevent attacks by woodpeckers (to which the plant was consecrated). According to the medieval signature theory, the peony was an effective remedy for brain and head diseases since flower buds resembled a skull complete of junctions (Coles, 1657), but all parts of the plant were used at some time to treat a large variety of affections. Today, all peony derivatives are out of order in western medicine as the whole plant is held to be toxic, but in China and elsewhere the medicinal use of arbustive peonies and their products is fluorishing.
In the first modern book of nature-true plant images, the fine illustration of *Paeonia officinalis* in Leonhart Fuchs's *New Kreüterbuch* (1543) is accompanied by a detailed description, with the bold opening "Der Sichtwurz seind zwey geschlecht/ weible und mennle" ("Peonies are of two sexes/ female and male"; though the "male" native to southern Europe was unknown to Fuchs). In Aldrovandi's herbarium (1551) at the University of Bologna, two specimens are marked *Poeonia foemina* and one *Poeonia mas*, corresponding to the major European species groups *Paeonia officinalis* s.l. and *P. mascula* s.l. The characteristics of both plants are well illustrated in Lobel's *Icones* (1581), with emphasis on the different "roots" and distinct shapes of the leaflets (Fig. 2).

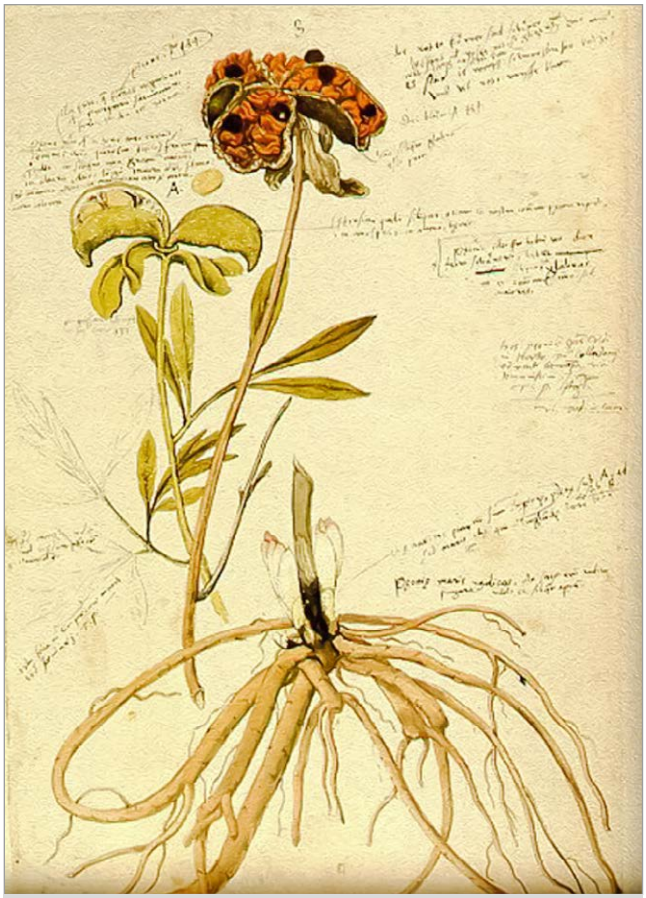

Fig. 1. A painting of peony fruits (follicles) and seeds, with hand annotations of C. Gesner, ca. 1550.

Fig. 2. M. Lobel's illustration of both herbaceous peony types, "female" (P. officinalis L.) and "mas" (P. mascula Mill.). Plantarum seu stirpium icones (1582), p. 682.

Peony populations of the Emilian Apennines (Emilian Apennine peonies, EAPs) have been known for centuries. Bertoloni's *Flora Italica* (1844) cites three localities of the Bologna district on hills on the left bank of river Reno near Vergato, where peonies are still frequent. The same sites plus an additional one (Jano near Sasso Marconi) are recorded by Cocconi in his *Flora della provincia di Bologna* (1883) and were sampled by other renowned botanists, hence represented in several herbaries in Italy (BOLO, FI, PAD, PI, RO, TO) and abroad. Notably, EAPs were known to Bertoloni as *Paeonia officinalis*, but for nearly one century most botanists (e.g. Cocconi, 1883; Fiori & Paoletti, 1898) referred them to *P. peregrina*. This eastern species is today acknowledged for Italy only in a few localities of Abruzzi (Pignatti, 2017).

The peculiarities of the EAPs were noticed by Stern in his monograph (1946), and he assigned these plants to the Balkanic–Caucasic species *P. arietina*. This species name dates back to G. Anderson (1818) who compared the twisted twin fruits (follicles), recumbent at maturity, to ram's horns (ram = *aries* in Latin). Subsequently, this taxon was treated at the rank of subspecies (Cullen & Heywood, 1964) but with attribution to *P. mascula*, hence *P. mascula* subsp. *arietina* (Anderson, 2018)) Cull. et Hey. Together with another subspecies recognized for Italy by Cullen & Heywood (1964), *P. officinalis* subsp. *villosa* (Huth) Cull. et Hey., the new subspecies *P. mascula* subsp. *arietina* was accepted in the authoritative *Flora Europaea* 2nd ed. (Akeroyd, 1993). This may possibly explain why Pignatti's first flora of Italy (1982) depicted *P. mascula* as occurring in several regions of northern Italy, whereas this species as intended today is limited to the south (Pignatti, 2017). However, Pignatti's first flora (1982) rightly ignored *P. mascula* subsp. *arietina* and considered EAP plants to belong to *P. officinalis* subsp. *villosa* (Huth) Cull. et Hey. Despite these precedents, EAPs were again referred to *P. officinalis* subsp. *officinalis*, without comment, in the monograph of Passalacqua & Bernardo (2004) on Italian peonies. In sum, if the rich presence of peonies in some parts of Emilian uplands was long known, the systematic treatments of these difficult taxa were contradictory and confusing. At least until the landmark paper of Hong *et al.* (2008), that following Stern (1946) relocated the EAPs within the species *P. arietina* forming a new species group with *P. parnassica* of Greece (see also Hong, 2021). Therefore, the subsequent assignment of EAPs to a subsp. *arietina* of *P. officinalis* (Passalacqua, 2009), endorsed by the new *Flora d'Italia* (Pignatti, 2017), seems misplaced. This point is discussed below.

Remarkably, river Reno to the west of Bologna represents an abrupt eastward limit to the Emilian distribution of *Paeonia*, possibly in relation to different rock substrates on the two river banks. It may be due to the relative isolation of the *Paeonia* population in this part of the northern Apennines that a peony lineage with Balkanic and near-Asiatic relationships, like *arietina*, could survive until today with its distinctive traits (Hong *et al.*, 2008). In the present paper we further

document the characteristics of these *Paeonia* populations of Emilian hills, with a plea for their recognition as a good species related to but definitely different from *P. officinalis*.

Plant distribution and documentation

The distribution of peonies in the Regione Emilia-Romagna is limited to its western part (Emilia) and covers hill and mountain ranges of Apennines in the provinces of Bologna, Modena, Reggio Emilia and Parma. Peonies are probably extinct in the district of Piacenza. Plants attributed to *P. officinalis* subsp. *italica* N.G. Pass. et Bernardo (Passalacqua & Bernardo 2004) also occur in the north-western part of Tuscany (provinces of Pistoia and Lucca), where they may come in contact with Emilian populations. Peonies are not present in the Tuscanian province of Prato to the east.

Fig. 3. Peonies of eastern Alps, *P. officinalis* subsp. *officinalis*. A) flowering plants; B) flower. Note the lanceolate leaves and triple carpel. Mt. Marzola (Trento), 1620 m; June 19, 2013.

We have sampled a few sites in the provinces of Bologna and Reggio Emilia (Regione Emilia) and in the province of Trento (Trentino), mainly:

- Bologna: Val Rio Maggiore near Jano (Sasso Marconi, Bologna: chestnut groves and deciduous woods of hop-hornbeam (*Ostrya carpinifolia*) with some downy oak (*Quercus pubescens*), *Sorbus torminalis* and *Acer opulifolium* at relatively low altitude (300-500 m); often accompanied by other understory geophytes such as *Helleborus viridis*, *Primula vulgaris*, *Daphne laureola, Pulmonaria officinalis*, *Lilium martagon*, *Athyrium filix-femina*.
- Reggio Emilia: hills near Viano (Mt. Benale; municipality of Scandiano) and Mt. Lusino, (Baiso), 300-600 m, deciduous woods with hop-hornbeam, downy oak and Scots pine;
- Trento: Mt. Marzola near refuge Bailoni, 1500-1600 m: beech-fir woods, in clearings and meadows.

Photographs were taken by the authors during numerous field surveys (2012-2022, April to July) or obtained from collaborators, using high definition cameras. Biometric measurements on leaves were performed on photos by inspecting 2-3 representative terminal segments for each plant.

Results

With respect to the peonies of the eastern Prealps (PAPs), generally attributed to the typical subspecies *Paeonia officinalis* subsp. *officinalis*, the plants of the Emilian Apennines (EAPs) feature several differences.

Leaves. Peony leaves have traditionally been an important basis for classification. There are marked differences between leaves of EAP and PAP populations, to be intended in a statistical sense because of marked intrapopulation variability. In comparison to PAPs (Fig. 3A), EAP plants usually present a lower size and lower number of ternate segments borne by bi- or tripartite leaves, but we shall not present such data since counts on photos are often unreliable. Leaf segments are initially ovoid to roundish in the immature, nonflowering EAP plant (Fig. 4A), and develop to an obovate-elliptic shape during further growth usually to a length of 8-10(-12) cm and diameter of 4-6 cm at maturity (Fig. 4B and Table 1). On the other hand, PAPs have narrower, lanceolate to lanceolate-elliptic leaf segments, 1.5-3 cm broad and 8-12(-14) cm long. Within this general type, single EAP plants or plant groups may have distinct leaf shapes suggesting a genetic basis for this trait, although variable growth effects of light exposure, temperatures, and water stress during spring months are possible. Fig. 4C shows a single terminal segment with three basally confluent lobes, a common feature in both EAP and PAP plants (and other strains). We have measured the sizes of the leaf segments of adult, flowering specimens of the three sites monitored. The data for the Emilian pop-

	Jano (Bologna) N = 49	Viano Benale (Reggio E.) N = 36	Mt. Marzola (Trento) N = 23
LL	(7)8-10(12) cm	(6)8-9(11) cm	(6)8-12(14) cm
LWR	2.70 ± 0.48 sd	2.76 ± 0.44 sd	4.42 ± 0.62 sd

Table 1. Morphometry of peony leaf segments from three sites, two in Emilian Apennines (*P. arietina*) and one in eastern Prealps (Mt. Marzola; *P. officinalis* subsp. *officinalis*). Reported are the estimated lengths (LL) and ratios of length to maximum width (LWR, based on 2-3 terminal segments per plant). LWR values represent means ± standard deviation (sd). N = number of plants.

ulations are rather homogenous and, in particular, the ratio of segment length to width appears to be a reliable marker (Table 1) yielding nearly identical values of R = 2.7-2.8 for Emilian peonies, with a significant difference to Alpine plants (R = 4.4).

Hairness. Pilosity is an important distinctive character for PAP *vs*. EAP plants (Passalacqua & Bernardo, 2004; Hong *et al.*, 2008; Pignatti, 2017). As also shown here, stiff, shiny hairs cover flower stalks and stems, while a villose, whitish hair felt fills up the lower (abaxial) surface of sepals, more elevated along the major veins (Fig. 5A-B). On the contrary, *P. officinalis* subsp. *officinalis* plants have glabrous or sparsely hairy stalks and sepals. The glaucous underside of leaf segments has a thin hair covering in EAPs, that is usually absent in PAPs.

Petal color. Peony flowers are quite showy and their colors are sometimes diagnostic (e.g. for *P. peregrina*), but all peonies of northern Italy seem to have fairly similar petal colors. Most EAP plants have intense red (crimson) flowers at the bud stage and initial anthesis (see Fig. 5 and 6A). Afterwards, the color tends to fade to mauve with a violet shade (Fig. 6B), apparently by dilution during petal cell extension. The fading process will continue following pollination, thus imparting a pink-violet color to senescent flowers (Fig.6 C-D). We are unable to notice consistent petal color differences between EAP and PAP populations examined.

Sexual organs. Stamens are very numerous in peonies and their color is always bright yellow in north-Italian taxa, probably indistinguishable between EAP and PAP plants. On the contrary, the number of carpels is partially diagnostic. According to Bertoloni (1844), *P. officinalis* (including both PAP and EAP plants) can have 2-4 carpels (later follicles) that are 2-3 for Pignatti (1982, 2017). G. Anderson (1818) considered twin "ram's horn" follicles as distinctive for his *P. arietina*, although Hong *et al.* (2008) report 2-3 carpels and sometimes more (occasionally 1 only). Bologna EAPs are generally endowed with two carpels (Fig. 7A-B-C), that at maturity become follicles, recumbent and divergent (Fig. 7D), but plants with 3 carpels do occur in hilly sites of the Reggio district (15-20%). On the other hand, carpels in PAP plants are commonly three (Fig. 3B), rarely two. According to Hong *et al.* (2008), carpel color in Anatolian populations of *P. arietina* varies from yellow to red, but it was always white in the plants we observed (also Passalacqua & Bernardo, 2004).

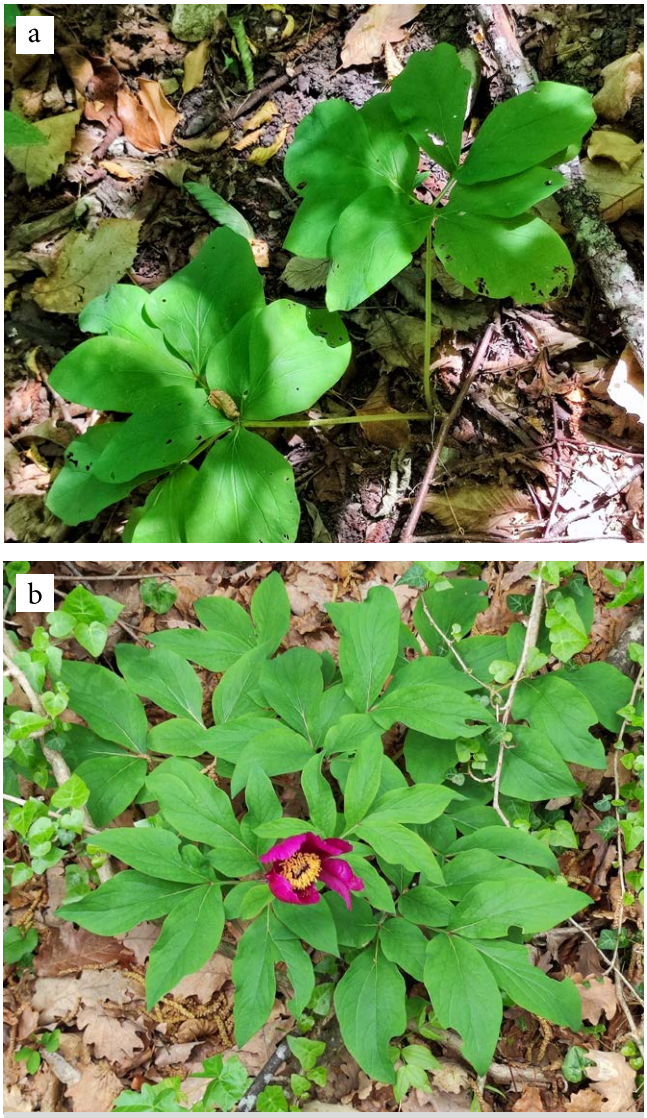

Fig. 4. Peony leaves, Bologna Apennine. A) young plants with broad, obovate basal leaves; B) adult plant with obovate-to elliptic leaves; C) terminal segment divided into three elongated lobes; glaucous underside thanks to a short hair covering. Val Rio Maggiore near Jano (Bologna), 370 m altitude. A and C: July 2, 2022; B: Apr. 27, 2022.

Rhizomes. Peony "roots" have been regarded as diagnostic markers since antiquity to denote the *P. officinalis* species group having tuberous rhizomes, as distinct from the carrot-like rhizomes of *P. mascula* (Figs. 1 and 2), and this basic difference remains fully valid (Passalacqua & Bernardo, 2004; Hong *et al.*, 2008). The *P. arietina* species group is characterized by tuber-like rhizomes, consistent with its kinship to *P. officinalis* (Hong *et al.*, 2008).

Ecology. The ecological relationships of EAP and PAP plants are different. EAP plants are found in fresh, northward exposed hill sites mainly on acidic soils (Passalacqua & De Giuseppe, 2009) covered by light deciduous woods, often in groupings (Fig. 8). However, some populations grow on chalky (basic) hills e.g. near Borzano (Albinea, Reggio E.). On the other hand, PAP plants (*P. officinalis* subsp. *officina-*

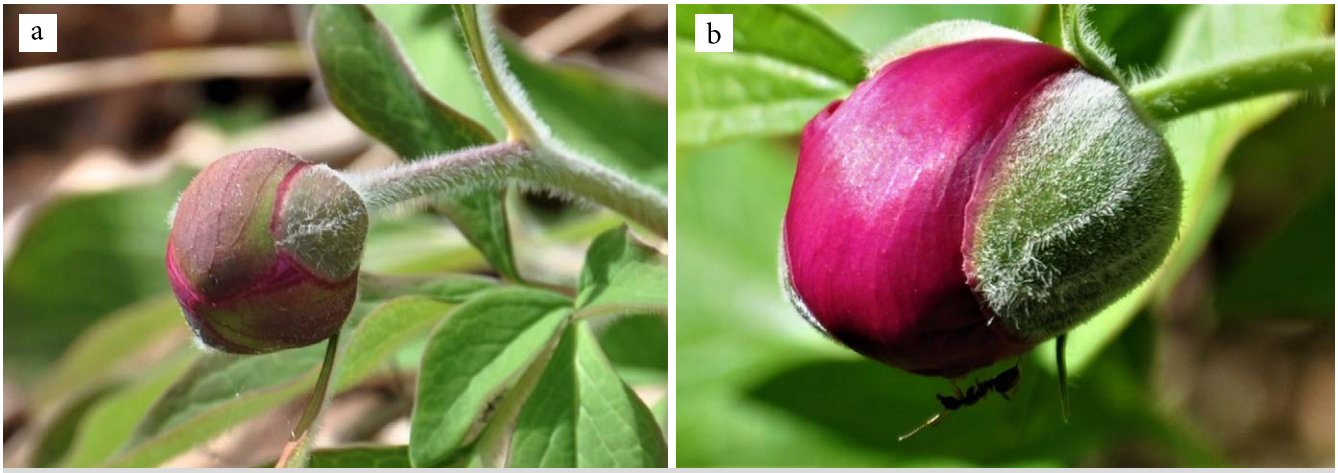

Fig. 5. A-B) Buds with crimson-red petals. Long, erect hairs on the stalks, and a dense felt covers the lower (abaxial) sepal surface. Val Rio Maggiore, 340 m. Apr 8, 2017.

Fig. 6. Flowers. A) a young flower; B-C) mature flowers; D) senescent. (A and B: Val Rio Maggiore, Apr. 27, 2022 and Apr. 1, 2017, respectively; C and D: Benale site (Viano, Reggio E.), 410 m. Apr. 23, 2016.

Fig. 7. Carpels/follicles. A) carpel with white, wool-like indument and unfertilized stigma; B) two villose carpels sitting upon a dentate, fleshy base within the stamen crown; note circinate fertilized stigmas; C) young follicles with 5 sepals; D) twin mature follicles, "ram's-horns". (A, B, C: Benale site, 530 m, Apr. 23, 2016; D: Val Rio Maggiore, July 2, 2022).

lis) of eastern Prealps are found on meadows, edge of beech-fir woods and clearings, 800-1700 m, invariably on basic soil of limestone or dolomite (see Prosser *et al.*, 2018). The scree habitat indicated for alpine *P. officinalis* subsp. *officinalis* (Passalacqua & Bernardo, 2004; Pignatti, 2017) is inconsistent with present and other observations (Hong *et al.*, 2008).

Discussion

Until recently, the taxonomy of peonies has been rather confusing. Antonio Bertoloni in his flora of Italy (1844) recognized *P. officinalis* as the principal species for northern and central Italy including the Bologna district, along with *P. mascula*, but since the half of the 19th century Italian authors have mostly treated Emilian *Paeonia* populations under the name *P. peregrina* (e.g. Cocconi, 1883; Fiori & Paoletti, 1898). Non-Italian specialists had other ideas, beginning with Stern who in his monograph (1946) assigned Emilian peonies to *P. arietina*, a Balkanic-west Asiatic species originally established by G. Anderson in 1818. Cullen & Heywood (1964) shifted putative *arietina* peonies to *P. mascula* as a subspecies: *P. mascula* subsp. *arietina* (Anderson) Cull. et Hey., possibly overestimating the systematic

Fig. 8. A peony "garden". Mt. Lusino woods near Baiso (Reggio E.), 530 m. Apr. 23, 2016.

relevance of their broad leaflets. At the same time, Cullen & Heywood (1964) established another subspecies *villosa* of *P. officinalis* for some Italian populations, *P. officinalis* subsp. *villosa* (Huth) Cull. & Hey. The protologues of both subspecies might match some characters of EAP plants.

The first Pignatti's flora (1981) while rejecting *P.* (*mascula*) *arietina* again reported the species *P. officinalis* for northern Italy, with subspecies *villosa* allegedly present in the Parmesan Appennine and some areas in central Italy, and subsp. *officinalis* covering the entire Alpine arc from west to east (and erroneously stated to be there sympatric with *P. mascula* subsp. *mascula*). The monograph of Italian peonies of Passalacqua & Bernardo (2004) reaffirmed *P. officinalis* as the sole species present in northern Italy with subspecies *officinalis*, *huthii*, and *banatica.* These authors also described a new subspecies *P officinalis* subsp. *italica* for central Italy, but skipped Emilian plants altogether, that were ascribed by the authors to *P. officinalis* subsp. *officinalis* without comment.

The genetics of *Paeonia* have been investigated for several decades. *Paeonia* is a phylogenetically and taxonomically complex group (Stebbins, 1938; Sang *et al.*, 1995). In particular, section *Paeonia* may have undergone complex reticulate evolution that contributed to obscure phylogenetic relationships (Sang *et al.,* 1997). While Stern (1946) regarded most species as autotetraploids derived from diploid ancestors, Stebbins (1948) by examining meiosis in some tetraploid species concluded that most of them were allotetraploids, as was later confirmed by comparing sequences of nuclear and chloroplast DNA (Sang *et al.*, 1997; Sang & Zhang, 1999). A paper by Hong *et al.* (2008) based on morphological evidence and clear statistics revived Stern's (1946) assignment of Emilian populations to the eastern species *P. arietina*. This analysis (Hong *et al.*, 2008) supports the existence of a species group consisting of *P. arietina* and *P. parnassica* of central Greece, distinct from *P. mascula* and closely related to the *P. officinalis* species group, including subsp. *banatica*. The conclusions of Hong *et al.* (2008) are well founded though possibly too clear cut, the more so in the lack of a survey of all *P. officinalis* subspecies. Previously, an important genetic study (Ferguson & Sang, 2001) had suggested an origin of tetraploid *P. officinalis* from *P. arietina* and *P. peregrina*, both tetraploids (2n = 20), by homoploidy.

Despite converging evidence for a regular species status in the international literature, *P. arietina* has been accepted in the Italian flora only at a subspecies level (*P. officinalis* subsp. *arietina* N.G. Passal.; Passalacqua, 2009). Accordingly, Pignatti's recent flora (2017) mentions four Italian subspecies of *P. officinalis* besides the nominal one *P. officinalis* subsp. *officinalis*: subsp. *huthii* Soldano for Maritime Alps on the French border; *banatica* Soò, on Karst near Trieste and perhaps in Lombardy; *italica* N.G. Passal. & Bernardo 2004 for central Italy (Marche, Abruzzo, Lazio, Umbria); *arietina* (Anderson) N.G. Passal. 2009 for Emilia.

We argue that treating the Emilian populations (EAPs) as a subspecies of *P. officinalis* L. is unjustified in the light of available data, including the present work, and contrasts with genetic evidence. In fact, *Paeonia arietina* though related to the *P. officinalis* complex, of which it may be an ancestor, differs from the latter in important morphological (and other) traits as reported above, and undoubtedly deserves the rank of an independent species. Moreover, it would be illogical to treat the parental species *P. arietina* (with *P. peregrina* as second partner: Ferguson & Sang, 2001) as a subspecies of the derived hybrid allotetraploid *P. officinalis.* And the implicit inclusion in west-European *P. officinalis* not only of Emilian peony populations, but of the Euro-Asiatic species *P. arietina* as a whole (at the rank of subspecies), is obviously untenable. Therefore, the Emilian peony populations should be correctly ascribed to the species *P. arietina* as previously proposed (Stern, 1946; Hong *et al.*, 2008) with the consequent fall of the name combination *P. officinalis* subsp. *arietina* N.G. Passal.

However, this conclusion needs to be corroborated by direct genetic studies on northen Appennine peony populations. Traits like triple carpels in some subpopulations (Reggio Emilia district) suggest the occurrence of phenotypic clines and call for more research to understand the true relationships of these highly hybridizing plants.

Acknowledgments

The collaboration of drs. Giuliano Cervi and Massimo Gigante in parts of this work is gratefully acknowledged. We also wish to thank the curator of the Orto Botanico of Bologna University dr. Umberto Mossetti for manifold assistance, in particular with herbarium specimens.

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