

WHAT IS *PAEONIA OFFICINALIS* SUBSP. *BANATICA* (ROCHEL) SOÓ 1960?

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(Received 22 March, 2005; accepted 10 September, 2005)

The taxon currently named *P. officinalis* subsp. *banatica* has been treated as a subspecies of *P. officinalis* by most authors. Recent genetic studies revealed that this taxon is an ancient allotetraploid hybrid carrying the genes of *P. mairei* and the ancestor of *P. officinalis*. Based on its current polyphyletic status, degree of genetic and morphological divergence, its geographical distribution and unique genetic constitution I argue that this viewpoint is incorrect, and this taxon should be recognised as an independent species.

Key words: evolutionary novelty, genetic and morphological divergence, polyphyly

INTRODUCTION

Paeonia officinalis L. subsp. *banatica* (Rochel 1828) Soó 1960 is a local endemic of the Carpathian Basin. It was first discovered and described by Anton Rochel during his field trip in the Banat region of Hungary (today Serbia and Montenegro, Vojvodina) in the late 1810s. He found this plant in the Deliblat Sand hills, and named it *P. banatica* (Rochel 1828). Later this taxon was discovered at a few other locations in what was then SC Hungary. Its contemporary distribution is restricted to the southern part of the Carpathian Basin. It has been collected in Yugoslavia near Čerevic at the foothills of the Fruška Gora, and in the Deliblat Sand hills, and in extreme SW Romania near Bazias along the Danube. Within the current borders of Hungary, it occurs only in the Mecsek Hills (Zengő, Hármas-hegy) between Hosszúhetény and Kisújbánya (Soó 1960, Csapody 1982, Kevey 1990).

The taxonomic treatment of *P. officinalis* subsp. *banatica* has had a varied history. Rochel (1828) regarded it as a distinct species, whereas others included it in *P. officinalis* L. as a subspecies or a variety. In his revision, Soó

(1960), for example, placed the taxon under *P. officinalis* L. as a subspecies, based on morphological similarities. He regarded differences in leaf segment width and number, and the indumentum on the adaxial side of leaves as minor not justifying delimitation of the taxon at the species rank.

P. officinalis L. essentially has been treated as an aggregate ("Formenkreis") of morphologically similar, but ecologically and geographically more or less distinct "microspecies". In the most recent taxonomic treatment of the genus of Culler and Heywood (revised by Akeroyd 1993), *P. officinalis* is divided into four subspecies: *P. officinalis* subsp. *officinalis*, *P. o.* subsp. *banatica*, *P. o.* subsp. *villosa* and *P. o.* subsp. *microcarpa* (= *P. humilis*). *P. officinalis* subsp. *officinalis* and subsp. *villosa* are both distributed from southwestern France to Albania (?) and to Italy in the southern Alps and the Apennines, respectively. *P. officinalis* subsp. *microcarpa* (*P. humilis*) occurs from southwestern France to southeastern Spain. Except for subsp. *officinalis* and subsp. *villosa*, all taxa have distinct geographical ranges (Akeroyd 1993) (Fig. 1).

DISCUSSION

Recent genetic studies (Sang *et al.* 1995, 1997) revealed that *P. officinalis* sensu Sang *et al.* (1997) (= *P. o.* subsp. *officinalis* and subsp. *villosa*) and *P. officinalis* subsp. *banatica* represent two distinct genetic lineages. The former taxon is part of an allotetraploid ($2n = 20$) group (*P. parnassica*, *P. arietina*, *P. humilis*, *P. officinalis*) of hybrid origin in which one parent was most likely *P. tenuifolia* L. ($2n = 10$). *P. banatica* also is an allotetraploid, but with a completely additive ITS sequence from both putative parents, *P. mairei*, a Far Eastern (China, Shaanxi Province) species and the ancestor of the *P. officinalis* hybrid group. *P. o.* subsp. *banatica* therefore is an ancient hybrid, but different from the taxa in the *P. officinalis* group (Fig. 2).

Apparently, the genetic divergence of *P. officinalis* subsp. *banatica* from *P. officinalis* is far greater than that among taxa within the *P. officinalis* group. Yet this group includes taxa that are recognised as distinct species. *P. arietina*, for example, has been considered a subspecies of *P. mascula* (Akeroyd 1993) and not a close relative of *P. officinalis* despite its apparently little genetic divergence in the ITS sequences from the latter. *P. o.* subsp. *banatica*, on the other hand, is considered only a subspecies of *P. officinalis*, while its status is very similar to that of *P. peregrina*. This taxon carries the nuclear genome of the common ancestor of the *P. officinalis* group, but also of the genome of *P. anomala*, a Euro-Siberian species (Fig. 2). Unlike *P. o.* subsp. *banatica*, it is recognised as a distinct species. All these suggest that morphological and genetic divergence

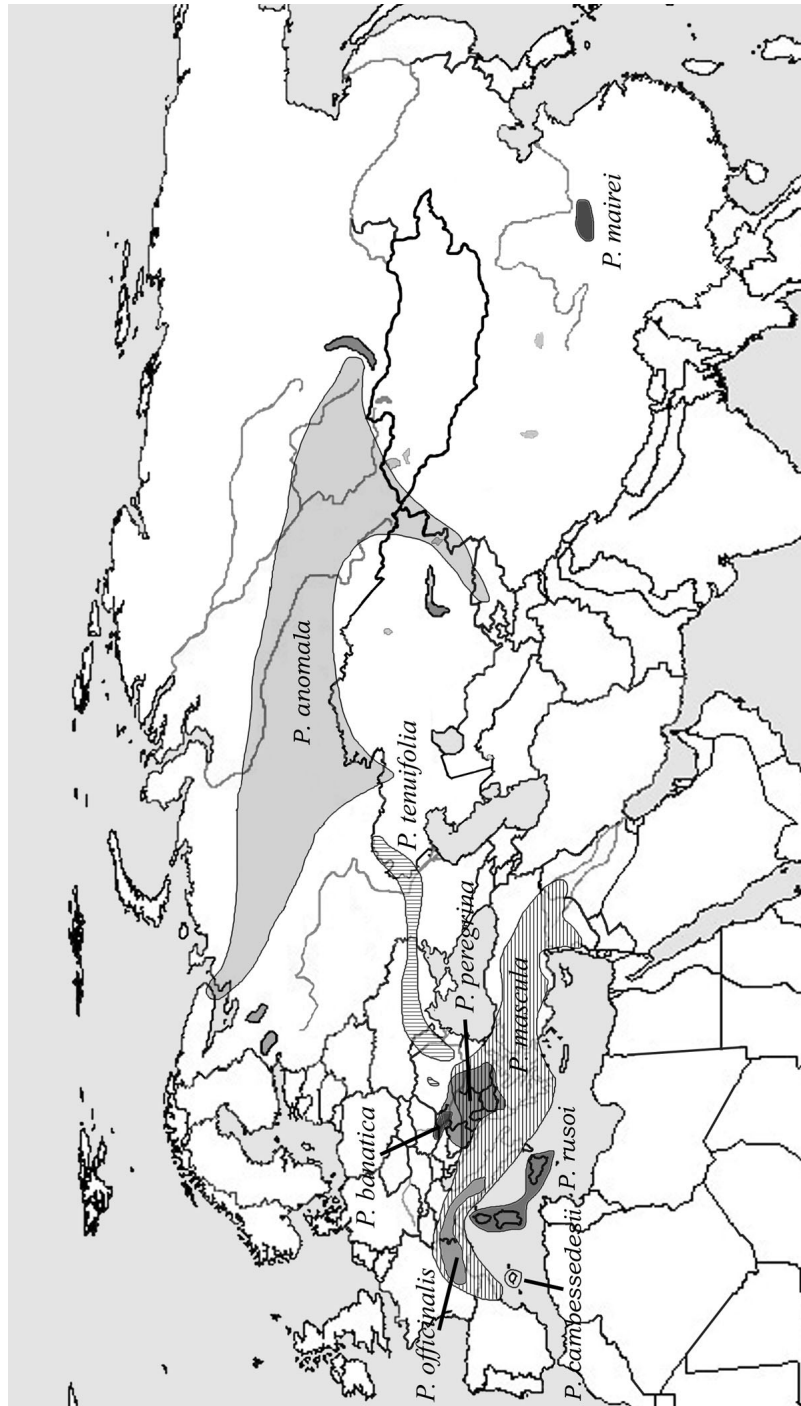


Fig. 1. Geographical distribution of the discussed *Paeonia* species (after Sang *et al.* 1997)

among taxa often is discordant, and most of the recent taxonomic treatments have been heavily based on morphology.

Why is P. banatica a distinct species?

In my opinion, *P. officinalis* subsp. *banatica* has been erroneously placed under *P. officinalis* L. There are several reasons why this taxon should be treated as a distinct species rather than a subspecies of *P. officinalis*.

Polyphyly within the genus

P. banatica apparently has arisen through hybridisation of *P. mairei* with the ancestor of the lineage leading to the *P. officinalis* allotetraploid group (Sang *et al.* 1997). Its ribosomal ITS sequences are totally additive (ancestor of the *P. officinalis* group and *P. mairei*, Sang *et al.* 1995, 1997), whereas the chloroplast *matK* sequence indicates the maternal ancestor being the common ancestor of the *P. officinalis* group (Sang *et al.* 1997). Differentiation within the latter, and

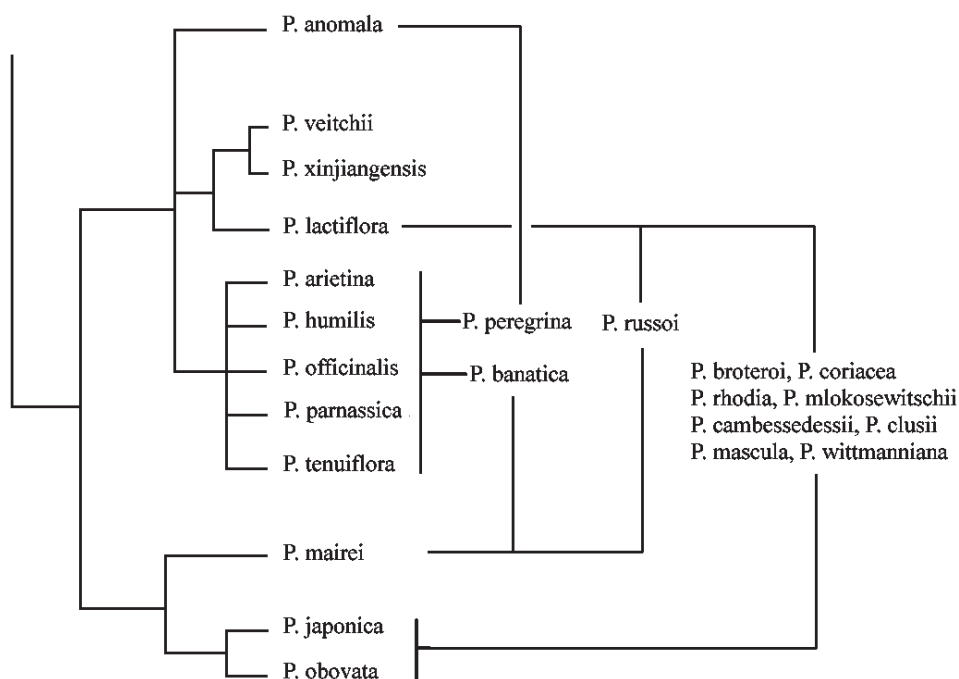


Fig. 2. Combined phylogenetic tree of the *P. officinalis* alliance based on ribosomal ITS and chloroplast *matK* DNA sequence data

therefore the evolution of *P. officinalis* must have followed this hybridisation event. *P. banatica* (like *P. peregrina*) is a (half-)sister taxon of the ancestor of *P. officinalis*, but not a (half-)sister taxon of *P. officinalis*. Because *P. banatica* carries the genes of the ancestor of *P. officinalis*, it must be older than the latter species, and therefore cannot be a subspecies of it. Consequently, the taxon *P. officinalis* as defined by Soó (1946, 1960) and Akeroyd (1993) is polyphyletic. Monophyly is preserved only when *P. banatica* is distinguished from *P. officinalis* at the species level.

Genetic divergence

Based on the ITS sequence data, genetic divergence of *P. banatica* from *P. officinalis* is significantly large as compared to other recognised species in the genus. This is particularly apparent when the degree of divergence is compared to taxa that are recognised as distinct species (for instance, *P. arietina* and *P. parnassica*).

Genetic divergence is not necessarily manifested in morphological divergence of the same degree (Sytsma and Smith 1992). There are many examples among plants where large morphological differences are associated with little genetic divergence (*Platanus orientalis* and *P. occidentalis*) or vice versa. In the genus *Paeonia*, *P. californica* and *P. brownii* are morphologically very similar and were formerly treated as conspecific (Sang *et al.* 1997). Their recognition as distinct species is warranted on the basis of their high degree of genetic and ecological divergence.

Morphological divergence

There are consistent morphological differences between *P. banatica* and *P. officinalis* L. (see Soó 1960). These differences are restricted primarily to leaf segmentation, segment size, and overall appearance. The degree of morphological divergence between the two taxa is little, but not necessarily less than between two generally recognised species. For instance, *P. mascula* (= *P. coralina*) also differs from *P. officinalis* primarily in leaf segmentation, the size of the segments, and petal colour. Apparently, genetic divergence in the nuclear genome was far less than morphological divergence in *P. mascula* subsp. *arietina* from *P. officinalis*. Despite these differences, the two species are frequently mistaken for one another. As discussed above, little morphological differentiation between distinct and well established species is not unusual in this genus (*P. californica* and *P. brownii*, Sang *et al.* 1997).

Morphological and simultaneous genetic differentiation are not necessarily accompanied with the emergence of reproductive isolating barriers be-

tween taxa. Intermediate forms in the Bazias population of *P. banatica* suggests potential hybridisation with *P. mascula* introduced in the area by monks (Soó 1960). It is not known, however, whether or not *P. banatica* and *P. officinalis* L. are reproductively isolated and thus satisfy the conditions of the biological species concept (Mayr 1963).

The available data suggest that *P. banatica* may be either a well established, distinct lineage genetically independent of (i.e. reproductively isolated from) *P. officinalis*, or it may represent a taxon currently with low levels of morphological differentiation but high degree of genetic differences. *P. banatica* thus may be on the way of becoming a well established species.

Geographical distribution

The two taxa have distinct and well isolated geographical ranges in Europe (Fig. 1). *P. banatica* is geographically well separated from all other taxa in the genus. The only exception is in the Deliblat Sand hill region in Vojvodina (Serbia), where *P. banatica* occurs in the relative proximity (within a few kilometres) of *P. tenuifolia*. Here hybridisation and gene flow between the two species have not been reported. Current ranges do not support the idea of recent or potential interbreeding and gene flow between the two taxa. The separate and/or independent distributions exclude the possibility of introgression and genetic exchange with members of the *P. officinalis* group, and ensure the independent evolution of *P. banatica*. Consequently, this species represents a separate evolutionary lineage essentially independent of other lineages in the *P. officinalis* group.

Paeonia banatica as an ancient evolutionary novelty

P. banatica represents a unique evolutionary novelty within the *P. officinalis* group. It is the only taxon that contains genetic traces of the Far Eastern *P. mairei*. Of other European species, only *P. cambessedessii* (Mallorca) and *P. rossii* (= *P. mascula* subsp. *rusoi*) (Sardagna, Corse, Sicily) carry the genes of *P. mairei*. Apparently, *P. banatica* has preserved a little part of the vegetation history of Eurasia since the late Tertiary, like the insular taxa in the Mediterranean (Sang *et al.* 1997). As such, its biological importance is extremely high.

CONCLUSIONS

The unique genetic constitution of *P. banatica* and the degree of genetic divergence from its relatives, its disjunct distribution and old age do not support the current taxonomic treatment of this taxon as a subspecies of *P. officinalis*. Rather, all these characteristics justify its treatment as a separate species even if its morphological divergence from other taxa may be relatively little compared to some others within the genus. In addition, the consistent phylogenetic treatment to avoid polyphyly in this genus would require that the taxonomic status of *P. officinalis* subsp. *banatica* be revised and its original species status restored. Thus, I suggest that this taxon be treated as a distinct species with its original valid name of *Paeonia banatica* Rochel 1828.*

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* Based on the genetic results the Hungarian delegation proposed to the Natura 2000 EU-Committee to adopt the *Paeonia banatica* Rochel as a strictly protected, valid species in October, 2001 in Brussels, and it was accepted (Borhidi, A., editor-in-chief, *pers. comm.*).