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Taxonomy and phylogeny of *Anemone patens* L. sensu lato (Ranunculaceae): A critical review

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Abstract: A critical review of botanical nomenclature for *Anemone patens* L. is given based on a rigorous literature analysis. Complete morphological characteristics and karyology of the taxon are compiled using data from the floristic treatments of Europe and North America. The phylogeny of *A. patens* in relation to a variety of contrasting historical, ecological and evolutionary factors acting through the species range transformation and speciation is elucidated.

Keywords: morphological characteristics, chromosome numbers, taxonomic considerations, origin, evolution

Introduction

Some plants, such as *Anemone patens* L. sensu lato from the buttercup or crowfoot family (Ranunculaceae), with very broad geographical range, highly expressed polymorphism, the existence of numerous transitional forms, convergent evolution, ability to cross and interbreed in a great variety of habitats, may become a nightmare for taxonomists. Arguably, *A. patens* is one of the most problematic taxa in the genus *Anemone* L., as far as circumscription and distribution are concerned, which was noted by many authors (e.g. ZÄMELS 1926; TZVELEV 2001). Taxonomic status of *A. patens* has been widely debated by botanists over a few centuries since the time it was first described by LINNAEUS (1753). As a result, the species was considered in floras and floristic treatments of Europe, Asia and North America under three genera (*Anemone*, *Pulsatilla* Miller, and *Clematis* L.) and over 20 different taxa.

A. *patens* is a perennial herb widespread through the temperate regions of the Northern Hemisphere, comprising different intraspecific taxa. It ranges from Europe to North America, passing through Central, North and Eastern Europe as well as Central and North Asia, and reaching the central part of North America covering a wide range of climatic and habitat conditions. The distribution of *A. patens* across many countries and scientific traditions additionally contributes to the taxonomic confusion regarding this species. Moreover, no critical review has ever been published for this species.

Therefore, main goals of this paper on *A*. *patens* are to: 1) compile morphological characteristics of the taxa based on the floristic treatments of Europe and North America, 2) conduct analysis of botanical nomenclature to review the species taxonomic status, and 3) elucidate the species origin and farther evolution in different parts of its range.

Morphological characteristics

This description of *A. patens* (Fig. 1) has been elaborated from published literature using both Flora Europaea (TUTİN & AKEROYD 1993) and Flora of North America (DUTTON et al. 1997).

Habit: perennial herb, silky–villose throughout, with erect (or spreading) aerial shoots 5–40(–60) cm tall and 5–10 mm wide, growing from many–headed vertical caudices. Only fibrous roots present. **Basal leaves**: redundant in a rosette (3–)5–8(–10), erect, alternate, 3-foliolate with each leaflet dissected dichotomously. Stipules absent. Petiole present 5–10(–13) cm long with hairs longer than the diameter of the petiole. Terminal leaflet petiolulate to nearly sessile, obovate in outline, (2.5–)3–5 cm long. Leaflets spreading, straight, veins palmate. Margins dichotomously dissected throughout, apex acute to obtuse; lateral leaflets 3–4–parted (±dichotomously); ultimate segments 2–4 mm wide. Base narrowly cuneate. Surfaces villous, hairs white or translucent, simple or stellate, straight, spreading or erect; moderately dense on the abaxial surface, sparse on the adaxial surface. **Inflorescences:** flowering stems clearly taller than the leaves; with leaves. Solitary flowers with a villous or glabrate peduncle; involucral bracts present, 3, 1–tiered, simple, different from basal leaves, (2–)2.5–4 cm long, bases clasping, connate, margins deeply laciniate throughout; segments usually 4–6, filiform to linear, unlobed, 1–2(–3) mm wide. Surfaces villous, rarely glabrous. **Flowers:** large, 5.5–8.5 cm in diameter, campanulate. Epicalyx absent. Conventional sepals, 5–8, free, oblong to elliptic, coloured in blue, purple or rarely near white. Villous on the abaxial surface, glabrous on the adaxial one. Petals present. Stamens 150–200. Stamen filament glabrous. Anthers yellow; long–cylindrical; (0.8–)1.1–1.3(–1.8) mm long. Nectaries present. Ovary carpels 30–45; apocarpous. Ovaries densely hairy. One stigma per ovary, one ovule per ovary. **Fruits:** heads of achenes spheric to ovoid; pedicel 10–18(–22) cm long. Achenes body ellipsoid to obovoid, 3–4(–6) × ca. 1 mm long; dry, brown, not winged, villous; beak curved, 20–40 mm long, long–villous, plumose, indehiscent. One seed per achene. Styles modified and persisting in fruit; remaining straight.

Fig. 1. *Anemone patens* in the vicinity of Saskatoon, Canada (photo V. Kricsfalusy)

Chromosome numbers

Study by HOOT et al. (1994) demonstrated that the chromosome base-number of the majority species of *Anemone* and *Pulsatilla* is n = 8. The karyotype of *Anemone* species consists of five metacentric, one submetacentric, and two satellite subtelocentric chromosomes (PUNINA & GRIF 1984).

A. patens is listed in the recent floristic compendia (TUTIN & AKEROYD 1993; DUTTON et al. 1997) and IPCN Chromosome Reports (2015) as diploid (2n = 16) in Europe, Asia and North America. However, the earlier study of this taxon (LÖVE 1954a) identified North American populations to be tetraploid (2n = 32) in contrast to diploid European and Asian populations (AGAPOVA et al. 1993; WEBER 2003). The more recent chromosome counts made on material from provinces of Alberta (TAYLOR & BROCKMAN 1966) and Manitoba (LÖVE 1982) in Canada identified *A. patens* as diploid (2n = 16). It seems that additional cytotaxonomic studies would be beneficial as they may shed light on evolutionary history of *A. patens* as well as give satisfactory explanation as to the species broad dispersal and high morphological variation.

It is well known that the number of polyploid plants in floras of different regions of the world increases with extreme environmental conditions (STEBBINS 1985).

The direct influence between environment and polyploid plants has been long established (see review by STEBBINS 1950). Their great adaptability and ecological plasticity in different environmental conditions may be caused by large genetic variation obtained during hybridization (LEVIN 2002). According to LÖVE (1954b), a taxon which has been unable to disperse to new areas or penetrate into new edaphic and climatic conditions may give rise to a polyploid which can do so. By an alteration in chromosome constitution, polyploid species acquired higher tolerances enabling them to penetrate into new areas and then easily expand to the wide range of biotopes (LEVIN 2002). As suggested by SAUER (1988), introgression and allopolyploid speciation show some sort of interplay between the processes of migration and evolution. This might be the possible scenario for spread and further evolution of *A. patens* in North American part of its range.

Taxonomic considerations

A. patens is commonly known under several names in different parts of the world, such as prairie crocus and eastern pasqueflower, being the most often in North America and respectively in Europe. Other descriptive common names applied to this species include: prairie smoke, prairie pasqueflower, American pasqueflower, European pasqueflower, sticky pasqueflower, pulsatille, crocus anemone, cutleaf anemone, gosling plant, lionsbeard, wild crocus, windflower, etc. It is interesting that the major common name in North America, the prairie crocus, is incorrect and misleading from a scientific point of view. It was given to this plant by the European settlers that colonized the American prairies, as it reminded them of the true crocus of Europe, which in fact belongs to the genus *Crocus* L. in the iris family (Iridaceae).

This species has been widely debated (Tab. 1) since the time it was first described by LINNAEUS (1753) from a specimen collected in Tobolsk, Siberia, in the former Russian Empire. Shortly after that, MILLER (1768) classified this species as *Pulsatilla patens* (L.) Mill., expressly distinguishing it from the genus *Anemone*. Later, specimens of this species collected in different parts of Europe and Asia were described under the names *A. longipetala* Schleich. ex Steud. (STEUDEL 1821), *A. wolfgangiana* Besser (BESSER 1826), *A. intermedia* G. Don (DON 1831), *P. angustifolia* Turcz. and *P. latifolia* Ruprecht (RUPRECHT 1854). Due to the work of TRAUTVETTER & MEYER (1856) the Siberian populations were classified as *P. patens* var. *wolfgangiana* (Besser) Trautv. & C.A. Mey. The name *P. latifolia* was applied by RUPRECHT (1854) to specimens of *P. halleri* (All.) Willd. ssp. *rhodopaea* (Stoj. & Stef.) K. Krause, as it is currently known (ref. to TUTIN & AKEROYD 1993). Recently, *P. latifolia* has been excluded from the taxonomic treatments as an illegitimate synonym (THE PLANT LIST 2013).

Given a wide geographical range of the species and it having extensive morphological variation, several taxa were described in Europe and Asia which led to difficulties in their ranks and synonymies. For example, *P. teklae* Zämelis (ZÄMELIS 1926), initially recognized in the first edition of Flora Europaea (TUTIN 1964), currently is considered to be synonym of *P. patens* ssp. *patens* in the second edition of Flora Europaea (TUTIN & AKEROYD 1993). Some names, for example, *P. patens* ssp. *asiatica* Krylov & Serg. (KRYLOV 1936) and *P. kiovensis* Wissjul. (WISSJULINA 1939), or others are not infrequent in the East European botanical tradition (e.g. MOSYAKIN & FEDORONCHUK 1999; TZVELEV 2001; CZEREPANOV 2007), but are rarely used in the West European floristic practice (TUTIN 1964; TUTIN & AKEROYD 1993).

Tab. 1. Accepted scientific nomenclature of *Anemone patens*.

Europe and Asia		**North America**	
A. patens L.	LINNAEUS 1753	*Clematis hirsutissima* Pursh	PURSH 1814
P. patens (L.) Mill.	MILLER 1768	*A. ludoviciana* Nuttall	NUTTALL 1818
A. longipetala Schleich. ex Steud.	STEUDEL 1821	*A. nuttalliana* DC.	CANDOLE DE 1817
A. wolfgangiana Besser	BESSER 1826	*A. nuttallii* (DC.) Nuttall	NUTTALL 1825
A. intermedia G. Don	DON 1831	*A. patens* var. *nuttalliana* (DC.) A.Gray	GRAY 1867
P. angustifolia Turcz.	TURCHANINOV 1840	*P. hirsutissima* (Pursh) Britton	BRITTON 1891
A. patens var. *multifida* Pritz.	PRITZEL 1841	*A. hirsutissima* (Pursh) MacMillan	MACMILLAN 1892
P. wolfgangiana (Besser) Ruprecht	RUPRECHT 1854	*A. patens* var. *hirsutissima* (Britton) Hitch.	HITCHCOCK 1892
P. latifolia Ruprecht	RUPRECHT 1854	*P. ludoviciana* (Nuttall) Heller	HELLER 1904
P. patens var. *wolfgangiana* (Besser) Trautv. & C.A. Mey	TRAUTVETTER & MEYER 1856	*A. patens* ssp. *multifida* (Pritz.) Hultén	HULTÉN 1944
A. patens var. *wolfgangiana* (Bess.) Koch	KOCH 1860	*A. patens* var. *multifida* Pritz.	GLEASON & CRONQUIST 1991
A. taroi (Makino) Takeda	TAKEDA 1910	-“-	DUTTON ET AL. 1997
P. patens ssp. *multifida* (Pritz.) Zämelis	ZÄMELIS 1926	-“-	KARTESZ & MEACHAM 2005
P. patens ssp. *latifolia* (Rupr.) Zämelis	ZÄMELIS 1926	-“-	VASCAN 2012
P. patens ssp. *uralensis* Zämelis	ZÄMELIS 1926		
P. patens ssp. *teklae* (Zämelis) Zämelis	ZÄMELIS 1926		
P. patens ssp. *flavescens* (Zucc.) Zämelis	ZÄMELIS 1926		
P. patens ssp. *asiatica* Krylov & Serg.	KRYLOV 1936		
P. flavescens (Zucc.) Juz.	YUZEPCHUK1937		
P. multifida (Pritz.) Juz.	YUZEPCHUK1937		
P. kioviensis Wissjul.	WISSJULINA 1939		
P. patens (L.) Mill. var. *kioviensis* (Wissjul.) Tzvelev	TZVELEV 2001		
P. patens var. *multifida* (Pritz.) S.H. Li & Y.Hui Huang	WANG ET AL. 2001		

There are a series of species, such as *P. wolfgangiana* and *P. kiovensis*, as well as several intraspecific taxa and hybrids described from Ukraine during the 19th and 20th centuries (WISSJULINA 1939, 1953). Their taxonomic value is dubious, and at present it is much more realistic to treat *P. patens* in a broad sense. However, TZVELEV (2001) in Flora of the Eastern Europe considered *P. patens* var. *kiovensis* (Wissjul.) Tzvelev as legitimate taxon. The Russian (Siberian) populations of *P. patens* were also often identified as separate taxa at the species or intraspecific levels. Nonetheless, all these taxa nowadays are considered to be synonyms of *P. patens* (Tab. 1). On the Far East, *A. taroi* Takeda was used as a synonym for *A. patens* (TAKEDA 1910).

In terms of intraspecific taxonomy, ZÄMELIS (1926) on the basis of the number and width of the leaf lobes, length of the petiolule's central segment, as well as flower colour divides *P. patens* into five subspecies: *P. patens* ssp. teklae (Zämelis) Zämelis and *P. patens* ssp. *latifolia* (Rupr.) Zämelis in Europe; *P. patens* ssp. *uralensis* Zämelis in Ural; *P. patens* ssp. *flavescens* (Zucc.) Zämelis, and *P. patens* ssp. *multifida* (G. Pritz.) Zämelis in Siberia.

Later, however, several authors described individual subspecies of *P. patens* as separate species. Thus, YUZEPCHUK (1937) distinguished three species: *P. patens* sensu stricto in Europe; *P. multifida* (G. Pritz.) Juz. and *P. flavescens* (Zucc.) Juz. in Siberia. In his opinion, the latter species includes *P. angustifolia* Turcz. as a local race. According to YUZEPCHUK (1937), the main diagnostic features to distinguish these species are the flower colour, number and width of the leaf segments. It should be noted that most authors (KRYLOV 1931; POPOV 1957; SERGIEVSKAJA 1964; PAVLOVA 1990), in floristic treatments of the flora of Siberia, consider the distinguishing of separate species unreasonable and perceive *P. patens* s.l., as a single species comprising a large number of intraspecific taxa.

The system, proposed by AICHELLE & SCHWEGLER (1957), generally was very similar to the previous one (YUZEPCHUK 1937) and repeated the same species. In subsequent studies, the trend toward separation of intraspecific taxa to the rank of species was consistent. Thus, ZIMMERMANN & MIEHLICH-VOGEL (1962) divided *P. multifida* и *P. fiavescens* into two separate species each. Therefore, the authors suggested system that consists of five species with particular geographic centres: *P. patens* s.str. in East Europe; *P. fiavescens* in Siberia; *P. angustifolia* in East Siberia; *P. multifida* in East and South Siberia; and *P. nuttaliana* (DC) Bercht. et Presl. in North America.

The efforts to prepare treatment of *A. patens* for North American flora resulted in numerous nomenclatural changes, including description of new species and varieties (Tab. 1). Initially, PURSH (1814) identified this species as *Clematis hisrsutissima* Pursh from a specimen collected by LEWIS & CLARK during their western expedition. Shortly afterwards, NUTTALL (1818) transferred *C. hirsutissima* to the genus *Anemone* as *A. ludoviciana* NUTTALL & DE CANDOLE (1817) reclassified it under the name *A. nuttalliana* DC. Shortly after that, NUTTALL (1825) restore his priority as *A. nuttalliana* (DC.) Nuttall. Later, BRITTON (1891) and MACMILLAN (1892) reconsidered *C. hirsutissima* as *P. hirsutissima*

(Pursh) Britton and *A. hirsutissima* (Pursh) MacMillan respectively. Some other nomenclatural combinations developed over this period of time are now considered illegitimate or superfluous, e.g. *P. nuttalliana* (DC.) Sprengel (THE PLANT LIST 2013).

During the second half of the 19th century, botanists noticed the similarity of the taxa described in North America with *A. patens* known from the Old World and classified them as its varieties; e.g. *A. patens* var. *nuttalliana* (DC.) A. Gray (GRAY 1867) or *A. patens* var. *hirsutissima* (Britton) Hitch. (HITCHCOCK 1892). This treatment gain more importance during the 20th century, and after the works of HULTÉN (1944), who identified the American populations as *A. patens* ssp. *multifida* (Pritz.) Hultén, there was little doubt about the Old and New World plants being the same taxon (e.g., HITCHCOCK et al. 1964; HITCHCOCK & CRONQUIST 1973). Most recent treatments of North American flora (e.g. GLEASON & CRONQUIST 1991; DUTTON et al. 1997; KARTESZ & MEACHAM 2005; VASCAN 2012) consider this taxon as. *A. patens* var. *multifida* Pritz (Tab. 1).

Based on the history of *A. patens* classification reviewed above, a major difference between the aforementioned botanical approaches can be recognised. While the vast majority of the taxonomic treatments of the flora of Europe and Asia include this taxon under the genus *Pulsatilla*, most American authors prefer to place it in the genus *Anemone*. However, there still remains some controversy over the taxonomic status of *A. patens* per se.

These controversial circumscriptions of the genera *Anemone* and *Pulsatilla* are present in more recent classifications as well. While some authors consider *Pulsatilla* to be a separate genus based mainly on morphological criteria (STARODUBTSEV 1991; TAMURA, 1995; ZIMAN et al. 2008), others argue that *Pulsatilla* should be subsumed within the *Anemone*, given recent molecular studies (e.g. HOOT et al. 1994, 2012; EHRENDORFER & SAMUEL 2001). In contrast, YARPAK (2011) considers the mentioned molecular studies to be too limited with an underrepresented number of taxa being considered. The author argues that morphological differences are clear, well known and based on a long botanical tradition, justifying priority choice for the genus *Pulsatilla*. In any case, it should be noted that this discussion turns around the phylogeny and evolution of the genera *Anemone* and *Pulsatilla* rather than taxonomic status of *A. patens*.

As mentioned before, intraspecific composition of the study taxon is also complicated. According to TUTIN & AKEROYD (1993), it includes three subspecies: *P. patens* ssp. *patens*, *P. patens* ssp. *multifida* and *P. patens* ssp. *flavescence*. PRITZEL (1841) coined the name *A. patens* var. *multifida* for the first time, using it to designate the Siberian populations. This name has priority over the commonly used *A. patens* var. *wolfgangiana* (KOCH 1860). It was not until the beginning of the 20th century when ZÄMELIS (1926) reclassified *A. patens* var. *multifida* as *P. patens* subsp. *multifida.* Later, JUZEPCZUK (1937) went beyond and considered *P. multifida* as a separate species. According to the author, *P. multifida* could be distinguished from *P. patens* by the strongly dissected leaf blades, narrower leaf segments and a distinct petiole. JUZEPCZUK's (1937) view was criticized by other authors who could not see a real difference between the Siberian and the North

American populations, and these authors suggested they should therefore be referred to as the same subspecies (HULTÉN 1944). It has been suggested that the observed differences were the consequence of differentiating geographic races (subspecies) within a continuous range of *P. patens* across the northern hemisphere (HULTÉN & FRIES 1986; LINDELL 2001). This taxon was also classified as *P. patens* var. *multifida* (Pritz.) S.H. Li & Y.Hui Huang in Flora of China (WANG et al. 2001).

There are two colour forms of *A. patens*, with rose and white flowers. *A. patens* var. *rosea* Cock., characterized by pink flowers, has been described by COCKERELL (1888) in the North America. The albino individuals have been described as var. *albo–lutea* in Europe (ZÄMELIS 1926) and f. *stevensonis* Boivin in North America (BOIVIN 1968).

According to BOBROV (1944), complex *A. patens* consists of the blue-purple European form and the yellow Siberian form, as well as the products of its hybridization. The resulting complex of plants includes individuals with blue-purple, yellow and white flowers. Currently, these original forms are distinguished by most taxonomists in separate species *P. patens* s.str. and *P. angustifolia*. TZVELEV (2001) believes that all the taxa from the section *Patentes* Czupov are the products of hybridization between these original species which later spun off as separate taxa.

Origin and evolution

Origin of *A. patens* and formation of its intraspecific structure was significantly influenced by the major climatic and geographic events during the Quaternary period. The great Pleistocene glaciations broke the continuous range of *A. patens* into different geographically isolated parts. This geographic disjunction gradually led to the isolation of a number of morphologically distinct subspecies in the European, Asian and North American parts of the species range. According to KLEOPOV's (1990) classification system of the geographic elements of flora, *A. patens* can be placed within the eastern European and southern Siberian geoelement, that includes plant species of open habitats, such as birch and aspen parklands, open coniferous forests, and grasslands which in the Siberian part of the range formed cold steppe-tundra. These species originated north of the southern steppes in Europe and Asia, and the disjunctions in their ranges occurred mainly on flooded areas during glaciation. KLEOPOV (1990) suggested that it clearly shows early Pleistocene age of the continuous ranges in this group of species and we may assume that this is true for *A. patens* as well. Phylogeographic study conducted by RONIKIER et al. (2008) indicates that *A. patens* is probably the oldest representative of the haplotype group that differentiated before the last stage of the Quartenary glaciation in Europe. The latter authors suggested that the lowland areas are the result of pre-glacial colonization and were re-colonized by populations survived in periglacial refugia in Europe and Scandinavia.

Apparently, *A. patens* penetrated into North America through long-vanished connection, the Bering land bridge (HOPKINS 1967), together with many other species of plants from Asia during the period of glacial transgressions. These waves of migrants spread on date to the early Holocene steppe-tundra and grassland biomes in North America (WILLIAMS et al. 2004), particularly in Alaska, Yukon and the Northwest Territories, as well as dispersed farther south across the continent. *A. patens* probably survived glaciation in regions south of the ice shield and north of it, in ice free refuges in Beringia. The species might have re-colonized the prairie region of Canada with the wave of grassland elements from the southwest and the Great Lakes region as the last continental Wisconsin glacier retreated. This could have happened about 10000–12000 years ago (WELLS 1970). The re-colonisation of the boreal region of Canada probably might have originated from refuges located in Beringia. Therefore, migrants from these southern and northern refuges were likely the sources for contemporary populations of *A. patens* occupying prairie and boreal biome of Canada.

The current range of *A. patens* reflects a variety of contrasting historical, ecological and evolutionary factors acting through the species range transformation and speciation. Understanding these processes can help to interpret the causes of the *A. patens* geographical variation and identify regions of the species high sensitivity to environmental change. This is of high conservation importance in light of threatened status of *A. patens* in Europe (BILZ et al. 2011) and some parts of North America (KRICSFALUSY & PONOMARENKO 2013), as well as priority need for accelerated taxonomic effort to better inform conservation planning and decision making (WEGE et al 2015). Therefore, the conducted analysis can inform important management implications which increasingly require more data on the systematics of threatened populations and intraspecific taxa.

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