

Copies of seven species and twenty hybrids of *Potentilla* (Rosaceae) obtained through experimental hybridization (Notes on *Potentilla* XXVI.)

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Abstract: Copies of Siberian species *Potentilla omissa*, *P. angarensis*, *P. approximata*, *P. tobolensis*, *P. acervata* and *P. chalchorum*, and Euro-Siberian species *P. intermedia* were created by experimental hybridization of their putative parents. Besides copies of these naturally occurring species, 20 hybrid combinations of *Potentilla*, which have mostly not been found in nature, were also obtained.

Keywords: experimental hybridization, hybrid species, *Potentilla*.

Introduction

During my travels in southern Siberia and northern Mongolia in 1961, my interest was drawn to certain species of the genus *Potentilla* which appeared to have arisen through hybridization. The most interesting of all was *P. tobolensis* Th. Wolf ex Juz. I was then convinced that this species, which occurs dispersedly in southwestern Siberia, originated by ancient hybridization between *P. argentea* L. and *P. supina* L. To prove the correctness of this opinion, I artificially crossed these two species and obtained a perfect copy of *P. tobolensis*. Encouraged by this success, I later tried to obtain other copies of naturally occurring Siberian and Mongolian species by crossing their putative parents. I succeeded in six further cases. I thus synthesized perfect copies

(with the exception of fertility) of *P. approximata* Bunge, *P. angarensis* Popov, *P. omissa* Soják, *P. acervata* Soják (syn.: *P. nudicaulis* sensu Juz.), *P. chalchorum* Soják and *P. intermedia* L.

Material and methods

For the hybridization experiments, I used eight species of the Siberian-Mongolian flora (five of which extend into Europe), three species commonly found in Siberia and Europe and three European species. The following species were used in the hybridization experiments: *P. argentea* L. (Siberia, Tatarskaya near Omsk), *P. chinensis* Ser. (China, Beijing), *P. conferta* Bunge (Mongolia, Songino near Ulaan-Baatar), *P. crantzii* (Crantz) Beck ex Fritsch (Slovakia, Malá Fatra), *P. longifolia* Willd. ex D. F. K. Schltl. (Mongolia, Ulaan-Baatar), *P. multifida* L. (Ulaan-Baatar), *P. norvegica* L. (Bohemia, Frymburk), *P. pensylvanica* L. (Mongolia, Zaysan near Ulaan-Baatar), *P. recta* L. (Bohemia, Praha), *P. sericea* L. (Siberia, near Baical), *P. supina* L. (Siberia, Ishim near Tyumen'), *P. tanacetifolia* Willd. ex D. F. K. Schltl. (Mongolia, near Ulaan-Baatar), *P. tergmina* Soják (Siberia, Irkutsk), *P. visianii* Pančić (Serbia, Zlatibor).

I carried out crossings of a total of 40 parent combinations, of which 14 combinations were unsuccessful and 26 yielded hybrid plants. The purpose of these experiments was to verify the origins of putative hybrid species and the participation of putative parents. I was also interesting in the fertility of hybrids. The experiments had no other objective, which is why karyology and modes of reproduction were not studied.

Results

The offspring of my interspecific hybridizations was completely sterile in 10 parent combinations (38% of combinations) and slightly fertile in 16 parent combinations (61%). This means that some specimens of such hybrids produced single vital achenes after free pollination (usually 1–3 achenes in flowers of a whole individual). In the next generation, the hybrids had either the same or a somewhat higher fertility. Surprising results were obtained by a cross between *P. argentea* and *P. supina*, where already in the F₁ generation, single fertile individuals produced virtually the same number of achenes as natural *P. tobolensis*.

Of 56 individuals of *P. argentea* × *P. supina*, 30 were sterile, 11 slightly fertile and 15 fertile. Further examples: *P. pensylvanica* × *P. tergmina*: none of the 49 individuals were sterile, 34 were slightly fertile, and 15 were fertile; *P. longifolia* × *P. pensylvanica*: of 7 individuals 2 were sterile, 5 were slightly fertile and none were fertile; *P. tanacetifolia* × *P. tergmina*: of 35 individuals 17 were sterile, 14 were slightly fertile and 4 were fertile; *P. argentea* × *P. multifida*: of 12 plants 7 were sterile, 4 were slightly fertile and 1 was fertile; *P. multifida* × *P. tergmina*: of 43 plants 10 were sterile, 33 were slightly fertile and none were fertile.

The number of fully developed achenes was on average between 0.004 and 0.35 achenes per flower. Examples: The mean number of achenes for a single

flower of *P. argentea* × *P. supina* was 1.15 [the mean number of achenes in *P. tobolensis*, which is its derivative, collected by me in Siberia (Omsk and Ishim) fluctuated between 6 and 7.5 achenes per flower]. *P. pensylvanica* × *P. tergemina* on average 0.035 achenes per flower (mean for 12,646 flowers); *P. longifolia* × *P. pensylvanica*: on average 0.021 achenes (mean from 804 flowers); *P. tanacetifolia* × *P. tergemina* on average 0.015 (mean for 11,103 flowers); *P. argentea* × *P. conferta* Bunge: on average 0.013 achenes (mean for 1,453 flowers); *P. multifida* L. × *P. tergemina*: on average 0.005 achenes per flower (mean for 15,956 flowers); *P. argentea* × *P. multifida*: on average 0.004 achenes per flower (mean for 1,453 flowers).

Apomixis was observed during all my hybridization experiments. The ratio of apomictically produced and hybrid individuals varied greatly. Examples: 1.34% of *P. multifida* × *P. tergemina* individuals were apomictic, 10% of *P. pensylvanica* × *P. tergemina*, 12% of *P. argentea* × *P. multifida* and 26% of *P. tanacetifolia* × *P. tergemina*. The hybridization of *P. argentea* × *P. supina* was repeated several times, and the number of apomictic plants obtained differed each time, ranging from 37% to 60%.

Survey

Copies of natural species

P. argentea × *P. conferta* (*P. approximata*)
P. argentea × *P. multifida* (*P. omissa*)
P. argentea × *P. tergemina* (*P. angarensis*)
P. argentea × *P. norvegica* (*P. intermedia*)
P. argentea × *P. supina* (*P. tobolensis*)
P. longifolia × *P. tanacetifolia* (*P. acervata*)
P. longifolia × *P. tergemina* (*P. chalchorum*)

Hybrids that could possibly arise in nature

<i>P. argentea</i> × <i>P. tanacetifolia</i>	<i>P. multifida</i> × <i>P. tergemina</i>
<i>P. chinensis</i> × <i>P. tergemina</i>	<i>P. norvegica</i> × <i>P. recta</i>
<i>P. conferta</i> × <i>P. pensylvanica</i>	<i>P. norvegica</i> × <i>P. supina</i>
<i>P. longifolia</i> × <i>P. multifida</i>	<i>P. norvegica</i> × <i>P. tanacetifolia</i>
<i>P. longifolia</i> × <i>P. pensylvanica</i>	<i>P. pensylvanica</i> × <i>P. tanacetifolia</i>
<i>P. multifida</i> × <i>P. pensylvanica</i>	<i>P. pensylvanica</i> × <i>P. tergemina</i>
<i>P. multifida</i> × <i>P. sericea</i>	<i>P. sericea</i> × <i>P. tergemina</i>
<i>P. multifida</i> × <i>P. tanacetifolia</i>	<i>P. tanacetifolia</i> × <i>P. tergemina</i>

Hybrids that not could arise in nature

P. crantzii × *P. tanacetifolia*
P. crantzii × *P. visianii* (*P. x dysgenes* Th. Wolf)
P. longifolia × *P. visianii*

Copies of natural species

***P. argentea* × *P. multifida* (*P. omissa*), *P. argentea* × *P. tergemina* (*P. angarensis*) and *P. argentea* × *P. conferta* (*P. approximata*)**

P. argentea in south Siberia hybridizes with three habitually similar species having pinnate leaves with deeply divided leaflets and straight petiole hairs; i.e., with *P. multifida*, *P. tergemina* and *P. conferta*. These, of course, significantly differ from each other, having a different length of petiole hairs and a different number of leaflet pairs. However, after hybridization with *P. argentea*, which has palmate leaves with shallowly toothed leaflets and very fine flexuous petiolar hairs, important characters of the three mentioned parent species disappear. Hybrid species and hybrids can be identified without difficulty only if their specimens are typical or if they grow together with their parents, which occurs rarely.

P. multifida has appressed, very short [0.2–0.8 (–1) mm] hairs on petioles and two pairs of leaflets. *P. tergemina* has patent, longer (1–2 mm) petiole hairs and three pairs of leaflets. Both have a white-tomentose leaflet underside and leaflets divided almost to the midrib. *P. conferta* is somewhat more dissimilar, having patent, conspicuously long petiole hairs (2–3 mm) and 4–5 pairs of leaflets with a less dense indumentum on the underside. Unlike the two previous species, *P. conferta* does not have leaflets divided almost to the midrib, and the entire plant is glandular.

In theory, the offspring of *P. argentea* × *P. conferta* should have a longer indumentum of petioles and a larger number of leaflets than the offspring of the other two combinations. Derivatives of *P. argentea* × *P. multifida* and *P. argentea* × *P. tergemina* should differ from one another mainly by the length of their petiole hairs. To check these assumptions experimentally, I carried out all three experimental crossings. The theoretical predictions were thus confirmed. Resulting F₁ hybrids were characterized as follows: *P. argentea* × *P. conferta* had pinnate lower cauline leaves with (2–)3 pairs of leaflets and petioles with (1.5–)2–2.5 mm long hairs. *P. argentea* × *P. tergemina* Soják had palmate or pinnate 2 (–3)-paired lower cauline leaves and petioles with 1.2–2 (–2.5) mm long hairs. *P. argentea* × *P. multifida* had palmate lower cauline leaves and petioles with 0.4–1 (–1.3) mm long hairs.

Except sterility, I obtained by crossing *P. argentea* with *P. conferta* an exact copy of *P. approximata* Bunge existing in nature. This is a steppe species growing throughout the southern part of West Siberia (KURBATSKIY 1988:150), in the eastern part of the former Soviet Central Asia, and its area of occurrence extends into Eastern Europe (South Urals region) and NW China (only Xinjiang). The record of it occurring in Talis Mts. refers to *P. lomakinii* Grossh. (vouchers in LE, DR).

By crossing *P. argentea* and *P. tergemina*, I obtained a copy of a taxon described as *P. angarensis* Popov. I collected this hybrid species at a number of sites along the Siberian arterial railway.

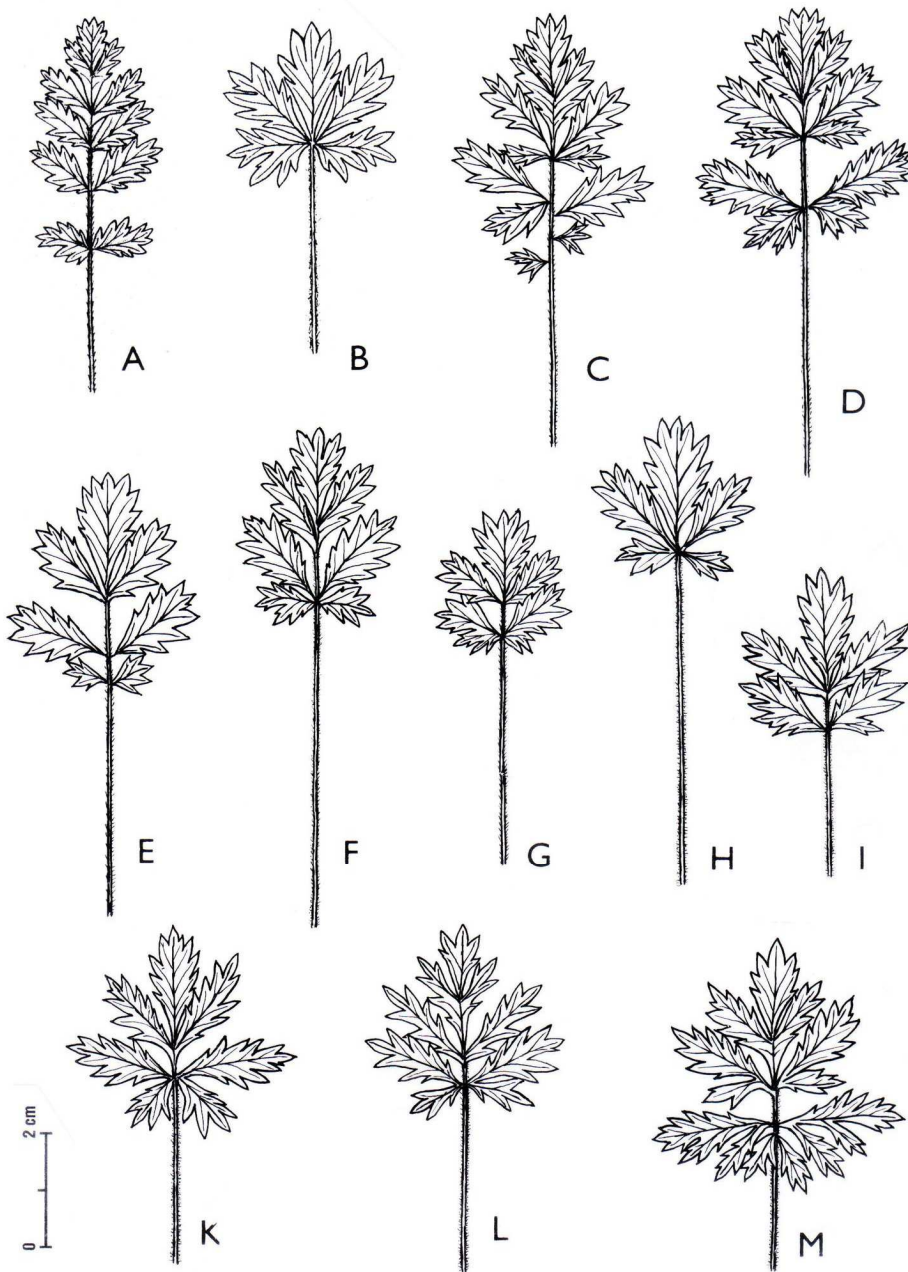


Fig. 1. Basal leaves: A) *Potentilla supina*; B) *P. argentea*; C-H) *P. argentea* × *P. supina* (*P. tobolensis*). Cauline leaves: I-M) *P. argentea* × *P. supina* (*P. tobolensis*).

By crossing *P. argentea* with *P. multifida*, I obtained hybrids corresponding to *P. omissa*, described from the southern coast of Lake Baikal. This species is frequent in the outskirts of Irkutsk, at the airport and even in the streets.

Differences found in experimentally obtained plants are often undetectable in plants collected in nature as a result of the predominating influence of the petiole indumentum of *P. argentea*. Discriminating between herbarium sheets of *P. angarensis* and *P. omissa* is therefore always difficult and often unreliable. It appears that most specimens found and collected in Siberia so far belong to *P. angarensis*. All hybrid species mentioned here spread independently of their parent species.

I used the pollen of the hybrid *P. argentea* × *P. multifida* to pollinate flowers of the parental species. In both cases I obtained perfectly sterile hybrid plants. The hybrid whose maternal plant was *P. argentea* had palmate basal leaves with leaves indented to half their width and petiole hairs 0.5–0.7 mm long. The hybrid obtained by pollinating *P. multifida* had subpalmate basal leaves, palmate lower cauline leaves with leaflets divided to the midrib and 0.2–0.5 mm long hairs on petioles.

***P. argentea* × *P. norvegica* (*P. intermedia*)**

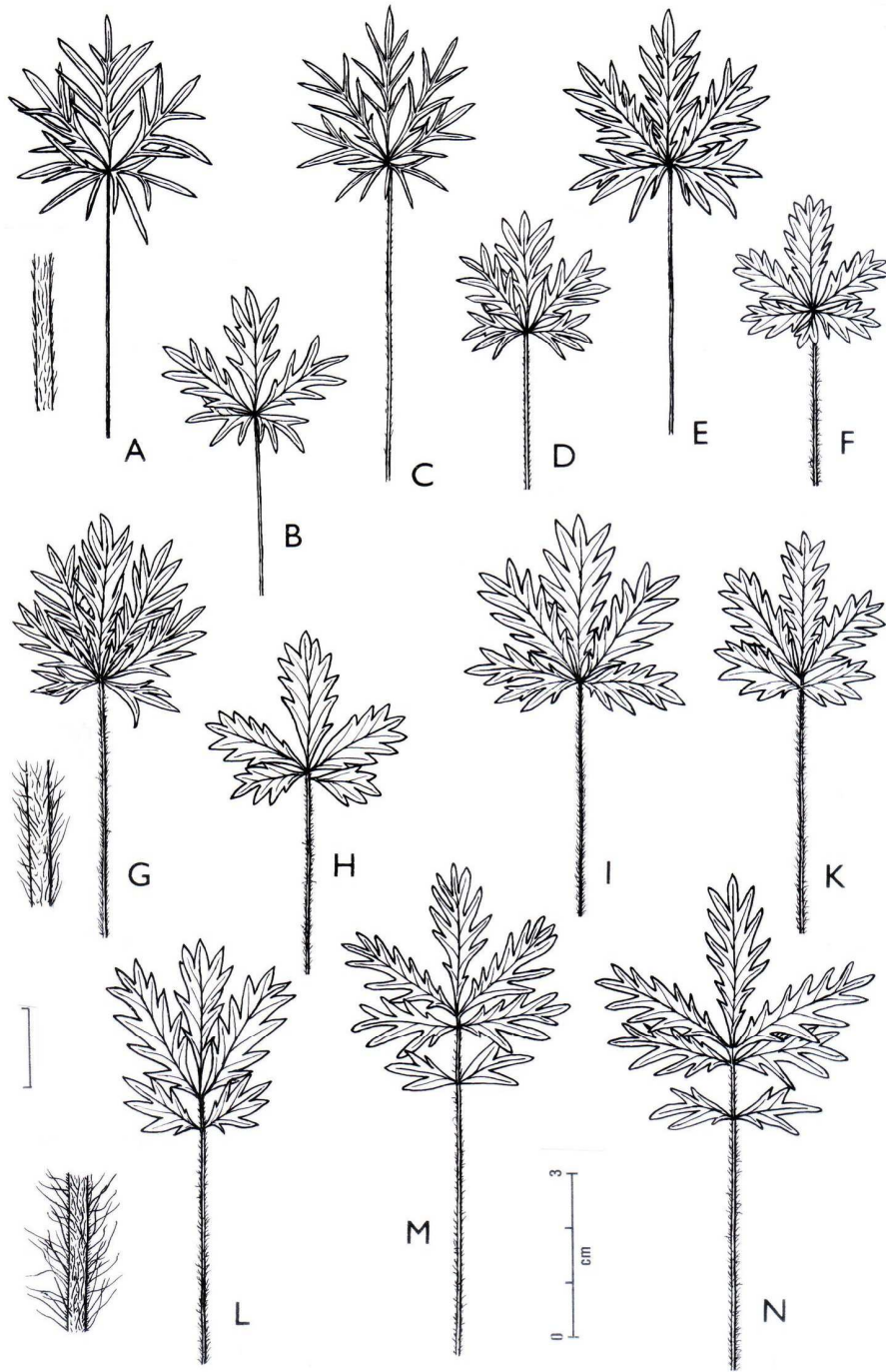
By crossing *P. argentea* with *P. norvegica* L. I obtained a perfect copy of *P. intermedia* (only sterile). All morphological characters including the indumentum of the underside of leaflets were identical with Linnaeus' specimens LINN 65517 and 65518. The underside of their leaflets was grey or greenish, not whitish-grey tomentose. I cannot recommend separating *P. heidenreichii* Zimmeter (nom. illeg., Art. 52.2e of the Code 2008), arisen from the same parent combination, as a different species. There is no dividing line between tomentose and non-tomentose forms. *P. intermedia* differs from *P. inclinata* Vill., which has the same leaflet indumentum, most of all in having small petals and anthers.

***P. argentea* × *P. supina* (*P. tobolensis*)**

The hybrid *P. argentea* × *P. supina* is the most interesting result of all of the 26 interspecific combinations obtained in culture. Both parent species are completely dissimilar. One has palmate tomentose leaves (with crisped hairs), the other pinnate non-tomentose leaves (with straight hairs). It is therefore easy to tell apomictically produced offspring from hybrid individuals.

Immediately after germination, experimentally obtained hybrids created leaf rosettes with strikingly polymorphic leaves. Some individuals had palmate leaves with a simply toothed middle leaflet. These individuals often remained permanently in the rosette stage and did not grow any stems. Other specimens had irregularly pinnate rosette leaves, mostly with 3 pairs of leaflets

Fig. 2. Basal leaves: A–E) *Potentilla argentea* × *P. multifida* (*P. omissa*); F–H) *P. argentea* × *P. tergemina* (*P. angarensis*); I–N) *P. argentea* × *P. conferta* (*P. approximata*). Petiole indumentum (scale bar: 3 mm) – above *P. argentea* × *P. multifida*; middle *P. argentea* × *P. tergemina*; bottom *P. argentea* × *P. conferta*.



and combined to different degrees the pinnate and palmate type of leaf (i.e., some lateral leaflets – often lower ones but sometimes also upper ones – were in groups of 4 in a false whorl). I repeated the crossing between the parent species seven times with essentially the same result except for one cross that resulted in all seedlings having two pairs of leaflets.

Unlike basal leaves, cauline leaves of hybrids showed little variability and were always a combination of a palmate and a pinnate leaf. The leaf blade had 5 bottom leaflets in a false whorl, in the middle of which the petiole continued upwards, bearing three further leaflets (these could alternatively be regarded as a single 3-sect leaflet), or the petiole above the 'whorl' carried two pairs of lateral leaflets. Both these types of leaf often co-occurred on the same stem.

The indumentum on the undersides of leaflets in *P. argentea* × *P. supina* is essentially the same as in all other hybrid species arisen through hybridization between the tomentose species *P. argentea* with any non-tomentose species of the Orthotrichae group (of these hybrid species, *P. inclinata* is most common in Europe).

The inflorescence of artificial hybrids tends to be conspicuously loose, their flowers are 1–1.3 cm in diameter, petals are 4–5 mm long, anthers measure 0.5–0.7 mm, and ripe achenes are ± 1.1 mm in length, straight on the abaxial side (lacking a protuberance). The artificial hybrids were identical with the naturally occurring species *P. tobolensis* in all characters including the tiniest details (except fertility). They had the same leaf shape, leaflet indumentum, size of floral organs etc.

The distribution of *P. tobolensis*, endemic to the former USSR, is presented in KURBATSKIY (1988) and SOJÁK (2009). Its native area spans from the southern Urals to the vicinity of Omsk. It has rarely been found introduced in Karelia, the Altai Mts and the Tien Shan Mts and in the Russian Far East (basin of river Ussuri and Sakhalin).

The *P. argentea* × *P. supina* hybrid does not arise in Europe. This may be due to the fact that a different subspecies of *P. supina* occurs in Europe than in Asia (European *P. s.* subsp. *supina* is tetraploid, while both Asian subspecies are octoploid).

I successfully backcrossed artificial hybrids between *P. argentea* and *P. supina* with *P. supina*. The resulting plants had basal and cauline leaves with 3–4 pairs of leaflets and a 3-sect terminal leaflet; the 'whorl' of leaflets at the base of the blade was usually absent; rarely it was present. The plants were difficult to distinguish from pure *P. supina* but were absolutely sterile. The participation of the *P. argentea* × *P. supina* hybrid in these backcrosses is evidenced by the occasional presence of double-toothed (or double-dissected) leaflets or 2-sect bottom leaflets of the blade. This sterile backcrossed hybrid was found introduced in Vladivostok.

***P. longifolia* × *P. tanacetifolia* (*P. acervata*)**

P. longifolia and *P. tanacetifolia* are two habitually similar species. They differ especially in the length of their indumentum, size petal and the shape of their inflorescence.

P. longifolia has petiole hairs 0.6–2 mm long, petals 3–5 mm long and a contracted, usually capitate inflorescence. The uppermost pair of leaflets is decurrent to the following leaflet pair. *P. tanacetifolia* has petiolar hairs (1.5–) 2–3 (–4) mm long, petals ± 6 mm long and a loose inflorescence. The uppermost pair of leaflets is not decurrent to the following leaflet pair.

Hybrids of *P. longifolia* × *P. tanacetifolia* obtained in culture have petiolar hairs (1–) 1.5–2.5 (–3) mm long, petals 5–7 mm long and a loose inflorescence. The uppermost pair of leaflets is shortly (1–10 mm) decurrent, sometimes non-decurrent.

I opine that the natural species *P. acervata* has originated from this parent combination. *P. acervata* has the same shape of leaves and leaflets and a petiolar indumentum of the same length as *P. longifolia*, from which it markedly differs in having large petals and a loose inflorescence. My experimental crossing of these two species resulted in almost completely sterile hybrids resembling *P. acervata*, having large petals and a loose inflorescence.

JUZEPCZUK (1941) was the first to distinguish and clearly define this species. He adopted the old name *P. nudicaulis* Willd. ex D.F.K. Schldl. without being able to see the type. The type specimen of *P. nudicaulis* is preserved in PR. This specimen is not identical with Juzepczuk's plant, but it corresponds to the hybrid *P. pensylvanica* L. × *P. sanguisorba* Willd. ex D.F.K. Schldl. I therefore replaced the name *P. nudicaulis* used by Juzepczuk (l.c.) by the name *P. acervata* (SOJÁK 1970, 2004).

P. acervata grows in the central part of South Siberia and from N Mongolia to NE China (for more information cf. SOJÁK 2007: 296).

***P. longifolia* × *P. tergemina* (*P. chalchorum*)**

P. longifolia and *P. tergemina* are not species that are similar in habit. They differ in their overall appearance, leaf shape and leaflet indumentum. Their hybrid is more or less similar to *P. tergemina*; a specialist would probably not anticipate the participation of *P. longifolia* in its origin.

The hybrid *P. longifolia* × *P. tergemina* obtained in culture is completely identical in all characters (except fertility) with the natural species *P. chalchorum* (its distribution is described in SOJÁK 2007, 2009). Both plants have the same leaf shape, indentation and leaflet indumentum, length of petiolar hairs, a glandular leaflet underside and sepals, and eglandular carpels.

The *P. longifolia* × *P. tergemina* hybrid differs from *P. tergemina* mainly in having less deeply reaching indents on leaflets (the central undivided part of the leaflet along the midrib is altogether 2–4 mm wide) and a sparser indumentum on the underside of leaflets. Its leaves have 4–5 pairs of leaflets. *P. tergemina* has leaflets that are divided almost to the midrib (their central undivided part is altogether 0.7–2 mm wide). Its leaves have 3 pairs of leaflets.

The hybrid has a grey or grey-green leaflet underside, covered with a not too dense tomentum consisting of flexuous or sometimes almost straight hairs (longer than found in *P. tergemina*), mostly patent all around; crisped hairs are missing, and the surface of leaflets is visible through the indumentum under

large enlargement. *P. tergemina* has a grey-white leaflet underside covered with a dense tomentum consisting of very fine crisped hairs; the surface of leaflets is not visible even under strong enlargement.

From the second parent, *P. longifolia*, the hybrid differs in a having a substantially different inflorescence (it is loose, not head-like contracted) and leaflets greyish on the underside with deeply reaching indents. *P. longifolia* has leaflets that are greenish on the underside, \pm shallowly toothed. The uppermost pair of leaflets are longly decurrent, and the whole plant is glandular with honey-coloured glands. It is therefore impossible to confuse these plants.

The artificial hybrid *P. longifolia* \times *P. tergemina* and the natural species *P. chalchorum* resemble *P. conferta* in their overall appearance. KURBATSKIY (1988) therefore merged these species. It cannot be proved, however, that these two species are related. *P. conferta* cannot be derived from hybrids between *P. longifolia* and *P. tergemina* because of its long indumentum on petioles, large glands on the underside of its leaflets and sepals and glandular carpels.

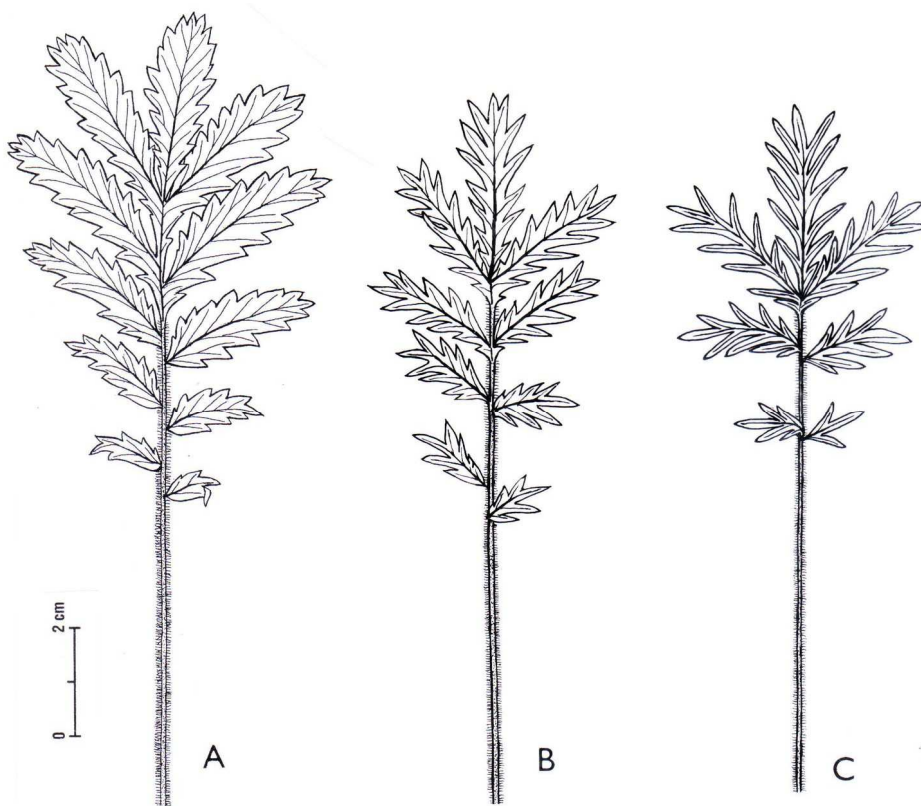


Fig. 3. Basal leaves: A) *Potentilla longifolia*; B) *P. longifolia* \times *P. tergemina* (*P. chalchorum*); C) *P. tergemina*.

P. chalchorum, on the other hand, has originated from this combination, which is convincingly evidenced by results of crossing experiments. The main difference between the two species resides in the length of the petiolar indumentum and the presence of large glands.

The hybrid *P. longifolia* × *P. tergemina* and the species *P. chalchorum* have short petiolar hairs (1–2 mm), while *P. conferta* has long hairs on petioles (2–3 mm). The hybrid, like *P. chalchorum*, has eglandular carpels, sepals without glands or with scattered, not too large glands, and the leaflet underside does not have sessile glands beneath the tomentum. *P. conferta* has glandular carpels. Its sepals and leaflet underside (beneath the tomentum) bear large, often yellowish and lightrefracting glands. Both these taxa are discontinuously separated in their morphology.

The hybrid between *P. longifolia* and *P. tergemina* obtained in culture also strongly resembles all hybrids arisen by crossing within the *P. multifida* group (*P. multifida* and *P. tergemina*) and *P. tanacetifolia* group (*P. tanacetifolia*, *P. longifolia* and *P. pensylvanica*). The most similar of these is *P. pensylvanica* × *P. tergemina*, which differs only slightly: its petiolar hairs are 1–2 mm long, while *P. longifolia* × *P. tergemina* has 0.5–1 mm long hairs on petioles. It is not certain whether this difference is retained in the second and third generation. Plants of these two combinations differ from other similar hybrids in having short, patent petiole hairs.

The hybrid *P. longifolia* × *P. tergemina* as well as the naturally occurring species *P. chalchorum* can also resemble hybrids in which *P. tergemina* is replaced by *P. sericea*, i.e. *P. conferta* × *P. sericea* (= *P. stepposa* Soják) and *P. sericea* × *P. tanacetifolia* (= *P. serrata* Soják). *P. stepposa* has leaflets indented in the same way as *P. chalchorum*, but because both its parents are characterized by a long indumentum (2–3 mm) on petioles. Its leaflet underside is whitish, and its tomentum tends to be denser than in *P. chalchorum*. *P. serrata* has an identical petiolar indumentum (2–3 mm long hairs) as the previous taxon, but its leaf shape is different (5–8 leaflet pairs), and the indentation of its leaflets often resembles *P. sericea*.

Hybrids that arise or can arise in nature

P. argentea × *P. tanacetifolia*

The hybrid *P. argentea* × *P. tanacetifolia* is not similar to any of its parents, but its overall appearance resembles hybrid species originated from crosses between *P. argentea* and species of the *P. multifida* aggregate (and also *P. conferta*), i.e. it especially resembles *P. approximata* and *P. angarensis*. From both of these species, the hybrid differs mainly in having larger flowers and 6–7 mm long petals. This small difference is stable.

This hybrid combination is not known from nature although its parental species meet in southern C Siberia. Its formation may be precluded by the different ecological preferences of its parents.

The hybrid has basal leaves with 3 pairs of leaflets, its leaflets are toothed less than half way to the midrib, greenish or greyish beneath, with short straight hairs between veins, petiole hairs are 1–2.5 mm long, obliquely patent.

P. chinensis* × *P. tergemina

The hybrid between *P. chinensis* and *P. tergemina* is somewhat closer to *P. tergemina* than to the latter parent. Unlike *P. chinensis* it has a substantially smaller number of leaflet pairs (4–5), and the base of its achenes lacks hairs. It often has a shorter indumentum on petioles and stems. It is sterile. Unlike *P. tergemina* it has a larger number of leaflets and markedly larger petals (cf. SOJÁK 2003). A natural hybrid of this combination, collected in the Russian Far East and in Mongolia, fully corresponds to artificial hybrid plants. The hybrid has been given the name *P. × recensita* Soják.

P. conferta* × *P. pensylvanica

P. conferta × *P. pensylvanica* is identical in most of its characters with *P. conferta*, not only in the shape of its leaves and leaflets but also in its petiole indumentum and sepals with numerous large, pale yellow glands. From pure *P. conferta*, the hybrid differs mainly in having less deeply divided leaflets [the middle undivided part of leaflets is 4–7 (–11) mm wide in hybrids and 1–4 (rarely to 5) mm wide in *P. conferta*]. The hybrid of this combination, as far as I know, has not been discovered in nature. Perhaps it has been overlooked because it is difficult to distinguish.

P. longifolia* × *P. multifida

This hybrid is unusually interesting. Its parental species are very different both in habit and in most taxonomically important characters, characters of *P. longifolia* being manifested as recessive in the hybrid and characters of *P. multifida* being dominant. The hybrid therefore resembles *P. multifida* in having leaves with two pairs of leaflets (rarely with 3-paired leaves admixed), leaves divided almost to the midrib with a small number of long lobes and petiole hairs appressed, 0.2–0.7 (–1) mm long. The hybrid differs from pure *P. multifida* in having mainly glandular sepals and a grey leaflet underside covered with a sparser tomentum. *P. longifolia* differs from the hybrid mainly by its large number of shallowly toothed leaflets (upper leaflets are longly decurrent); the entire plant has numerous, honey-coloured, shortly stalked glands.

Would this hybrid, which is completely sterile, exist in nature, it would be probably regarded as a microspecies from the complex of *P. multifida*, and nobody would anticipate the participation of *P. longifolia* in its origin.

P. longifolia* × *P. pensylvanica

This inconspicuous hybrid is characterized by sepals covered with dense, dirty yellowish-brown glands, basal leaves with 4–5 pairs of leaflets, whose underside is greenish or slightly greyish, between veins with short, patent, straight (sometimes slightly bent) hairs and petioles with 1–1.5 mm long, patent hairs.

The hybrid is similar in habit to plants arisen from the hybrid combination *P. conferta* × *P. pensylvanica*, but its leaflet underside is densely tomentose and whitish, and its petiole hairs are up to 3 mm long. The hybrid is remarkably similar to the combination *P. pensylvanica* × *P. tanacetifolia*, which differs, it seems, in having pale lemon-coloured, often lightrefractive glands on sepals. The hybrid probably arises in nature, but I have not seen any such specimens.

P. multifida* × *P. pensylvanica

Hybrids of this combination have leaves with 2–3 pairs of leaflets that are greyish-white on the underside, densely hairy, and petiole hairs that are erecto-subpatent, short [(0.5–)1–1.5 mm]. The very similar hybrid *P. multifida* × *P. tanacetifolia* has a markedly sparser indumentum on the leaflet underside, grey or greyish-green, and *P. longifolia* × *P. multifida* has shorter [0.4–0.6 (–0.7)] petiole hairs.

P. multifida* × *P. sericea

The artificial hybrid between *P. multifida* and *P. sericea* differs from other hybrids obtained in culture by its short petiole indumentum (0.4–1.5 mm) and small number of leaflets, i.e., (2–)3 pairs.

This hybrid is secondarily extremely similar to *P. tergemina*, and if it would occur naturally, these two could be easily misidentified. Most straightforward is their separation based on their petiole indumentum; petiole hairs of the hybrid are not horizontally patent as in *P. tergemina* but erect upwards (subpatent). Hybrid individuals are sterile.

P. multifida* × *P. tanacetifolia

P. multifida and *P. tanacetifolia* are fundamentally different in all taxonomically important characters as well as their overall appearance. *P. multifida* has 2 pairs of leaflets divided to the midrib, whitish-tomentose beneath, petioles with very short appressed hairs. *P. tanacetifolia* has (4–) 5–7 pairs of shallowly toothed leaflets, green beneath with straight hairs and long patent hairs on petioles. The artificial hybrid combines the characters of its parental species, but is closer to *P. multifida* in its overall appearance.

The *P. multifida* × *P. tanacetifolia* hybrid has leaves with 2 (rarely 3) pairs of deeply divided leaflets (their lobes reach 5/9 to 9/10 of their breadth, sometimes reach to the midrib), the leaflet underside is grey or greyish-green, slightly or intermediately densely hairy (the surface of leaflets is well visible between the hairs) with appressed, straight hairs or patent, short, ± straight hairs, petioles have straight hairs, 0.5–1.5 mm long, appressed or often obliquely patent. Sepals have very small, sparse glands. A similar hybrid, *P. multifida* × *P. pensylvanica*, differs in having more densely hairy leaflets that are grey-whitish beneath.

P. multifida* × *P. tergemina

P. multifida and *P. tergemina* are related species, which differ in having a different number of leaflets and a different petiole indumentum. *P. multifida* has 2

pairs of leaflets (the terminal leaflet usually has 3–4 pairs of lobes) and short [0.2–0.7 (–1) mm] appressed petiole hairs. *P. tergemina* has 3 pairs of leaflets (the terminal leaflet tends to have 4–6 pairs of lobes) and a longer (1–2 mm), patent petiole hairs. By hybridizing these two species I attempted to test the hypothesis that the East-Asian–North-American species *P. bimundorum* Soják originated by their hybridization. Although the hybridization experiment was a success, the hybrid sterile individuals obtained were not identical in important characters with *P. bimundorum* but with *P. multifida*. Their leaves had 2 pairs of leaflets and a short (0.5–1 mm) petiole indumentum, while *P. bimundorum* has leaves with 3 pairs of leaflets and 0.7–2 mm long petiole hairs. The presumed hybridogenous origin of *P. bimundorum* therefore was not verified.

P. norvegica* × *P. recta

It appears that this interesting hybrid has not yet been found in nature. This is perhaps due to different habitat requirements of its parents, which usually do not co-occur. The hybrid stands between the parental species. It could be overlooked or mistaken for *P. norvegica* because it has small petals. It can be identified by its palmate (5-foliolate) basal and cauline leaves. Its anthers are similar to those of *P. recta*.

P. norvegica* × *P. supina

This hybrid has every expectation to be found in nature because both of its parents often grow side by side (e.g., along banks of fish ponds). It could very easily be missed, since it is difficult to distinguish from non-hybridized *P. supina*. It would be given away by its sterility (abundant production of achenes is typical of both of its parents). The hybrid has basal and lower cauline leaves with 2–3 pairs of leaflets; typical *P. supina* has a larger number of leaflets.

P. norvegica* × *P. tanacetifolia

The distribution areas of these two species overlap considerably, but their hybrid has not been found. This is probably because the species differ in their ecological requirements and do not grow in the same habitats. The hybrid would probably be immediately identified in nature because its parents are completely different. One has pinnate leaves and large petals, the other ternate leaves and small petals.

The artificial hybrid has leaves of basal rosettes pinnate with 2 pairs of leaflets (rarely admixed are ternate leaves or leaves with 3 pairs of leaflets); the terminal leaflet has an unusually long petiolule (0.5–2 cm). Cauline leaves are palmate, 5-foliolate (ternate or subpinnate leaves are sometimes admixed). Petals are ± as long as sepals.

P. pensylvanica* × *P. tanacetifolia

This hybrid is more or less intermediate between its parents in all taxonomically important characters including the indumentum of petioles and the underside of leaflets, and the size of petals. Hairs of the petiole indumentum are

(1–) 1.5–2.5 mm long. The leaflet underside between veins has dense, straight, patent hairs. Its petals are 5 (–5.5) mm long and longer than sepals.

The hybrid *P. pensylvanica* × *P. tanacetifolia* is very close to the hybrid *P. longifolia* × *P. pensylvanica*. It differs mainly in the length of its hairs on petioles, and the colouration of glands on sepals.

P. pensylvanica* × *P. tergemina

This artificial hybrid is identical in habit with *P. longifolia* × *P. tergemina* (*P. chalchorum*). In the F₁ generation it differs only in having a longer petiole indumentum (1–2 instead of 0.5–1 mm). It is not certain whether this difference is stable. Would the derivatives of both these combination occur in nature, it would be very difficult to separate them.

P. sericea* × *P. tergemina

Although the parents of this hybrid are not too distinct, their hybrid cannot be mistaken for them. It can be easily identified based on the following set of characters: petiole hairs long (2–2.5 mm), leaflet underside with a dense, whitish tomentum, basal leaves with a large number (3–6) of leaflet pairs and a usually very loose inflorescence.

P. tanacetifolia* × *P. tergemina

The hybrid of *P. tanacetifolia* and *P. tergemina* stands between its parents in its morphology but is closer to *P. tergemina* in its habit because it usually has relatively deeply divided leaflets. The participation of *P. tanacetifolia* manifests itself in a long petiole indumentum, i.e., petioles of inner leaves of the basal rosette have (2–)2.5–3 mm long hairs. The underside of leaflets is ± grey, its indumentum is more or less intermediate between its parental species. Similar hybrids with a long petiole indumentum and *P. conferta*, have sepals with numerous large, yellowish glands, while *P. tanacetifolia* × *P. tergemina* has eglandular sepals or rarely with minute, sparse, colourless glands.

Hybrids that cannot originate in nature

P. crantzii* × *P. tanacetifolia

A hybrid of this parental combination cannot arise spontaneously in nature. The distribution area of *P. crantzii* ends in the Urals. The hybrid is very close to *P. crantzii* in its habit because stems of both species are virtually identical. Leaves of the hybrid are subpinnate with 2 pairs of leaflets (sometimes with almost palmate leaflets admixed) or pinnate with 3 pairs of leaflets (2 uppermost pairs of leaflets being strongly approximate and the bottommost pair being remote).

***P. crantzii* × *P. visianii* (*P. xdysgenes*)**

According to my findings, *P. xdysgenes* is a hybrid between *P. crantzii* and *P. visianii*. It occurs from time to time in European botanical gardens. The source of

its achenes is the botanical garden in Belgrade. I also raised it from achenes of *P. visianii* sent to me from Belgrade. The most striking feature of this hybrid is its leaf shape. It combines, in an interesting way, palmate and pinnate leaves: 2–4 outer leaflets grow from a single point, and the petiole continues on the middle between them and bears 1–2 pairs of lateral, longly decurrent leaflets. This leaf type must arise by hybridization between a species with palmate leaves (*P. crantzii*) with a species with pinnate leaves (*P. visianii*). A similar type of leaf is found in *P. tobolensis* from S Siberia and can also occur in some American species.

P. longifolia* × *P. visianii

The hybrid between *P. longifolia* and *P. visianii* does not at all resemble *P. longifolia* but is so similar to *P. visianii* that it is difficult to distinguish it from this unhybridized parent species. Characters of *P. longifolia* practically do not occur. The hybrid is sterile and cannot originate in nature (the distribution areas of the parental species preclude it).

The artificial hybrid has basal and lower cauline leaves with ± 4 pairs of leaflets, the uppermost pair of leaflets is longly decurrent, lateral leaflets have (3–)4–5 pairs of shallow, blunt teeth. The inflorescence is loose. Petals are 5–8 mm long.

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