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**Autor:** Soják, Jiří  
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# Notes on *Potentilla* (Rosaceae). VIII. *P. nivea* L. agg.

JIŘÍ SOJÁK

## RÉSUMÉ

SOJÁK, J. (1989). Notes sur *Potentilla* (Rosaceae). VIII. *P. nivea* L. agg. *Candollea* 44: 741-762. En anglais, résumés français et anglais.

Le lectotype de *Potentilla nivea* L. (LINN 655.43) appartient à l'espèce avec des poils droits (longs ou courts) sur les pétioles, nommée jusqu'à présent soit *P. hookeriana* Lehm. sensu Hult. soit *P. arenosa* (Turcz.) Juz. Le nom proposé par Linné doit être utilisé dans ce sens. Le taxon avec des pétioles couverts de poils floconneux, appelé jusqu'ici *P. nivea* L. (sensu Hult.), est décrit dans cette contribution comme *P. prostrata* Rottb. subsp. *floccosa* Soják. Les plantes parentes à poils droits et floconneux sur les pétioles doivent être nommées comme *P. prostrata* subsp. *prostrata*. *P. prostrata* subsp. *chamissonis* (Hult.) Soják qui est semblable à soit tous les pétioles couverts par des poils longs et droits, soit que quelques pétioles sont accompagnés par des poils flexueux ou bouclés, plus courts. *P. prostrata* est considérée comme une espèce d'origine hybridogène dérivée de *P. nivea* L. non Hult. (*P. arenosa*) × *P. crebridens* (*P. matsuokana* subsp. *crebridens*). Une espèce nouvelle est décrite de Japon.

## ABSTRACT

SOJÁK, J. (1989). Notes on *Potentilla* (Rosaceae). VIII. *P. nivea* L. agg. *Candollea* 44: 741-762. In English, French and English abstracts.

The lectotype of *Potentilla nivea* L. (LINN 655.43) belongs to a species with straight hairs (both short and long) on the petioles, which has been called *P. hookeriana* Lehm. sensu Hult. or *P. arenosa* (Turcz.) Juz. The Linnaean name should be accepted in this sense. A taxon with petioles covered exclusively with floccose hairs, up to now named *P. nivea* L. (sensu Hult.), is described as *P. prostrata* Rottb. subsp. *floccosa* Soják. Related plants with both straight and floccose (or crispate) hairs on the petioles should bear the name *P. prostrata* subsp. *prostrata*. A similar form, *P. prostrata* subsp. *chamissonis* (Hult.) Soják has either all petioles covered with long straight hairs, or some of them also have short flexuose or crispate hairs. *P. prostrata* is considered as a hybridogenous species derived from the parental combination of *P. nivea* L. non Hult. (*P. arenosa*) × *P. crebridens* (or more exactly, *P. matsuokana* subsp. *crebridens*). A new species, *P. jezoensis* Soják, is described from Japan.

## Introduction

*Potentilla nivea* L. s.l. belongs to the section *Niveae*, one of the most intricate groups of the whole genus. The taxonomic complexity of this section is due to the fact that its members can hybridize comparatively easily. Thus, sometimes it is not simple to draw a line between hybrids and species, and also the identification of various hybrids derived from morphologically similar parents is complicated. Hybrid plants usually are fertile, and exhibit a tendency to stabilize into hybridogenous species. It is not easy to find at what stage of its development a hybrid population acquires the character of hybridogenous species, and subjective decisions are usually adopted.

The majority of the species belonging to the section *Niveae* are characterized by ternate leaves with white tomentum beneath, lateral stems, and short subterminal styles. Species with quinate leaves (*P. saundersiana* group, *P. hookeriana* group) represent products of hybridization between the sections *Niveae* and *Pensylvanicae* (*Multifidae*). Species having leaves (at least some of them)

with sparse (more or less reduced) tomentum, have come into being as a result of hybridization between members of *Niveae* and representatives of other sections, mainly *Aureae*.

The section *Niveae* is comparatively homogeneous (but its limits towards the section *Pensylvanicae* are sometimes rather obscure as a result of hybridization). It comprises two morphologically isolated species and five species aggregates.

Taxonomically isolated species are *P. leucophylla* Pallas (Transbaikalia, Mongolia and W. Manchuria) and *P. delavayi* Franchet (Yunnan). The former possesses coriaceous leaflets of an unusual shape, the latter has not dilated stigmas, and is characterized by well developed cauline leaves.

*P. saundersiana* agg. is a homogeneous group of 4-5 Sino-Himalayan species having unthickened styles at the base. *P. sino-nivea* Hult. has ternate leaves, the other members of this group have quinate ones.

*P. uniflora* agg. consists of three closely related Arctic species and two species occurring in the Soviet Far East. The hybridogenous *P. villosula* Jurtz. represents a link between *P. uniflora* agg. and a very distinctive *P. villosa* Pallas (which grows in the coastal zone of the Pacific regions, and in its general habit closely approaches the Himalayan *P. venusta* Soják of the *P. argyrophylla* group). The species of the *P. uniflora*-*P. villosa* complex possess a characteristic indumentum of petioles (very long, conspicuously thin straight hairs along with sparse or abundant crispate hairs), and sometimes broad epicalyx-segments.

*P. evestita* agg. is a heterogeneous assemblage of young species that came into being through hybridization between members of the section *Niveae* and species with non-tomentose leaves (primarily from the section *Aureae*). The members of this group occur in Asia (from Soviet Central Asia and Kashmir to the Chukotskiy Nat. Okrug), more rarely in North America.

*P. hookeriana* agg. comprises seven species derived from those intersectional hybrids of *Niveae* × *Pensylvanicae* that have quinate leaves. (The species of the same origin having pinnate leaves belong to the section *Pensylvanicae*.) *P. hookeriana* agg. is distributed both in Asia (from Kashmir to the Arctic) and North America (cf. SOJÁK, 1986).

The last group of the section to be mentioned is *P. nivea* agg. Its members are widely distributed not only in Asia (in the territories extending from the Urals to Japan, in the Soviet Central Asia, Mongolia and in eastern China) but also in Europe (from Scandinavia to the Urals, and rarely also in the Alps), and in the Caucasus; they are not infrequent in North America, either. They grow from the forest-steppe zone to the Arctic islands; in the steppe and semi-desert regions they occur exclusively in the mountains. The group is characterized by ternate leaves, herbaceous leaflets with white tomentum beneath and with (3-)4-7(-14) pairs of teeth, narrow epicalyx-segments (except for *P. jezoensis* Soják; its taxonomic position within this section, however, is rather controversial), and styles slightly to strongly thickened at the base.

*P. pringlei* S. Wats., included in the group *Niveae* by RYDBERG (1908), has very long styles and belongs to another section. The group *Concinnae* Rydberg not only comprised the *P. concinna*-*P. fastigiata* agg., but also two species of the section *Niveae*, viz. *P. quinquefolia* Rydb. and *P. modesta* Rydb., both identical with *P. hookeriana* Lehm. non auct. in my opinion.

At the beginning of this century, two accounts of the *P. nivea* agg. were published (WOLF, 1908; RYDBERG, 1908), both studies being out-of-date now in view of the modern evidence. Wolf, who treated *P. nivea* very broadly, lumped all the members of this aggregate (and some representatives of other groups) under this latter name. Rydberg adopted much narrower species concept but based his treatment of *P. nivea* s.l. on unsuitable diagnostic features. The decisive contribution towards understanding the taxonomy of this group was made by JUZEPCZUK (1941) who was the first to evaluate properly the differences in the indumentum of petioles. He divided *P. nivea* s.l. into four species in the USSR (later on he recognized a further one, cf. JUZEPCZUK, 1955). This conception was followed by HULTÉN (1945) who divided the Scandinavian *P. nivea* s.l. into two species. In an excellent account of the Arctic members of the section *Niveae*, JURTZEV (1984) succeeded in clearing up the doubtful points in the taxonomy of the northern taxa of the Old World. Particularly, his delimitation of *P. nivea* L. s. Hult. and *P. crebridens* Juz. is important for further discussion in the present study.

### Taxonomy and phylogeny

*Potentilla crebridens* Juz. and *P. arenosa* (Turcz.) Juz. (*P. hookeriana* auct.) seem to represent ancestral taxa within the *P. nivea* agg. Both possess a combination of morphological features that cannot be derived from any other recent member of the genus, while, on the other hand, the other taxa of the *P. nivea* agg., judging from their morphology, might be derivatives of *P. crebridens*, *P. arenosa* and their hybrid.

***Potentilla arenosa* (Turcz.) Juz. (*P. hookeriana* Lehm. s. Hult. non s. orig.).**

*P. arenosa* has petioles only with straight hairs, partly long and stiff, partly very short thin ones. Its epicalyx-segments are oblong elliptical or lanceolate; styles are thickened and conspicuously papillose at the base. *P. arenosa* occurs from the basins of the rivers Pechora and Kama to Chukotka, the southernmost localities are found in Mongolia, and, furthermore, it grows in Alaska and Canada.

***Potentilla crebridens* Juz.**

*P. crebridens* has petioles covered only with floccose, extremely thin hairs, its epicalyx-segments in the younger (upper) flowers are narrowly linear, styles only slightly thickened at the base (often without papillosity or with rare small papillae). Its leaflets are broad with short teeth. The typical forms having the leaflets with 6-14 pairs of teeth occur in the Baikal Lake region (they reach the southern part of the Central Siberian Plateau in the north), in Mongolia and China. The plants with lower number of teeth to the leaflets (4-9), but otherwise answering to the typical *P. crebridens*, have been found to occur in the mountains of southern Siberia and Mongolia, in the Vilyuyskoye Plato, from the Baikal Lake region to the mouth of the Lena river, and to Chukotka, in the southern part of the Soviet Far East, in Korea, northern Alaska, and in the Richardson Mts. in Canada. Until recently these plants were considered as identical with the European *P. nivea* L. s. Hult. Only Jurtzev revealed that they belong to *P. crebridens*, described them as *P. crebridens* subsp. *hemicryophila*, and defined concisely the differences between the latter and the true *P. nivea* L. s. Hult. Thus it became possible to solve the problem of the origin of *P. nivea*. In this way, Jurtzev also confirmed the specific status of *P. crebridens*. (In Southern Siberia and Mongolia, *P. crebridens* subsp. *crebridens* gradually changes in *P. crebridens* subsp. *hemicryophila* in high mountain altitudes; previous authors were therefore of the opinion that there is no gap between *P. crebridens* and *P. nivea*, and some of them, as MALYSHEV (1965) considered *P. crebridens* as a variety of *P. nivea*).

***Potentilla nivea* L. sensu Hult.**

*P. nivea* has petioles covered exclusively with floccose hairs, and, upon comparison with both subspecies of *P. crebridens*, it possesses narrower leaflets with longer teeth, broader epicalyx-segments, and thicker styles with more thickened and more densely papillose base. It is relatively frequent in northern part of Asia from the Yenisey river to Chukotka, scattered in the mountains of southern Siberia, Mongolia and in Tarbagatay, in North America it is locally common from Alaska to New Foundland and in the Rocky Mts., reaching Utah and Colorado in the south. Furthermore, it is known to occur in Greenland, in the mountains of Scandinavia, in northeastern Finland, in the regions of Severnyy, Pripolyarnyy and Polyarnyy Urals, in the Caucasus, and in the Alps. It has been reported to occur in the Appennines (CARUEL, 1860, 1894; NEGODI, 1944) but I have not seen any specimen of this species from that region, and consider its occurrence in the Appennines as doubtful (cf. PIGNATTI, 1982).

According to the herbarium material of *P. nivea* I was kindly given by V. V. Petrovsky and B. A. Jurtzev, and in agreement with the JURTZEV work (1984), there are not only plants exclusively with floccose tomentum on the petioles in Siberia and the Chukotka region. In many plants also thicker, straight or flexuose hairs of variable density can be observed on some or all petioles. Plants with both floccose and thicker, straight hairs are met with as scattered individuals or groups in the populations of the typical *P. nivea*, or form local populations of their own. In fact, it is



impossible (and would be quite artificial) to treat the plants with and without thicker straight hairs as separate taxa because both forms are fully identical in other characters, and occur very often together in mixed populations. JURTZEV (1984) thus included both north Asian forms into one subspecies, *P. nivea* subsp. *mischkinii*. The Alpine-Scandinavian subspecies, *P. nivea* subsp. *nivea*, include exclusively plants with petioles lacking the thicker hairs.

In my opinion, these two forms (with and without straight thicker hairs on the petioles) have never been distinct from each other, nor they did amalgamate as a result of hybridization between *P. nivea* and *P. arenosa*, either. This is due to the fact that *P. nivea* is a hybridogenous species derived from the *P. crebridens* × *P. arenosa* parentage, hence it inevitably includes both types of indumentum on the petioles. (Of course, *P. nivea* hybridizes with both its parental species, which increases the overall variability.)

In Siberia, Chukotka and Mongolia, hybridization between *P. arenosa* and *P. crebridens* is common. Along with various nothomorphs of more or less intermediate appearance that were described as *P. × drymeja* Soják from Mongolia, and as *P. × tomentulosa* Jurtz. from northern Asia, a nothomorph comes into being possessing the indumentum to the petioles similar or even identical to *P. crebridens*. Such a nothomorph, morphologically almost indistinguishable from the European *P. nivea*, can be found in hybrid swarms, or forms micropopulations of its own. A hypothesis can be suggested that, in the territory west of the Urals, the originally very variable hybrid complex lost many of its genotypes, and the intermediary nothomorphs survived only locally and rarely, while the nothomorphs lacking straight hairs ("the true *P. nivea*") became stabilized and have an independent character now. This nothomorph penetrated southwards to the Alps independently although the plants with scattered straight hairs can very rarely be found there, as well. In Greenland, Canada and Alaska, the situation is similar to that in Siberia: forms with both types of the indumentum on the petioles occur there, but "the true *P. nivea*" is more common and clear-cut than in Siberia.

In my opinion, *P. nivea* cannot be derived from *P. crebridens* subsp. *hemicryophila* directly; its origin should be searched for among those hybrid populations of *P. crebridens* × *P. arenosa* that lost the straight hairs on the petioles. The following arguments can be given in favour of this hypothesis:

1. *P. nivea* differs from *P. crebridens* in five characters (narrower leaflets with longer teeth, broader epicalyx-segments, and more thickened styles with more papillae at the base); all of them are typical for the hybrids between *P. crebridens* and *P. arenosa*. This suggests that *P. nivea* has *P. arenosa* among its parental species. If *P. nivea* has evolved directly from *P. crebridens*, it would be highly improbable that all the changes point towards *P. arenosa*.

2. At the localities with recent hybridization between *P. crebridens* and *P. arenosa*, it is possible to find individuals (or local subpopulations) within the hybrid swarms, that exactly match the morphology of the "true European *P. nivea*". I have studied such populations in north Mongolia (northern slopes of Mt. Bogd-uul near Ulaan-Baatar, Soják, 26.7.1965, PR). I am convinced that the same morphotype can be obtained from experimental crosses between the above species.

3. The presence of some straight hairs in the petioles that can be considered as a trace of influence of *P. arenosa*, is found throughout the whole range of *P. nivea*. It is common in northern Asia, North America as well as in Scandinavia. However, also in the Alps where the "true *P. nivea*" seems to be best stabilized, individuals are rarely met with having straight thick hairs dispersed in some of the petioles (e.g. Tirol: Sterzing and Kitzbühl; France: Lautaret); I have even studied specimens with numerous thick straight hairs in a few petioles (Helvetia, A. Braun s.d., PR; Vallesia, Gletscherberg, Thomas s.d., LE). *P. crebridens* which is not derived from hybrids of the *P. arenosa* parentage obviously cannot show analogous variability.

4. Through the hybridization between *P. crebridens* and *P. pamirica* Wolf (which has pinnate leaves and only the straight hairs on the petioles) not only intermediate nothomorphs came into being. There is also a nothomorph having exclusively floccose indumentum on the petioles and on veins on the leaflet undersides. This latter plant can be distinguished from the typical *P. crebridens* only by the presence of quinate leaves (an influence of pinnate leaves of *P. pamirica*,

and, at the same time, the only evidence of the hybrid origin of this plant). This taxon named *P. chamaeleo* var. *byssina* Soják also exhibits a tendency to stabilize its micropopulations; the existence of this nothomorph represents an important argument in favour of my opinion on the origin of *P. nivea*. It is evident, anyway, that (as with many other hybrid combinations) not only a complex of intermediate nothomorphs appears in the progeny of *P. crebridens* × *P. arenosa*; nothomorphs approaching the parental species can be found, too.

The absence of straight hairs in “the true *P. nivea*” need not be a result of the segregation within the progeny of *P. crebridens* × *P. arenosa*. Another possible, or even very likely, explanation is that back crosses between the hybrid and *P. crebridens* took place. This problem which might be a good subject for an experimental study, is interesting from the evolutionary point of view. However, according to the Art. H. 4 of the Code, it has no nomenclatural relevance in this case.

The Alpine populations of *P. nivea* have a quite uniform shape of leaflets and the teeth to the leaflets: the teeth are conspicuously approximated (with margins touching each other or overlapping), widely oblong, blunt, in 4-6 pairs. The Scandinavian populations have leaflets and the teeth identical to those of the Alpine plants (in Lappland and in the mountains of southern Norway, populations occur having often 2-4 pairs of remote long acute teeth to the leaflets, but these also have some straight or flexuose thick hairs on the petioles, and should therefore be regarded as hybrids, *P. nivea* × *P. chamissonis*). The Alpine-Scandinavian populations of *P. nivea* are markedly homogeneous, in contrast to the Siberian ones.

In north Asia, *P. nivea* usually has the teeth to the leaflets remote (not touching each other), oblong-triangular, sometimes acute. The forms corresponding to those from the Alps are rare in Siberia and Chukotka. From the viewpoint of the origin of *P. nivea*, it is not important how common those forms are in north Asia; the very presence of them there can be considered as a substantial fact supporting my ideas on the origin and the status of *P. nivea*.

The forms identical to the Alpine-Scandinavian ones predominate in North America but morphotypes characterized by acutely dentate leaflets, matching those occurring in Asia, can also be found throughout this territory. Moreover, both types are linked by intermediate forms. In some regions of Quebec (e.g. Gaspé Pen.) a form of *P. nivea* grows having broad leaflets with short teeth, and thus imitating *P. crebridens* subsp. *hemicryophila*.

The Caucasian *P. nivea* is conspicuously distinct from the Alpine and northern plants. Its leaflets have (6-)7-8(-9) pairs of short approximated teeth, and they are almost indistinguishable from those of *P. crebridens*. The only reason why the Caucasian plants are classed together with *P. nivea* is the presence of comparatively broad, lanceolate to oblong epicalyx-segments (linear epicalyx-segments are absent even from the upper young flowers).

The Caucasian taxon should be considered as a marginal aberrant morphotype of *P. nivea*, very close to *P. crebridens*. With regard to its geographical isolation and constant character combination, this taxon is accorded subspecific status below.

### **Potentilla chamissonis** Hult.

*P. chamissonis*, in my opinion, came into being in the way parallel to that of *P. nivea*, i.e. through stabilization of one of the nothomorphs of the *P. crebridens* × *P. arenosa* parentage. While *P. nivea* evolved from a nothomorph closer to *P. crebridens*, *P. chamissonis* is derived from a nothomorph matching *P. arenosa* in the leaflet shape and indentation but having the indumentum of petioles (at least in some petioles or in some individuals of the population) intermediate between those of *P. arenosa* and *P. crebridens*. *P. chamissonis* possesses 3-4 pairs of remote, often oblong-triangular, sometimes acute teeth to the leaflets. Leaflets are divided more deeply than these of *P. nivea*, sometimes approaching *P. arenosa* var. *pinnatisecta* Jurtz.

*P. chamissonis* does not represent a very homogeneous taxon. Some of the plants that are classed in it have all the petioles covered only with long straight hairs, some others have this type of indumentum in a part of the petioles (the other petioles have also shorter flexuose or subcrispate hairs along with the long straight ones). Sometimes the shorter hairs are developed on all the petioles, and such plants in fact represent intermediates between *P. chamissonis* and *P. × drymeja* (incl. *P. × tomentulosa*).

The flexuose or subcrispate hairs on the petioles of *P. chamissonis* provide evidence for suggested origin of this taxon: it is derived from an intermediate nothomorph of the *P. crebridens* × *P. arenosa* parentage. During the evolution of *P. chamissonis*, however, a process of the reduction of the shorter hairs on the petioles took place. This process is met with frequently in the Arctic forms of *P. arenosa* in Siberia and Canada, and from time to time can be observed in the hybrids between *P. arenosa* and *P. crebridens*, taking place not only in some or all the petioles of the plant but also in some or all the individuals of a local population.

*P. chamissonis* occurs in Scandinavia, in the territory extending from Kola Pen. to the Tazovskiy Pen. at the mouth of the Ob' river, in Novaya Zemlya, Svalbard, Greenland and in Canada.

In the territories that are very far from the geographical range of *P. chamissonis* as suggested by HULTÉN (1945) and JURTZEV (1984), for instance in Yakutia, Chukotka (the East Siberian Sea coast, Korobkov, Petrovsky & Saponova s.n., 13.8.1972, PR) or in Mongolia (Hatgal near the Hövsgöl Nuur, Soják s.n., 15.8.1965, PR), some individuals within the hybrid populations of *P. crebridens* × *P. arenosa* may possess petioles partially or entirely lacking shorter hairs. These plants, in fact, match *P. chamissonis* morphologically, and demonstrate its origin.

Achenes of such a "copy" of *P. chamissonis* from the latter locality (the Hövsgöl Nuur, Mongolia) were cultivated in the experimental garden at Průhonice near Praha; the progeny was quite uniform morphologically, and identical to the Scandinavian *P. chamissonis* in the petiole indumentum.

### **Potentilla kuznetzowii** (Gowor.) Juz.

According to JUZEPCZUK (1941), *P. arenosa* is confined to eastern Siberia. It should be characterized by small leaves with short petioles, leaflets with dense straight hairs above and on the venation beneath, often blunt stipules to the cauline leaves, and flowers 8-10 mm in the diameter. Juzepczuk believed that, in western Siberia, Novaya Zemlya and in the territory from the Urals to Kola Pen. and Scandinavia, another similar species occurred. It is *P. kuznetzowii*, with long petioles to the basal, often larger leaves with scattered straight hairs on the leaflets' upper side and on the venation beneath, with acute stipules to the cauline leaves, and flowers 10-15 mm in diameter. HULTÉN (1945) ignored the Juzepczuk data on the occurrence of *P. kuznetzowii* in Scandinavia and Karelia-Lapland region, in spite of the fact that he was aware of the occurrence of the only taxon of *P. nivea* agg. with straight hairs on the petioles in these regions. He described this latter taxon as *P. chamissonis* referring to the Juzepczuk description of *P. kuznetzowii* and supposing that *P. kuznetzowii* and *P. arenosa* (*P. hookeriana* sensu Hult.) are identical. Juzepczuk gives only *P. nivea* and *P. kuznetzowii* for the Urals, and the only specimen that Hultén had at his disposal from there answered to the south Siberian *P. arenosa* (*P. hookeriana* sensu Hult.).

The specimens of *P. kuznetzowii* annotated by Juzepczuk (in LE) show very clearly that he included in it both the western taxon (later described as *P. chamissonis*) and the populations from the Urals and western Siberia belonging to *P. arenosa*. The use of the name *P. chamissonis* depends on the identity of the type of the earlier *P. kuznetzowii*. The type is missing for the time being.

JURTZEV (1984), on the basis of Juzepczuk's description of *P. kuznetzowii*, used this name as a substitute for *P. chamissonis*. This solution is questionable, however, because the description can hardly be a satisfactory criterion. It should be emphasized that JUZEPCZUK in a later work (1959) accepted the Hultén name for the plants with straight hairs on the petioles, growing in the Kola Peninsula. If the type of *P. kuznetzowii* belonged to *P. chamissonis*, it would mean that JUZEPCZUK (1959) was not able to recognize the species introduced by him. This does not seem to be very likely. When the name *P. chamissonis* is used at the rank of subspecies, which I recommend, the Hultén name should be given priority.

The Curator of the herbarium in Ottawa (DAO) kindly placed at my disposal an extensive material of the *P. nivea* agg. from Canada. I have found that the majority of the specimens deposited under the name *P. chamissonis* there in fact belong either to the *P. uniflora* agg. or to various intermediates between *P. arenosa* and *P. nivea*. Among the numerous specimens from DAO, only four herbarium sheets (all from the Northwest Territories) agree with *P. chamissonis* from Scandinavia and Greenland. In view of the fact that *P. chamissonis* is very rare in Canada, and is confined to the regions with common occurrence of *P. arenosa* × *P. nivea* that is very variable there (some of the hybrid populations exhibit a tendency of reduction of the shorter petiole hairs), it can easily



be suggested that *P. chamissonis* need not have penetrated to Canada from Greenland, and that it might have come into being independently in Canada.

### **Potentilla nipharga** Rydb.

The typical *P. arenosa* has both long and dense, very short straight hairs on the petioles. In the Arctic territories of Siberia and Canada, the atypical forms with sparse or lacking short hairs on some of the petioles are not rare (the type specimen of *P. basanensis* Serg. belongs to this form). Plants with deeply divided leaflets, described as *P. arenosa* var. *pinnatisecta* Jurtz. are also frequent in these regions. Along with the above forms, plants having the petioles with both long hairs and dense, curved or slightly flexuose short hairs (usually a little longer than those of typical *P. arenosa*), are widely distributed in Canada. Very likely, these populations were influenced by introgressive hybridization. This taxon, which is called *P. nipharga*, forms quite gradual transitions to the typical *P. arenosa*, and to the intermediary nothomorph of *P. arenosa*  $\times$  *P. nivea* on the other side of its morphological range.

I recommend to treat *P. nipharga* as a variety of *P. arenosa*. On the other hand, only weak arguments can be given against treating it as a marginal nothomorph of a hybrid between *P. crebridens*  $\times$  *P. arenosa* or *P. nivea*  $\times$  *P. arenosa*. This variety not only occurs in North America but also in northern Asia and Mongolia. Its occurrence in Greenland is very surprising, as the typical *P. arenosa* is absent from this region. The origin of var. *nipharga* in Greenland can be accounted for in several ways:

1. it penetrated to Greenland from Canada without any change;
2. it indicates the possibility that the typical *P. arenosa* reached Greenland in the past;
3. it represents remains of the original hybrid complex of *P. crebridens*  $\times$  *P. arenosa* from Siberia;
4. it is a result of the character segregation in *P. chamissonis*.

The literature records of the occurrence of *P. arenosa* (*P. hookeriana* auct.) apparently refer to this intermediate taxon. One specimen of var. *nipharga* from Greenland was identified by Jurtzev as *P. kuznetzowii* (*P. chamissonis*)  $\times$  *P. arenosa* (Nordmann, 15.7.1911, LE).

### **Potentilla nivea-P. chamissonis** complex

In order to summarize the above chapter, the following points should be emphasized: within the hybrid populations of *P. crebridens*  $\times$  *P. arenosa* in northern Asia, not only the intermediate plants can be found but also the forms approaching the respective parental species in the indumentum of the petioles and indentation of the leaflets. Furthermore, nothomorphs with more or less reduced density of shorter petiole hairs occur in those populations. In the territory west of the Urals, outside the geographical range of the parental taxa, the genetical and morphological variability decreased to reach the present situation when the intermediate nothomorphs have become rare while the marginal nothomorphs gradually stabilized to form homogeneous independent populations. That is why they were regarded as distinct species, *P. nivea* and *P. chamissonis*. Neither in the Urals, nor in Scandinavia, Greenland, Canada, nor Alaska, however, such a geographical or genetical isolation took place to lead to a distinct morphological limits of these taxa. In the present paper, *P. nivea* as well as *P. chamissonis* are therefore treated as subspecies of one hybridogenous species. There are some limited regions isolated from the extensive geographical range of the complex *P. nivea-P. chamissonis*, where scarce populations of the two subspecies penetrated independently (viz. Svalbard and Novaya Zemlya in the north, the Alps in the south), but this can hardly justify the specific treatment for both taxa.

The plants with the intermediary petiole indumentum (with both straight and crispate hairs) might have evolved in two ways: they belong to the progeny of either *P. crebridens*  $\times$  *P. arenosa* or *P. nivea*  $\times$  *P. chamissonis*. Evidently, in north Europe and America we are not able to distinguish the primary hybrids of the Siberian origin (that represent the ancestor of *P. nivea* and *P. chamissonis*) from the products of the secondary hybridization between *P. nivea* and *P. chamissonis*. Products of these two ways are indistinguishable morphologically. Nevertheless, from both the

evolutionary and nomenclatural viewpoints, this question is not important, as both hybrids are derived from the same genetical basis (*P. arenosa* and *P. crebridens* represent the parental or ancestral species in both cases).

JURTZEV (1984: 172) also considered the hybrid origin of *P. chamissonis* (*P. kuznetzowii* sensu Jurtzev) and *P. nivea*: "There are good reasons to suppose that *P. kuznetzowii* s.str. (*P. chamissonis* Hult.) might have originated as a result of introgression of *P. nivea* s.l. and *P. arenosa*. In this case, however, the features of the later predominate. As regards the "true" *P. nivea* from the Scandinavian mountains and the Alps, it might have evolved from the Siberian *P. crebridens* subsp. *hemicryophila* (migration in the periglacial zone during the cold and arid period of the Pleistocene), or from *P. mischkinii* [*P. crebridens*  $\times$  *P. arenosa* or *P. nivea*  $\times$  *P. chamissonis*] as a result of the severe selection pressure against the plants with the features of *P. chamissonis*. The latter possibility is less probable..."

### ***P. nervosa* Juz.**

*P. nervosa*, which is endemic to Soviet Central Asia, has leaflets very similar to those of *P. crebridens* subsp. *crebridens* but its petioles have both floccose tomentum and straight stiff hairs (Juzepczuk overlooked the latter, and gives only floccose hairs in the protologue of his new species). Theoretically, it might be also derived from the hybrid combination *P. crebridens*  $\times$  *P. arenosa*. In terms of morphology, it answers to the nothomorph, the position of which can be expressed as *P. crebridens* subsp. *crebridens*  $>$  *P. arenosa*. However, such an origin of *P. nervosa* is uncertain. The absence of convergent forms among the Mongolian and Siberian nothomorphs *P. crebridens* subsp. *crebridens*  $\times$  *P. arenosa* speaks against the above hypothesis, as well as the considerable stability of the populations of *P. nervosa*.

### **Potentilla matsukana Makino**

*P. matsukana* was described from Japan, and later it was also collected in Korea (e.g. Mt. Baekdoo, PR) and the Soviet Far East (Sikhote Alin' and southern Sakhalin, LE and PR). This taxon, believed to be identical with *P. nivea* s.str., is very close to *P. crebridens* subsp. *hemicryophila* having the same petiole indumentum, and similar shape of leaflets and their teeth. Small, 1-2-flowered specimens of *P. matsukana* usually have larger calyces and broader epicalyx-segments than in the medium sized specimens of *P. crebridens*. However, the larger plants with more flowers per stem possess the calyces and epicalyx-segments of the same size and shape, respectively, as those of *P. crebridens* subsp. *hemicryophila*.

The Japanese plants are often remarkable in having rounded teeth to the leaflets but sometimes the teeth are acute. The only constant and consistent difference between *P. crebridens* and *P. matsukana* consists in the length of styles: *P. crebridens* has the styles (0.8-)1.0-1.2(-1.4) mm long while *P. matsukana* has (1.3-)1.4-1.6(-1.7) mm long styles. In view of the fact that the above minor difference is of a quantitative character (the extreme values overlap a little), I have arrived, after some hesitation, at the conclusion that both taxa should better be treated as subspecies than as separate species. This opinion (as it is usual in such problematic cases) is subjective and may depend on the number of the specimens studied.

### **Potentilla jezoensis Soják**

The last taxon to be discussed here is the Japanese *P. jezoensis*. It has petioles covered exclusively with floccose, extremely thin hairs, which points to *P. matsukana*, but its epicalyx-segments are ovate to elliptical, which is a feature of *P. villosa* Pallas and *P. vahliana* Lehm. It differs from all the members of the section *Niveae*, except for the Chinese *P. delavayi* Franchet, in having unusually long styles. The evolutionary relationships of *P. jezoensis* are unclear. On the basis of its petiole indumentum, it can be included in the *P. nivea* agg., or, taking its broad epicalyx-segments into account, into the *P. uniflora*-*P. villosa* group. Nevertheless, it represents a marginal element in both groups.



### Nomenclature

*P. nivea* L. was described from the Lappland mountains and from Siberia. The diagnose is brief, and can be referred to any member of the aggregate. The only synonym given by Linnaeus is doubtful (*Fragaria sterilis, foliis subtus incanis, magno flore albo*. Vaill. Paris. 55?) and refers to a white-flowered French representative of another section. A problem of the typification of *P. nivea* L. was not so important until JUZEPCZUK (1941) divided the Siberian *P. nivea* into three species, and HULTÉN (1945) the Lappland *P. nivea* into two species. Juzepczuk did not deal with the typification of *P. nivea* and restricted the Linnaean name to cover the plants with floccose indumentum, without giving any evidence to support his opinion. HULTÉN (1945) evaluated the photographs of both syntype specimens in LINN, and arrived at the conclusion that "one apparently being *P. nivea* as described here [i.e. sensu Juzepczuk] and the other being *P. chamissonis*". He therefore followed Juzepczuk in including in *P. nivea* the plants with tomentose petioles.

In 1983 I examined the Linnaean plants in London, and found that one of the Hultén identifications was wrong. The plant No. 655.43 belongs to the typical *P. arenosa* (and comes from Siberia) while No. 655.44 is *P. chamissonis* (very likely, the plant was collected in Lappland). For the sake of completeness, it should be noted that there is no other Linnaean material connected nomenclaturally with the name *P. nivea*. According to the Curators of the herbaria of BM, H, S, SBT, UPS and Institut de France, Paris, there is not any specimen annotated by Linnaeus in the above collections. There are some reasons in favour of the suggestion that the taxon with floccose hairs on the petioles (*P. nivea* sensu Hultén) was not studied by Linnaeus before 1753. According to STEARN (1957), the Siberian plant collected by Gmelin should play a role of the type.

The name *P. nivea* L. is to be used instead of *P. arenosa* (Turcz.) Juz. of the Russian authors, and of *P. hookeriana* Lehm. erroneously introduced by HULTÉN (1945) on the basis of Lehmann's incorrect diagnose (cf. SOJÁK, 1986).

In order to avoid confusion, the name *P. nivea* L. will have to be given for sometime with a note directing the attention to the fact of changed conception of the name (e.g. *P. nivea* s. orig. or *P. nivea* L. non auct.). There is no danger that the name *P. nivea* might become a source of error. Hultén's misidentification of the photograph of the type seems to be a very insufficient reason for rejection of the Linnaean name.

A name of the taxon with only floccose hairs on the petioles should be therefore searched for. In the section *Niveae* there are three taxa with only floccose indumentum of the petioles (*P. matsukana*, *P. crebridens*, *P. crebridens* subsp. *hemicryophila*) but all of them are specifically distinct from *P. nivea* auct. non L.

If we accept that *P. nivea* auct. non L. came into being through stabilization of a nothomorph of *P. crebridens* × *P. nivea* L. non auct. (*P. arenosa*), and taking the Art. H.4 of the Code into account, the correct name for *P. nivea* auct. non L. ought to be searched for among the specific epithets given to another taxon derived from the same parentage. The oldest name being in agreement with the above conditions is *P. prostrata* Rottb. 1770.

Dr. Bent Fredskild of Copenhagen (C), was so kind as to send me a photograph of the general habit, and details of the petiole indumentum of the type specimen of *P. prostrata* (the plant is deposited in Egede, Herbarium vivum). Furthermore, I had sent to Dr. Fredskild a series of petioles with all the types of indumentum encountered in the *P. nivea* agg., and he selected three petioles approaching most closely those of *P. prostrata*. The above material (the photograph and the petioles returned) allows to conclude that *P. prostrata* has all the leaves ternate [in contrast to *P. subquinata* (Lange) Rydb.] and the petioles with both stiff thick, slightly flexuose or straight hairs and thin crispate hairs. The type of *P. prostrata* was collected in Greenland. Very similar but not identical petioles can be found in *P. × mischkinii* Juz. from the Kola Peninsula.

*P. prostrata* is considered here as a collective hybridogenous species, consisting of four groups of forms (originally nothomorphs) that, with regard to the level of their differentiation, should be treated as subspecies. A subspecies lacking the straight hairs on the petioles is described as *P. prostrata* subsp. *floccosa* Soják (= *P. nivea* auct. non L.) in the present paper. Plants with reduced short flexuose-crispate hairs in some or all petioles bear the name *P. prostrata* subsp. *chamissonis* (Hult.) Soják, and the plants with both straight and crispate hairs in all the petioles should be called

*P. prostrata* subsp. *prostrata*. The fourth subspecies is represented by Caucasian plants which answer to *P. prostrata* subsp. *floccosa* in the shape of the epicalyx-segments and the petiole indumentum, but in the shape and number of the leaflet teeth they correspond to *P. matsukana* subsp. *crebridens*.

JURTZEV (1984) came to a similar conclusion independently; he treated *P. mischkinii* (my *P. prostrata* subsp. *prostrata*) as a subspecies of *P. nivea* L. s. auct. (my *P. prostrata* subsp. *floccosa*). The only difference between the two conceptions is that I also treat Jurtzev's *P. kuznetzowii* as a subspecies *P. prostrata* subsp. *chamissonis*.

If the latter taxon is accorded a specific status, a problem arises of the typification of *P. kuznetzowii*. The type specimen, in 1969 certainly deposited in LE, is missing now. As the locus classicus region of *P. kuznetzowii* harbours two similar taxa of this group, the type specimen may belong to any of them with the same probability. However, this is not the main problem for me, as the Hultén name should be given a priority at the rank of subspecies.

The taxa that have been referred to as *P. × drymeja* Soják and *P. × tomentulosa* Jurtz. are included in *P. prostrata* subsp. *prostrata*. A level of differentiation and stabilization of them is lower than that of *P. prostrata* subsp. *floccosa* and *P. prostrata* subsp. *chamissonis*; therefore I do not consider it as advisable to treat them as a separate subspecies of *P. prostrata*.

If *P. chamissonis* and *P. nivea* auct. non L. were accorded specific status, in spite of the arguments given in the present study, it would be necessary to treat *P. prostrata* subsp. *floccosa* as a separate species, *P. prostrata* (incl. *P. mischkinii*) would have to be regarded, for formal geographical reasons, as a hybrid between *P. chamissonis* and *P. floccosa*, and the name *P. × drymeja* would become correct for the hybrids *P. crebridens* × *P. nivea* L. non auct. (*P. arenosa*).

*P. matsukana* and *P. crebridens* are considered here as conspecific at the rank of subspecies; for the priority reasons the former name is adopted for the species. A more detailed evidence for this conception is given above.

The original type specimen of *P. matsukana* is not extant and that is why I select a neotype. The neotype comes from Mt. Togakushi, a locality where the species was described from. (Type specimen has been unsuccessfully searched for in MAK, TI and TNS.)

*P. hookeriana* Lehm. non Hult. represents an independent species endemic to America. It is characterized by its quinate leaves (cf. SOJÁK, 1986). *P. quinquefolia* Rydb. (type PR!) and *P. modesta* Rydb. (type NY!) should be relegated to the synonymy of the above name.

An isotype of *P. basanensis* Serg. (from the Kuznetskiy Alatau, LE!) belong to the true (not hybridized) *P. nivea* L. non Hult. with sparse short hairs on the petioles.

*P. sajanensis* A. Polozh. (from the Sayany Mts.) is an unclear taxon having petioles covered with both straight and crispate hairs, and conspicuously deeply divided leaflets.

*P. coriacea* Soják is a species of hybrid origin derived from *P. leucophylla* Pallas × *P. nivea* L. non Hult. (or *P. leucophylla* × *P. matsukana* subsp. *crebridens*).

A survey of the changing views on the nomenclature of *P. nivea* s.l. is given in what follows:

HULTÉN (1945)	JURTZEV (1984)	Present author
<i>Potentilla hookeriana</i> Lehm. <i>P. nivea</i> L. <i>P. chamissonis</i> Hult. — — <i>P. nervosa</i> Juz. p.p.	<i>Potentilla arenosa</i> (Turcz.) Juz. <i>P. nivea</i> L. <i>P. kuznetzovii</i> (Gow.) Juz. <i>P. × tomentulosa</i> Jurtz. <i>P. nivea</i> subsp. <i>mischkinii</i> (Juz.) Jurtz. p.p. <i>P. crebridens</i> Juz.	<i>Potentilla nivea</i> L. <i>P. prostrata</i> Rottb. subsp. <i>floccosa</i> Soják <i>P. prostrata</i> subsp. <i>chamissonis</i> (Hult.) Soják <i>P. prostrata</i> subsp. <i>prostrata</i> <i>P. prostrata</i> subsp. <i>prostrata</i> <i>P. matsukana</i> Mak. subsp. <i>crebridens</i> (Juz.) Soják

**Potentilla nivea** L., Sp. Pl. 499. 1753 — *Fragaria nivea* (L.) Crantz Inst. 2: 179. 1766 — *P. nivea* subsp. *chionodes* Hiit., Arch. Soc. Zool. Bot. Fenn. Vanamo 2: 25. 1949 nom. inval., quoad nomen et typum non quoad plantam Hiitoneni. **Lectotypus:** LINN 655.43!; cf. Stearn Intr. Sp. Pl. 127. 1957.

**Potentilla nivea** var. **nivea**

*Potentilla nivea* γ [var.] *arenosa* Turcz., Bul. Soc. Nat. Mosc. 14: 607. 1843 — *P. arenosa* (Turcz.) Juz., Fl. SSSR 10: 137. 1941 — *P. nivea* subsp. *hookeriana* var. *arenosa* (Turcz.) Hiit., Arch. Soc. Zool. Bot. Fenn. Vanamo 2: 26. 1949. **Typus:** Turczaninow s.n., LE!

*Potentilla basanensis* Serg., Sist. Zam. Mat. Gerb. Tomsk. Gos. Univ. 77-78: 11. 1954. **Isotypus:** Titov s.n., LE!

*Potentilla hookeriana* auct. non Lehm.: Hult., Bot. Notis. 1945: 138. 1945; Ball, Pawlowski & Walters, Fl. Europ. 2: 41. 1968 & al.

**Potentilla nivea** var. **nipharga** (Rydb.) Soják, stat. nov.

*Potentilla nipharga* Rydb., N. Am. Fl. 22/4: 332. 1908. **Typus:** Onion s.n., NY!

**Potentilla prostrata** Rottb., Skr. Kjøbenh. Selsk. Laerdoms Vidensk. Elsk. 10: 453. 1770. **Typus:** Egede s.n., C, photo!**Potentilla prostrata** subsp. **prostrata**

*Potentilla mischkinii* Juz., Fl. Murman. Obl. 4: 323. 1959 — *Potentilla nivea* subsp. *mischkinii* (Juz.) Jurtz., Arkt. Fl. SSSR 9/1: 173. 1984. **Holotypus:** Mischkin 111, LE!

*Potentilla* × *drymeja* Soják, Folia Geobot. Phytotax. 5: 111. 1970. **Holotypus:** Deyl & Soják s.n., PR!

*Potentilla* × *tomentulosa* Jurtz., Arkt. Fl. SSSR 9/1: 318. 1984. **Holotypus:** Jurtzev & Petrovsky 298, LE!

**Potentilla prostrata** subsp. **chamissonis** (Hult.) Soják, comb. nov.

*Potentilla chamissonis* Hult., Bot. Notis. 1945: 140. 1945 — *P. nivea* subsp. *chamissonis* (Hult.) Hiit., Arch. Soc. Zool. Bot. Fenn. Vanamo 2: 25. 1949 — *P. hookeriana* subsp. *chamissonis* (Hult.) Hult., Bot. Notis. 1945: 139. 1945 nom. inval.; Hult., Comments Fl. Al. 73. 1967; Hult. in: Böcher, Holmen & Jakobsen, Fl. Greenl. 56. 1968 — *P. nivea* var. *chamissonis* (Hult.) Lid, Norsk Svensk Fl. 409. 1963 nom. inval. **Holotypus:** Cederstrahle s.n., S!

?*Potentilla nivea* var. *kuznetzowii* Gowor., Fl. Urala 532. 1932 — *P. kuznetzowii* (Gowor.) Juz., Fl. SSSR 10: 137. 1941 — *P. nivea* subsp. *hookeriana* var. *kuznetzowii* (Gowor.) Hiit., Arch. Soc. Zool. Bot. Fenn. Vanamo 2: 25. 1949. **Typus:** LE, n.v.

**Potentilla prostrata** subsp. **floccosa** Soják, subsp. nov.

*Potentilla nivea* subsp. *chionodes* Hiit., Arch. Soc. Zool. Bot. Fenn. Vanamo 2: 25. 1949 nom. inval., quoad plantam et conceptionem Hulténi et Hiitoneni (sine descr. lat.) non quoad nomen Linnaei.

*Potentilla nivea* auct. non L.: Juz. Fl. SSSR 10: 135. 1941; Hult., Bot. Notis. 1945: 129. 1945; Ball, Pawlowski & Walters, Fl. Europ. 2: 41. 1968; Jurtz., Arkt. Fl. SSSR 9/1: 169. 1984 & al.

Caules (3-)5-15(-20) cm alti, pilis crispato-floccosis obtekti. Folia ternata, (1-)2-10 cm longa. Petioli pilis crispato-floccosis omnibus tenuibus vestiti (i.e. pilis rectis rigidulis nullis). Foliola 0.5-2.5 cm × 0.5-1.6 cm magna, elliptica vel oblongo elliptica, rarius obovata, basi cuneata, dentibus utrinque 3-6(-7) aut latis (apice obtusis vel rotundatis) marginibus obtegentibus vel tangentibus aut ± triangularibus (apice acutis) marginibus a sese remotis, plerumque (1-)1.5-4 × 1-2(-3) mm magnis, supra pilis rectis (raro etiam crispatis) induta, subtus albo-tomentosa (nervatura plerumque tantum tomento obtecta). Flores 1-1.7 cm in diam. Episepala oblonga vel lanceolata, obtusa, sepalis breviora, interdum aequilonga. Petala lutea, 4-7 mm longa. Stylus basi ± distincte incrassatus et papillosus, 1-1.2 mm longus. Nuculae maturae olivaceae, 1.4-1.8 mm longae.

A *P. prostrata* subsp. *prostrata* petiolis pilis tantum crispato-floccosis tenuibus vestitis (i.e. pilis rigidulis rectis nullis) differt. A *P. matsukana* (incl. *P. crebridens*), cui vestitu petiolorum in men-

tem revocat, foliolis angustioribus, dentibus eorum profundioribus, episepalis latioribus, stylis basi saepe magis intumescens et papillosus distat.

**Typus:** France, Hautes-Alpes: Le Lautaret, à Prime-Messe, *Faurie* s.n., 1909, PR.

***Potentilla prostrata* subsp. *ciscaspica* Soják, subsp. nov.**

Petoli tantum pilis crispato-floccosis vestiti. Foliola intermedia  $\pm$  elliptica (basi cuneata), dentibus utrinque (6-)7-8(-9) parvis densis (apice obtusis vel rotundatis). Episepala lanceolata vel oblonga, non linearia (in floribus inferioribus  $\pm$  1.5 mm, in supremis  $\pm$  0.8 mm lata). Petala  $\pm$  5.5 mm longa. Stylus basi leviter intumescens et  $\pm$  papillosus.

A *P. prostrata* subsp. *floccosa* foliolorum dentibus pluribus (non 3-6) brevioribusque differt. A *P. matsukana* subsp. *crebridentis*, cui habitu simillima, episepalis omnibus latioribus distat.

**Typus:** Daghestan: g. Bazardyuzi, v. 7-8 km yuzhn. s. Kurush, 3200 m, *Prima & Syunyakov* s.n., 1970, PR.

***Potentilla matsukana* Makino, Bot. Mag. Tokyo 16: 161. 1902. Neotypus:** Mt. Togakushi (Omoteyama), Prov. Shinano (= Pref. Nagano), Tadao Muzuno s.n., 1909, MAK 106 382!

***Potentilla matsukana* subsp. *matsukana***

***Potentilla matsukana* subsp. *hemicryophila* (Jurtz.) Soják, comb. nov.**

*Potentilla crebridentis* Juz. subsp. *hemicryophila* Jurtz., Arkt. Fl. SSSR 9/1: 318. 1984. **Holotypus:** Zhukova & Petrovsky 66-28, LE!

***Potentilla matsukana* subsp. *crebridentis* (Juz.) Soják, stat. nov.**

*Potentilla crebridentis* Juz., Bot. Mat. Gerb. Bot. Inst. Komar. Akad. Nauk SSSR 17: 218. 1955 — *P. nivea* var. *crebridentis* (Juz.) Malysch., Opred. Visokogor. Rast. Yuzhn. Sib. 169. 1968, comb. inval. **Holotypus:** Sukachev & Poplavskaya 579, LE!

***Potentilla nervosa* Juz., Fl. SSSR 10: 610. 1941. Typus:** Juzepczuk s.n., LE!

***Potentilla jezoensis* Soják, spec. nov.**

Caules 10-20 cm alti, ascendentes, interdum decumbentes, 1-2 mm crassi, superne vel a medio laxe ramosi, pilis floccosis tenerrimis tecti. Folia radicalia ternata. Stipulae in vivo ferrugineae; auriculae  $\pm$  5-10  $\times$  3-5 mm magnae, glandulis minutis et dorso pilis crispatis et rectiusculis obsitae. Petioli pilis omnibus tenerrimis floccosis tecti (pilis crassiusculis rectis nullis). Foliolum intermedium ambitu ellipticum vel obovatum, basi late cuneatum, sessile vel brevipetiolulatum, (1.5-)2.5-4.5  $\times$  (1.2-)1.5-2.5(-3) cm magnum, crenatum, crenis utrinque 5-8, ca. (1.5-)2-4(-5)  $\times$  (1.5-)2-4(-5) mm magnis, supra  $\pm$  viride, opacum, pilis haud longis rectiusculis appressis usque patentibus mediocriter densis (interdum item glandulis minutis) tectum, subtus albidum, pilis crispato-floccosis dense tomentosum (nervatura concolori). Folium caulinum 1(-2), bene evolutum, ternatum, sessile vel brevipetiolatum, stipulis magnis extus tomentosum, foliolis  $\pm$  1-2 cm longis, crenis utrinque 2-4. Inflorescentia 2-5-flora, insigniter laxa (i.e. pedicellis florum pseudoterminalem 1.5-3 cm, florum lateralium  $\pm$  3-6 cm longis). Episepala elliptica vel ovata, 3.5-6  $\times$  (1.3-)2-4 mm magna, pilis longis rectis et item brevibus rectis, curvatis vel crispatis (tum tomentum verum formantibus) vestita; sepala  $\pm$  triangularia, 4-6  $\times$  2-4 mm magna, pilis  $\pm$  rectis longis et item brevibus (et saepe glandulis minutis) induta. Petala lutea,  $\pm$  7 mm longa, sepalis longiora. Antherae 0.5-0.7 mm longae. Stylus basi modice sed distincte intumescens et papillis insignis ornatus, 1.6-1.8 mm longus. Nuculae maturae brunneae,  $\pm$  2 mm longae, leviter sculpturatae.

A *P. prostrata* (= *P. nivea* auct.) et *P. matsukana* (incl. *P. crebridentis*) episepalis latis (2-4 mm) ellipticis vel ovatis et stylis 1.6-1.8 mm longis differt. A speciebus *P. uniflorae* agg. petiolorum pilis omnibus floccosis tenerrimis (i.e. pilis rectis crassiusculis nullis) distinguitur.

**Typus:** Japonia, Yezo [Hokkaido]: prov. Ishikari, Mt. Yubari, Hara 337, 1933, LD.



## Key

- 1a. All (short and long) hairs on the petioles  $\pm$  straight ..... 2
- 1b. Petioles with long straight hairs and short, strongly flexuose (or crispate) hairs, or all hairs crispate-floccose ..... 5
- 2a. All petioles with long and numerous short hairs ..... 3
- 2b. At least some petioles with both long and sparse or lacking short hairs ..... 4
- 3a. Short petiole hairs (0.05-)0.1-0.2 mm long,  $\pm$  straight, patent.... **P. nivea** var. **nivea**
- 3b. Short petiole hairs (0.15-)0.2-0.3 mm long, curved or slightly flexuose, patent to sub-appressed ..... **P. nivea** var. **nipharga**
- 4a. Short petiole hairs  $\pm$  straight, patent, (0.05-)0.1-0.2 mm long; long petiole hairs usually stiffer and thicker ..... **P. nivea** var. **nivea**
- 4b. Short petiole hairs curved or slightly flexuose, subpatent (forward-pointing), about 0.2-0.3 mm long; long petiole hairs usually softer and thinner  
**P. prostrata** subsp. **chamissonis**
- 5a. Petioles exclusively with extremely thin, soft floccose or crispate hairs (thicker stiff  $\pm$  straight hairs lacking) ..... 6
- 5b. Petioles with thicker stiff long straight or flexuose hairs and thin soft short crispate or flexuose hairs ..... 11
- 6a. Epicalyx-segments  $\pm$  2-4 mm wide; styles 1.6-1.8 mm long ..... **P. jezoensis**
- 6b. Epicalyx segments narrower; styles shorter ..... 7
- 7a. Leaflets with 6-14 pairs of teeth ..... **P. matsuokana** subsp. **crebridens**
- 7b. Leaflets with 3-9 pairs of teeth ..... 8
- 8a. Styles (1.3-)1.4-1.6(-1.7) mm long ..... **P. matsuokana** subsp. **matsuokana**
- 8b. Styles (0.8-)1.0-1.2(-1.4) mm long ..... 9
- 9a. At least upper (i.e. younger) flowers with very narrow, linear epicalyx-segments; styles often not thickened at the base, and not papillose; leaflets broad, usually with short teeth  
**P. matsuokana** subsp. **hemicryophila**
- 9b. All flowers with epicalyx-segments oblong to lanceolate; styles slightly thickened and with small papillae at the base ..... 10
- 10a. Leaflets with (6-)7-8(-9) pairs of short teeth ..... **P. prostrata** subsp. **ciscaspica**
- 10b. Leaflets with 3-6(-7) pairs of longer teeth ..... **P. prostrata** subsp. **floccosa**
- 11a. Leaflets with 6-9(-12) pairs of teeth ..... **P. nervosa**
- 11b. Leaflets with 2-5(-7) pairs of teeth ..... 12
- 12a. All petioles with long  $\pm$  straight hairs and numerous short crispate or flexuose hairs  
**P. prostrata** subsp. **prostrata**
- 12b. Short crispate or flexuose hairs sparse or lacking at least on some petioles  
**P. prostrata** subsp. **chamissonis**



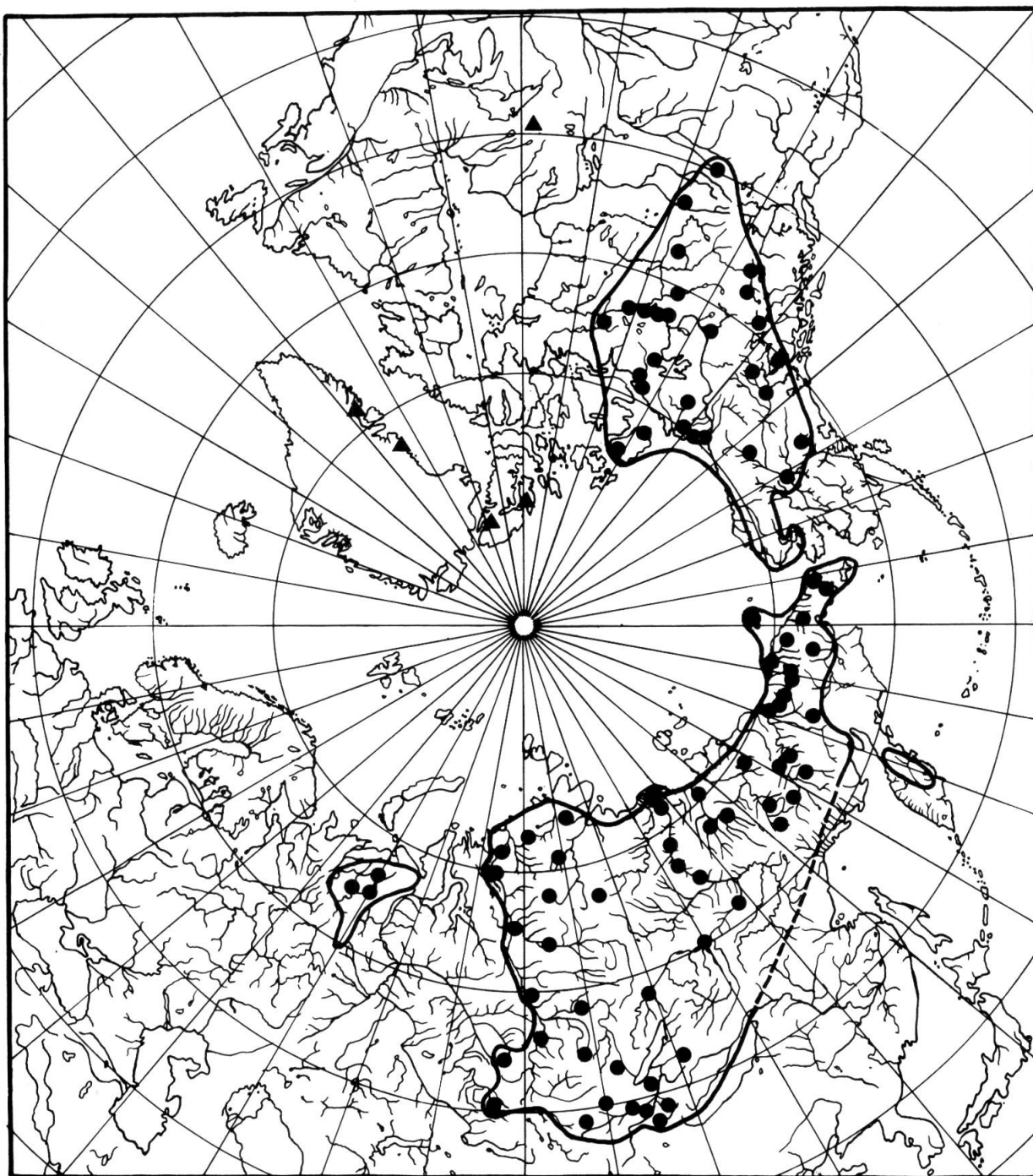


Fig. 1. — Distribution of *Potentilla nivea* L. non Hult. var. *nivea* (= *P. hookeriana* auct., *P. arenosa*).  
● herbarium specimens studied; ▲ localities of *P. nivea* var. *nipharga* outside the distribution range of *P. nivea* var. *nivea* (occurrence of *P. nivea* var. *nipharga* inside the range of *P. nivea* var. *nivea* is not included in the map).

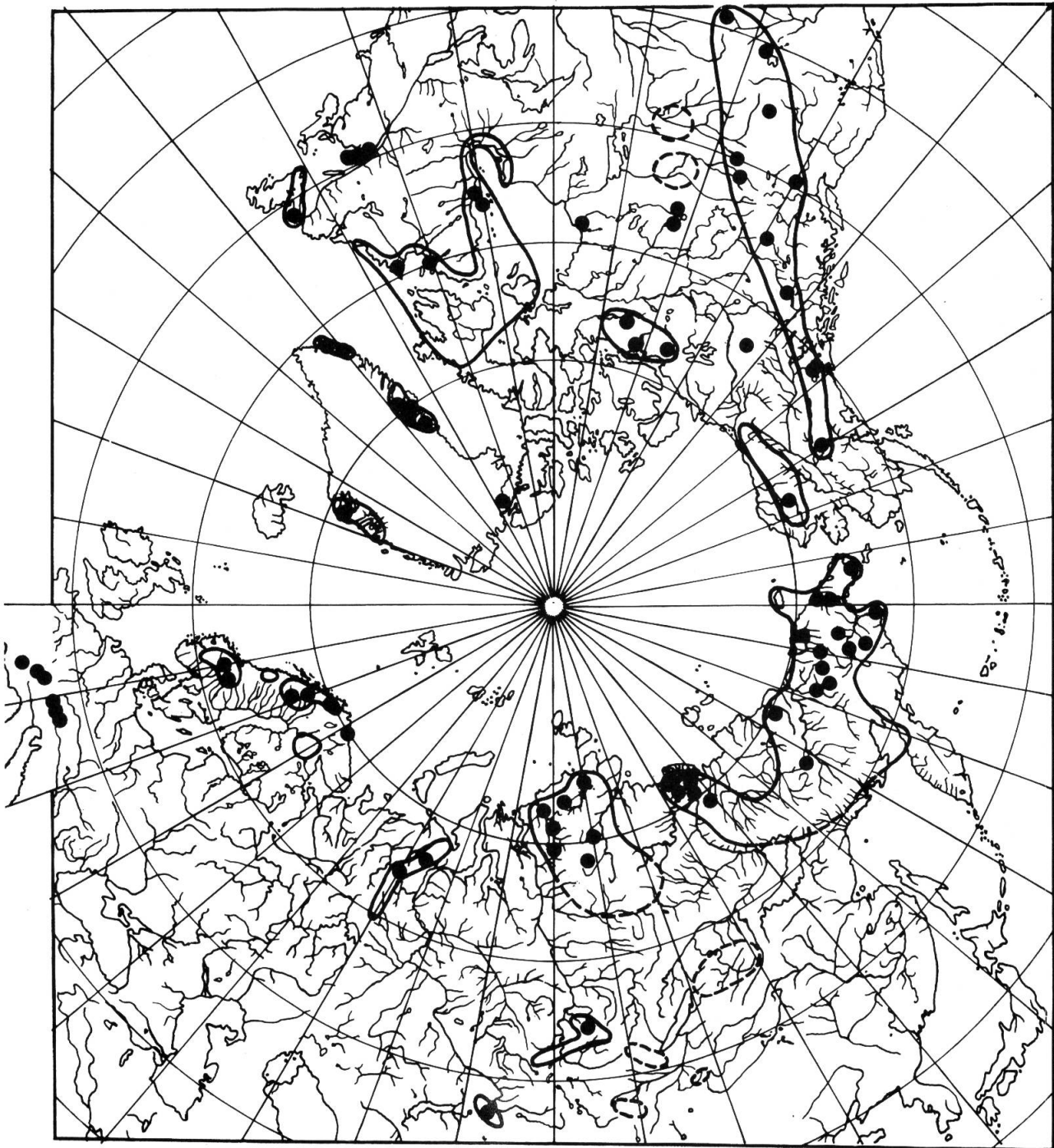


Fig. 2. — Overall distribution of *Potentilla prostrata* subsp. *floccosa* (= *P. nivea* auct.).

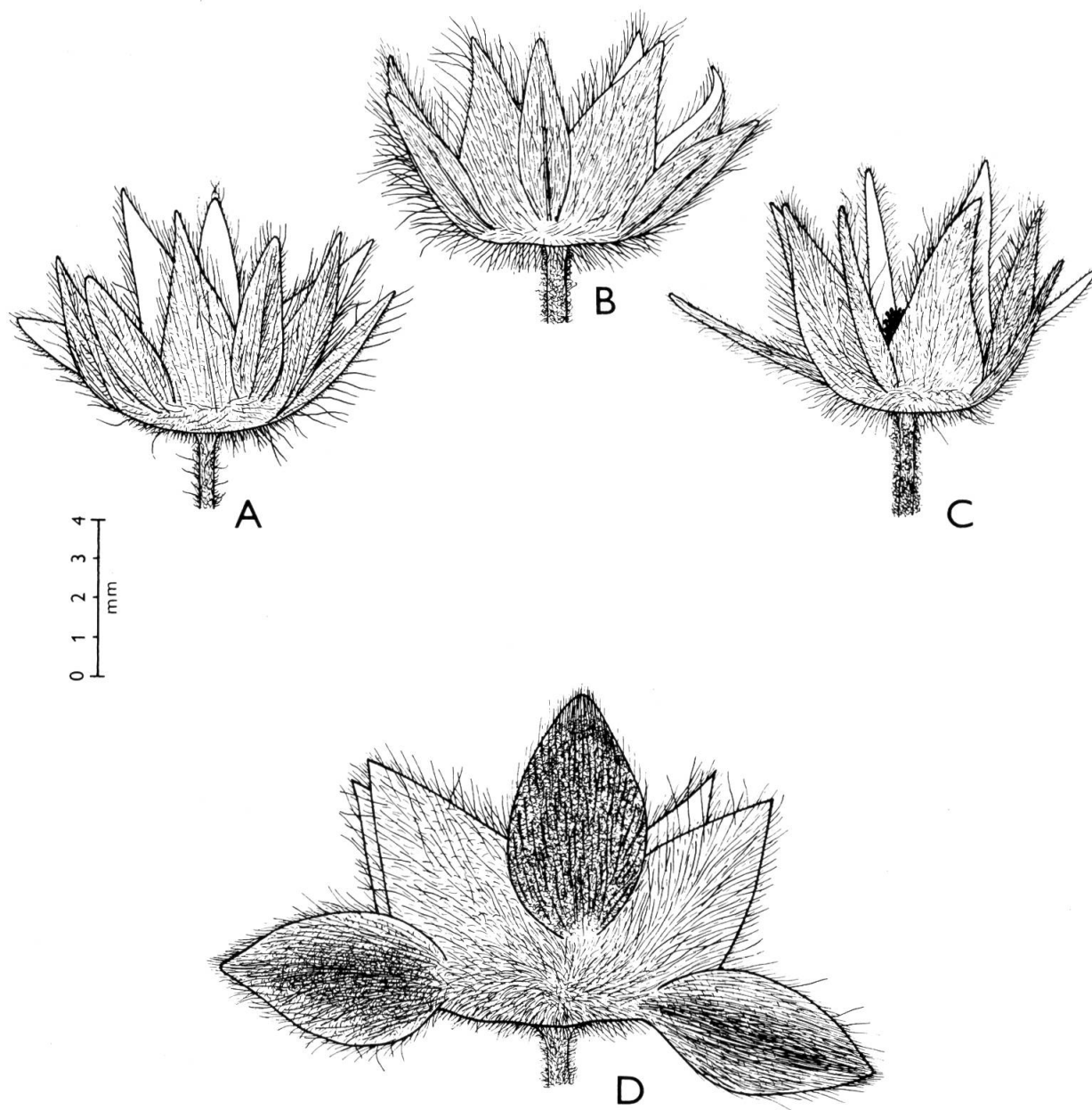


Fig. 3. — Calyx: **A**, *Potentilla nivea* L. non Hult. (= *P. hookeriana* auct., *P. arenosa*); **B**, *P. prostrata* subsp. *floccosa* (= *P. nivea* auct.); **C**, *P. matsukana* subsp. *crebridentis*; **D**, *P. jezoensis*.

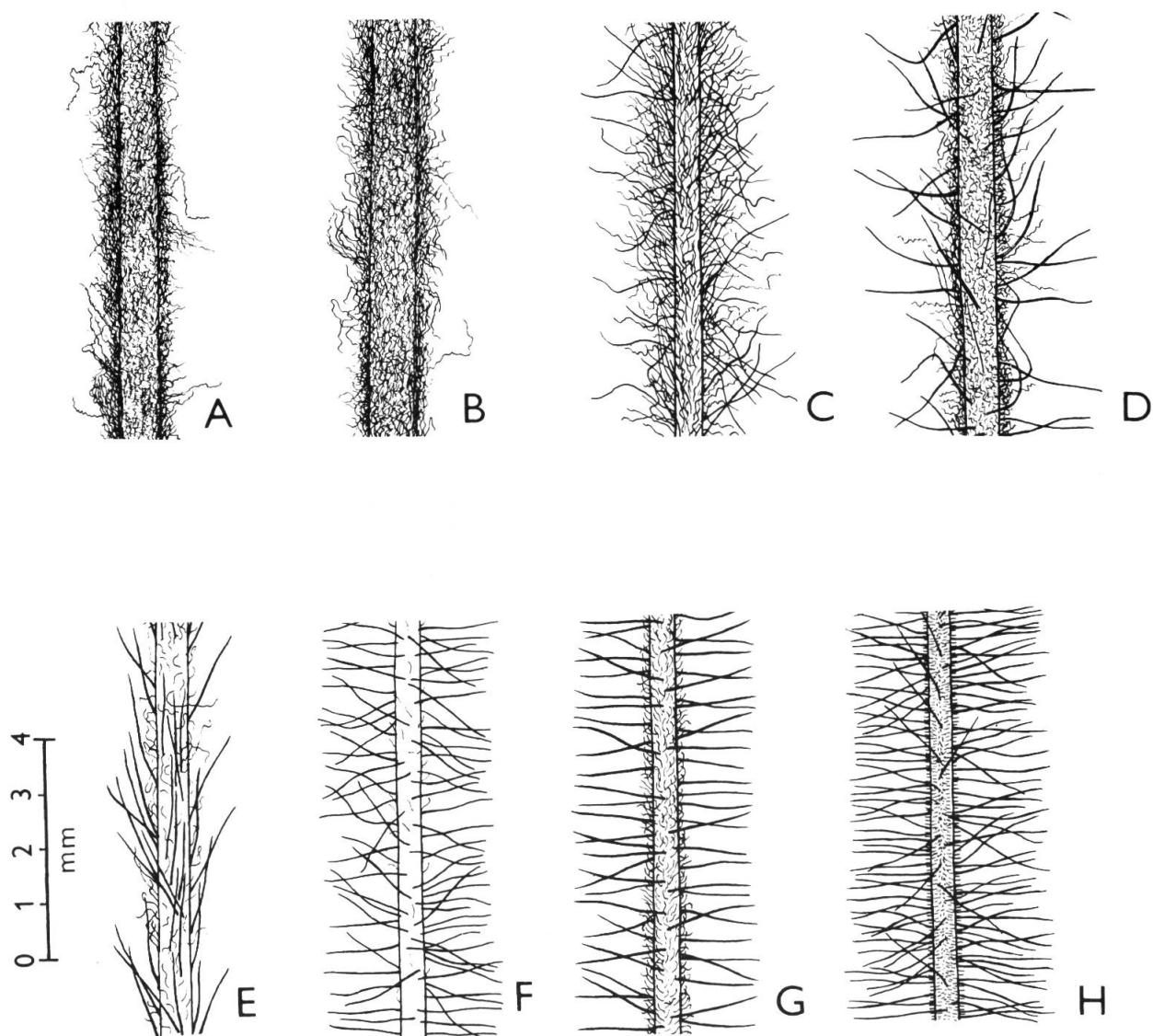


Fig. 4. — Indumentum of the petioles: **A**, *Potentilla matsukana* subsp. *crebridens*; **B**, *P. prostrata* subsp. *floccosa* (= *P. nivea* auct.); **C-D**, *P. prostrata* subsp. *prostrata*; **E-F**, *P. prostrata* subsp. *chamissonis*; **G**, *P. nivea* var. *nipharga*; **H**, *P. nivea* L. s. orig. var. *nivea* (= *P. hookeriana* auct., *P. arenosa*).

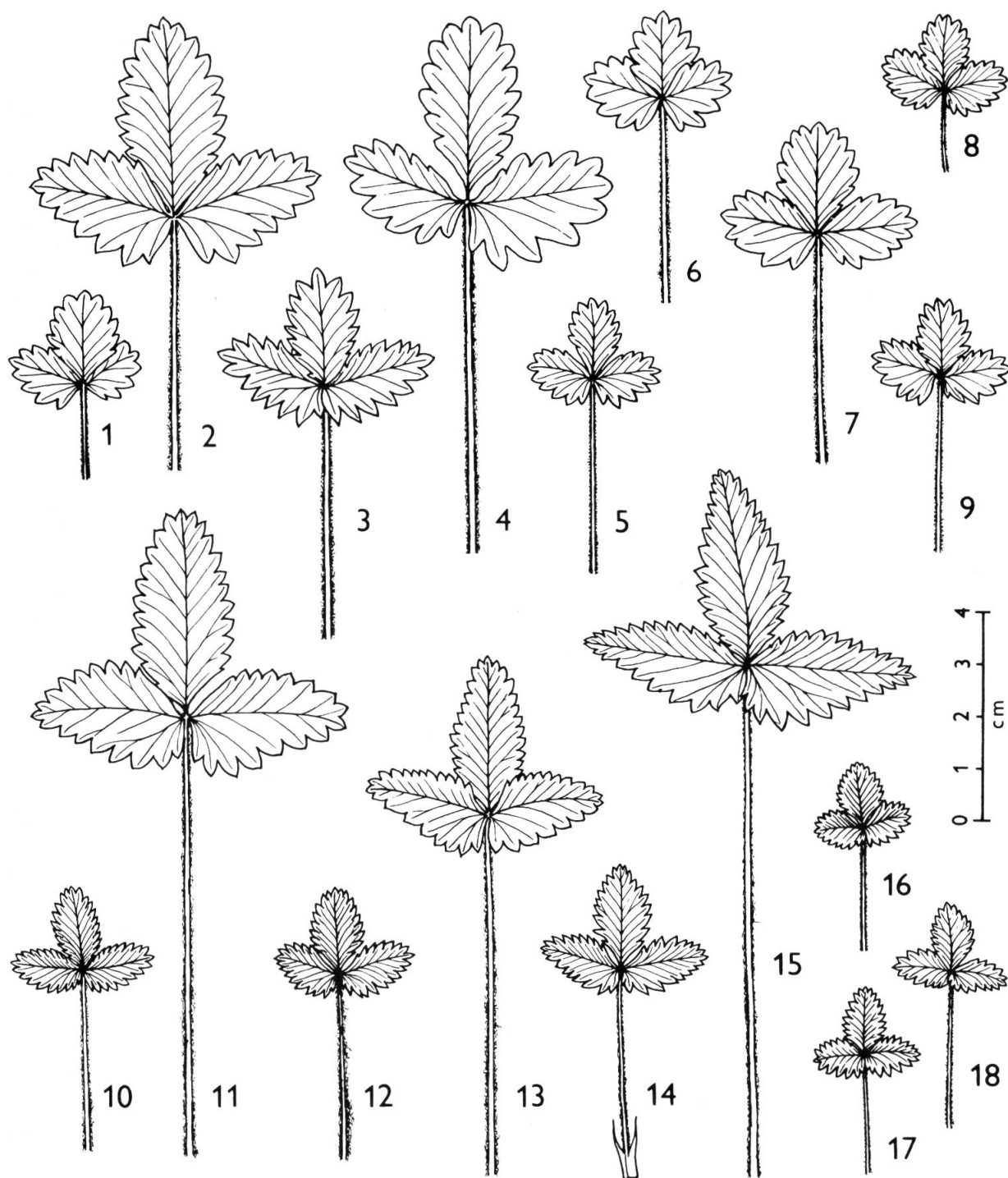


Fig. 5. — Basal leaves: 1-9, *Potentilla matsuokana* subsp. *matsumokana* (1, 3, 5-9, Japan; 2, 4, Soviet Far East); 10-18, *P. matsuokana* subsp. *crebridentis* (10, 11, 13, 15-18, Mongolia; 12, Baikal L.; 14, Shanxi, China).



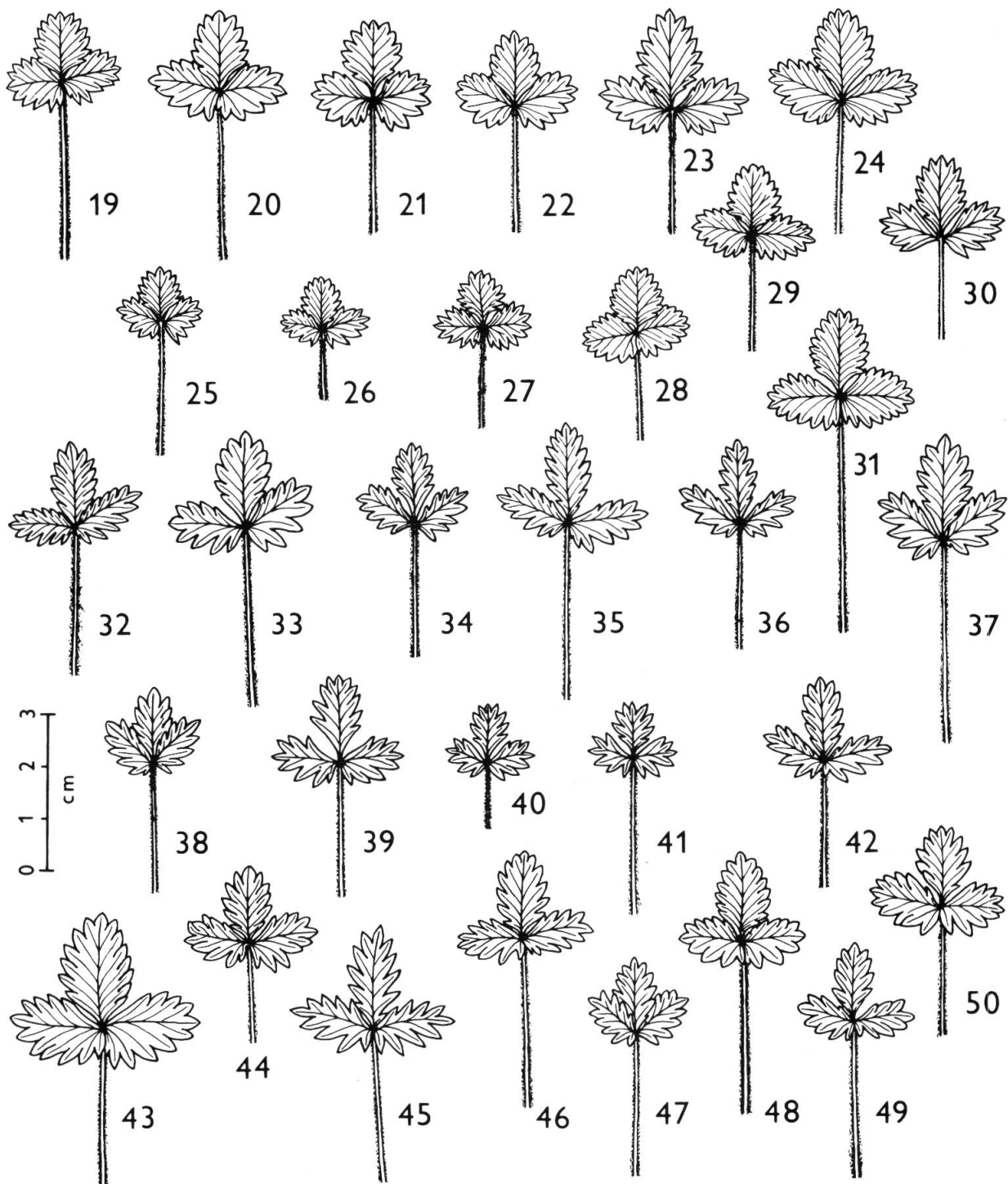


Fig. 6. — Basal leaves: 19-31, *Potentilla matsuoekana* subsp. *hemicryophila* (19, Yakutia; 20, 26, 27, Wrangel Isl.; 21-25, 28, Chukotka; 29-31, Alaska); 32-50, *P. prostrata* subsp. *floccosa* (32-37, the French Alps; 38-45, Tirolean Alps; 46-47, Sweden; 48-49, Norway; 50, E. Canada).

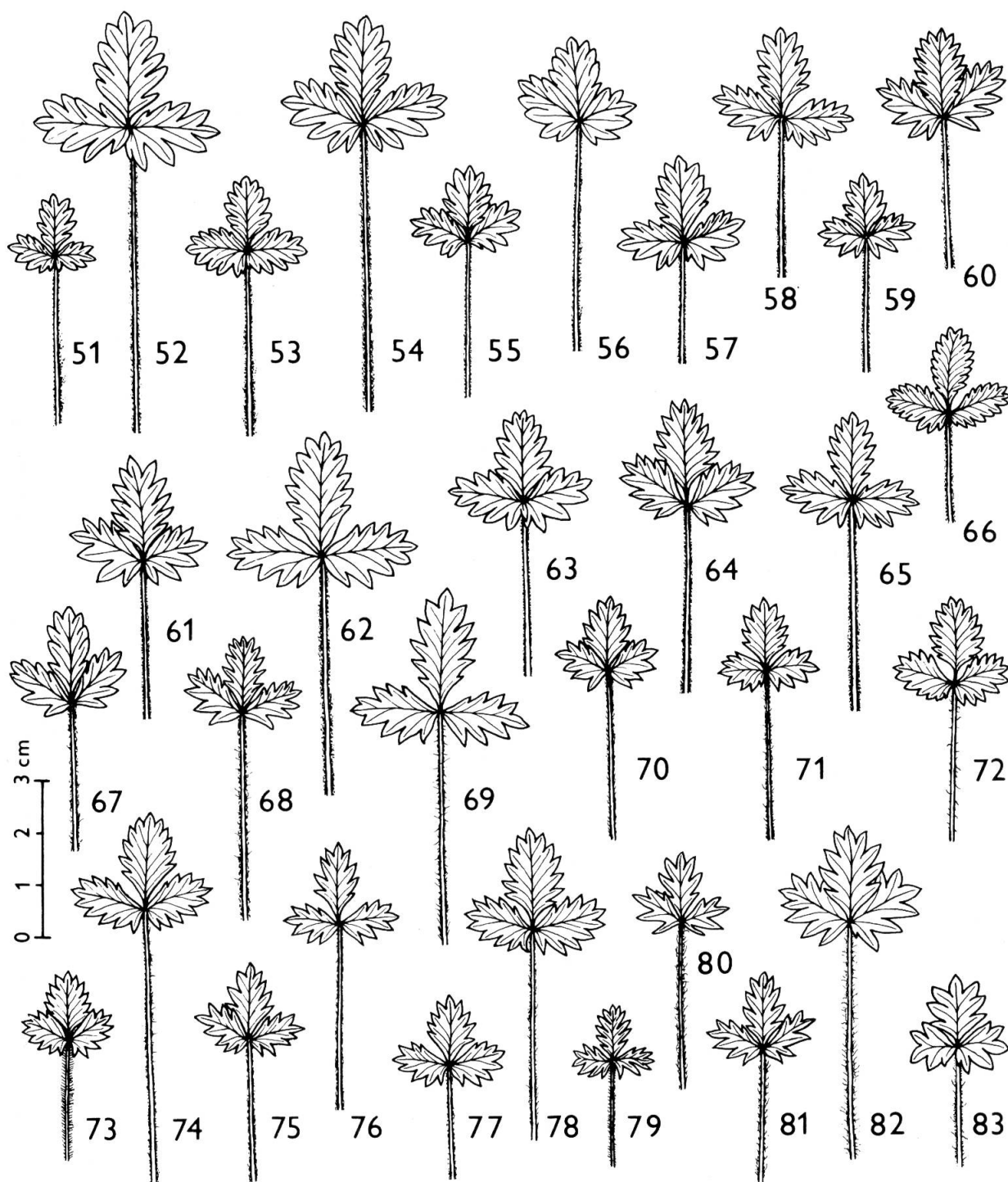


Fig. 7. — Basal leaves: 51-65, *Potentilla prostrata* subsp. *floccosa* (51-54, Norway; 55-62, Yakutia; 63-65, Chukotka); 66, *P. prostrata* subsp. *ciscaspica* (Caucasus); 67-83, *P. prostrata* subsp. *prostrata* (67-68, Chukotka; 69-78, Mongolia; 79-82, Sweden; 83, Greenland).

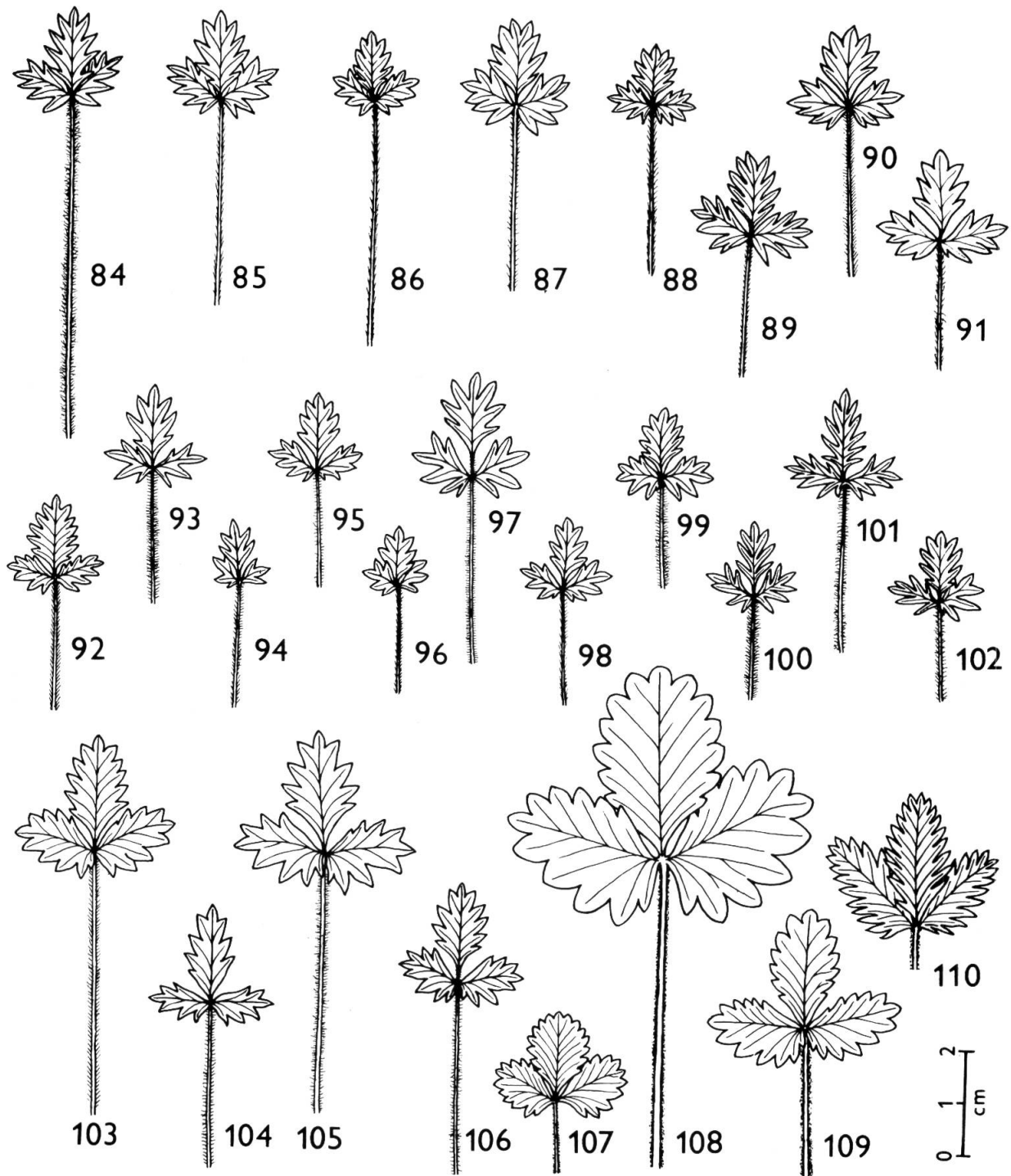


Fig. 8. — Basal leaves: **84-91**, *Potentilla prostrata* subsp. *chamissonis* (84-88, Sweden; 89, Svalbard; 90-91, Greenland); **92-106**, *P. nivea* L. non auct. = *P. hookeriana* auct. (92-94, 103, Yakutia; 95-102, Chukotka; 104-106, Mongolia); **107-109**, *P. jezoensis* (Japan); **110**, *P. nervosa* (Soviet Central Asia).

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