DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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THE GENUS *POTENTILLA* L. IN ESTONIA, LATVIA AND LITHUANIA: DISTRIBUTION, MORPHOLOGY AND TAXONOMY

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To the memory of Prof. Liivia-Maria Laasimer

CONTENTS

PREFACE

Estonia, Latvia and Lithuania occupy a position which appears not only politically but also floristically intermediate between the East and West: they are traversed by the borderline separating the eastern and western Baltic geobotanical provinces (Laasimer 1965, Ahti *et al.* 1968). Therefore about 1/4 of the Estonian spontaneous flora consists of the so-called margin species (Kask, Laasimer 1987). In larger genera of the Estonian flora (*Carex, Alchemilla, Taraxacum, Salix, Juncus*) the percentage of the species reaching their distribution margins is also about 20–25%, while in the genus *Potentilla* it is higher, nearly 40%.

It can be supposed that plants inhabiting central parts of their areal and those populating margin areas have a different morphology since the latter are exposed to more extreme habitat conditions, and therefore the possibility of differentiation of new taxa there can be greater (Grant 1981).

Besides, when considering also the well-known fact that many *Potentilla* species are apomictic, either obligatory or facultative, one can understand how interesting, challenging, and problematic and therefore worth studying this genus is.

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications, which are referred to in the text by their Roman numerals.

I Leht, M. 1989. The genus *Potentilla* L. in the Baltic republics. Leaf epidermis. — Proc. Estonian Acad. Sci. Biol. 38: 33–39 (in Russian, summary in English).

II Leht, M. 1990. The genus *Potentilla* L. in the Baltic republics. Pollen and seeds in SEM. — Proc. Estonian Acad. Sci. Biol. 39: 28–33 (in Russian, summary in English).

III Gudžinskas, Z. & Leht, M. 1991. New data on the *Potentilla* L. (*Rosaceae*) genus in the Lithuanian flora. — Ecology. The Lithuanian Academy of Sciences. 1: 106–116 (in Russian, summary in English).

IV Leht, M., Eglite, Z. & Lapele, M. 1996. *Potentilla* L. — In: Kuusk, V., Tabaka, L. & Jankevičienė, R. (eds.). Flora of the Baltic countries. Compendium of vascular plants. Tartu, Eesti Loodusfoto. 2: 68–79.

V Leht, M., Eglite, Z. & Lapele, M. 1996. *Comarum* L. — In: Kuusk, V., Tabaka, L. & Jankevičiene, R. (eds.). Flora of the Baltic countries. Compendium of vascular plants. Tartu, Eesti Loodusfoto. 2: 67–68.

VI Leht, M. 1996. Cladistic analysis of the data published in the "Monographie der Gattung Potentilla" by Th. Wolf. — Proc. Estonian Acad. Sci. Biol. 45: 171–180.

VII Leht, M. 1997. Distribution and nomenclature problems of the Baltic taxa of the genus *Potentilla* L. — Bothanica Lithuanica. Suppl. 1: 15–27.

VIII Leht, M. & Paal, J. Variation in *Potentilla* sect. *Aureae* Wolf in the Baltic states. — Nordic J. Bot. (accepted).

IX Leht, M. & Paal, J. 1997: Variation of *Potentilla erecta* (*Rosaceae*) in Estonia. — Ann. Bot. Fenn. 34: (accepted).

X Leht, M. & Paal, J. Variation of *Potentilla* L. sect. *Rivales* Wolf and the nearest taxa in the Baltic states — Folia geobot. et phytotax. (submitted).

XI Leht, M. & Reier, Ü. Chromosome number and sexual type of *Potentilla fruticosa* L. in Estonia and Latvia. — Acta. Bot. Fenn. (manuscript).

List of other relevant publications

Leht, M. 1984: Synonyms of Estonian cinquefoils (*Potentilla* L.). — In: Lekavičius, A. (ed.). Flora of the Baltic Countries and its history. Vilnius, pp. 81–84 (in Russian).

Leht, M. 1987. The genus *Potentilla* in the Baltic republics in connection with some taxonomical problems. — In: Laasimer, L. & Kull, T. (eds.). The Plant Cover of Estonian SSR. Flora, Vegetation and Ecology. Tallinn, pp. 123–132.

Leht, M. 1987. The genus *Potentilla* L. in the Baltic republics. — Proc. Estonian Acad. Sci. Biol. 36: 220–226 (in Russian, summary in English).

Leht, M. 1991. Micromorphological characters in the taxonomy of the Baltic genus *Potentilla* L. — Scripta Botanica 6: 150–164 (in Estonian, summary in English).

Leht, M. 1993. How to count species in the genus *Potentilla* L.? — Schola Biotheoretica 19: 15–21 (in Estonian).

Leht, M. 1994. *Potentilla erecta* Räusch. in Estonia. — Proceedings of XVII Estonian Naturalists' Congress. Tartu, pp. 89–96 (in Estonian).

Leht, M. 1994. Troublesome cinquefoils. — Lutukka 10: 72–76 (in Finnish, summary in English).

Leht M. 1995. Alpine taxa from g. *Potentilla* L. sect. *Aureae* Wolf. in Estonia, Latvia and Lithuania. — VI Intern. Symp. IOPB. Variation and Evolution in Arctic and Alpine Plants. Programme and Abstracts. Trømso, p. 48

Leht, M. & Paal, J. 1996. Morphometrics of Baltic taxa from g. *Potentilla* L. sect. *Aureae* Wolf on their areal bordeline. — Origin and Evolution. Abstracts. Fith Intern. Congress of Systematic and Evolutionary Biology. Budapest, p. 265.

1. INTRODUCTION

As currently understood, the genus *Potentilla* L. with its 400–500 species is one of the largest in the family *Rosaceae*. Its centre of variation is thought to be in the mountains of Central Asia (Shah *et al.* 1992), whence it has spread over the whole Northern hemisphere, with *P. anserina* reaching Australia, as well (Meusel *et al.* 1965).

The representatives of the genus *Potentilla* are highly polymorphic taxa as the genus is subject not only to phenotypic variation but also to interspecific hybridization. Several species were suspected to be of hybrid origin already by earlier researchers (Ascherson & Graebner 1900–1905, Wolf 1908 etc.).

By now it has become clear that interspecific hybridization and apomixis are common in the genus *Potentilla* (Ball *et al.* 1968). The occurrence of apospory (apomixis) was first mentioned in case of this genus by Forenbacher (1914), the phenomenon was demonstrated experimentally by Müntzing (1928). Being amphimictic in central parts of its areal, some species may be apomicitc at its edge (Müntzing 1958). Also species propagating both vegetatively with runners and generatively with seeds occur. In facultative apomicts, the choice between sexual and alternate reproductive behaviour depends on pollen: pollen from distant relatives increases the level of apomixis. However, ploidization or hybridization of apomicts can lead back to sexual reproduction (Richards 1994). Therefore, because of the parallel variation of characters and occurrence of reticulate evolution in the genus, it is useful to study the genus both with cladistic and phenetic methods.

The last taxonomist to deal with the whole genus was Theodore Wolf whose "Monographie der Gattung *Potentilla*" (1908) was based on about a hundred studies of earlier researchers; he recognized 305 species with 336 varieties and 294 forms. In his system the genus is subdivided into subgenera mostly on the basis of style characters.

Among recent researchers, only Jiří Soják has been consemed with the taxonomy of the whole genus with a special focus on the morphology of anthers (Soják 1985a). Owing to the growing popularity of DNA methods, taxonomists have again taken up research into the whole genus (Tørtsen Eriksson). Nowerdays taxonomists mostly deal either with some groups of taxa or some species (Bente Eriksen — sect. *Niveae*; Yrjö Vasari — *P. erecta*; Ove Eriksson — *P. anserina*, etc.), with species from a certain region (Vladimir Kurbatsky — Siberian *Potentillas*) or with special problems connected with Potentillas (Sven Asker, Svante Holm — apomixis, Romana Czapik — embryology, Valentina Czevtayeva — anatomy, etc.).

This thesis is based on papers devoted to *Potentilla* species growing in Estonia, Latvia and Lithuania: their morphology and anatomy, nomenclature problems, distribution and taxonomy of more common native taxa.

2. OBJECTIVES

1. To establish the taxonomic composition of the genus *Potentilla* in Estonia, Latvia and Lithuania as well as to establish the distribution of its taxa in the Baltics.

2. To find out new characters, useful for delimiting taxa in the genus *Potentilla*, in addition to traditional macromorphological characters used in descriptions already by Wolf.

3. To study the interspecific variation and structure of *Potentilla* species common in Estonia, Latvia and Lithuania with a special consideration of “margin” species.

4. To study intergeneric variation of the genus *Potentilla* as well as the ranks of taxa and relationships between them.

5. To determine the chromosome numbers of Estonian *Potentilla* species.

3. MATERIAL AND METHODS

The material studied was collected mostly in 1983–1988 and 1996; herbarium specimens from the Herbarium of the Institute of Zoology and Botany (TAA), University of Tartu (TU) and University of Helsinki (H) were also used.

Macromorphological characters were measured on air-dry herbarium material with a binocular microscope MBS-2 or a ruler.

For studying **micromorphological characters**, herbarium material or material fixed with FAA (formalin, alcohol, acetic acid) were used. Slides were investigated with a Carl Zeiss Jena microscope "Ergaval" (16 × 40).

For studying the **surface** of leaves, pollen grains and seeds with scanning electron microscope (Tesla BS 301), air-dry or dried at critical point material was used.

The material collected is preserved in TAA.

Data processing

For **phenetic analysis**, data were standardized and Ward's clustering method with the Manhattan distance as a resemblance measure was used. For further optimization of the classification by k-means clustering, the result served as the initial group membership vector. Cluster analysis was performed by SYN-TAX 5.0 program package (Podani 1993).

Principal components analysis was used for the ordination of ln-transformed data (CANOCO package, version 3.1; Ter Braak, 1990, and CANODRAW package, version 3.0; Smilauer, 1992).

To calculate means and standard errors, and to estimate the importance of characters within clusters on the basis of variation analysis, the SAS program package (SAS Institute Inc. 1994) was employed.

The adjacency and distinctness of clusters were calculated with the SYN-CONT program (compiled by J. Paal, S. Kolodyazhnyi and A. Kink).

Cladistic analysis was made with PAUP ver. 3.1.1. (Swofford 1993).

4. RESULTS

4.1. Distribution (papers III, IV, V, VII)

Genus *Potentilla* L. (*Rosaceae*) is represented by 24 species in three Baltic countries: 18 in Estonia, 22 in Latvia and 19 in Lithuania. 60% of the species reach their areal border here, and only in case of five species (*P. argentea* L., *P. erecta* Räusch., *P. anserina* L., *P. norvegica* L., *P. palustris* (L.) Scop.), their Baltic localities lie in the central part of the distribution area.

Seven species of Baltic cinquefoils are rather rare adventives with a different distribution pattern in each of the three countries (VII). The most recent newcomers, *P. multifida* L. and *P. longifolia* Willd., were found in Lithuania in 1988 and 1989, respectively (III). Nowerdays *P. bifurca* L. and *P. supina* L. grow in several places in Latvia and Lithuania; however, Estonian herbaria supply only with old data and specimens from the 1930ies. *P. goldbachii* Rupr. is known already for many years from Estonia and Latvia, whereas in Lithuania it was first found only in 1989 (III). *P. recta* L. is an old rare adventive which is now expanding in all three Baltic countries. The most confusing adventive species in the Baltics, *P. canescens* Bess., reached Estonia and Lithuania in the 1950ies but is still lacking (or not yet found) in Latvia.

Of spontaneous species, the most common in highly different habitats is *P. anserina*. *P. argentea* can be found growing abundantly on dry mineral soils over the whole territory. *P. erecta* is a very usual species both on moist mineral and peaty soils, while *P. norvegica* is quite usual. *P. palustris* occurs nearly everywhere on swampy soils. Growing in various habitats *P. reptans* L., is frequent in West Estonia, rare in its eastern part and rather frequent in Latvia and Lithuania. *P. heidenreichii* Zimm. is found locally in all three countries on meadows, grasslands, roadsides and ruderal places, whereas *P. intermedia* L. s. str., which grows in similar habitats, is met with in very few localities only (IV, V).

The most interesting distribution pattern among Baltic cinquefoils is observed in case of the *P. verna* group from the sect. *Aureae*, all species of which populate open habitats on shallow soils, mostly alvars (VII). *P. crantzii* (Crantz) Beck is usual in Estonia, very rare in Latvia and absent from Lithuania. *P. neumanniana* Rchb. occurs only in West and North-West Estonia, *P. subarenaria* Borb. in West and North-West Estonia and in Central Latvia. *P. arenaria* Borkh., which is lacking in Estonia, grows abundantly in Central Latvia on sandy banks of the River Daugava and even more abundantly in similar habitatas in Lithuania. *P. subarenaria* (*P. arenaria* × *P. neumanniana*) does not occur together with either of its parents: in Estonia it sometimes grows densely together with *P. neumanniana*, while its Latvian localities lie close to the habitatas of *P. arenaria*. Unfortunately, earlier floristic literature (Vilberg 1925, Enari *et al.* 1943) evidently contains some misinterpretation regarding the taxon, as *P. arenaria* was claimed to occur in Estonia. These incorrect data have reached the maps of Hultén (1950) and Hultén and Fries (1986), too.

The only Baltic representatives of the *P. collina* group, *P. silesiaca* Uechtr., *P. thyrsiflora* Hülsen and *P. leucopolitana* J. M. Müller, are found very locally in Latvia and Lithuania; in Estonia they have not yet been encountered. These species are inhabitants of dry, poor, mostly sandy, soils (IV).

P. anglica Laich. was refound, after a nearly hundred-year gap, near Riga, Latvia, in 1988 (III). There exist very old literature data on its occurrence in Estonia too, but with no herbarium material available, these data cannot be accepted. However, there exist herbarium specimens from the 1930ies with *P.* × *mixta* and *P.* × *italica* (putative hybrids of *P. erecta*, *P. reptans* and *P. anglica*) from five Estonian localities (identifications were confirmed by Prof. Romana Czapik). In July 1997, *P.* × *mixta* was refound from one of the localities.

P. fruticosa L. s. str. is the only shrubby *Potentilla* in the Baltic area. It is growing in North-West Estonia and in Central Latvia on shallow soils on alvars and in juniper shrubs (IV).

4.2. Nomenclature problems of Baltic *Potentilla* species (papers IV, VII)

Among cinquefoils (*Potentilla* L.) growing in Estonia, Latvia and Lithuania, *P. intermedia* L., *P. heidenreichii* Zimm. and *P. canescens* Bess. have been the most confusing for local botanists. While the other Baltic *Potentilla* species have not given rise to nomenclature problems, these three have been troublesome for taxonomists in other regions as well (VII).

P. intermedia was described as early as 1767; in 1860 Ruprecht separated from it *P. intermedia* β. *canescens* Rupr. which in 1870 was assigned the rank of a species and named *P. digitato-flabellata* Heidenr. by F. A. Heidenreich. Since the same name had been used for another taxon (*P. digitato-flabellata* Braun), Alber Zimmeter renamed the taxon *P. heidenreichii* Zimm. in 1884 which is now the valid name (Leht 1994).

P. intermedia and *P. heidenreichii* are considered to be separate species by several authors (Juzepczuk 1941, Stankov & Taliev 1949, Galenieks 1957, Eichwald 1962, Sergievskaya 1981, Natkevičaitė-Ivanauskienė 1971, Kobeleva 1976 etc.), whereas some do not recognize *P. heidenreichii* as a taxon at all (Ball *et al.* 1968, Garcke 1972, Rothmahler 1976, etc.). *P. heidenreichii* has also been treated as a subspecies or a variety of *P. intermedia* (Ruprecht 1860, Wolf 1908, Syreischikov 1907, Hegi 1922–1923, Hiitonen 1934, Maevsky 1954, Raciborski *et al.* 1955, etc.).

The different taxonomic viewpoints concerning *P. intermedia* and *P. heidenreichii* are related to problems of distinguishing between *P. heidenreichii* and *P. canescens*, as well as to errors in their nomenclature that are mostly mistakes in the use of their synonyms (IV).

The two best-known synonyms of *P. canescens* are *P. inclinata* Vill. and *P. adscendens* Walst. & Kit. However, not all taxonomists have regarded them as full synonyms (Zimmeter 1884, Juzepczuk 1941, Czerepanov 1973, Dostal 1982). All three names can be encounted in older Baltic floristic literature but in the sense of *P. heidenreichii* (Glehn 1860, Lehmann 1895, Vilberg 1925, etc.): the descriptions added to the floristic lists correspond to *P. heidenreichii*. Also, older sheets of Estonian herbaria display several specimens of *P. heidenreichii* labelled as *P. inclinata* or *P. adscendens*.

Therefore, although *P. inclinata* and *P. adscendens* are older synonyms, it would be better to use the name *P. canescens* Bess., since the other names have been involved in too much confusion. It seems that the real *P. canescens* reached Estonia and Latvia in the middle of this century, as the first herbarium specimens were collected in the 1950ies. All earlier hints to the occurrence of *P. canescens* in Estonia are mistakes and should be ascribed to *P. heidenreichii* (IV, VII).

4.2.1. List of the Baltic genus *Potentilla* L.

In comparison with some of my earlier articles and also with the “Flora of the Baltic Countries” Vol. 2, the use of synonyms and the taxonomic ranks of some taxa in the “Key-book of Estonian Vascular Plants” (ed. M. Leht, in print) as well as in the “List of Estonian Plants” (compiled by T. Kukk, in print) will be somewhat different. Therefore the list of the Baltic gen. *Potentilla* as currently recognized will be given. For some more profoundly studied species also varities are listed.

List of the Baltic genus *Potentilla*

Sect. Fruticosae Th. Wolf
    1. P. fruticosa L. s. str.
Sect. Bifurcae Th. Wolf
    2. P. bifurca L.
Sect. Anserinae Th. Wolf
    3. P. anserina L.
        ssp. anserina
            var. anserina
            var. sericea Hayne

Sect. Palustres Th. Wolf
    4. P. palustris (L.) Scop.
Sect. Multifidae Rydb.
    5. P. multifida L.
Sect. Argenteae Th. Wolf
    6. P. argentea L.
        ssp. argentea
            var. argentea
            var. decumbens (Jord.) Focke
            var. demissa (Jord.) Lehm.
            var. grandiceps (Zimm.) Roy & Cam
            var. tenerrima (Vel.) Th. Wolf
        ssp. impolita = var. incanescens Focke
    7. P. leucopolitana J. M. Mueller
    8. P. silesiaca Uechtr.
    9. P. thyrsiflora Hülsen
Sect. Tanacetifoliae Th. Wolf
    10. P. longifolia Willd.
Sect. Rivales Th. Wolf
    11. P. supina L.
    12. P. norvegica L.
    13. P. heidenreichii Zimm.
    14. P. intermedia L.
    15. P. canescens Bess.
Sect. Rectae Th. Wolf
    16. P. recta L.
Sect. Chrysanthae Th. Wolf
    17. P. goldbachii Rupr.
Sect. Aureae Th. Wolf
    18. P. crantzii (Crantz) Beck
    19. P. neumanniana Rchb.
    20. P. arenaria Borkh.
    21. P. subarenaria Borbas
Sect. Tormentillae Rydb.
    22. P. erecta (L.) Räusch.
        var. erecta
        var. strictissima (Zimm.) Hegi
    23. P. anglica Laich.
    24. P. reptans L.
    P. × mixta
    P. × italica

4.3. Surface of epidermis, pollen and seeds (papers I, II)

The leaf surface of *Potentilla* is covered with simple and glandular hairs. Unicellular trichomes of different length and diameter have a smooth, wavy or tuberculate surface, the surface of multicellular stellate hairs is smooth. Glandular hairs of the Baltic *Potentilla* species have in most cases a similar structure, only the shape of the glandular hair's head of *P. crantzii* and *P. reptans* is different, being wider and shorter (I).

The type of trichomes is thought to be a very good character for identifying taxonomically complicated taxa (Aneli 1976, Edmonds 1982). *P. argentea* and *P. impolita* have been described as species mostly on the basis of their hairiness density. However, as their trichomes are exactly of the same type, and as the density of hairs is a very variable character (Rousi 1965), there is no ground for separating them as different species, at least on the basis of hairiness characters.

The study of the hairs of *P. arenaria, P. neumanniana* and *P. subarenaria* confirms the hybrid origin of the last species. *P. arenaria* has only stellate hairs with 15 to 40 branches; *P. neumanniana* has only straight unicellular hairs; the hair cover of *P. subarenaria* is intermediate, with straight unicellular hairs and stellate hairs having fewer (3–10) branches.

Most of the stomata of *Potentilla* are anomocytic and differ only in their size: the smallest are found in *P. silesiaca*, the largest in *P. neumanniana* and *P. norvegica*. Among anomocytic stomata another type was found — nearly all Baltic species have also some hemiparacytic stomata (stomata with one subsidiary cell). In the epidermis of *P. neumanniana* and *P. norvegica* some contiguous stomata were found as well (I).

Pollen morphology is a useful tool in verifying species identifications based on macromorphological features (Hebda *et al.* 1988), and the study of exine sculpturing with SEM is considered a powerful criterion at the interspecific level (Weber-El Ghobhary 1986). However, these aids do not work in case of all plant species, e.g. Edmonds (1984) failed to demonstrate the occurrence of exine patterns which could be of practical taxonomic use in differentiating between the species belonging to the g. *Solanum* sect. *Solanum.*

This is namely the case with *Potentilla*; the pollen of the studied cinquefoils is monomorphic: their grains are isopolar, tricolpate, the exine is meridionally striped (II).

In addition to *Potentilla* pollen grains, also pollen from seven closely related genera of the subfam. *Rosoideae* was studied comparatively using SEM.

The pollen grains of the genera *Geum* and *Fragaria*, which belong to the tribe *Potentilleae*, are very similar to the grains of the genus *Potentilla.* The genus *Rubus* has also been included in the tribe *Potentilleae*, but its pollen and fruits are so different from those of the other genera that it should form a tribe of its own.

Heteromorphism of pollen grains in the tribe *Sanguisorbeae* indicates that this tribe is not a natural taxon but a combined one: the pollen surface of *Alchemilla* is papillate, that of *Agrimonia* is covered with whitled stripes, that of *Sanguisorba* is slightly granulous and sixcolpate, and that of *Poterium* nearly noncolpate with stripes and rows of very small papillae (II).

Subgenera in the genus *Potentilla* are mostly based on the structure of styles. As pollen grains are monomorphic, the question arises whether differences in the form and position of the style are taxonomically so important that subgenera should be distinguished on this basis: hybridization is not prevented by differences in style morphology.

However, the study of **seed morphology** reveals some differences between subgenera: in the subgen. *Hypargyrium* seeds are small (about 1 mm long), in the subgen. *Dynamidium* they are about 1.5 mm long, and seeds of *P. anserina*, the only Baltic representative of the subgen. *Chenopotentilla*, are about 2 mm long. The sculpture of the seedcoat is also different: in the subgen. *Hypargyrium* the network pattern is formed by clear cell wall lines, in the subgen. *Dynamidium* the network is formed of emerged cell edges, the surface of cells being flat, in *P. anserina* it resembles parchment.

4.4. Taxonomic analysis of Baltic *Potentilla* taxa

The following chapters are devoted to more variable and problematic species in the Baltics, including all Baltic representatives of the sections *Aureae*, *Argenteae* and *Rivales*, *P. erecta* from the sect. *Tormentillae*, as well as our only shrubby cinquefoil *P. fruticosa*. Adventive taxa were not studied in detail because of the scantiness of available material, as was also the case with *P. anglica* (sect. *Tormentillae*). *P. anserina* was not considered as it was very thoroughly studied by Rousi (1965), and *P. palustris* was excluded because it appeared quite monomorphic. The distribution of *P. mixta* and *P. italica* needs to be checked and more material gathered in order to study these species together with *P. reptans*.

4.4.1. Section *Aureae* Wolf (papers IV, VIII)

All four Baltic representatives of the genus *Potentilla* L. section *Aureae* Wolf, *P. neumanniana* Rchb. (*P. tabernaemontani* Ascher.), *P. arenaria* Borkh., *P. subarenaria* Borb. and *P. crantzii* (Crantz.) Beck (IV), are morphologically as well as cytologically polymorphic. Wolf (1908), for example, has divided *P. crantzii* into 15 varieties and 6 forms, *P. tabernaemonatni* into 10 varieties and 27 forms and *P. arenaria* into 12 forms, using only macromorphological characters.

Smith (1963a, b), studying British material, has stated that *P. crantzii* is relatively homogenous containing both hexaploids and heptaploids, whereas *P. neumanniana* is both cytologically and morphologically more variable.

According to Asker (1986), *P. crantzii* is apomictic in Sweden. Although there occurs distinct morphological variation even between adjacent sites, it is doubtful if the Swedish material ought to be divided into different subtaxa. *P. neumanniana* is extremely variable on Gotland (Asker 1985), from where Johansson (1905) described five different taxa, whereas in the neigbouring parts of Sweden its variation is smaller. In the Nordic countries the species is apomictic as is *P. arenaria*. In Central Europe, howevr, sexual populations of *P. arenaria*, *P. neumanniana* and *P. crantzii* have been found (Czapik 1962).

In the Baltic region where the taxa reach their distribution boundaries the species are significantly distinct, including *P. subarenaria* which is certainly a species of a hybrid origin. At the same time, the species are morphologically quite varyable: it is possible to establish subclusters (morphotypes) which, too, are in most cases distinct (VIII).

The most important characters in distinguishing clusters are those pertaining to the epidermis: characters of stellate hairs and glandular hairs and the number of cells. Macromorphological characters (incl. those used by Wolf in his species descriptions) appeared less important than micromorphological characters, the most useful among the former being the length of sepals and stipules and the number of teeth.

P. subarenaria was divided into two clusters, one of which resembles more one parent species, *P. neumanniana*, the other is closer to the other parent, *P. arenaria*. So *P. subarenaria* occupies a linking position between these two species, and there is no sense in attempting to divide it.

P. crantzii is morphologically the most different of the four, although its clusters resemble to some extent *P. neumanniana*. The morphs of *P. crantzii* are mostly adjacent to each other in the multidimensional character space. Chromosome numbers have been counted for three populations with only 2n=42 being identified, which points to the possibility of the existence of apomixis, in this case, too, and makes it complicated to establish the taxonomic rank of the morphs.

P. neumanniana is the most varyable species of the four though not so varyiable as it is on Gotland. Morphs of *P. neumanniana* certainly need to be studied more in detail in order to judge of their taxonomic rank, as far as use of morphological characters only seems to be insufficient. The varieties established by Wolf did not agree very well with our material; however, it can be admitted that his var. *typica, neumanniana, longipes* and *ballotii* are prevailing in Estonia.

The only chromosome number identified up to now is 2n=42, which idicates the existence of apomixis in this species, as well (VIII).

4.4.2. Section *Rivales* Wolf and section *Argenteae* Wolf (papers X, VI)

Potentilla L. section *Rivales* Wolf is represented by four species in the Baltic states: *P. supina* L., *P. norvegica* L., *P. intermedia* L. and *P. heidenreichii* Zimm.

Taxonomically, the nearest species to sect. *Rivales* in the Baltics are rare adventives *P. canescens* Bess. (sect. *Argenteae* Wolf), *P. recta* L. (sect. *Rectae* Wolf) and *P. goldbachii* (sect. *Chrysanthae* Wolf), as well as two native species, *P. argentea* L. s.l. and *P. collina* Wib. from the section *Argenteae* Wolf.

P. intermedia s.l. is supposed to be a stable hybrid of *P. argentea* s.l. ($2n=28$, 42) and *P. norvegica* ($2n=70$) (Janchen 1957). After establishing $2n=56$ for *P. intermedia* s.l., Skalinska and Czapik (1958) suggested that *P. intermedia* s.l. has arisen with the involvment of only hexaploid *P. argentea*. However, polyploids of the genus *Potentilla* are in general apomictic, just as is the case with *P. norvegica* (Asker 1970a, b). And also it is difficult to explain the origin of the tetraploid *P. intermedia* ($2n=28$) from *P. norvegica* because of its high chromosome number. Asker (1970a) suggests that *P. intermedia* consists of apomictic biotypes which have resulted from crosses between *P. argentea* and *P. norvegica*, or perhaps even between other members of the sections *Argenteae* and *Rivales*; the origin of *P. intermedia* s.l. remains to be tested experimentally.

In Wolf's system (1908) *P. canescens* Bess. belongs to the sect. *Argenteae*, however when characters from Wolf's descriptions were used for cladistic analysis (VI), *P. canescens* was placed much closer to the representatives of the sect. *Rivales* and *Rectae*.

When tracing connections between *P. argentea*, *P. heidenreichii* and *P. canescens* according to cluster analysis, *P. canescens* stands nearer to *P. heidenreichii* than to *P. argentea*. *P. canescens* appeared adjacent to and indistinct with only one small *P. argentea* subcluster. *P. collina*, the other representative of the sect. *Argenteae*, is not connected with *P. canescens* at all. At the same time, *P. canescens* is mainly adjacent to *P. heidenreichii* from the sect. *Rivales* (X).

In Wolf's (1908) system, *P. canescens* does not belong to the same section as *P. heidenreichii*, *P. norvegica* and *P. supina*. In fact, it is much nearer to these species than *P. recta* and *P. goldbachii* are, since *P. canescens* specimens do not form a separate cluster as *P. recta* and *P. goldbachii* do, but belong to mixed clusters together with specimens of *P. heidenreichii*, *P. norvegica* and *P. supina*. Therefore, *P. canescens* cannot be placed taxonomically as far from *P. heidenreichii*, *P. norvegica* and *P. supina* as *P. recta* and *P. goldbachii* are stand (i.e. not into a separate section). More likely, *P. canescens* belongs to the same section (sect. *Rivales*) as these three species do. The closeness of *P. canescens* to this section is well demonstrated by the indistinctness of its species-cluster with *P. heidenreichii* and *P. norvegica* as well as by its adjacency to these clusters (X).

In *P. argentea* s.l. material, *P. impolita*, *P. argentea* var. *argentea*, var. *decumbens*, var. *demissa*, var. *grandiceps* and var. *tenerrima* were identified. Hence, differences between these taxa are very small, and all six clusters obtained are mixed clusters containing specimens from 3–5 varieties. The specimens of *P. collina*, which is a very close relative of *P. argentea* s.l., stand in a separate cluster, which indicates a greater difference between *P. collina* and *P. argentea* than there is between the varieties of *P. argentea.*

P. impolita specimens did not cluster into a separate group as the "model" species *P. collina, P. canescens* and *P. heidenreichii* did, but formed mixed clusters with different varieties of *P. argentea.* Therefore, *P. impolita* is not worthy of the rank of either the species or evidently that of the subspecies, even on the basis of morphological characters, and should be referred to as a variety of *P. argentea* (X).

Asker (1986) suggests that the diploid chromosomal type (*P. argentea* s. str.) is more common in the north and the hexaploid (*P. impolita*) in the south, and that the two types come into contact in the southern part of the Scandinavian Peninsula. No strict correlation has been found between the ploidy level and morphological characters in *P. argentea* s.l. (Holm 1996). Although very few chromosome counts have so far been made on Estonian material, different numbers (2n=14, 28, 42) have been established. When identified only on the basis of morphological characters, *P. argentea* s.str. is more common in Estonia, Latvia and Lithuania; however, there occur intermediates and often also mixed populations. Therefore the "contact territory" of diploids and hexaploids is not confined to southern Scandinavia but extends also to Estonia, Latvia and Lithuania (X).

4.4.3. *Potentilla erecta* (L.) Räusch (paper IX)

Being a genetically and phenotypically widely varying taxon, *P. erecta* has been treated quite differently: Hegi (1922) has summarized its interspecific taxonomy and listed 19 taxa of different ranks and taxonomic significance (excluding synonyms) that can be joined under the name of *P. erecta* (L.) Räusch. Also, the multitude of synonyms, more than 30 (Leht 1984), points to its variability.

Variation of *P. erecta* has been thoroughly studied by Vasari (1968) in Finland and by Richards (1973) in Great Britain. They established three different races (subspecies): two in Great Britain and three in Finland (Richards 1973).

On the British Isles, the most common is the race growing on lowlands, identified as *P. erecta* ssp. *erecta.* The uplands race (500 m a.s.l.), *P. erecta* ssp. *strictissima* (Zimm.) A. J. Richards, is rarer. In Finland, *P. erecta* ssp. *strictissima* dominates, and *P. erecta* ssp. *erecta* occurs mostly in SW part of the country (Richards 1973).

The race growing on a thick peat layer in North Finland represents a new subspecies which Vasari has not yet described. Vasari (1968) suggests that the northern race is an old constituent of the Finnish flora, while his southern race, as interpreted by him before discussions with Richards (*P. erecta* ssp. *erecta* and

P. erecta ssp. *strictissima* together), is likely to have migrated from the south during the post-glacial climatic optimum.

In Estonia, both *P. erecta* ssp. *erecta* and ssp. *strictissima* occur, ssp. *strictissima* being more common. Therefore, the theory of their migration from the south to Finland (Vasari 1968) seems to be plausible.

Often *P. erecta* ssp. *erecta* and ssp. *strictissima* grow together, and their intermediates seem to be common. However, it was not possible to delimit the two subspecies even at the level of small clusters; all obtained clusters were mixed ones.

Since Estonia is a low-lying country (maximum elevation 318 m), ssp. *strictissima* grows here in habitats different from those it favours on the British Isles and in Central Europe. *P. erecta* ssp. *strictissima* and ssp. *erecta* have no ecological or geographical preference in Estonia: they both grow on various soils, in rather wet places and in moderately moist habitats. Intermediates can be found everywhere (IX).

Already Wolf (1908), when characterizing his varieties of *P. erecta* (he recorded 6), mentioned that four of them (incl. var. *strictissima* and var. *typica*) are sometimes difficult to distinguish and that there exist intermediate forms.

According to our material, these taxa are much more variable and transitional in Estonia than on the British Isles and hence are not worthy of the rank of the subspecies but should rather be referred to as varieties, since the rank of the subspecies (race) is used for taxa that have their own geographical areal and/or established ecological preference (IX).

As the material appeared to be morphologically quite varying and the obtained clusters distinct, the interspecific taxonomy of the species needs further investigation over a more extensive area of distribution with the use of more elaborated methods (DNA and/or isozyme analysis etc.).

4.4.4. *Potentilla fruticosa* L. (paper IV, XI)

P. fruticosa L. s. l. has been divided into two species by Klackenberg (1983) according to the sexual type of flowers and the ploidy level: *P. fruticosa* L. s. str. is a dioecious tetraploid taxon growing in North Europe and North Asia, *P. floribunda* Pursh a hermaphroditic diploid occurring in South Europe, Siberia, West and East Asia and North America. Consequently, it could be supposed that Estonian and Latvian shrubby cinquefoils are dioecious tetraploids. However, Eichwald (1962) states in the Estonian Flora that *P. fruticosa* is diploid and hermaphroditic. Vilbaste (1953), the author of the only study on the Estonian *P. fruticosa*, says nothing either about its ploidy level or sexual type.

In Estonia, *P. fruticosa* grows on alvars in the NW part of the territory — a large, vigorous, rather dense population between Harku, Keila and Vääna, and two smaller separate populations at Enge and Ohukotsu where *P. fruticosa*, being intolerant to shading, seems to decline as a result of afforestation. In the Latvian locality, which lies on dolomite in the valley of the River Abava near Kandava (Čuzupurvs Botanical Reserve), *P. fruticosa* is viable and abundant as well (IV).

As all the plants studied were dioecious and tetraploid (2n=28), it can be stated that shrubby cinquefoils belong to *Potentilla fruticosa* L. s.str in Estonia and Latvia. Hermaphroditic plants were found only among ornamentals, and the only chromosome number obtained from hermaphroditic material was diploid.

Preconditions for the generative propagation of the species are very favourable, as the seedset of plants is good and germination percentage rather high (27.4–40.8%). However, seedlings were found only in a few places, merely on open soil; young plants of firm generative origin were not encountered. The soil on which the seedlings were growing was very thin, disturbed by freezing and flood, which makes the survival of young plants very hard. Therefore, reproduction by seeds cannot be important here, weheras vegetative reproduction must be prevailing. However, in suitable conditions *P. fruticosa* may be a colonizing species. In Ohukotsu and Enge, where the species is declining due to the thickening of the forest, no seedlings were found; and the bushes were smaller, with several dry branches (XI).

In the Vääna-Harku locality, *P. fruticosa* stands are in some places very dense, in others — moderate. The species flowers abundantly here and the seedset is good, the population is very viable but not extending its distribution here.

Vegetative spread occurs by creeping stems directly below soil surface, in some cases the plant is thus capable to cover a large area (Elkington & Woodell 1963). In Baltic localities, vegetative spread or, in our case rather, renewal, takes place namely in such a way. However, *P. fruticosa* does not colonize surrounding areas, but is in some places even diminishing. Therefore, one can agree with the opinion of Eilart & Eilart (1974) about *P. fruticosa* being a relic but not an introducent in Estonia and Latvia (XI).

4.5. Cladistic analysis of the genus *Potentilla* (paper VI)

The results of cladistic analysis support the conclusions, drawn from the study of pollen exine sturcture, that the use of mostly style charcters for distinguishing subgenera is not justified.

When analyzing with cladistic methods all morphological characters used by Wolf (1908) in his descriptions of species, the subgenera based on style characters (shape and position) turn out to be polyphyletic (VI).

On the other hand, several of Wolf's sections are supported as being monophyletic; e.g. the section *Aureae* of *Gomphostylae,* consisting of *P. crantzii, P. arenaria, P. neumanniana* and *P. gelida*, appears a distinct clade with the last species being the farthest. According to Soják (1985b), *P. gelida* can be considered the primitive ancestor of the others. The sections *Argenteae*, *Graciles*, *Rectae* and *Niveae* in *Conostylae* also prove monophyletic in the consensus tree.

One species from the section *Argenteae*, *P. canescens*, is connected with *P. recta* and falls into the same clade with other members of the section *Rectae*.

Based on the cladistic analysis, Wolf's sections are more natural groupings as they are mostly monophyletic. The same conclusions were achieved by Soják (pers. comm. 1995) on the basis of comparative morphology of anthers and styles in the tribe *Potentilleae*. Soják (1987) also suggests that in Wolf's group *Potentillae trichocarpae* (comprised of *Rhopalostylae* and *Nematostylae*) it is not necessary to retain the category of subgenus between the genus and its sections.

The contradiction between the results of cladistic analysis and the subgeneral groupings proposed by Wolf arises, without doubt, partly from the polygenic nature and parallel variation of morphological characters, partly from differential weights given to the characters by Wolf (style characters being weighted more highly). Wolf performed the grouping of species on the basis of overall morphological similarity, with an emphasis on style characters.

4.6. Preliminary list of chromosome numbers of Estonian *Potentilla* species (papers IX, X)

Species	Locality	2n
P. palustris	Nugissaare	28
P. fruticosa	Enge	28
	Ohukotsu	28
	Niitvälja	28
	Vääna	28
P. argentea s. str.	Haanja	14
P. argentea s.l.	Salme	28
	Salme	42
	Tartu	42
	Vormsi	42
ssp. impolita	Salme	42
	Vormsi	42
P. norvegica	Saare	56
P. heidenreichii	Piusa	28
	Valgjärve	28
P. reptans	Salme	28
	Virtsu	28
P. erecta	Lakesoo	28
	Osmussaar	28
	Valgjärve	28
P. crantzii	Osmussaar	42
P. neumanniana	Osmussaar	42
P. anserina	Tartu	28

5. CONCLUSIONS

The genus *Potentilla* L. s.l. is represented by 24 species in Estonia, Latvia and Lithuania. 60% of them reach their areal borderlines in the Baltics (about 40% if only spontaneous species are considered). Seven species are quite rare adventives here; among spontaneous species only in case of five do their Baltic localities lie in the central part of the distribution area.

Pollen grains of all Baltic *Potentilla* species are monomorphic and have therefore no importance in the identification of species or intergeneric taxa. However, they appeared useful in delimiting tribes in the subfam. *Rosoideae*. The surface of seeds had discriminative importance at the level of subgenera. At the specific and interspecific levels, the most discriminative characters were micromorphological characters which proved in some cases more important than all macromorphological characters.

Among the Baltic representatives of the sect. *Aureae*, the most varyable species is *P. neumanniana*, though not so varyable as on Gotland. It can be clustered into morphs but their taxonomic rank needs further studying. *P. subarenaria* is undoubtedly a species of hybrid origin; occupying morphologically an intermediate position between its parents, its division into subtaxa is not justified. For *P. neumanniana* and *P. crantzii*, only the chromosome number 2n=42 has been identified, which refers to the possibility of the occurrence of apomixis.

P. canescens must be placed into the sect. *Rivales* but not into the sect. *Argenteae*. This species reached the Baltics in the 1950ies, and all earlier hints about its occurrence here are erraneous: in fact, *P. heidenreichii* was meant. *P. heidenreichii* (sect. *Rivales*) is a varying taxon which can be divided into morphs, whereas *P. norvegica* is much more homogenous.

P. argentea s.l. is morphologically highly varyable: six varieties could be identified in the material. *P. impolita* is not worthy of the rank of the species, it must be referred to as a subspecies (or even a variety).

P. erecta is represented by two subtaxa in Estonia; however, since there exist very many intermediate forms, and no differences in ecology or distribution occur, these taxa belong to the rank of the variety but not the subspecies, viz. var. *erecta* and var. *strictissima* (Zimm.) Hegi.

The subgenera of the genus *Potentilla* were created by Wolf on the basis of style morphology. However, as the pollen of all species studied appeared monomorphic, it seemed that the importance of style characters had been overestimated. This viewpoint is supported also by cladistic analysis according to which the subgenera did not come out as monophyletic groups, whereas most of the sections did.

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ABSTRACT

This thesis presents the results of multivariate and cladistic analysis of the genus *Potentilla* as well as of SEM studies of leaves, pollen and seeds surfaces of the Baltic *Potentilla* taxa.

In the sect. *Aureae* Wolf the most varying species is *P. neumanniana* Rchb: it can be clustered into morphs but their taxonomic rank needs further research. Since *P. subarenaria* Borkh. is undoubtedly a species of hybrid origin occupying a morphologically intermrdiate position between its parents, it is not justified to attempt to divide it into subtaxa. For *P. neumanniana* and *P. crantzii* (Crantz) Beck, only the chromosome number 2n=42 has been determined, which refers to the possible occurrence of apomixis.

P. erecta Räusch. is represented by two subtaxa in Estonia; however, as there exist very many intermediate forms, and no ecological or distributional differences were found between them, these taxa belong to the rank of variety, not to subspecies, viz. var. *erecta* and var. *strictissima* (Zimm.) Hegi.

In the sect. *Rivales* Wolf, *P. heidenreichii* Zimm. is a varyable taxon which can be divided into morphs, whereas *P. norvegica* L. is much more homogenous. Also *P. canescens* Bess. must belong to the sect. *Rivales*, not to the sect. *Argenteae*. It reached the Baltics in the 1950ies, and all earlier hints about its occurrence here are erraneous: in fact, *P. heidenreichii* was meant.

P. argentea s.l. is morphologically very varyable with six varieties being identified in the material. *P. impolita* is not worthy of the rank of the species and should be referred to as a subspecies (or even a variety).

The subgenera of the genus *Potentilla* were created by Wolf mostly on the basis of style morphology. However, as the pollen of all species studied appeared monomorphic (isopolar, tricolpate, exine meridionally striped), the importance of style characters seemed overestimated. This opinion is supported also by cladistic analysis according to which the subgenera were not formed as monophyletic groups, whereas most of the sections did.

PEREKOND MARAN (*POTENTILLA* L.) EESTIS, LÄTIS JA LEEDUS: LEVIK, MORFOLOOGIA JA TAKSONOOMIA

Kokkuvõte

Eestis, Lätis ja Leedus kasvab 24 liiki maranaid (*Potentilla* L.), millest seitse on üsna haruldased tulnukad. Spontaansetest liikidest on siin oma levila piiril 40% (60%, kui arvestada ka tulnukaid). Ainult viie liigi puhul on Baltikum enamvähem areaali keskosas.

Enim taksonoomilisi ja nomenklatuurseid probleeme on Balti maranaist põhjustanud ilmselt karvane (*P. heidenreichii* Zimm.), keskmine (*P. intermedia* L.) ja hallikas maran (*P. canescens* Bess.). Karvast ja keskmist maranat on käsitletud eraldi liikidena, alamliikidena või varieteetidena, samuti ühe taksonina. Hallika marana tuntuimad sünonüümid on *P. adscendens* Walst. et Kit. ja *P. inclinata* Vill., mida kohtab paljudes varasemates Baltimaid puudutavates floristilistes töödes. Lisatud kirjeldused vastavad *P. heidenreichii* tunnustele. Ka vanade herbaareksemplaride seas on *P. heidenreichii* taimi, mille etiketil seisab *P. adscendens* või *P. inclinata*. Tõeline *P. canescens*, Kesk-Venemaa stepitaim, jõudis Baltikumi alles 1950. aastail. Kuigi P. *inclinata* ja *P. adscendens* on vanemad sünonüümid kui *P. canescens*, on nendega olnud palju segadust ja mitmetimõistmist, nii et parem on kasutada nimetust *P. canescens*.

Wolfi (1908) süsteemis kuulub *P. canescens* koos *P. argentea* L. ja *P. collina* rühmaga sektsiooni *Argenteae* Wolf, aga sektsioonide *Argenteae* ja *Rivales* Wolf võrdlev feneetiline analüüs ja kogu perekonna kladistiline analüüs osutasid, et *P. canescens* on palju lähemal sektsiooni *Rivales* (*P. heidenreichii, P. intermedia, P. norvegica* ja *P. supina*) kui sektsiooni *Argenteae* liikidele. Seega on õigem paigutada *P. canescens* sektsiooni *Rivales*.

P. argentea s. l. materjalist on võimalik eristada kuus Wolfi püstitatud varieteeti ja liik (*s. str.*) *P. impolita*. Klasteranalüüsi tulemustest aga ilmneb, et *P. impolita* pole kindlasti liigi tasemel takson, vaid alamliik või isegi varieteet, sest ta ei eristu sugugi selgemalt kui varieteedid.

P. erecta sees on varem eraldatud kolm alamliiki, millest kaks, *ssp. erecta* ja *ssp. strictissima*, esinevad ka Eestis. Nad on siin aga väga üleminevate tunnustega, neil on palju vahevorme ning puuduvad erinevused ökoloogilistes nõudlustes ja levikus. Feneetilise analüüsi põhjal tuleks neid taksoneid käsitleda varieteetidena, mitte alamliikidena.

Baltimail oma levila piirile jõudnud sektsiooni *Aureae* liikidest on kõige varieeruvam *P. neumanniana* Rchb. See jaguneb mitmeks morfotüübiks, mille taksonoomiline tasand vajab edaspidist määratlemist. *P. subarenaria* Borbas on kindlasti hübriidse päritoluga liik, mille eksemplarid eristusid kaheks klastriks, millest üks sarnanes ühega, teine teise vanemliigiga. Liigi küllaltki ülemineva loomuse pärast pole alamtaksonite eristamine põhjendatud.

Eestis ja Lätis kasvavad põõsasmaranad on diöötsilised tetraploidid, nii et nad kuuluvad liiki *Potentilla fruticosa s. str.* Diploidne kahesuguliste õitega *P. floribunda* esineb vaid haljastuses.

Liigisisese varieeruvuse selgitamisel on kõige informatiivsemad mikromorfoloogilised tunnused: karvade tüüp, rakkude arv, õhulõhede arv jne. Kõik maranate tolmuterad on monomorfsed: piklik-elliptilised, kolmevaolised, triibulise pinnaga, seega neil perekonnasiseste taksonite eristamisel väärtust ei ole. Küll aga on tolmutera pinna tunnused informatiivsed triibuste tasemel alamperekonnas *Rosoideae*: tolmutera ehituse alusel peaks perekonna *Rubus* eraldama triibusest *Potentilleae* iseseisvasse triibusesse; kõigi triibuse *Sanguisorbeae* esindajate tolmuterad on aga niivõrd erinevad, et see triibus pole ilmselt loomulik, vaid kunstlik takson.

Lähtudes kladistilises analüüsis samadest tunnustest, mida kasutas Wolf (1908) oma süsteemi loomisel, ei osutunud monofüleetilisteks alamperekonnad, küll aga enamik sektsioone. Vastuolu kladistilise analüüsi tulemuste ja Wolfi empiiriliselt loodud taksonoomiliste üksuste vahel on tõenäoliselt tingitud morfoloogiliste tunnuste paralleelsest evolutsioonist perekonnas, samuti tunnustele erisuguse kaalu andmisest.

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I

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Малле ЛЕХТ

POTENTILLA L. В ПРИБАЛТИКЕ

ЭПИДЕРМИС ЛИСТА

Применение в ботанике сканирующего электронного микроскопа (СЭМ) существенно расширило технические возможности морфологического и таксономического исследования растений. В. Э. Джунипер и К. Э. Джеффри (1986) отмечают, что СЭМ дает прямую и наиболее простую возможность для изучения поверхности растений.

Цель настоящей работы — изучение с помощью СЭМ поверхности эпидермиса листа (волоски, воск, устьица) и уточнение некоторых вопросов систематики прибалтийских лапчаток. Исследовали эпидермис нижней и верхней поверхности листа 16 видов лапчаток трех подродов.

Материал и методика

Препараты из нежных тканей необходимо предварительно подготовить к просмотру в СЭМ во избежание сморщивания их в вакууме. Существует несколько способов фиксации препаратов: химические методы, замораживание в жидком азоте, лиофилизация (freeze-drying), сушка в критической точке (critical point drying).

Для применения этих трудоемких методов необходима специальная аппаратура. Во многих случаях для исследования твердых тканей (древесина, семена, пыльца и т. д.) можно воспользоваться более простыми методами, например, изучать нефиксированные напыленные растительные препараты (Terrell, Wergin, 1981; Bačič, 1981; Vyas, Chaudhary, Joshi, 1982 и др.). Итальянские ученые (Cappalletti, Casadoro, 1977) сравнивали препараты, полученные сушкой в критической точке, а также быстрым высушиванием. На нефиксированных препаратах отмечались артефакты, но авторы полагают, что и таким способом можно получить достаточно полезной информации. Нередко более качественных результатов можно достичь со свежеприготовленными образцами, не подверженными какой-либо обработке (Stant, 1981; Dwivedi, Ahmad, 1985; Джунипер, Джеффри, 1986 и др.). На рис. 1 изображен эпидермис свежего, не напыленного листа лапчатки — клетки в нормальном состоянии, деформаций нет. Однако изучение свежеприготовленных препаратов требует быстрого выполнения всех операций по приготовлению и анализу, так как сморщивание клеток начинается уже через 4—5 мин после помещения препарата в вакуум. Приемлемую же информацию можно получить иногда даже в течение 15 мин.

Сухой растительный материал можно исследовать как с применением напыления, так и без этого.

В настоящей работе использовали в основном нефиксированный, высушенный на воздухе (при комнатной температуре) материал. Образцы, вырезанные из средней части листа, приклеивали на носители препаратов клеем ПВА. Перед напылением клей высушивали на нагревательном столике. Напыляли золотом в ионном напылителе фирмы «Joel Fine Coat» (Япония). Работу выполняли в лаборатории электронной микроскопии Таллиннского политехнического института на СЭМ Tesla BS 300.

При использовании гербарного (нефиксированного) материала следует учитывать, что поверхность растений часто загрязнена яйцами насекомых, пылью, песком или спорами грибов, гифы которых проникают в толщу листа через устьица и кутикулу. К артефактам могут привести также заболевания растений (рис. 2). В настоящей работе не использованы загрязненные и сильно деформированные образцы.

Тип волосков изучали на 20—25 экземплярах обычных видов, на 8 экземплярах *P. canescens* и *P. silesiaca* и на 2 экземплярах *P. thyrsiflora* и *P. leucopolitana*.

Волоски и устьица измеряли в световом микроскопе фирмы «Ergaval» (ГДР). Для удаления эпидермиса гербарный или фиксированный в FAA материал подвергали мацерированию сначала в концентрированной HNO_3 с приместью $HClO_4$, затем в NH_3OH. После этого препарат промывали в дистиллированной воде, окрашивали, обезвоживали и просматривали в глицерине.

Из обычных в Прибалтике видов изучали 20 экземпляров, из редких — 2—5 (*P. thyrsiflora, P. silesiaca, P. leucopolitana, P. intermedia, P. canescens,* т. е. все доступные гербарные экземпляры). Измеряли не меньше пяти устиц на нижней и на верхней поверхности листа и 3—5 железистых трихом.

Результаты

Трихомы. Подрод *Hypargyrium* Fourr. Секция *Argenteae* Th. Wolf. Опушенность *P. argentea* L. и *P. impolita* Wahl. состоит из простых одноклеточных волосков — нитчатых и железистых. Структура железистых волосков у большинства лапчаток одинакова — имеются трехклеточная головка диаметром около 20 мкм и 3—6-клеточная ножка. Простые волоски прямые бугорковые (диаметр бугорков 1,5—3 мкм), извилистые же — гладкие. Диаметр и размер стенок прямых волосков больше, чем у извилистых (рис. 3). То что стенки извилистых волосков тоньше, подтверждается и на неудачно высушенных препаратах — там эти волоски иногда выглядят плоскими, бугорковые же волоски сохраняют всегда нормальный вид.

Волосистость *P. canescens* Bess. выражается в наличии коротких и длинных гладкостенных трихом разного диаметра, встречаются и жезезистые волоски.

Подсекция *Collinae* Zimm. *P. silesiaca* Uecht. имеет наряду с одноклеточными длинными волосками и звездчатые волоски (рис. 4), которые имеют ветвей меньше (4—6), чем *P. arenaria,* они длиннее и не образуют гнезд (рис. 5). За исключением гладких волосков, на листьях *P. leucopolitana* P.-J. Müll. отмечаются такие же бугорковые трихомы, как на листьях *P. argentea*. У *P. thyrsiflora* (Hüls.) Zimm. встречаются только гладкостенные трихомы.

Секция *Rivales* Th. Wolf. *P. intermedia* L. и *P. heidenreichii* Zimm. имеют волоски одинакового типа — кроме железистых (размеры головки 29,0×33,4 мкм) встречаются одноклеточные толстостенные длинные волоски с гладкой и волнистой поверхностями (рис. 6). Диаметр разноповерхностных волосков более или менее одинаковый и составляет 10—19 мкм. Гладкие одноклеточные простые волоски *P. norvegica* L. имеют довольно большой диаметр (18—35 мкм).

Подрод *Dynamidium* Fourr. Секция *Aurea* Th. Wolf. На листьях *P. tabernaemontani* Asch. встречаются кроме железистых трихом одноклеточные гладкостенные короткие волоски. Нижняя поверхность листа *P. subarenaria* Borb. (*P. tabernaemontani*×*P. arenaria*) имеет многоклеточные маловетвистые (3—7 (10)) звездчатые волоски (рис. 7). У

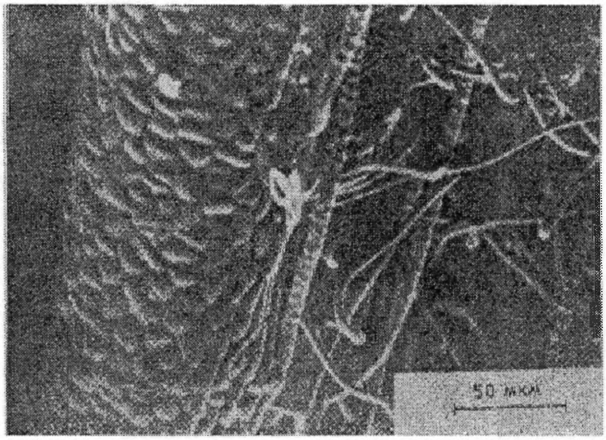

Рис. 1. Эпидермис свежего, не напыленного листа *P. argentea.* Epidermis of a fresh, uncoated leaf of *P. argentea.*

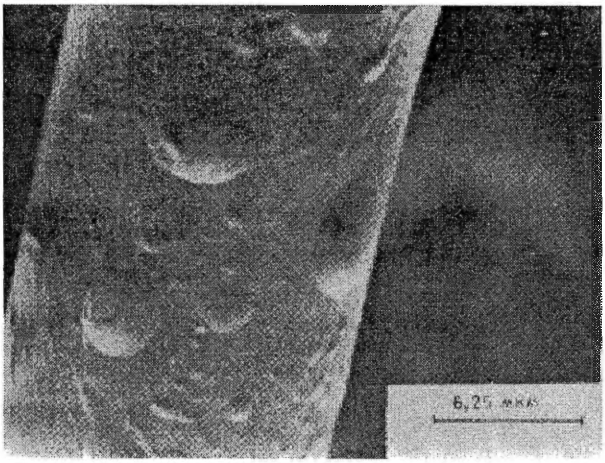

Рис. 2. Измененная поверхность волоска *P. crantzii.* The transformed surface of a hair of *P. crantzii.*

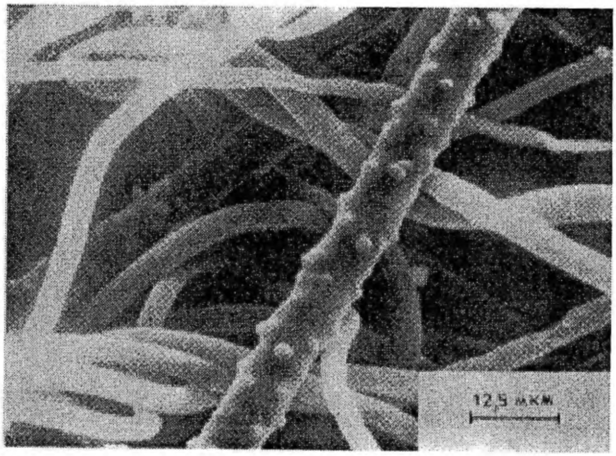

Рис. 3. Гладкие и бугорковые волоски на верхней стороне листа *P. impolita.* Smooth and tuberculate hairs on the upper surface of a leaf of *P. impolita.*

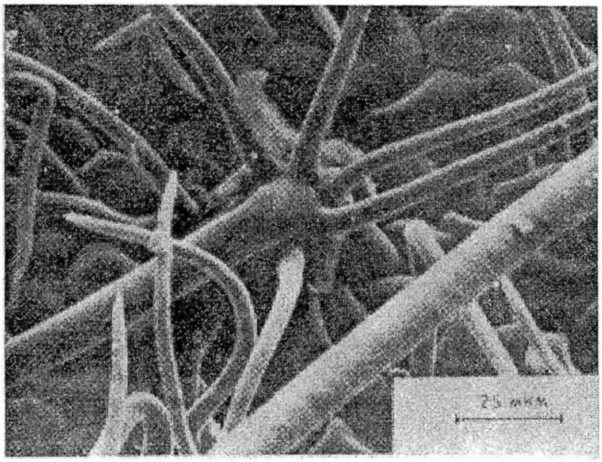

Рис. 4. Звездчатый волосок на верхней стороне листа *P. silesiaca*. A stellate hair on the upper surface of a leaf of *P. silesiaca*.

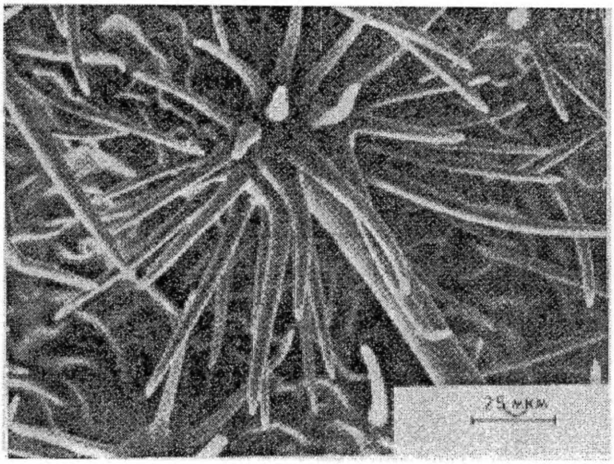

Рис. 5. Верхняя сторона листа *P. arenaria*. The upper surface of a leaf of *P. arenaria*.

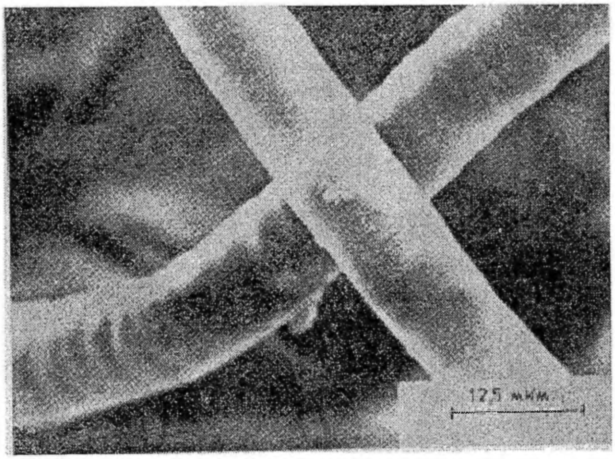

Рис. 6. Гладкие и волнистые волоски на нижней стороне листа *P. intermedia*. Smooth and wavy hairs on the lower surface of a leaf of *P. intermedia*.

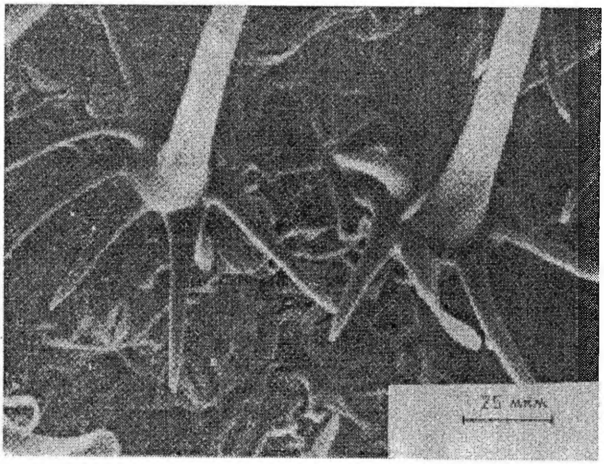

Рис. 7. Нижняя сторона листа *P. subarenaria*. The lower surface of a leaf of *P. subarenaria*.

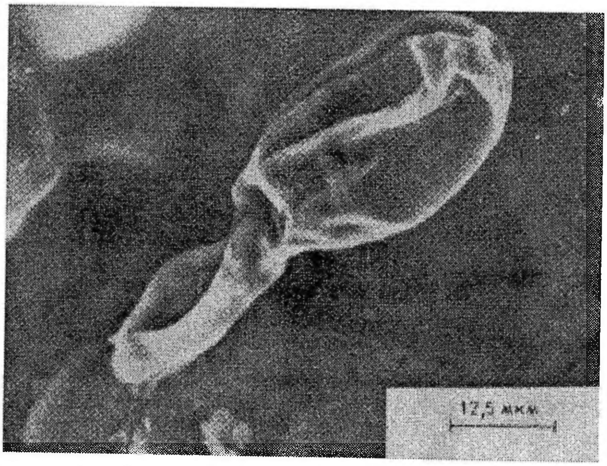

Рис. 8. Железистый волосок *P. tabernaemontani*. A glandular hair of *P. tabernaemontani*.

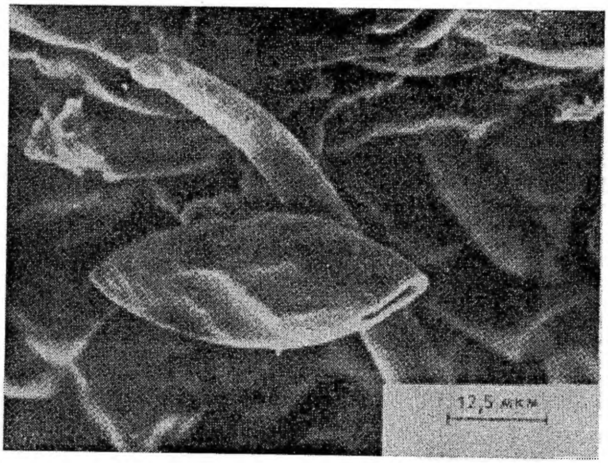

Рис. 9. Железистый волосок *P. crantzii*. A glandular hair of *P. crantzii*.

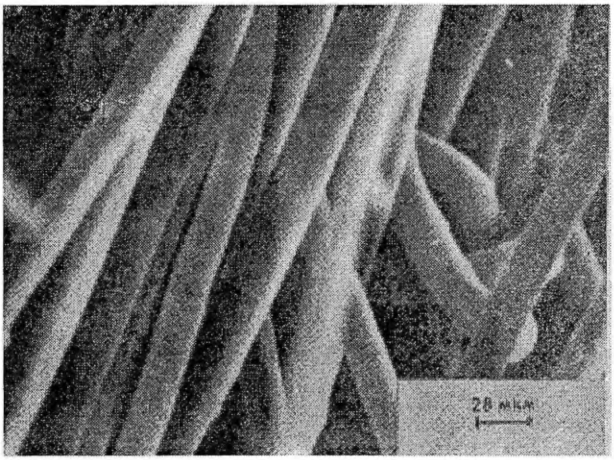

Рис. 10. Длинные гладкие прямые и вьющиеся волоски *P. anserina.* Long smooth straight and curled hairs of *P. anserina.*

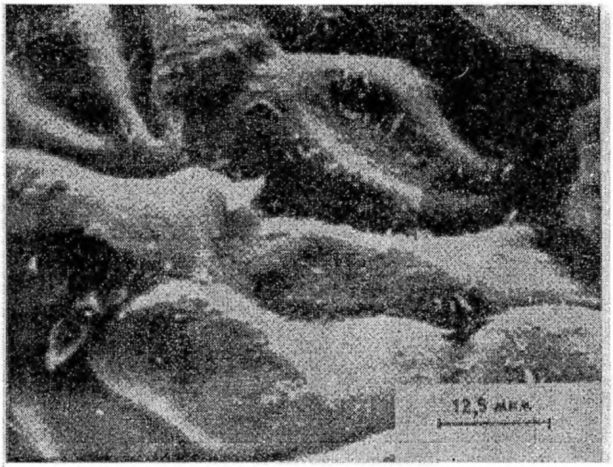

Рис. 11. Воск на верхней стороне листа *P. heidenreichii.* Wax on the upper surface of a leaf of *P. heidenreichii.*

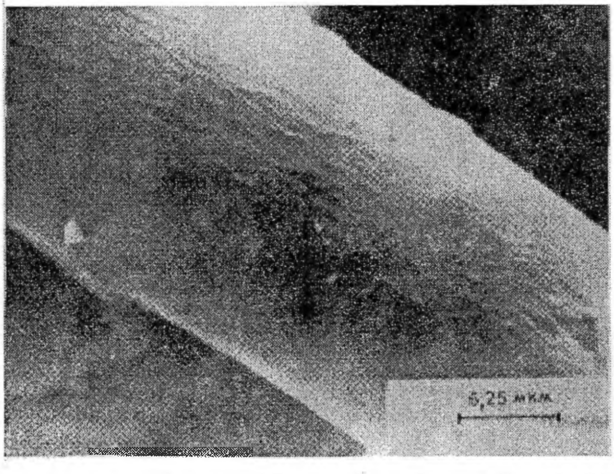

Рис. 12. Гладкий волосок *P. canescens.* A smooth hair of *P. canescens.*

второго предка этого вида, *P. arenaria* Borkh., волоски только звездчатые и железистые, одноклеточные простые волоски отсутствуют. Звездчатые волоски состоят из 15—40 гладкостенных лучей, расположенных в двух или трех гнездах с одним длинным лучом в центре (рис. 5).

У четвертого представителя, *P. crantzii* (Crantz) Beck, наблюдаются только гладкие прямые волоски. Форма головки железистых волосков этого вида несколько отличается от таковых других видов прибалтийских лапчаток (рис. 8, 9).

Очень похожи строением волосков эпидермиса листа прибалтийские виды из секции *Tormentillae* — *P. reptans* L. и *P. erecta* (L.) Räusch. Их гладкостенные одноклеточные длинные волоски различаются только диаметром, составляя соответственно 15—25 и 18—35 мкм.

Подрод *Chenopotentilla* Focke. Единственный прибалтийский представитель этого подрода — *P. anserina* L. Он характеризуется двумя типами гладких волосков — прямыми и извилистыми (рис. 10).

По уменьшению диаметра волосков прибалтийские лапчатки можно расположить в данной последовательности: от *P. erecta, P. norvegica, P. tabernaemontani* до *P. argentea, P. silesiaca* и *P. leucopolitana*. Самые крупные железистые трихомы наблюдаются у *P. crantzii* (56,9× 59,1 мкм) и *P. norvegica* (40,2×31,7 мкм).

Воск. Листья всех видов, но не всех экземпляров одного вида лапчаток покрыты восковым налетом, выполняющим защитную функцию (рис. 11).

Устьица всех розоцветных, в том числе лапчаток, только аномоцитные (Чевтаева, 1979; Гасанов, 1962 и др.). Они окружены ограниченным числом клеток, не отличающихся по размерам и форме от остальных клеток эпидермы (Metcalfe, Chalk, 1950).

Большинство устьиц у представителей рода *Potentilla* оказались аномоцитными — устьица окружены 4—6 (очень редко тремя) эпидермальными клетками. Размеры устьиц разных видов различаются — самые маленькие устьица у *P. silesiaca* — у вида с приподнимающимися побегами из сухих местообитаний (19,1×15,6 мкм). У этого вида на верхней

Размеры устьиц ($\bar{x}\pm m_{\bar{x}}$), мкм

Dimensions of stomata, μm

Вид Species	Верхняя сторона Upper side		Нижняя сторона Lower side	
	Длина Length	Ширина Width	Длина Length	Ширина Width
P. norvegica L.	28,1±0,6	20,4±0,4	25,0±0,3	19,9±0,3
P. heidenreichii Zimm.	29,5±0,8	23,4±0,8	23,6±0,2	18,5±0,2
P. tabernaemontani Asch.	27,5±0,3	21,5±0,3	26,9±0,2	21,2±0,2
P. crantzii (Crantz) Beck	25,3±0,3	18,6±0,3	24,7±0,3	18,3±0,3
P. subarenaria Bomb.	24,8±0,3	18,7±0,3	23,5±0,3	17,9±0,3
P. arenaria Borkh.			21,1±0,4	16,1±0,3
P. argentea L.			25,5±0,7	18,9±0,5
P. silesiaca Uecht.			19,1±0,3	15,6±0,3
P. leucopolitana P.-J. Müll.			21,1±0,5	17,1±0,9
P. thyrsiflora (Hüls.) Zimm.			27,9±0,5	20,8±0,5
P. reptans L.	22,2±0,3	17,5±0,3	20,3±0,2	16,6±0,2
P. erecta (L.) Räusch.			24,6±0,2	19,2±0,2
P. anserina L.	25,7±0,6	18,7±0,5	21,2±0,4	15,7±0,4
P. canescens Bess.			25,8±0,8	19,6±0,4
P. intermedia L.	28,1±1,2	21,3±0,7	25,2±0,5	20,0±0,6

стороне листа устьиц мало. Низкорослые виды из сухих мест лучше защищены от ветра (*P. tabernaemontani*, *P. subarenaria*, *P. arenaria*), их устьица крупнее и на верхней стороне листа их больше. Самые большие устьица имеют *P. norvegica*, *P. erecta* и *P. heidenreichii* из умеренно влажных местообитаний. Размеры устьиц всех видов лапчаток на верхней стороне крупнее, чем на нижней (таблица).

Среди аномоцитных устьиц многих видов *Potentilla* автором обнаружены и устьица с одной побочной клеткой, отнесенные некоторыми исследователями к гемипарацитным (Van Cotthem, 1970; Wilkinson, 1979). Отмечая сходство этого типа с парацитным, Г. П. Уилькинсон указывает, что гемипарацитные устьица могут встречаться среди парацитных, но редко. Я. А. Инамдар (Inamdar, 1969) и другие индийские исследователи (Patel, Inamdar, 1971) отмечают, что устьица с одной побочной клеткой встречаются как среди аномоцитных, так и среди некоторых других типов. В устичной системе Я. Д. Пателя (Patel, 1979), состоящей из 44 типов, устьица с одной побочной клеткой названы гемипарацитными, а у Н. А. Анели (1975) — латерицитными.

Среди названных выше типов автором обнаружены некоторые не часто встречаемые аномалии — два устьица подряд в цепочке у *P. norvegica* и два устьица, соединенные боком у *P. tabernaemontani* и названные соседними (contigous stomata) в английской литературе и двойниковидными у Н. А. Анели.

Обсуждение

К описанному К. Линнеем в 1753 г. виду *P. argentea* L. последующие систематики относились по-разному. В 1814 г. Г. Валенберг выделил из него вид *P. impolita* Wahl. Из *P. argentea* и *P. impolita*, в свою очередь, выделено несколько видов — в 1852 г. *P. tenuiloba* Jord., в 1884 *P. dissecta* (Wallr.) Zimm и др. Но далеко не все систематики признают выделенные из *P. argentea* таксоны самостоятельными видами. *P. impolita* считают подвидом или вариететом *P. argentea* (Ascherson, Graebner, 1905; Ball и др., 1968; Garcke, 1972; Gleason, 1968; Hegi, 1922—1923; Dostal, 1982; Wolf, 1908 и др.), *P. impolita* — самостоятельным видом (Юзепчук, 1941; Черепанов, 1981; Чевтаева, 1981; Borhidi, Isepy, 1965; Eichwald, 1962; Galenieks, 1957; Marklund, 1933—1934; 1940; Natkevicaitė-Ivanauskienė, 1971; Rothmahler, 1976 и др.). Два последних автора признают *P. tenuiloba* и *P. dissecta* также самостоятельными видами.

Наиболее важным признаком при определении *P. argentea* и *P. impolita* является густота опушения на листьях. Верхняя сторона листа у *P. argentea* должна быть зеленой, почти голой или негусто опушенной, у *P. impolita* она тускло-серо-зеленая, нередко беловато-серо-войлочная. Признак опушения все же очень изменчив — верхняя половина растения может быть покрыта как у типичного *P. argentea*, нижняя — как у *P. impolita* и наоборот. Опушение изменяется также в зависимости от времени года.

На основе экспериментов выращивания *P. anserina*, А. Роуси (Rousi, 1965) доказал, что густота опушения зависит от условий местопроизрастания — в основном от влажности почвы и воздуха. Неизменным же признаком является тип волосков. Это подтверждают и ботаники Т. Я. Мякушко и А. Ф. Ильинская (1984) относительно большинства украинских видов лапчаток — типы волосков на листьях, чаще листиках и цветоножках неизменные, а их количество может варьировать в зависимости от фазы развития и экологических условий.

Волоски *P. argentea* и *P. impolita* одинаковые, а такой изменчивый признак, как густота опушения не является диагностически ценным. На основе этого можно сказать, что признаки опушения не позволяют выделить *P. impolita, P. tenuiloba* и *P. dissecta* самостоятельными видами.

Таксономически сложной, принятой в разном объеме группой, является также подсекция *Collinae* из секции *Argentea.* Из этой группы в Прибалтике растут *P. silesiaca, P. thyrsiflora, P. leucopolitana.* При идентификации этих внешне похожих видов выяснилось, что кроме трудно опознаваемых макроморфологических признаков можно опираться и на строение волосков.

Некоторые трудности таксономического порядка связаны также с иерархизацией двух близких таксонов из секции *Rivales* — *P. intermedia* и выделенного из него *P. heidenreichii.* С трудностями связано и различение *P. heidenreichii* от фенотипически сходного представителя секции *Argentea* — *P. canescens* (Лехт, 1987 *а, б*).

При различении *P. intermedia* от *P. heidenreichii* густота опушения и тип волосков являются не единственными признаками — информативными оказываются также окраска растения и толщина листьев.

Хорошим признаком идентифицирования вида является, кроме различий в габитусе, форме листочков и зубчиков, тип волосков. Поверхность листьев *P. canescens* покрыта короткими и длинными гладкостенными волосками разного диаметра, волнистостенные волоски отсутствуют (рис. 12).

Практически только по типу волосков идентифицируются фенотипически очень похожие *P. tabernaemontani* и *P. subarenaria* (*P. arenaria*×*P. tabernaemontani*) из секции *Aurea.* Строение волосков подтверждает предположение о гибридном происхождении *P. subarenaria* — его звездчатые волоски промежуточны между одноклеточными волосками *P. tabernaemontani* и многоветвистыми звездчатыми волосками *P. arenaria.* При том *P. subarenaria* — несомненно самостоятельный вид, он произрастает и на таких территориях, где один из его предков отсутствует (Лехт, 1987*б*).

Промежуточными между *P. arenaria* (21,1×16,1 мкм) и *P. tabernaemontani* (26,9×21,2 мкм) являются также размеры устьиц *P. subarenaria* (23,5×17,9 мкм).

В заключение можно сказать, что тип волосков является одним из важнейших признаков идентификации сложных, часто спорных видов рода *Potentilla.* Это относится к определению таких видов, как *P. heidenreichii, P. canescens, P. sileciaca, P. thyrsiflora* и *P. leucopolitana.* На гибридное происхождение *P. subarenaria* указывает также строение волосков этого вида.

Автор выражает признательность У. Каллавус за проведение анализов.

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POTENTILLA L. BALTIKUMIS

Lehe epidermis

Uuritud 16 maranaliigi lehtedel esinevad liht- ja näärmekarvad. Sileda, näsalise või lainelise pinnaga üherakulised lihtkarvad ja siledapinnaliste harudega mitmerakulised tähtkarvad on läbimõõdult ja pikkuselt erinevad. Näärmekarvad on enamikul balti maranaist ühesuguse ehitusega (erinevad veidi *P. crantzii* (Crantz) Beck ja *P. reptansi* L. omad). Karvade tüüp on makromorfoloogiliste tunnuste kõrval väga hea liike eristav tunnus.

Põhiliselt karvasuse tiheduse alusel (see on aga väga muutlik tunnus) iseseisvate liikidena eristatud *P. argentea* L. ja *P. impolita* Wahl. karvad on täiesti ühesuguse ehitusega, seepärast pole põhjust neid taksoneid iseseisvateks liikideks pidada.

P. arenaria Borkh., *P. tabernaemontani* Asch. ja *P. subarenaria* Borb. karvade uurimine kinnitab viimase liigi hübriidset päritolu — *P. arenaria*'l on ainult 15—40-harulised tähtkarvad, *P. tabernaemontani*'l ainult sirged üherakulised lihtkarvad, *P. subarenaria*'l aga sirged üherakulised karvad ja väheharulised tähtkarvad (harusid 3—10).

Enamik balti maranate õhulõhesid on anomotsüütsed, erinedes vaid mõõtmetelt: kõige väiksemad on *P. silesiaca* Uecht. õhulõhed ja kõige suuremad *P. norvegica* L. ja *P. tabernaemontani* omad. Anomotsüütsete õhulõhede seas leiti enamikul liikidel ka hemiparatsüütseid õhulõhesid (ühe kaasrakuga õhulõhed) ja üksikuid pidevaid (*contiguous*) õhulõhesid *P. norvegia*'l ja *P. tabernaemontani*'l.

Malle LEHT

THE GENUS *POTENTILLA* L. IN THE BALTIC REPUBLICS

Epidermis of the leaf

The leaf surface of 16 *Potentilla* species studied are covered with simple and glandular hairs. The simple unicellular trichomes of different length and diameter have smooth, wavy or tuberculate surface. The branches of multicellular stellate hairs have a smooth surface. The glandular hairs of the majority of the Baltic *Potentilla* species are of similar structure (those of *P. crantzii* (Crantz) Beck and *P. reptans* L. somewhat different).

The type trichomes is a very good character for indentifying taxonomically complicated taxa.

P. argentea L. and *P. impolita* Wahl. have been described as independent species mostly on the basis of their hairiness density. Whereas their trichomes are exactly of the same type, the density being a very variable character, there is no ground for separating them as different species, at least on the basis of hairiness characters.

Study of the hairs of *P. arenaria* Borkh., *P. tabernaemontani* Arch. and *P. subarenaria* Borb. assures the hybrid origin of the last mentioned species. *P. arenaria* has only stellate hairs with 15 to 40 branches, *P. tabernaemontani* only straight unicellular hairs, the hair cover of *P. subarenaria* being intermediate with its straight unicellular hairs and stellate hairs having less (3—10) branches.

Most of the stomata of *Potentilla* are anomocytic and differ only in their size — the smallest are those of *P. silesiaca* Uecht., the largest ones of *P. tabernaemontani* and *P. norvegica* L. Among the anomocytic stomata another type was found — nearly all the Baltic species have also some hemiparacytic stomata (stomata with one subsidiary cell). In the epidermis of *P. tabernaemontani* and *P. norvegica* some contiguous stomata were also found.

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Малле ЛЕХТ

POTENTILLA L. В ПРИБАЛТИКЕ

ПЫЛЬЦЕВЫЕ ЗЕРНА И СЕМЕНА

Изучение морфологии пыльцевых зерен с помощью сканирующего электронного микроскопа (СЭМ) решает многие проблемы по выяснению внутривидовой систематики некоторых родов, например, *Aegitalis, Trillium, Cicer, Ephedra, Salvia, Paeonia, Paris, Rubus* и др. (Brisson, Peterson, 1976; Weber-El Ghobary, 1985; Lamba, Gupta, 1981 и др.).

Целью данной работы было изучение морфологии семян и пыльцевых зерен прибалтийских видов рода *Potentilla* L. и близких ему родов из семейства *Rosaceae* для выяснения важности некоторых генеративных признаков в систематике рода.

Материал и методика

С помощью СЭМ изучали пыльцу и семена гербарного материала всех прибалтийских видов лапчаток *Potentilla* L. (21 вид из 4 подродов). Изучали 5—8 экземпляров, из редких видов — в зависимости от количества доступного материала (Лехт, 1987; 1988).

От каждого экземпляра брали 3 зрелых пыльника и 3—5 зрелых семян. Пыльники приклеивали с помощью двухсторонней липкой ленты на столики и разбивали иглой. Семена приклеивали клеем ПВА или липкой лентой. Препараты покрывали тонким слоем золота (методом напыления) и просматривали с помощью СЭМ TESLA BS 300 в лаборатории электронной микроскопии Таллиннского политехнического института и TESLA BS 301 в Институте зоологии и ботаники АН ЭССР.

Результаты

Пыльцевые зерна

Все изученные прибалтийские лапчатки имеют изополярные трехбороздные пыльцевые зерна продолговато-эллипсоидальной, иногда немного округленной формы. Размеры пыльцевых зерен в одном пыльнике иногда сильно варьируют (рис. 1), довольно часто встречаются деформированные зерна (рис. 2), что зависит, вероятно, от степени их зрелости.

Размеры пыльцевых зерен прибалтийских лапчаток варьируют в следующих пределах: полярная ось от (18)20 до 35(40) мкм, экваториальный диаметр от (10)12 до 18(20) мкм. Маленьких зерен меньше, чем больших. Длина полярной оси пыльцевых зерен одного вида варьирует в основном в пределах 10 мкм и экваториальный диаметр в пределах 5 мкм (таблица).

По шкале Г. Эрдтмана (Erdtman, 1945), где группы размеров пыльцевых зерен установлены с учетом длины полярной оси, пыльцевые зерна *Potentilla* относятся к группе средних (от 25 до 50 мкм).

Орнаментация экзины пыльцевых зерен у всех видов рода *Potentilla* струйчатая (рис. 3—13). Скульптурные элементы длинные, расположены более или менее меридионально и параллельно; иногда соединяются анастомозами или запутаны между собой. Варьирует их высота и ширина — на фотографиях это хорошо видно по четко или слабо выра-

Пределы варьирования размеров пыльцевых зерен прибалтийских лапчаток
Potentilla L.

Observed range of dimensions of pollen grains of the Baltic cinquefoils *Potentilla* L.

Вид Species	Число измеренных зерен Number of measured grains	Длина полярной оси, мкм Length of the polar axis	Длина экваториального диаметра, мкм Length of the equatorial axis
P. norvegica	20	40,7 — 23,9	12,4 — 19,6
P. erecta	20	33,5 — 26,7	13,7 — 17,6
P. argentea	20	20,8 — 31,5	9,8 — 15,6
P. crantzii	10	22,4 — 31,6	12,6 — 18,1
P. tabernaemontani	15	23,8 — 35,7	12,1 — 18,3
P. arenaria	15	24,3 — 30,9	13,6 — 18,9
P. subarenaria	26	27,2 — 36,0	13,3 — 17,9
P. goldbachii	10	25,4 — 38	13,9 — 19,8
P. anserina	11	26,2 — 31,1	13,9 — 16,2
P. reptans	11	25,3 — 34,4	13,2 — 15,3
P. fruticosa	10	23 — 28,5	11,8 — 16,8
P. bifurca	7	20,5 — 32,7	13,6 — 17,3
P. canescens	6	20,9 — 28	15,2 — 18,4
P. leucopolitana	9	17,9 — 34,6	14,5 — 17,3

женному рисунку экзины. Экзина, по нашим данным, неперфорированная. Орнаментация пыльцевых зерен слабее всего выражена у *P. subarenaria* Borb. и *P. silesiaca* Uecht. Частота струек у разных зерен различается очень мало.

Для сравнения были просмотрены также пыльцевые зерна некоторых представителей близких к *Potentilla* родов из подсемейств *Rosoidea*. Рисунок пыльцевых зерен *Geum* L., *Fragaria* L. и *Comarum* L. в основном такой же, как у лапчаток — струйчатый, неперфорированный, пыльцевые зерна продолговато-эллипсоидальные, трехбороздные (рис. 14—16).

Поверхность пыльцевых зерен у остальных наблюдаемых родов существенно отличается (рис. 17—23). Экзина *Rubus* L. шиповатая, перфорированная, у *Alchemilla* L. — покрыта рядами нежных невысоких бугорков, у *Filipendula* Adans. бугорки крупнее и расположены рассеянно. Скульптура микроспор *Rosa* L. состоит из извилистых густо расположенных штрихов, межштриховая экзина перфорированная. Орнаментация *Agrimonia* L. напоминает скульптуру *Rosa*, но не имеет перфорации. Пыльцевые зерна всех названных родов трехбороздные, а *Sanguisorba* L. — шестибороздные, со слабовыраженным гранулярным рисунком. Зерна *Poterium* L. без четких борозд, с тремя выступами, поверхность мелкозернистая.

За исключением *Filipendula*, все изученные пыльцевые зерна подсемейства *Rosoideae* можно отнести к группе средних по Г. Эрдтману. Пыльцевые зерна *Filipendula* самые маленькие в подсемействе *Rosoideae* и принадлежат к группе мелких (10—25 мкм).

Семена

Строение поверхности семян в роде *Potentilla* различается больше, чем строение поверхности пыльцевых зерен.

Семена яйцевидные или продолговато-яйцевидные, не совсем регулярной формы, коричневые, бугристые, морщинистые.

Рисунок поверхности семян нами исследовался на трех уровнях. При маленьких увеличениях (200×) распознаваемый рисунок формируется из широких, довольно плоских штрихов, покрывающих спинную сторону семени. На спинке штриха обычно образуется невысокий гребень. Вся поверхность сетчатая. На этом уровне виды не различить между собой (рис. 24—26).

При средних увеличениях (1000—2000×) становится хорошо заметной сетчатая структура, рисунок у разных подродов разный.

У *P. argentea* L., *P. impolita* Wahl., *P. canescens* Bess., *P. intermedia* L., *P. norvegica* L. и других видов из подрода *Hypargyrium* Fourr. границы клеток нечеткие, петли образуются из-за углубления центра и выступающих краев клеток. При больших увеличениях (6000×) поверхность клеток гладкая (рис. 27—29).

У *P. tabernaemontani* Asch., *P. crantzii* (Crantz) Beck, *P. arenaria* Borb., *P. subarenaria*, *P. erecta* (L.) *Hampe*, *P. reptans* L. (подрод *Dynamidium* Fourr.) сетчатый рисунок образуется из ясно выраженных межклеточных линий. Центральная часть клетки обычно не углубляется (рис. 30—32). При больших увеличениях поверхность клеток гладкая.

У *P. anserina* L. сетчатость формируется тоже из межклеточных линий, но поверхность эпидермиса слегка морщинистая и напоминает пергамент. Центральные части клеток не углублены, но по краям эпидермис немного возвышен (рис. 33).

У всех этих видов семена без волосков. Длинными прямыми волосками покрыты семена *P. fruticosa* L. (рис. 34).

Отличаются и размеры семян: самые мелкие в подроде *Hypargyrium* (средняя длина *P. argentea* 0,85 мм; *P. heidenreichii* 0,99 мм; *P. norvegica* 0,9 мм). У видов из подрода *Dynamidium (P. subarenaria* 1,68 мм; *P. erecta* 1,6 мм; *P. reptans* 1,3 мм) семена крупнее, у *P. anserina*, единственного прибалтийского представителя подрода *Chenopotentilla* — самые крупные (длиной от 1,8 до 2,2 мм). Измеряли в среднем 50 семян.

Обсуждение

Трехбороздные зерна, т. е. зерна с тремя меридиональными бороздами, по-видимому, являются основным типом, характерным для двудольных. Этот тип не известен для других семенных растений. Трехбороздный тип считают примитивным, в процессе эволюции из него по одной линии образовались многобороздный и безбороздный типы. В пределах другой линии зерна с единственной дистальной бороздой по отношению к положению споры в тетраде привели к образованию проксимального однобороздного, двухбороздного, многобороздного и безбороздного типов. Форма и величина пыльцевых зерен, видимо, практического значения при классификации не имеют, хотя очень крупные или очень мелкие пыльцевые зерна характеризуют некоторые таксоны (Имс, 1964).

Скульптурирование экзины, несомненно, связано со способом опыления. У энтомофильных растений зерна скульптурированные, у анемофильных — нет. Энтомофилию считают примитивным способом опыления (Фегри, Пэйл, 1982).

Среди изученных нами пыльцевых зерен видов подсемейства *Rosoideae* только *Sanguisorba officinalis* L. и *Poterium sanguisorba* L. оказались малоскульптурированными (первая из них шестибороздная, вторая — с неясными бороздами). Это единственные анемофильные виды среди изученных. По теории А. Имса (1964) и К. Фегри и Л. ван дер Пэйла (1982), они, по всей вероятности, более развиты среди изученных.

Известно, что строение генеративных органов растений консервативнее, чем вегетативных. В семействе *Rosaceae* большинство родов по строению цветка очень похожи, варьируют в основном размеры цветка и цвет лепестков.

В цветке гинецей имеет более консервативную структуру, чем наружные части цветка. Наиболее изменчивой частью гинецея считают рыльце, служащее органом восприятия пыльцевых зерен. Известно, что поверхность рыльца и ткани столбика проявляют избирательность в отношении прорастания пыльцевого зерна и роста пыльцевой трубки (Фегри, ван дер Пейл, 1982).

В роде *Potentilla* многообразной частью в цветке является гинецей, хотя К. Ферги и Л. ван дер Пэйл (1982) считают его самой консервативной частью цветка. Т. Вольф разделил род *Potentilla* на подроды в основном по форме и месту отхождения столбика от завязи (Wolf, 1908). По тем же принципам составлял свою систему лапчаток СССР С. В. Юзепчук (1941). Он разделил род *Potentilla* на 7 подродов. Прибалтийские лапчатки принадлежат к четырем из них. Эта система с некоторыми изменениями используется и сейчас.

В отличие от системы Т. Вольфа, С. В. Юзепчук относит *P. fruticosa* (*Dasiphora fruticosa*) в самостоятельный род *Dasiphora*, а *P. palustris* (*Comarum palustre*) — в род *Comarum*. П. В. Бал и другие (Ball и др., 1968) объединяют подроды *Hypargyrium, Dynamidium* и *Chenopotentilla* в подрод *Potentilla*, а *P. fruticosa* и *P. palustris* относят к самостоятельным подродам рода *Potentilla*.

Важным диагностическим признаком является в этой системе форма и место отхождения столбика. В других родах семейства *Rosaceae* форма столбика такой диагностической важности не имеет (кроме рода *Geum*, где у всех прибалтийских видов форма столбика отличается).

Струйчатая орнаментация поверхности пыльцевых зерен у всех прибалтийских видов одинакова (рис. 23—33), существенных различий нет и в их размерах. Аналогична поверхность у пыльцевых зерен *Fragaria, Comarum* и *Geum*.

Хотя внешняя форма и место отхождения столбика в роде *Potentilla* довольно различные, эта разница не является препятствием при гибридизации — в роде много видов, которые возникли именно этим путем (среди прибалтийских видов *P. subarenaria, P. silesiaca* и др.). Так в подроде *Potentilla* (напоминаем, что он состоит из 3 подродов С. В. Юзепчука) встречаются гибриды между большинством (3/4) видов этого подрода (Ball и др., 1986).

Экспериментально были получены гибриды при скрещивании *Potentilla* и *Fragaria*; *Comarum* и *Fragaria*. Жизнеспособные семена развивались после нескольких скрещиваний, но до взрослых растений вырастали только гибриды *P. fruticosa* × *F. vesca*; *P. fruticosa* × *F. grandiflora*; *Comarum palustre* × *F. vesca* и *C. palustre* × *F. grandiflora*, которые все оказались стерильными (Ellis, 1962).

Этот эксперимент указывает на близость *Fragaria, Comarum* и *Potentilla*, а также на то, что преграда, которая могла бы препятствовать гибридизации, т. е. взаимодействию пыльцевой трубки со столбиком, внешний вид которого отличается в разных подродах, не надежная. Это наводит на мысль, что различия в форме столбика не имеют таксономически столь важного значения, чтобы главным образом по этому признаку выделять подроды в роде *Potentilla*.

Оказывается, что поверхность семян в роде *Potentilla* не так однообразна, как поверхность пыльцевых зерен. Скульптура поверхности и размеры семян различаются у представителей разных подродов (рис. 24—34).

Опираясь на морфологию главных генеративных органов, гинецея и семян, можно утверждать, что подроды в роде *Potentilla* — естественные таксоны, хотя пыльцевые зерна у всех лапчаток одинаковые. Остается неясным, почему эволюция привела к внешнему разнообразию гинецея, в то время как пыльцевые зерна остались однообразными?

Рис. 1—23. Пыльцевые зерна.

Figs 1—23. Pollen grains.

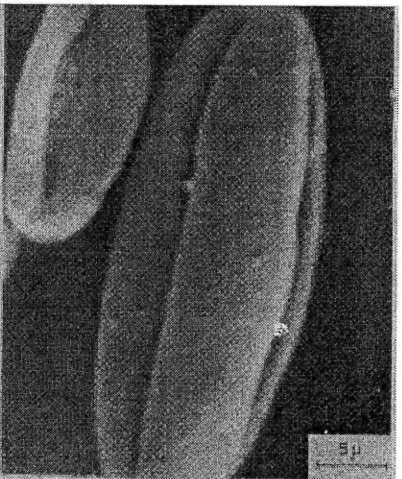

Рис. 1. *P. subarenaria.*

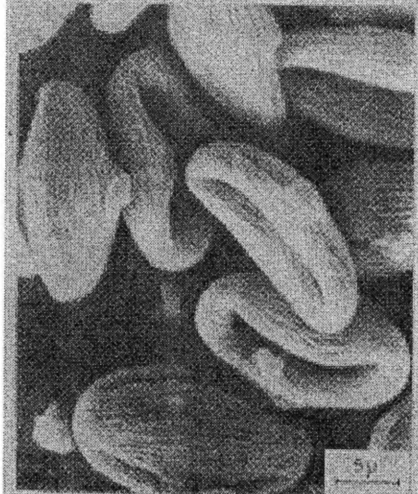

Рис. 2. *P. argentea.*

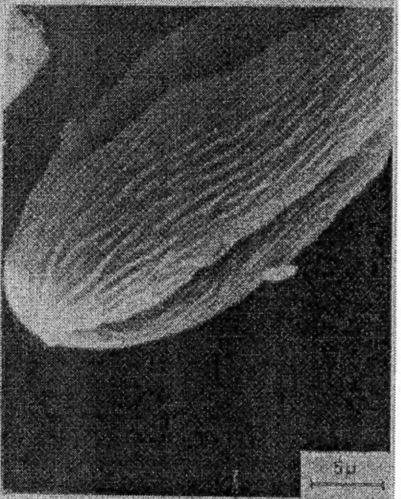

Рис. 3. *P. supina.*

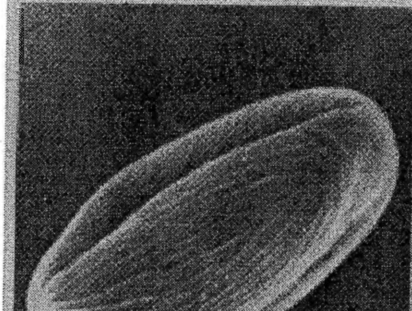

Рис. 4. *P. argentea.*

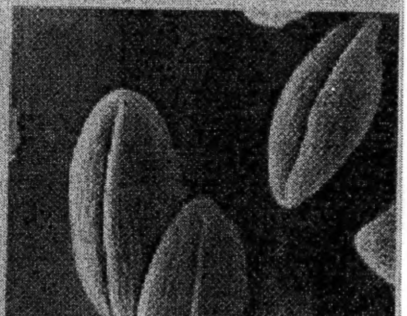

Рис. 5. *P. fruticosa.*

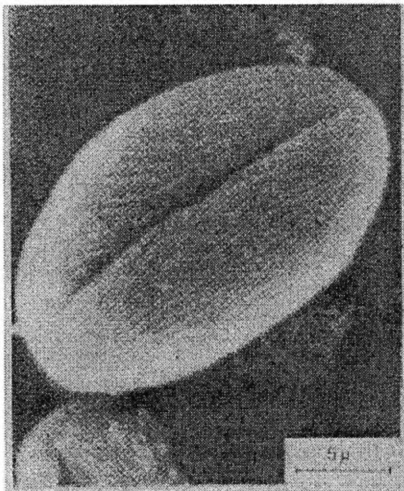

Рис. 6. *P. neapolitana.*

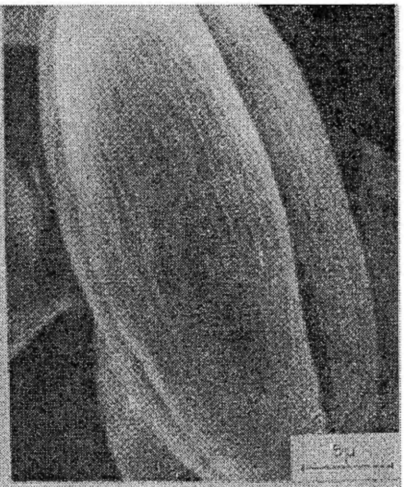

Рис. 7. *P. erecta.*

Рис. 8. *P. arenaria.*

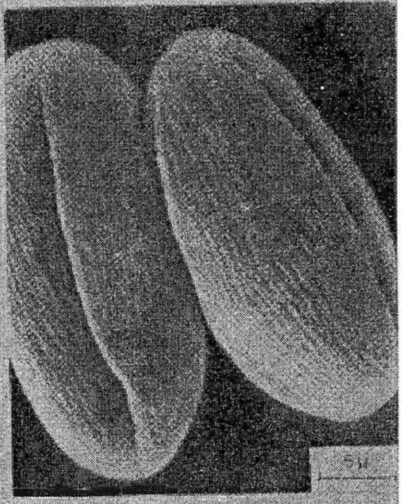

Рис. 9. *P. subarenaria.*

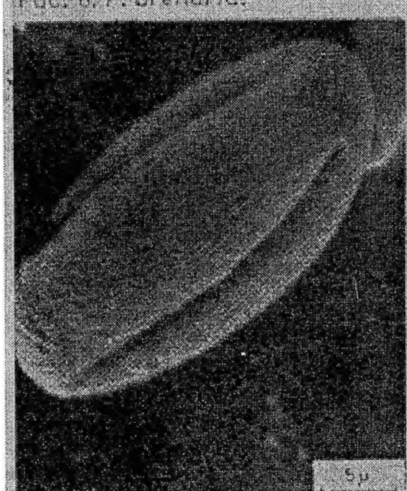

Рис. 10. *P. crantzii.*

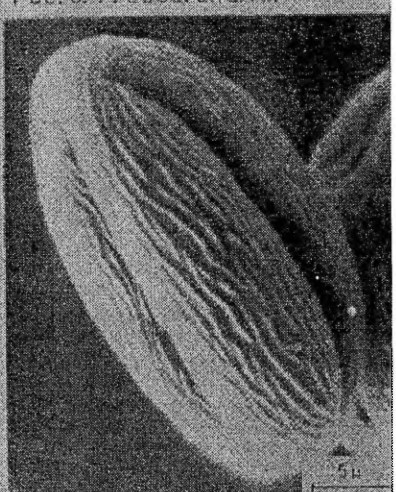

Рис. 11. *P. bifurca.*

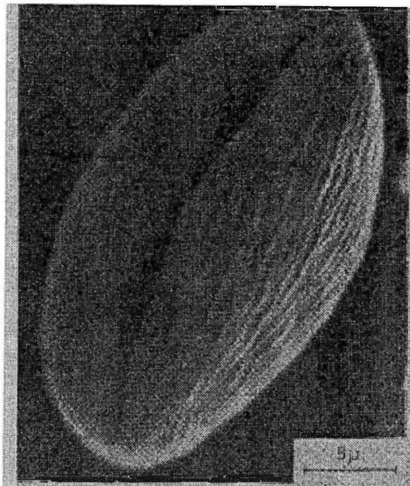

Рис. 12. *P. anserina*.

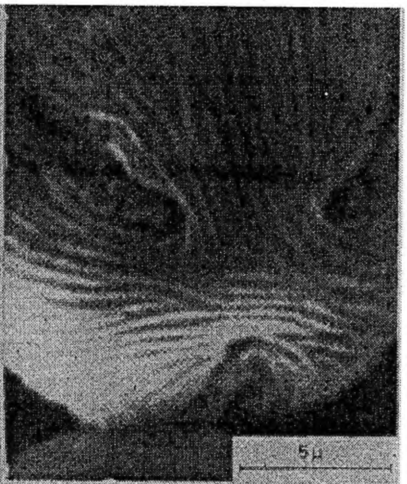

Рис. 13. *P. canescens*.

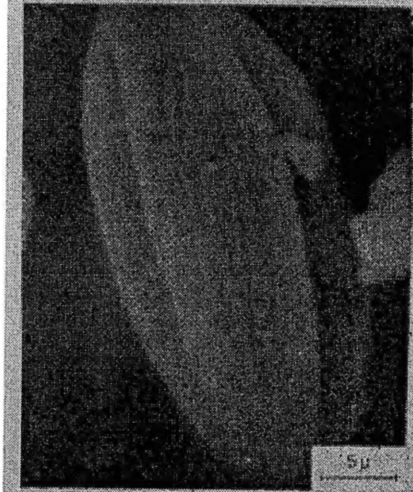

Рис. 14. *Geum rivale*.

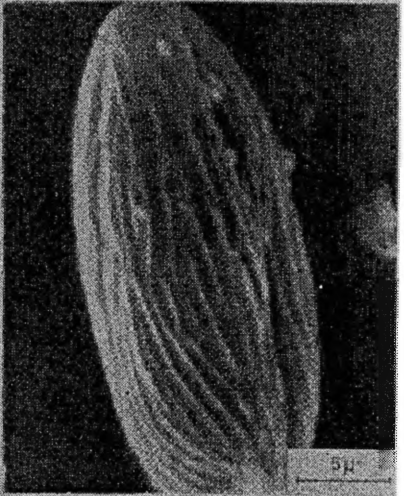

Рис. 15. *Fragaria vesca*.

Рис. 16. *Comarum palustre*.

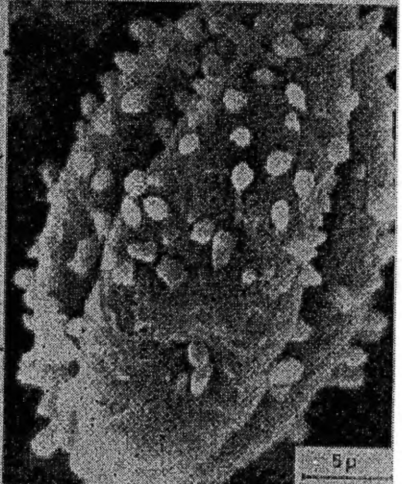

Рис. 17. *Rubus chamaemorus*.

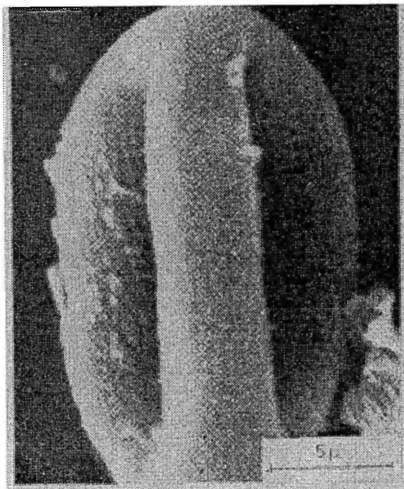

Рис. 18. *Alchemilla wichurae.*

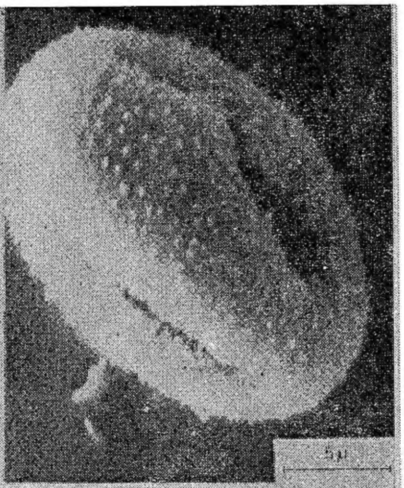

Рис. 19. *Filipendula ulmaria.*

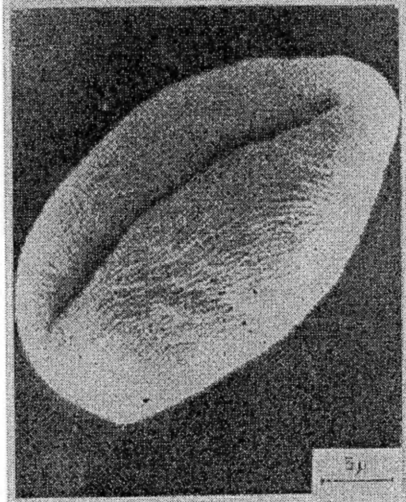

Рис. 20. *Rosa majalis.*

Рис. 21. *Agrimonia eupatoria.*

Рис. 22. *Sanguisorba officinalis.*

Рис. 23. *Poterium sanguisorba.*

Рис. 24—34. Семена.

Figs. 24—34. Seeds.

Рис. 24. *P. goldbachii.*

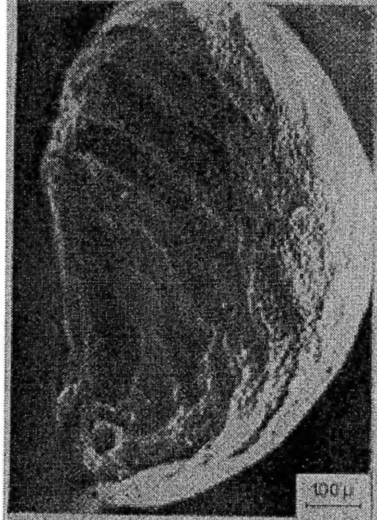

Рис. 25. *P. argentea.*

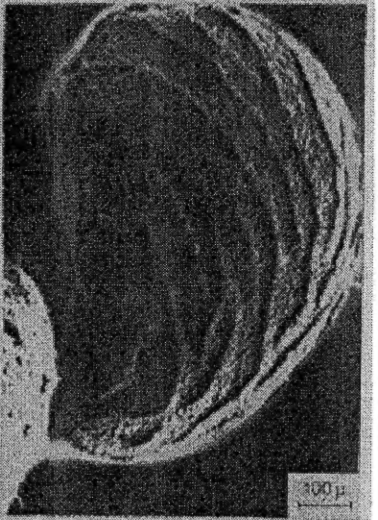

Рис. 26. *P. arenaria.*

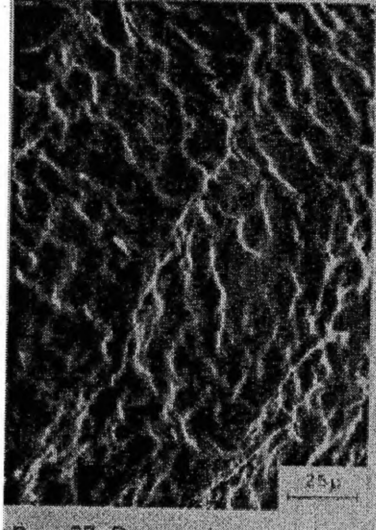

Рис. 27. *P. argentea.*

Рис. 28. *P. argentea.*

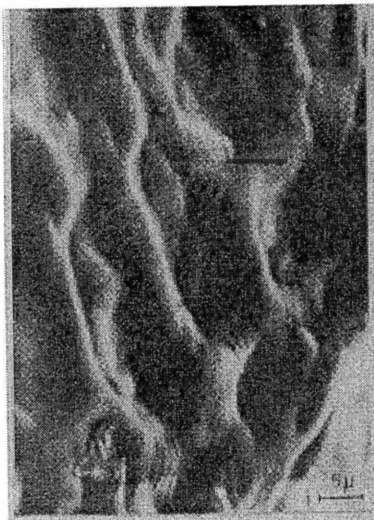

Рис. 29. *P. goldbachii.*

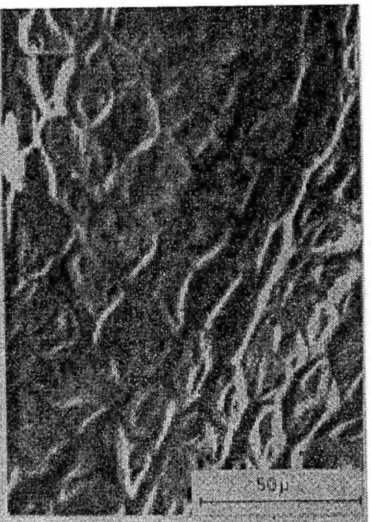

Рис. 30. *P. crantzii.*

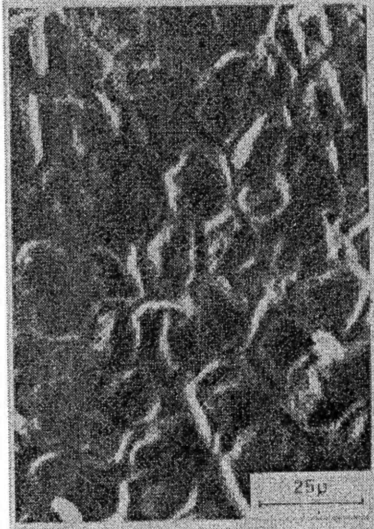

Рис. 31. *P. tabernaemontani.*

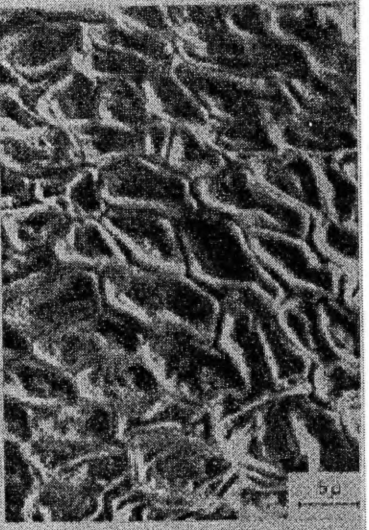

Рис. 32. *P. erecta.*

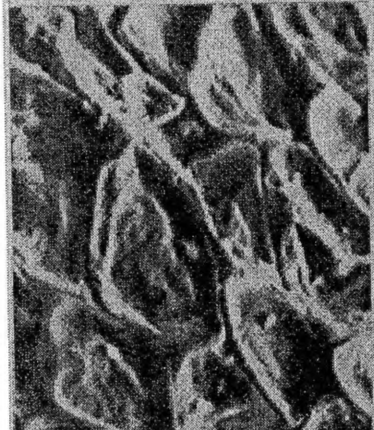

Рис. 33. *P. anserina.*

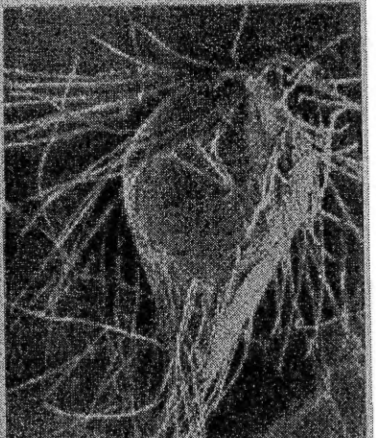

Рис. 34. *P. fruticosa.*

По строению пыльцевых зерён, гинецея и семян можно утверждать, что *Comarum palustre*, *Dasiphora fruticosa* и *Potentilla* sp. sp. принадлежат к роду *Potentilla*, как и считают авторы «Флоры Европы». Но в пределах рода надо использовать систему подродов С. В. Юзепчука — подроды *Hypargyrium*, *Dynamidium* и *Chenopotentilla* нельзя соединять в один подрод.

Роды подсемейства *Rosoideae* соединены в 5 трибусов. К трибусу *Potentillae* принадлежат роды *Geum*, *Fragaria*, *Comarum*, *Potentilla* и *Rubus*. По строению генеративных органов, *Rubus* в этот трибус не входит — экзина пыльцевых зерен не струйчатая, как у остальных, а шиповатая, перфорированная; семена не на поверхности гипантии, а в сочных костяниках. В другие трибусы *Rubus* тоже не входит. В трибусе *Ulmariae* только один род — *Filipendula*. В трибусе *Sanguisorbae* их больше — *Alchemilla*, *Agrimonia*, *Poterium* и *Sanguisorba*. По строению пыльцевых зерен (рис. 18, 21—23) этот трибус выглядит очень разнообразно, пыльцевые зерна очень разные. У трибуса сборный, а не естественный характер. О гетерогенности этого трибуса пишут М. М. Федорончук и В. Д. Савицький (1987).

Признаки генеративных органов — пыльцевых зерен, семян и гинецея оказались таксономически полезными не на уровне вида, а в подразделениях выше вида. Исходя из морфологии семян, формы и места отхождения столбика можно утверждать, что к самостоятельным подродам рода *Potentilla* принадлежат *Comarum palustre* и *Dasiphora fruticosa*. Следует обратить внимание на то, что подроды *Hypargyrium*, *Dynamidium* и *Chenopotentilla* нельзя объединять в один подрод. По строению пыльцевых зерен видно, что роды *Fragaria*, *Potentilla*, и *Geum* близкие, а род *Rubus* отличается от них и заслуживает самостоятельного трибуса; строение пыльцевых зерен в трибусе *Sanguisorbae* указывает на его сборный (не естественный) характер.

Автор выражает благодарность У. Каллавус, М. Рахи и Н. Кирьяновой за проведение анализов на СЭМ.

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POTENTILLA L. BALTIKUMIS

Tolmuterad ja seemned

Skaneeriva elektronmikroskoobi abil uuriti 21 Baltikumi maranaliigi (*Potentilla* L.) ja neile lähedaste perekondade (alamsugukonnast *Rosoideae*) liikide tolmuterade ja seemnete pindu. Maranate tolmuterad on ühesugused — piklik-elliptilised, kolmevaolised, triibulise pinnaga. Samasugune on ka maranatega ühte triibusesse kuuluvate perekondade *Geum*, *Fragaria* ja *Comarum* esindajate tolm. Samasse triibusesse (*Potentillae*) on arvatud ka perekond *Rubus*, mille tolmuterade pinna ja viljade ehitus erineb ülejäänud perekondade omast niivõrd, et ta peaks kuuluma omaette triibusesse. Triibuse *Sanguisorbae* tolmuterade ehituse võrdlemine osutab sellele, et vaadeldud triibus pole loomulik, vaid kunstlik takson. *Alchemilla* liikide tolm on madalate näsadega, *Agrimonia* tolmuterade pinna mustri moodustavad pööristesse ühinenud triibud, *Sanguisorba* tolmuterad on koguni kuuevaolised ja väga väikeste näsakestega, tolmuterad perekonnas *Poterium* on selgete vagudeta, kolme suurema köbrukesega, väga peeneteralise pinnamustriga.

Perekonnas *Potentilla* on alamperekonnad püstitatud põhiliselt emakakaelte ehituslike iseärasuste põhjal. Kuna tolmuterad on aga täiesti ühesuguse ehitusega, tekib küsimus, kas on õige emakakaela ehitust nii tähtsaks pidada, et selle alusel alamperekonnad püstitada. Alamperekondadevaheliste «piiride» õigsust kinnitab aga ka seemnete ehitus: seemnepinna morfoloogia ja ka seemnete mõõtmed erinevad alamperekondade lõikes.

Kõigi vaadeldud generatiivsete tunnuste põhjal võib Baltikumi maranate näitel öelda, et alamperekonnad selles perekonnas on loomulikud taksonid. S. Juzeptšuki süsteemi alamperekondi *Chenopotentilla*, *Hypargyrium* ja *Dynamidium* pole õige ühendada üheks alamperekonnaks, nagu tehakse «Euroopa flooras»; *Comarum palustre* ja *Dasiphora fruticosa* kuuluvad iseseisvate alamperekondadena perekond *Potentilla* koosseisu.

Malle LEHT

POTENTILLA L. IN THE BALTIC REPUBLICS

Pollen grains and seeds

Surfaces of pollen grains and seeds of 21 species of the Baltic cinquefoils and of some species from 9 closely related genera of the subfam. *Rosoideae* were studied using scanning electron microscope. The pollen of studied cinquefoils is monomorphic: their grains are isopolar, tricolpate, the exine is meridionally striped. The pollen grains of the genera *Geum*, *Fragaria* and *Comarum* which belong to the tribe *Potentillae* are very similar to the grains of *Potentilla*. The genus *Rubus* has also been included in the tribe *Potentillae*, but its pollen and fruits are so different from those of other genera that it should make up a tribe of its own. The heteromorphism of pollen grains in the tribe *Sanguisorbae* indicates that the tribe is not a natural taxon but a combined one: the pollen surface of *Alchemilla* is papillate, that of *Agrimonia* is covered with whitled stripes, that of *Sanguisorba* is slightly granulous and sixcolpate, and that of *Poterium* nearly noncolpate with stripes and rows of very small papillae.

Subgenera in the genus *Potentilla* are mostly based on the structure of styles. As pollen grains are monomorphic, a question arises whether the differences in the form and the position of the style are taxonomically so important that subgenera should be distinguished on this basis. However, the study of seeds reveals some differences between subgenera : in subgen. *Hypargyrium* the seeds are small (about 1 mm long), in subgen. *Dynamidium* they are about 1.5 mm long, and the seeds of *P. anserina*, the only Baltic representative of the subgen. *Chenopotentilla*, are about 2 mm long. The sculpture of the seedcoat is also different: in subgen. *Hypargurium* the network pattern is formed by clear cellwall lines, in subgen. *Dynamidium* the network is formed by emerged cell edges, the surface of cells being flat, in *P. anserina* it resembles parchment paper.

On the basis of all generative characters examined it may be concluded that the genus *Potentilla* consists of subgenera. However, the subgenera *Chenopotentilla*, *Dynamidium* and *Hypargyrium* (Juzeptchuck, 1941) should not be joined into one subgenus, as it has been done in "Flora Europaea" (1968); *Comarum palustre* and *Dasiphora fruticosa* belong to the genus *Potentilla*, to the subgenera of their own.

III

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З. Гуджинскас, М. Лехт

НОВЫЕ ДАННЫЕ О РОДЕ *POTENTILLA* L. (*ROSACEAE*) ВО ФЛОРЕ ЛИТВЫ

Введение

Род *Potentilla* – один из крупнейших и наиболее таксономически сложных родов семейства *Rosaceae*. Сложность заключается в том, что некоторые систематики понимают виды sensu lato, а другие – sensu stricto, постоянно описывают новые таксоны или изменяется статус уже описанных (Лехт, 1987). Основой этих субъективных проблем является «трудный характер» рода – лапчатки размножаются вегетативно, половым путем и апомиктически, встречаются и гибриды. Среди европейских лапчаток обнаружены гибриды между 3/4 видов. Кроме того, на краю ареала вид может вести себя по-иному, чем в центре: в группе *P. argentea* s. l. встречаются все варианты размножения, начиная с полных апомиктов и кончая совершенно сексуальными растениями (Müntzig, 1958). Некоторые виды возникли гибридогенно, но в настоящее время являются облигатными апомиктами.

В Литве недостаточно хорошо изучены видовой состав рода и распространение отдельных видов. До 1987 г. в республике было известно 17 видов *Potentilla*, один из которых – в качестве культивируемого (Natkevičaitė-Ivanauskienė, 1971). Однако 2 вида – *P. tenuiloba* Jord., *P. dissecta* (Wallr.) Zimm. – объединены с *P. argentea*, *P. impolita*. В Прибалтике этот род был представлен 21 видом (Лехт, 1987; Leht, 1987). В 1988 г. после 100-летнего перерыва прибавился еще 1 вид из Латвии – *P. anglica* Laich. (Leht, 1989).

В результате проведенных нами исследований флора Литвы пополнилась 4 видами рода: *P. bifurca* L., о котором уже сообщалось ранее (Гуджинскас, 1989), *P. goldbachii* Rupr., *P. multifida* L., *P. longifolia* Willd. Данные о распространении *P. multifida*, *P. longifolia* приводятся впервые не только для флоры Литвы, но и для флоры Прибалтики в целом. Существовала большая вероятность обнаружения *P. goldbachii*, поскольку он известен в соседних республиках, а в Латвии – даже на юго-восточной границе. Возможна вероятность обнаружения в Литве *P. canescens* Bess., который растет на юго-восточной границе Латвии, в Белоруссии и Калининградской обл.

Значительно пополнились сведения о распространении *P. heidenreichii* Zimm., *P. intermedia* L., *P. supina* L., *P. norvegica* L., которые в Литве считались редкими или очень редкими (Leht, 1987).

Целью настоящей работы явилось исследование видового состава лапчаток (*Potentilla*) в Литве, уточнение распространения некоторых редких видов, а также критическая обработка гербарного материала, имеющегося в гербариях республики.

Методика

В 1987–1989 гг. были обследованы синантропные местообитания и собран гербарный материал, насчитывающий свыше 70 гербарных листов представителей рода *Potentilla*. Критическая обработка гербарного материала по данному роду, хранящегося в Гербарии Института ботаники Литовской академии наук (BILAS) и в Гербарии Кафедры ботаники и генетики Вильнюсского университета (WI), позволила исправить ошибки в определении таких таксономически сложных видов, как *P. intermedia*, *P. heidenreichii*. Литературные данные по этим видам учитывались лишь в том случае, когда они сопровождались диагнозами видов.

Составлены точечные карты распространения некоторых видов. Приведены краткие морфологические описания новых для флоры Литвы видов, составлен ключ для определения прибалтийских видов рода *Potentilla*. Для заносных видов указывается степень натурализации.

Гербарные образцы, подтверждающие нахождение данных видов в Литве, хранятся в Гербарии Института ботаники Литовской академии наук (BILAS).

Результаты и их обсуждение

а. Новые адвентивные виды. *P. bifurca* L. Sp. Pl. 497. 1753. Одревесневающий у основания полукустарничек высотой до 35 см.

Стебли, черешки листьев и цветоножки волосистые. Листья с 2–7 парами боковых листочков, длиной 5–25 и шириной 3–10 мм. Конечный листочек, как правило, 3–лопастный. Прилистники продолговатые, цельные или надрезанные, в нижней части сросшиеся с черешком. Немногочисленные цветки в верхушечном соцветии. Орешки гладкие или слабоморщинистые. *P. bifurca* – восточноевропейско–центральноазиатский вид. В пределах первичного ареала растет в степях, на остепененных лугах, по залежам. О нахождении этого вида в Литве (г. Варена) нами уже сообщалось ранее (Гуджинскас, 1989).

Трехлетние наблюдения за состоянием популяции позволили сделать следующие выводы. В Литве *P. bifurca* цветет во второй половине мая – начале июня. В исследуемой популяции, которая занимает около 150 м^2 при довольно большой плотности растений, цветет только около 5 % индивидов. В течение 1987–1989 гг. образования семян не отмечалось. Вид размножается в Литве, по–видимому, только вегетативным способом. Эпекофит.

P. goldbachii Rupr. Fl. Ingr. 1:319. 1860. Многолетнее растение высотой 15–45 см. Стебли у основания восходящие. Прикорневые листья пальчатые, с (5)5–7 листочками, с обеих сторон зеленые, волосистые. Листочки длиной 1,5–4,5 и шириной 0,6–2 см, зубчатые. Цветки диаметром 12–17 мм, в многоцветковом щитковидно–метельчатом соцветии. Чашечка до 1,5 раза короче венчика, волосистая. Орешки морщинистые.

Распространена в Центральной и Южной Европе, Западной Сибири (Курбатский, 1988).

Некоторые авторы этот вид относят к *P. thuringiaca* Bernh. ex Link. (Ball et al., 1968), а некоторые считают самостоятельным, близкородственным *P. thuringiaca*. *P. thuringiaca* считают западноевропейским видом, а *P. goldbachii* – восточноевропейско–западносибирским (Юрцев, 1984).

В Прибалтике вид ранее был известен из Латвии (Табака и др., 1988) и Эстонии (Лехт, 1987) в качестве заносного. Для Литвы вид приводится впервые.

В Литве впервые *P. goldbachii* обнаружена в г. Кедайняй на территории железнодорожной станции (ж.–д. ст.), на слабозадерненном склоне ж.–д. насыпи, на месте разгрузки вагонов, 13.08.1988. Позже обнаружено еще несколько местонахождений: г. Шяуляй, территория ж.–д. ст., задерненный склон ж.–д. насыпи, 30.08.1988; г. Панявежис, территория ж.–д. ст., задерненный склон ж.–д. насыпи, 26.09.1989; Варенский р–н, территория ж.–д. ст. Валькининкай, между ж.–д. линиями, 19.08.1989; Пренайский р–н, территория ж.–д. ст. Мауручяй, задерненный склон ж.–д. насыпи, 03.09.1989 (рис. 1).

В большинстве случаев обнаруживались небольшие группы растений на задерненных, реже слабозадерненных склонах ж.–д. насыпи, насчитывающие

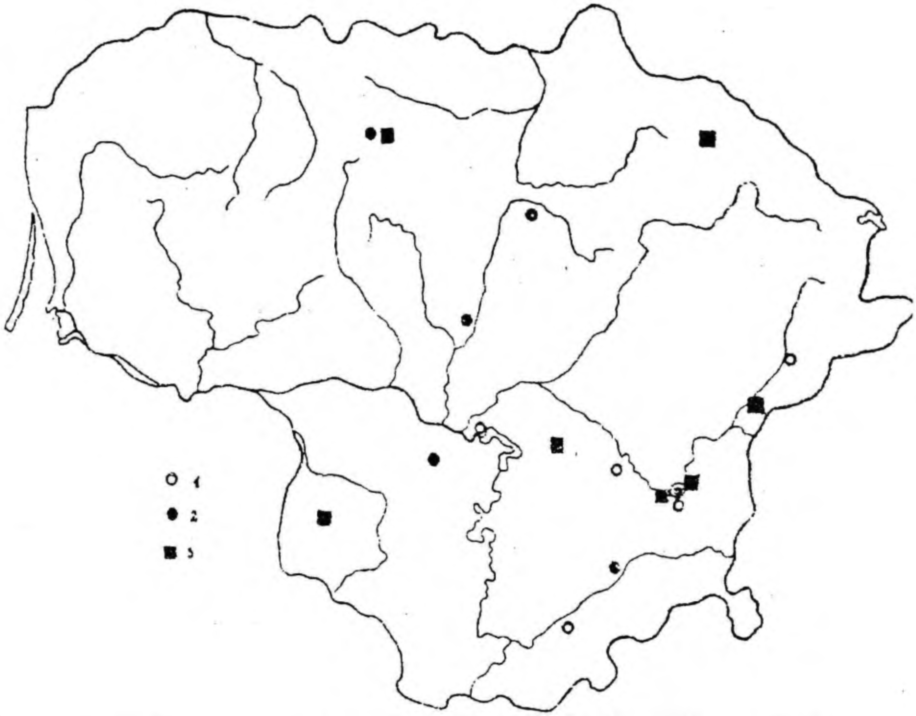

Рис. 1. Распространение *Potentilla intermedia* (1), *P.goldbachii* (2), *P. supina* (3)

от нескольких до 30–40 индивидов. Во всех случаях были собраны цветущие и плодоносящие растения. Бид способен внедряться в полусомкнутые сообщества. Эпекофит.

P. longifolia Willd. ex Schlecht. Ges. Naturf. Freunde Berlin (Mag.) 7:278. 1816 (*P. viscosa* Donn. ex Lehm.). Многолетнее растение с прямым стеблем высотой 15–60 см. Прикорневые листья и нижние стеблевые листья с 3–5(6) парами листочков, с обеих сторон зеленые, железистые, опушенные простыми волосками. Листочки длиной 1,5–5 и шириной 0,5–2 см, надрезанно–крупнозубчатые. Цветки немногочисленные, в щитковидном соцветии. Чашечка густожелезистая, волосистая, равна венчику или длиннее. Наружные линейные чашелистики равны или длиннее яйцевидно–ланцетных внутренних Орешки гладкие или слабоморщинистые.

В пределах первичного ареала вид растет в степях, по суходольным лугам каменистым склонам, в разреженных лесах (Курбатский, 1988). Вид распространен в Сибири, Средней Азии, Монголии. В Европе вид встречается в восточных районах Центральной России (Ball et al., 1968; Курбатский, 1988)

P. longifolia найдена в г. Алитус, в промышленном районе, на слабозадерненном склоне подъездных к хлебокомбинату ж.–д. путей, 28.07.1989, 1 цветущий экземпляр с не вполне созревшими семенами. По–видимому заносится с зерном. Эфемерофит.

Необходимо отметить, что растения, собранные нами в г. Алитус, по некоторым признакам приближаются к *P. acervata* Sójak (столбик с неясными сосочками у основания, растение покрыто разреженными короткостебельчатыми железками), а по некоторым - к *P. longifolia* s. str. (цветки диаметром 10–15 мм, в немногоцветковом щитковидном соцветии, чашечка длиннее венчика). Поэтому мы его рассматриваем как *P. longifolia* s.l.

P. multifida L. Sp. Pl. 496. 1753. Многолетнее растение. Стебли высотой 5–60 см, приподнимающиеся или простертые, часто дуговидные. Прикорневые листья сверху зеленые, волосистые или слабовойлочные, снизу – серо– или беловойлочные. Листочки рассечены почти до средней жилки на линейноланцетные или линейные сегменты. Цветки диаметром 7–10 мм, в немногоцветковом метельчатом соцветии; чашечка почти равна венчику. Орешки гладкие или слегка морщинистые.

Вид распространен в юго-восточной части Европы, Сибири, Средней, Центральной и Восточной Азии (Курбатский, 1988). В качестве заносного вид известен из Московской (Макаров, Игнатов, 1983) и Калининской (Малышева, 1980) областей. В пределах первичного ареала вид растет в степях, по сухим лугам, каменистым склонам, залежам, вдоль дорог.

В Литве *P. multifida* впервые обнаружена в г. Шяуляй, на территории товарной ж.-д. ст., на задерненном склоне ж.-д. насыпи, у площадки для разгрузки вагонов, 30.08.1988 и 06.08.1989. В 1988 г. найдено около 15 плодоносящих растений. При повторном обследовании местонахождения в 1989 г. было найдено свыше 30 растений, половина из которых были ювенилы. Это позволяет сделать вывод, что растения дают жизнеспособные семена и вид укрепляется в полусомкнутом сообществе, в котором преобладают *Poa pratense, Medicado falcata, Artemisia campestre, A. vulgare, Achillea millefolium, Potentilla argentea, P. heidenreichii* и др. Эпекофит.

Необходимо отметить, что растения, собранные в г. Шяуляй, по некоторым признакам приближаются к близкородственному с *P. multifida* L. виду *P. tergemina* Sójak. Жилки собранных нами растений с нижней стороны листьев негусто опушены прямыми волосками, а стебли и черешки листьев оттопыренно-волосистые. У *P. multifida* s. str. жилки нижней стороны листьев с немногими прямыми волосками, а стебли и черешки листьев прижато-волосистые. Однако эти признаки недостаточно устойчивы, и трудно указать точную принадлежность растений из Шяуляй к какому-нибудь одному из нескольких выделяемых из объема *P. multifida* s. l. более мелких видов.

6. Новые данные о редких видах. P. intermedia L. – восточно-европейский бореальный сорный вид, широко распространившийся в Европе. Ареал вида доходит до восточно-европейской лесотундры (Юрцев, 1984).

В Литве вид считают заносным (Natkevičaitė-Ivanauskienė, 1971). В литературе имеются указания о нахождении вида в г. Вильнюс, Пасвальском р-не (Понишкелис) (Natkevičaitė-Ivanauskienė, 1971), в Шяуляй (Мотекайтите, 1985), Зарасайском (Балтришкес) и Тяльшяйском (Кегай) районах (Tupčiauskaitė, 1987). Однако после критической обработки гербарного материала оказалось, что сборы из Пасвальского, Зарасайского и Тяльшяйского районов относятся к *P. heidenreichii* Zimm., а образцы *P. intermedia* были только из Вильнюса. Проверить точность определения образца из г. Шяуляй (Мотекайтите, 1985) оказалось невозможным из-за отсутствия гербарного образца.

В настоящее время выявлен ряд новых местонахождений *P. intermedia* в Литве: г. Вильнюс, Жямейи–Паняряй, задерненный склон ж.-д. насыпи, 04.06.1983; г. Вильнюс, территория товарной ж.-д. ст., ж.-д. пути, 04.06.1988; г. Вевис (Тракайский р-н), территория ж.-д. ст., ж.-д полотно, 09.09.1987; г. Каунас, территория товарной ж.-д. ст., слабозадерненный склон ж.-д. насыпи, 06.09.1987; г. Варена, территория хлебокомбината, склон ж.-д. насыпи, 31.05.1989; Швянчёнеляй (Швянчёнский р-н), подъездные к хлебокомбинату ж.-д. пути, 28.06.1989 (рис. 1).

P. heidenreichii Zimm. – восточно-европейский бореальный сорный вид, выделенный из *P. intermedia* L. s. l. А. Цимметером (Zimmeter, 1884). Этот таксон часто считают подвидом или вариететом *P. intermedia*, или даже «игнорируют» его, не признавая его как самостоятельный таксон. В старой прибалтийской ботанической литературе очень часто использовали в смысле *P. heidenreichii* Zimm. неправильный синоним *P. inclinata* Vill. *P. inclinata* Vill. является синонимом *P. canescens* Bess. (*P. adscendens* Waldst. et Kit.) – степного вида, являющегося редким пришельцем в Латвии и Эстонии.

В литературе для Литвы вид ранее был констатирован только из Вильнюса и Кайшядорского (Дарсунишкис) (Natkevičaitė, 1951; Natkevičaitė-Ivanauskienė, 1971) и Игналинского (Симонишкес) (Апаля, 1977) районов.

Однако после критической обработки гербарного материала оказалось, что многие экземпляры этого вида определялись как *P. intermedia*. Ошибочным оказалось определение экземпляров из Кайшядорского (Дарсунишкис) р–на, а из Игналинского (Симонишкес) р–на отсутствуют гербарные образцы. Имеются гербарные образцы *P. heidenreichii* только из Йонишкелиса, Вильнюса, Варенского (ж.–д. ст. Матуйзос)(BILAS), Тяльшяйского (Кегай) и Зарасайского (Балтришкес) районов (WI).

В настоящее время авторами выявлен ряд новых местонахождений *P. heidenreichii* в Литве: г. Вильнюс (Балтупяй, Вилкпеде, Науйни–Вильня, Жверинас, ж.–д. станция), Вевис (Тракайский р–н), Дукштас (Игналинский р–н), Лентварис (Тракайский р–н), Гайжюнай (Йонавский р–н), Кайшядорис, Каунас (ж.–д. станция, Жямойи–Фреда), Клайпеда, Крятинга, Кедайняй, Кибартай (Вилкавишкский р–н), Бездонис (Вильнюсский р–н), Мариямполе (бывший Капсукас), Швянчёнеляй (Швянчёнский р–н), Дягучяй (Зарасайский р–и), Пажеймяне (Швянчёнский р–н), Радвилишкис, Шяуляй (рис. 2). Во всех случаях найдены группы растений, насчитывающие от нескольких до нескольких сот индивидов. В республике сейчас известно 43 местонахождения: 34 – на склонах ж.–д. насыпей и в других местообитаниях, приуроченных к железным дорогам, а 9 – в других синантропных местообитаниях: возле дорог, на пустырях, свалках и т.д.

Рис. 2. Распространение *Potentilla heidenreichii* Zimm: *1* – по данным авторов, 2 – по гербарным данным

P. norvegica L. – евразиатский бореальный субконтинентальный сорный вид. В Северной Америке встречается особая раса – *P. monspeliensis* L., которую часто включают в объем *P. norvegica* L. s. l., являющегося циркумполярным видом. В качестве заносного и натурализовавшегося вид известен из Новой Зеландии и Южной Америки (Юрцев, 1984).

В основной части своего ареала вид обычен на участках с нарушенной растительностью. Может быть, поэтому вид в Литве считают заносным (Natkevičaitė, 1951; Natkevičaitė-Ivanauskienė, 1971), что является весьма спорным.

В настоящее время известно свыше 40 местонахождений *P. norvegica* в следующих районах Литвы: Аникщяйском (Аникщяй), Алитусском (Алитус, Даугай, Мирославас, Обялия), Акмянском (Ужвянтис), Биржайском (Даужгиряй), Варенском (Варена, Друскининкай, Дубичяй, Марцинконис, Рудня, Пувочяй), Вильнюсском (Вильнюс, Мицкунай, Бездонис), Зарасайском (Тильже, Дягучяй), Игналинском (Казимеравас, Спечкус, Калтаненай, Гинучяй), Йонишкском (Жагаре), Йонавском (Упнинкай), Кайшядорском (Круонис), Крятингском (Паланга), Молетском (Молетай, Миндунай), Мажяйкском (Аукcодис), Пасвальском (Йонишкелис), Паневежском (Жалёйи), Пренайском (Бирштонас), Рокишкском (Южинтай), Тракайском (Вевис, Дусмянис, Балтойи-Воке, Палукнис), Укмяргском (Жямайткемис), Утянском (Вайшноришкес), Швянчёнском (Швянчёнис, Лаукагалис, Бааранава), Шальчининкском (Тятенай, Пирчюпяй), Шяуляйском (Шяуляй). Все местонахождения сосредоточены в основном в восточной и юго-восточной частях республики, а в центральной и северной встречается редко. В западной части Литвы известны одиночные местонахождения, а в юго-западной вид не констатирован. Это можно объяснить тем, что вид является субконтинентальным.

P. supina L. – распространен в Европе, на Кавказе, в Средней Азии и Северной Африке, а в качестве заносного – в Северной Америке (Natkevičaitė-Ivanauskienė, 1971). В Литве вид ранее был известен как очень редкий, только из г. Вильнюса (Natkevičaitė-Ivanauskienė, 1971).

В результате исследований выявлен целый ряд новых местонахождений P. supina: г. Вильнюс, ул. Майронё, сорное место у р. Вильняле, 02.07.1988; г. Кайшядорис, территория ж.-д. ст., слабозадерненный склон ж.-д. насыпи, 19.06.1988 и 13.07.1989; г. Рокишкис, территория ж.-д. ст., ж.-д. полотно, 14.09.1988; г. Шяуляй, территория ж.-д. ст., незадерненный склон ж.-д. насыпи, 30.08.1988; г. Вилкавишкис, территория хлебокомбината, ж.-д. линия, 02.09.1989; г. Вильнюс, территория товарной ж.-д. ст., склон ж.-д. насыпи, 19.06.1989; г. Вильнюс, ж.-д. ст. Паняряй, распределительные пути, 22.06.1989; ж.-д. ст. Пабраде (Швянчёнский р-н), ж.-д. линия у платформы для разгрузки вагонов, 30.07.1989. Во всех случаях растения цвели и плодоносили (рис. 1). Эпекофит.

в. *Вопросы хорологии.* В результате исследований живого и гербарного материалов видов рода *Potentilla*, их местопроизрастаний, а также изучения литературных данных возникли некоторые соображения, связанные с хорологией *P. intermedia, P. heidenreichii, P. norvegica, P. supina*. В Литве виды *P. intermedia, P. heidenreichii* считаются заносными (Natkevičaitė, 1951; Natkevičaitė-Ivanauskienė, 1971), а на соседних с Литвой территориях принимаются в качестве спонтанных синантропных видов (Leht, 1987; Лехт, 1987; Табака и др., 1988). Вольф (Wolf, 1908) *P. intermedia* L. s. l. считает спонтанным в северных и средних провинциях европейской части России и Южной Скандинавии. Сейчас *P. intermedia, P. heidenreichii* растут в основном около железных дорог и на других рудеральных местообитаниях, и это наблюдается в пределах всего ареала обоих видов (Кобелева, 1976; Юрцев, 1984). Кроме того, литературные данные о них имеются с первой половины XIX в. (Ledebour, 1844; Wiedemann, Weber, 1852), когда железные дороги, являющиеся главным источником заносных видов, были еще слабо развиты. Приуроченность к рудеральным местообитаниям можно объяснить тем, что эти виды отличаются небольшой конкурентоспособностью, им нужны сухие, открытые местообитания, какими и являются рудеральные места. Поэтому мы считаем, что эти 2 вида в Литве являются спонтанными.

Мы считаем, что необоснованным является и то, что *P. norvegica* в Литве рассматривается как заносный вид (Natkevičaitė, 1951; Natkevičaitė-Ivanauskienė, 1971). В Литве так же, как в Эстонии и Латвии, этот вид обитает в основном на торфяных почвах, на берегах каналов, около дорог, по краям болот, иногда на железных дорогах и в других рудеральных местообитаниях. Может быть, поэтому вид и принимается в качестве заносного. Однако *P. norvegica* в пределах всего своего ареала растет на участках с нарушенной

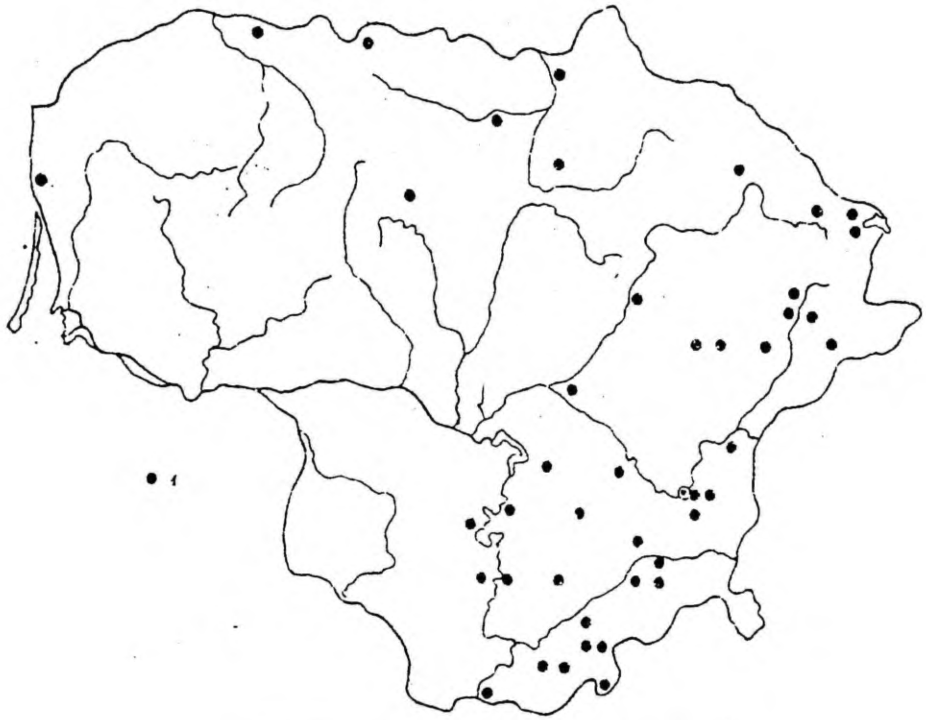

Рис. 3. Распространение *Potentilla norvegica* (*1*)

растительностью. Литературные данные об этом виде имеются уже с начала XIX в. (Grindel, 1803; Jundzill, 1811). Характер распространения этого вида в республике (рис. 3) хорошо отражает его субконтинентальный характер. Мы считаем, что *P. norvegica*, как и предыдущие 2 вида, в Литве является спонтанным.

P. supina ранее М. Наткевичайте (Natkevičaite, 1951) приводила для Литвы как заносный вид, но во «Флоре Литовской ССР» (Lietuvos TSR flora, 1971) она уже не указывает на то, что вид заносный. Мы думаем, что *P. supina*, появившийся в Литве в 40–е годы (первая находка в 1945 г. в г. Вильнюс (WI)), является типичным заносным видом с довольно низкой степенью натурализации и обитает только в местообитаниях с полностью уничтоженной или очень сильно нарушенной естественной растительностью.

Ключ для определения видов рода *Potentilla* L. Прибалтики

1. Листья перистые 2
– Листья пальчатые или тройчатые 7
2. Кустарники или полукустарники, одревесневающие у основания . . 3
– Однолетние, двухлетние или многолетние травы 4
3. Кустарники с цельнокрайними листочками и большими (20–30 мм) цветками . . . . 1. *P. fruticosa* L.
– Невысокие полукустарнички с одревесневающими у основания стеблями и одревесневшими подземными частями; конечные листочки, как правило, 3–лопастные . . . . 2. *P. bifurca* L.
4. Растения с ползучими, укореняющимися в узлах побегами; листья с многочисленными острыми зубцами, цветки одиночные, диаметром 15–20 мм . . . . 3. *P. anserina* L.
– Растения без ползучих побегов, цветки в соцветиях 5
5. Одно– или двухлетние травы с тонкими простертыми или

восходящими стеблями, цветки диаметром 5–6 мм; соцветие рыхлое, чашелистики длиннее венчика . . . . .4. *P. supina* L.

Многолетние травы с прямым или дугообразно восходящими стеблями. 6

Верхняя сторона листьев зеленая, нижняя – беловойлочная; чашечка почти равна венчику или немного короче его; растения без железистых волосков; стебли дугообразно восходящие . . . . 5. *P. multifida* Lehm.

Листья с обеих сторон зеленые, все части растения с железистыми волосками; чашечка длиннее венчика; стебли прямостоячие . . . . 6. *P. longifolia* Willd.

Листья тройчатые 8

Листья пальчатые, с 5–7(8) листочками 10

Нижние стеблевые листья черешчатые 9

Все стеблевые листья без черешков, с большими листообразными глубоконадрезанными прилистниками, цветки 4–членные, одиночные на длинных цветоносах . . . . 7. *P. erecta* (L.) Rausch.

Многолетники с утолщенным корневищем, цветки 4–членные, стебли часто лежащие, осенью могут укореняться в узлах; растения почти голые или покрыты немногочисленными прижатыми волосками . . . . *P. anglica* Laich.

Одно– или двухлетние растения с 5–членными цветками; волоски жестковатые, отстоящие; конечные листочки иногда 3–лопастные . . . . 8. *P. norvegica* L.

0. Стебли приподнимающиеся или прямые, цветки в рыхлых соцветиях 11

Стебли ползучие, укореняющиеся в узлах, цветки одиночные, большие (диаметром 15–25 мм) . . . . 9. *P. reptans* L.

1. Прикорневые листья ко времени цветения высыхают 12

Во время цветения розетки прикорневых листьев сохраняются . . 17

2. Высокие, прямые, ветвистые только в пределах соцветия растения с мягкими длинными и короткими оттопыренными волосками (самым волосистым является соцветие), листочки удлиненно–овальные, с острыми равномерными зубцами 13

Растения с дугообразно приподнимающимися ветвистыми стеблями, листья с немногочисленными прижатыми волосками до войлочных, листочки обратнояйцевидные, часто лопастные, зубчики неравные, тупые 14

.3. Большие растения (высотой 30–70 см), с длинными и короткими оттопыренными волосками, цветки большие (диаметром 15–25 мм) . . . .*P. recta* L.

- Растения поменьше (высотой 15–50 см), с прижатым войлоком и длинными рыхлыми оттопыренными волосками, цветки диаметром 10–15 мм . . . .*P. canescens* Bess.

14. Листочки в верхней половине неравно глубоконадрезанные, с острыми зубцами, внизу цельнокрайние, клиновидные, по краям завернутые, внизу беловойлочные 15

- Листочки с неравными тупыми зубцами, конечные часто 2– или 3–лопастные, снизу с немногими прижатыми волосками до серовойлочных, края листочков незавернутые 16

15. Листочки только снизу беловойлочные, сверху зеленые . . . . 11. *P. argentea* L.

- Листочки снизу беловойлочные, сверху седоватые от волосков . . . . 12. *P. impolita* L.

16. Листочки светло–зеленые, очень тонкие, почти голые; стебли зеленые . . . . 13. *P. intermedia* L.

- Листочки снизу волосистые, до войлочных, сверху темно–зеленые, листочки плотные, стебли часто

красноватые . . . . 14. *P. heidenreichii* Zi
17. Листочки с прижатыми волосками (почти голые) до войлочных, прикорневые листья пятерные . . . .
– Листочки покрыты длинными и короткими оттопыренными волосками, высота растений 20–50 см, прикорневые листья семер (редко пятерные), длинночерешчатые . . . . . 15. *P. goldbachii* Ru
18. Листочки почти голые, с немногими прижатыми волосками или серые от звездчатых волосков . . . .
– Листочки снизу войлочные, растения похожи на *P. argentea* . . . .
19. Растения без звездчатых волосков . . . .
– Растения со звездчатыми волосками . . . .
20. Растения высотой 10–20 см, почти голые, корневище плоское благодаря двухрядному расположению коричневых, голых, чешуйчатых прилистников . . . . *P. crantzii* (Crantz) Be
– Растения высотой 5–15(20) см, подушкообразные, листочки с прижатыми простыми волосками, корневище округлое, черное; на прилистниках прикорневых листьев короткие, белые, жесткие волоски . . . . *P. tabernaemontani* As
21. На нижней стороне листочков среди простых волосков имеются звездчатые волоски с 3–10 ветвями . . . . *P. subarenaria* Bo
– Растения серые от покрывающих их многоветвистых (15–40 ветвей) звездчатых волосков; простые волоски отсутствуют . . . . 16. *P. arenaria* Bork
22. На листочках среди простых волосков одиночные длинные ветвис звездчатые волоски . . . . 17. *P. silesiaca* Uech
– Звездчатые волоски отсутствуют 2
23. Листочки с 2–4 равномерными тупыми зубчиками на обоих краях верхняя сторона с прижатыми шелковистыми волосками . . . . 18. *P. leucopolitana* Mu
– Листочки с глубоконадрезанными лопастями, с 4–7 острыми зубчиками на обоих краях . . . . 19. *P. thyrsiflora* Zimn

Примечание. В таблицу включены все виды рода *Potentilla*, встр ющиеся в Прибалтийских республиках. Виды, которые во флоре Л отсутствуют, в таблице приведены без порядкового номера.

Таким образом, в настоящее время во флоре Прибалтики род *Pote* представлен 24, а во флоре Литвы – 19 видами. 2 вида, описанные во «Ф Литовской ССР», – *P. tenuiloba* Jord., *P. dissecta* (Wallr.) Zimm. – в насто время не признаются в ранге самостоятельных видов.

Заносными в Литве являются *P. bifurca, P. goldbachii, P. longifoli multifida, P. recta, P. supina.* Мы считаем, что 3 вида, ранее считавш заносными, – *P. intermedia, P. heidenreichii, P. norvegica* – в Литве являю спонтанными.

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NAUJI DUOMENYS APIE *POTENTILLA* L. (*ROSACEAE*) GENTĮ LIETUVOS FLOROJE

Reziumė

Lietuvoje anksčiau buvo žinoma 17 sidabražolių (*Potentilla* L.) rūšių. 1987–1989 m., atlikus floristinius tyrimus sinantropinėse augimvietėse, buvo rastos 4 naujos rūšys – dvišakė sidabražolė (*P. bifurca* L.), Goldbacho sidabražolė (*P. goldbachii* Rupr.), daugiaskiltė sidabražolė (*P. multifida* L.) ir ilgalapė sidabražolė (*P. longifolia*). 2 iš jų – *P. multifida* ir *P. longifolia* pirmą kartą rastos ne tik Lietuvoje, bet ir visose Baltijos šalyse. *P. multifida* pirmą kartą rasta 1988 m. Šiauliuose. *P. goldbachii* rasta 5 vietose: pirmą kartą 1988 m. Kėdainiuose, o vėliau – Šiauliuose, Panevėžyje, Valkininkuose (Varėnos raj.) ir Mauručiuose (Prienų raj.). *P. bifurca* rasta 1987 m. Varėnoje, kur jos augimvietė ant seno geležinkelio pylimo šlaito užima apie 150 m² plotą. *P. longifolia* rasta 1989 m. Alytuje.

Labai pagausėjo duomenų apie *P. heidenreichii, P. intermedia, P. supina* ir *P. norvegica*, kurios anksčiau buvo žinomos kaip labai retos ir retos rūšys, paplitimą. Aptariami šių rūšių chorologijos klausimai. Manome, jog *P. heidenreichii, P. intermedia* ir *P. norvegica* yra spontaninės rūšys. Lietuvoje yra 6 užnėštinės sidabražolių rūšys: *P. bifurca, P. goldbachii, P. longifolia, P. multifida, P. recta* ir *P. supina*.

Pateikiamos naujų rūšių morfologinės charakteristikos ir lentelė Baltijos respublikose augančioms sidabražolėms apibūdinti.

Dabar Baltijos respublikose yra žinomos 24, o Lietuvoje – 19 sidabražolių rūšių. 2 rūšys – *P. tenuiloba* Jord. ir *P. dissecta* (Wallr.) Zimm., aprašytos „Lietuvos TSR floroje", dabar nepripažįstamos savarankiškomis rūšimis. Yra didelė tikimybė Lietuvoje rasti dar 2 užnėštines šios genties rūšis - *P. anglica* ir *P. canescens*, kurios auga kaimyninėse respublikose.

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1990.04.25

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NEW DATA ON THE *POTENTILLA* L. (*ROSACEAE*) GENUS IN THE LITHUANIAN FLORA

Summary

The *Potentilla* genus was represented in the Lithuanian flora by 17 species. After floristic investigations in synantropic habitats in 1987–1989 4 species new for the Lithuanian flora were found: *P. bifurca, P. multifida, P. goldbachii* and *P. longifolia*. Two of them – *P. multifida* and *P. longifolia* – are new for the flora of all the Baltic republics.

Information on the distribution of *P. heidenreichii, P. intermedia, P. norvegica* and *P. supina*, which were very rare or rare in Lithuania was considerably expanded.

P. multifida was first found in Lithuania in 1988 on the railway embankment in Šiauliai. *P. goldbachii* was discovered in 5 localities: first in 1988 in Kėdainiai, later in Šiauliai, Panevėžys, Valkininkai (Varėna district) and Mauručiai (Prienai district). *P. bifurca* was found in 1987 in Varėna, where it grows on the old railway embankment and occupies about 150 square metres. *P. longifolia* was found in 1989 in Alytus.

We suppose, that *P. heidenreichii, P. intermedia* and *P. norvegica* are spontaneous whereas *P. bifurca, P. goldbachii, P. longifolia, P. multifida, P. recta* and *P. supina* are adventitious in Lithuania. Morphological characteristics of the new species and a key to *Potentilla* ones which are known in the Baltic republics are

given.

Now the *Potentilla* genus is represented by 19 species in the Lithuanian flora and by 24 species in that of the Baltic republics. Two species – *P. anglica* and *P. canescens* – may be found in Lithuania, as they occur in the neighbouring countries.

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Реферат

НОВЫЕ ДАННЫЕ О РОДЕ *POTENTILLA* L. (*ROSACEAE*) ВО ФЛОРЕ ЛИТВЫ

З. Гуджинскас, М. Лехт – Ekologija. 1991. Nr. 1. P. 106-116.

Приводятся данные о 4 новых заносных (*P. bifurca*, *P. goldbachii*, *P. longifolia*, *P. multifida*) и 4 редких (*P. intermedia*, *P. heidenreichii*, *P. norvegica*, *P. supina*) для флоры Литвы видах рода *Potentilla*, обнаруженных в 1987–1989 гг. во время флористического обследования синантропных местообитаний.

Для новых видов приводится краткая морфологическая характеристика, общее распространение, известные местонахождения в Литве, степень натурализации. Для редких видов приводятся новые местонахождения, карты распространения и критические замечания по их хорологии.

Дается ключ для определения видов рода *Potentilla* Прибалтики.

Иллюстраций 3, библиогр. 23 назв.

IV

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11. *Potentilla* L.[*] Sp. Pl. 495. 1753.
Maran; retējs; sidabražolė; лапчатка.

Таблица для определения балтийских видов[**]

1\. Листья перистые 2

– Листья пальчатые или тройчатые 5

2\. Растения с ползучими, в узлах укореняющимися побегами. Листья с многочисленными острыми зубцами, цветки одиночные, 1,5-2 см в диам.

3\. *P. anserina* L.

– Побеги не ползучие, не укореняющиеся, листочки цельнокрайние 3

3\. Одно- или двухлетние травянистые растения с тонкими стеблями, цветки 5-6 мм в диам., соцветие рыхлое, чашелистики длиннее венчика

10\. *P. supina* L.

– Кустарники или полукустарники одревесневающие при основании, чашелистики короче венчика 4

4\. Кустарники с цельнокрайними листочками и большими (2-3 см диам.) цветками

1\. *P. fruticosa* L.

– Невысокие полукустраники с деревянистыми подземными частями, конечные листочки обычно 3-2-лопастные, цветки 8-15 мм диам.

2\. *P. bifurca* L.

5\. Листья тройчатые 6

– Листья пальчатые, с 5-7 (8) листочками 8

6\. Нижние стеблевые листья черешчатые 7

– Все стеблевые листья без черешков, с большими листообразными глубоко надрезанными прилистниками, цветки четырехчленные, одиночные, на длинных цветоносах.

20\. *P. erecta* (L.) Räusch.

7\. Многолетники с утолщенным корневищем, цветки четырехчленные, стебли обычно лежащие, осенью нередко укореняющиеся в узлах; растения почти голые или слабо прижатоволосистые

21\. *P. anglica* Laich.

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Authors: M. Leht; Z. Eglīte; M. Lapelė.

[**] Составила М. Лехт.

– Одно- или двухлетние растения с 5-мерными цветками; волоски жестковатые, оттопыренно отстоящие. Конечные листочки иногда 3-лопастные
11. *P. norvegica* L.

8. Стебли приподнимающиеся или прямые, цветки в рыхлых соцветиях 9

– Стебли ползучие, укореняющиеся в узлах, цветки одиночные, большие, 1,5-2,5 см диам.
22. *P. reptans* L.

9. Прикорневые листья ко времени цветения высыхают, цветущие побеги густо облиственные 10

– Во время цветения розетка прикорневых листьев сохраняется 15

10. Высокие, прямые, ветвистые только в пределах соцветия растения с мягкими, длинными и коротко оттопыренными волосками (наиболее волосистым является соцветие), листочки удлиненно-овальные, с острыми равномерными зубцами 11

– Растения с дугообразно приподнимающимися ветвистыми стеблями, листья с немногими прижатыми волосками до войлочных, листочки обратнояйцевидные, часто лопастные, зубчики неравные, тупые 12

11. Крупные растения, 30-70 см высоты, с длинными и коротко оттопыренными волосками, цветки большие, 1,5-2,5 см диам.
14. *P. recta* L.

– Растения не крупные, 15-50 см высоты, с хорошо выраженным войлочком и длинными рыхлыми оттопыренными волосками, цветки 1-1,5 см диам.
6. *P. canescens* Bess.

12. Листочки в верхней половине неравно глубоко надрезанные, с острыми зубцами, внизу цельнокрайние, клиновидные, по краям завороченные, по крайней мере снизу беловойлочные 13

– Листочки с неравными тупыми зубцами, конечные часто 2- или 3-лопастные, снизу с немногими прижатыми волосками до серовойлочных, края листочков незавороченные 14

13. Листочки только снизу беловойлочные, сверху зеленые
4. *P. argentea* L.

– Листочки снизу беловойлочные, сверху более менее опушенные
5. *P. impolita* L.

14. Листочки светло-зеленые, очень тонкие, почти голые; стебли зеленые
13. *P. intermedia* L.

– Листочки снизу волосистые до войлочных, сверху темно-зеленые, плотные; стебли часто красноватые
12. *P. heidenreichii* Zimmet.

15(9). Листочки с прижатыми волосками (почти голые) до войлочных, прикорневые листья пятерные 16

– Листочки покрыты длинными и коротко оттопыренными волосками, растения 20-50 см высоты, прикорневые листья семерные (редко пятерные), длинночерешчатые
15. *P. goldbachii* Rupr.

16. Листочки почти голые или серые, покрытые немногими прижатыми или звездчатыми волосками 17

– Листочки снизу войлочные, растения похожие на *P. argentea* 20

17. Растения без звездчатых волосков 18

– Растения с звездчатыми волосками 19

18. Растения 10-25 см высоты, почти голые, корневище плоское благодаря двухрядному расположению коричневых, голых, чешуйчатых прилистников
16. *P. crantzii* (Crantz) G. Beck ex Fritsch
– Растения 5-15 (20) см высоты, подушкообразные, листочки с прижатыми простыми волосками, корневище округлое, черное; на прилистниках прикорневых листьев короткие белые жесткие волоски
17. *P. tabernaemontani* Aschers.
19. На нижней стороне листочков среди простых волосков звездчатые многоветвистые (3-10) волоски
19. *P.* × *subarenaria* Borb. et Zimmet.
– Растения серые от покрывающих их многоветвистых (15-40) звездчатых волосков, простых волосков нет
18. *P. arenaria* Borkh.
20. На листочках среди простых волосков одиночные длинно-ветвистые звездчатые волоски
8. *P. silesiaca* Uechtr.
– Звездчатых волосков нет 21
21. Листочки с 2-4 равномерными тупыми зубчиками по краям, сверху прижатыми шелковистыми волосками
7. *P. leucopolitana* P. J. Muell.
– Листочки с глубоко надрезанными лопастями, с 4-7 острыми зубчиками по краям
9. *P. thyrsiflora* Zimmet.

Key to the Baltic species*

1. Leaves pinnate 2
– Leaves digitate or ternate 5
2. Stems creeping, rooting at the nodes, leaflets regularly toothed, flowers 1.5-2.0 cm in diam., solitary
3. *P. anserina* L.
– Stems are not creeping, not rooting at nodes, leaflets have no teeth 3
3. Annual or biennial herbs with week stems, flowers 5-6 mm in diam., petals shorter than sepals, numerous
10. *P. supina* L.
– Shrubs or undershrubs, petals longer than sepals 4
4. Many-branched shrubs with entire leaflets and large flowers (2-3 cm in diam.)
1. *P. fruticosa* L.
– Low undershrubs with woody underground parts, leaflets 2- to 3-fid at apex, flowers 8-15 mm in diam.
2. *P. bifurca* L.
5. Leaves ternate 6
– Leaves digitate, with 5-7(8) leaflets 8
6. At least lower stem-leaves petiolate 7
– All stem-leaves without petioles, with large stipules resembling leaflets. Stems erect, flowers 4-merous, solitary on long petioles
20. *P. erecta* (L.) Räusch.

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* Compiled by M. Leht.

7. Perennials with stout rhizomes, flowers 4-merous, stems often lying on the ground, rooting at the nodes in autumn, leaflets covered with few adpressed hairs
21. *P. anglica* Laich.

– Annual or biennial herbs with 5-merous flowers. Sometimes the topmost leaflet is divided into three lobes. Leaflets covered with unpressed harsh solitary hairs
11. *P. norvegica* L.

8. Ascendent or erect plants, flowers in inflorescences 9

– Stems creeping, rooting at nodes, flowers large, 1.5-2.5 cm in diam., solitary
22. *P. reptans* L.

9. Basal rosette of leaves dead at flowering time, flowering stems with several leaves 10

– Plants with a living basal rosette of leaves at flowering time 15

10. Plants erect, high, branching in the inflorescence only, covered with long soft unpressed hairs (inflorescence being most hairy) leaflets oblong-ovate, with regular sharp teeth 11

– Plants with ascendent branching stems, leaflets obovate-cuneate, sometimes lobed, with irregular, obtuse teeth, covered with sparse adpressed to tomentose hairs 12

11. Large plants, 30-70 cm high, covered with long and short erect hairs, flowers large, 1.5-2.5 cm in diam.
14. *P. recta* L.

– Somewhat smaller herbs, 15-20 cm high, grey-tomentose with some long simple hairs, flowers 1.0-1.5 cm in diam.
6. *P. canescens* Bess.

12. Leaflets white-tometose at least beneath, deeply incise-dentate at the top, entire at the base, with edges rolled beneath 13

– Leaflets irregulary obtuse-toothed but not deeply incised, although the terminal leaflet of basal leaves may be 3-lobed, glabrous to grey-tomentose beneath, with edges not rolled beneath 14

13. Leaflets white-tomentose beneath, green above with some straight adpressed hairs
4. *P. argentea* L.

– Leaflets tomentose both above and beneath
5. *P. impolita* L.

14. Leaflets thin, light-green, nearly glabrous, plane. Stems green
13. *P. intermedia* L.

– Leaflets more or less grey-tomentose beneath, dark green, thick. Stems sometimes reddish
12. *P. heidenreichii* Zimmet.

15(9). Leaflets with adpressed hairs (nearly glabrous) to tomentose, basal leaves usually 5-merous 16

– Leaflets with long and short erect hairs, plants 20-50 cm high, basal leaves long-petioled, with 7 leaflets (rarely with 5)
15. *P. goldbachii* Rupr.

16. Leaflets nearly glabrous or grey because of stellate hairs 17

– Leaflets tomentose beneath, plants resemble *P. argentea* 20

17. Plants with simple hairs only 18

– Plants with stellate hairs 19

18. Plants 10-25 cm high, nearly glabrous, withered brown stipules of basal leaves making rootstock flat
16. *P. crantzii* (Crantz) G. Beck ex Fritsch

– Plants 5-15 (20) cm high, with adpressed simple hairs, rootstock black, roundi: Edges of stipules of basal leaves covered with coarse white straight hairs
17. *P. tabernaemontani* Asche

19. 3-10 branched stellate hairs between simple hairs beneath the leaflet
19. *P.* × *subarenaria* Borb. ex Zimm

– Leaflets grey from 15-40 branched stellate hairs, without simple hairs
18. *P. arenaria* Borl

20. Long-branched stellate hairs between simple hairs
8. *P. silesiaca* Uech

– Plants without stellate hairs . . . .

21. Leaflets with 2-4 obtuse regular teeth on both sides, with silky hairs above
7. *P. leucopolitana* P. J. Mue

– Leaflets deeply incised with 4-7 sharp teeth on both sides
9. *P. thyrsiflora* Zimm

1. subgenus *Trichothalamus* (Lehm.) Reichenb.

1. ***Potentilla fruticosa*** L. Sp. Pl. 495. 1753; Grindel, Bot. Taschenb. 162. 1803, si auct.; Ledeb. Fl. Ross. 2: 61. 1843; Wied. et Weber, Beschr. phan. Gew. Esth-, Liv-Curl. 276. 1852; Kuprev. et al. Vadovas 122. 1934; Ball, Pawł. et Walters in Fl. Euro 2: 39. 1968; Natk.-Ivanausk. in Liet. fl. **4**: 163. 1971. – *Dasiphora fruticosa* (L.) Ryd in Mem. Dep. Bot. Columbia Univ. 2: 188. 1898; Juz. in Fl. URSS **10**: 69. 1941; Eich' in Eesti fl. 2: 315. 1956 et in ed. 2. 2: 317. 1962; Galenieks in Latv. fl. 3: 74. 1957. Põõsasmaran; krūma čuža; krūminė sidabražolė; курильский чай кустарниковый.

♄. 20-120 (150) cm.

VI-VIII.

II A 2; B. VII A 5.

В природе только в Эстонии и Латвии, редко. Местами в регионе культивирует как декоративное растение. В Литве одичавший (13b; 21b).

In nature only in Estonia and Latvia, rare. Locally cultivated for ornament in tl region. In Lithuania runs wild (13b; 21b).

2; 12d.

2. subgenus *Schistophyllidium* Juz. ex Fed.

★ 2. ***Potentilla bifurca*** L. Sp. Pl. 497. 1753; Juz. in Fl. URSS **10**: 81. 1941; Enari al. Kodumaa taimestik 182. 1943; Bickis et Rasiņš in Bickis, Latv. augu not. 188. 194 Eichw. in Eesti fl. 2: 322. 1956 et in ed. 2. 2: 324. 1962; Galenieks in Latv. fl. 3: 9 1957; Ball, Pawł. et Walters in Fl. Europ. 2: 39. 1968; Gudžinskas et Leht in Ekologi (Vilnius) 1: 107. 1991. – Sämpmaran; dakšainais retējs; dvišakė sidabražolė; лапчатк вильчатая.

♃. 5-25 cm.

VI-VIII.

VII A 2; B 2, 4.

На территории региона очень редко.

Very rare in the Baltic region.

1b, e; 2; 9a; 10a; 14c; 15a; 22a; 30.

3. subgenus *Chenopotentilla* (Focke) Juz.

3. ***Potentilla anserina*** L. Sp. Pl. 495. 1753; Fischer, Naturgesch. Livl. 244. 1778, sine auct.; B. S. Jundz. Opis. rośl. 274. 1791; Wied. et Weber, Beschr. phan. Gew. Esth-, Liv- u. Curl. 272. 1852; Juz. in Fl. URSS **10**: 221. 1941; Eichw. in Eesti fl. **2**: 344. 1956 et in ed. 2. **2**: 347. 1962; Galenieks in Latv. fl. **3**: 87. 1957; Natk.-Ivanausk. in Liet. fl. **4**: 185. 1971. – *P. anserina* subsp. *anserina*: Ball, Pawł. et Walters in Fl. Europ. **2**: 40. 1968. – Hanijalg; maura retējs; žąsinė sidabražolė; лапчатка гусиная.
♃. 5-20 cm.
V-VIII.
II A 1a, b; B 1, 2; C; D 1. IV B; C. VI Aa; Ba; Da; Ea; Fa. VII A; B; C.
На всей территории региона, очень часто.
Very common throughout the territory.

Изменчивость. Варьирует по степени опушенности.
Variability. Varies in its hairiness.

4. subgenus *Hypargyrium* (Fourr.) Juz.

4. ***Potentilla argentea*** L. Sp. Pl. 497. 1753; Fischer, Zusätze Naturgesch. Livl. 120. 1784, sine auct.; B. S. Jundz. Opis. rośl. 275. 1791; Wied. et Weber, Beschr. phan. Gew. Esth-, Liv- u. Curl. 274. 1852; Juz. in Fl. URSS **10**: 145. 1941; Eichw. in Eesti fl. **2**: 324. 1956 et in ed. 2. **2**: 326. 1962; Galenieks in Latv. fl. **3**: 88. 1957; Ball, Pawl. et Walters in Fl. Europ. **2**: 41. 1968; Natk.-Ivanausk. in Liet. fl. **4**: 164. 1971. – *P. tomentosa* Gilib. Fl. Lith. **5**: 254. 1782. – *P. tenuiloba* Jord. Pug. pl. nov. 67. 1852; Natk.-Ivanausk. in Liet. fl. **4**: 165. 1971. – Hõbemaran; sudraba retējs; tikroji sidabražolė; лапчатка серебристая.
♃. 10-40 (50) cm.
VI-VIII.
I A 5. II A 1c, 2. IV B 2; C. V 1, 2, 3. VII A 2, 3, 4, 5; B 3, 4, 5, 6b, c, d, 8, 9, 10; C.
Очень часто по всему региону.
Very common throughout the Baltic region.

5. ***Potentilla impolita*** Wahlenb. Fl. Carpat. 155. 1814; Juz. in Fl. URSS **10**: 146. 1941; Snarskis, Vadovas 436. 1954; Eichw. in Eesti fl. **2**: 325. 1956 et in ed. 2. **2**: 327. 1962; Natk.-Ivanausk. in Liet. fl. **4**: 167. 1971; Pēters. et Birkm. Latv. augu not. ed. 2. 212. 1980. – *P. neglecta* Baumg. Enum. stirp. Transs. **2**: 63. 1816; Ball, Pawł. et Walters in Fl. Europ. **2**: 41. 1968. – *P. dissecta* (Wallr.) Zimmet. Gatt. Potent. 13. 1884; Natk.-Ivanausk. in Liet. fl. **4**: 168. 1971. – P. argentea γ. dissecta Wallr. Sched. crit. 237. 1822. – Läiketu maran; blāvais retējs; pilkoji sidabražolė; лапчатка неблестящая.
♃. 20-40 (60) cm.
VI-VIII.
I A 5. II A 1c, 2. IV B 2; C. V 1, 2, 3. VI Fa. VII A 2, 3, 4; B 3, 4, 5, 6b, c, d, 8, 9, 10.
Часто по всей территории региона.
Frequent on the whole territory of the region.

⋆ 6. ***Potentilla canescens*** Bess. Fl. Galic. **1**: 330. 1809; Juz. in Fl. URSS **10**: 147. 1941; Bitzky, Latw. augu not. **1**: 105. 1920; Galenieks in Latv. fl. **3**: 88. 1957. – *P.*

inclinata Vill. Hist. pl. Dauph. 3: 567. 1788; Ball, Pawł. et Walters in Fl. Europ. **2**: 41. 1968. – Hallikas maran; sirmais retējs; –; лапчатка седоватая.
♃. 15-50 cm.
E, La: VI-VIII.
VII A.
Только в Эстонии и Латвии, очень редко.
Very rare, only in Estonia and Latvia.
1e, f; 2; 5a; 15a; 22a.

7. ***Potentilla leucopolitana*** P. J. Muell. in Billot. Annot. 278, 1862; Juz. in Fl. URSS **10**: 151. 1941; Galenieks in Latv. fl. **3**: 90. 1957; Natk.-Ivanausk. in Liet. fl. **4**: 171. 1971. – –; Veisenburgas retējs; vaisenburgiškė sidabražolė; лапчатка вейсенбургская.
♃. 10-25 cm
La, Li: V-VII.
I A 5. II A 1c. IV C 1. VII A 2; B 4, на песчаных склонах; on sandy slopes.
Только в Латвии и Литве, очень редко.
Very rare, only in Latvia and Lithuania.
1e; 20a; 26b; 29b, c; 30.

8. ***Potentilla silesiaca*** Uechtr. in Jahresb. Schles. Ges. Vaterl. Cult. **44**: 82. 1867; Natk.-Ivanausk. in Liet. fl. **4**: 170. 1971. – –; Silēzijas retējs; silezinė sidabražolė; -.
♃. 10-20 cm.
La, Li: VI, VII.
II A 1. V 3. VII A 2; B 4; на сухих склонах; on dry slopes
Только в Латвии и Литве, очень редко.
Very rare, only in Latvia and Lithuania.
1e; 14c; 26b; 28a, b.

9. ***Potentilla thyrsiflora*** Zimmet. in A. Kerner, Sched. Fl. exsicc. Austro-Hung. **2**: 21. 1882; Juz. in Fl. URSS **10**: 150. 1941; Snarskis, Vadovas 435. 1954; Galenieks in Latv. fl. **3**: 91. 1957; Natk.-Ivanausk. in Liet. fl. **4**: 168. 1971. – –; ķekarziedainais retējs; puokštinė sidabražolė; лапчатка пирамидкоцветковая.
♃. 10-25 cm.
La, Li: VI, VII.
II A 1a; на сухих травянистых склонах; on dry grassy slopes.
Очень редко; в Эстонии не встречается.
Very rare; absent in Estonia.
12b; 20c.

⋆ 10. ***Potentilla supina*** L. Sp. Pl. 497. 1753; Fischer, Naturgesch. Livl. 244. 1778, sine auct.; Wied. et Weber, Beschr. phan. Gew. Esth-, Liv- u. Curl. 271. 1852, in textu; Juz. in Fl. URSS **10**: 165. 1941; Snarskis, Vadovas 435. 1954; Eichw. in Eesti fl. **2**: 327. 1956 et in ed. 2. **2**: 329. 1962; Galenieks in Latv. fl. **3**: 84. 1957; Ball, Pawł. et Walters in Fl. Europ. **2**: 42. 1968; Natk.-Ivanausk. in Liet. fl. **4**: 173. 1971. – Lamav maran; zemais retējs; pavirtusioji sidabražolė; лапчатка низкая.
⊙, ⊖. 10-40 cm.
VI-VIII (IX).
VI Ba. VII B 1, 3, 4.
Редко в регионе.
Rare in the region.
1b, e, f; 2; 12a; 14c; 19a; 21a; 22a; 23; 26b; 28b; 31b.

11. ***Potentilla norvegica*** L. Sp. Pl. 499. 1753; Grindel, Bot. Taschenb. 162. 1803, sine auct.; B. S. Jundz. Opis. rośl. 276. 1791; Wied. et Weber, Beschr. phan. Gew. Esth-, Liv- u. Curl. 271. 1852; Juz. in Fl. URSS **10**: 167. 1941; Eichw. in Eesti fl. **2**: 329. 1956 et in ed. 2. **2**: 331. 1962; Galenieks in Latv. fl. **3**: 79. 1957; Ball, Pawł. et Walters in Fl. Europ. **2**: 42. 1968; Natk.-Ivanausk. in Liet. fl. **4**: 174. 1971. – *P. trifolia* Gilib. Fl. Lith. **5**: 249. 1782. – Norra maran; Norvēģijas retējs; šiaurinė sidabražolė; лапчатка норвежская.

⊙, ⊖. (10) 20-70 cm.

VI-IX.

I B 4. VII A; B 1, 3, 4, 6c, d, 8, 10; C.

На территории региона довольно часто, местами изредка. Не отмечен в 16; 18; 20c; 25; 26; 27; 28a.

Rather frequent in the region, locally rather rare. Not recorded from 16; 18; 20c; 25; 26; 27; 28a.

12. ***Potentilla heidenreichii*** Zimmet. Gatt. Potent. 10. 1884; Juz. in Fl. URSS **10**: 170. 1941; Snarskis, Vadovas 436. 1954; Eichw. in Eesti fl. **2**: 332. 1956 et in ed. 2. **2**: 335. 1962; Galenieks in Latv. fl. **3**: 91. 1957; Natk.-Ivanausk. in Liet. fl. **4**: 177. 1971. – *P. intermedia* L. Mant. 76. 1767, p.p.; Ball, Pawł. et Walters in Fl. Europ. **2**: 42. 1968, p.p. – *P. inclinata* auct.: Ledeb. Fl. Ross. **2**: 47. 1843; Wied. et Weber, Beschr. phan. Gew. Esth-, Liv- u. Curl. 275. 1852. – *P. canescens* auct.: Vilberg, Eesti taimestik ed. 2. 134. 1925. – *P. adscendens* auct.: Vilberg, Eesti taimestik 48. 1922. – Karvane maran; Heidenreiha retējs; šiukšlyninė sidabražolė; лапчатка Гейденрейха.

♃. 15-30 cm.

VI-VIII.

II A 1c. V 3, 4. VII A 1, 2, 3a, 4, 5; B 1, 3, 4, 5, 6c, d, 8, 10; C.

На всей территории региона, довольно часто, реже в Литве.

Rather frequent throughout the region, rarer in Lithuania.

13. ***Potentilla intermedia*** L. Mant. 76. 1767; Wied. et Weber, Beschr. phan. Gew. Esth-, Liv- u. Curl. 275. 1852; Juz. in Fl. URSS **10**: 170. 1941; Snarskis, Vadovas 436. 1954; Eichw. in Eesti fl. **2**: 330. 1965 et in ed. 2. **2**: 333. 1962; Galenieks in Latv. fl. **3**: 80. 1957; Ball, Pawł. et Walters in Fl. Europ. **2**: 42. 1968, p.p.; Natk.-Ivanausk. in Liet. fl. **4**: 176. 1971. – Keskmine maran; vidējais retējs; tarpinė sidabražolė; лапчатка средняя.

♃. 15-50 (60) cm.

VI-VIII.

III A 5. V 3. VII A 2, 3b, 5; B 1, 3, 4, 10.

На территории региона довольно редко.

Rather rare in the region.

1b, e; 2; 5d; 9a; 10a; 13b; 14a, c; 15a; 22a; 23; 26b; 29c; 30.

★ 14. ***Potentilla recta*** L. Sp. Pl. 497. 1753; B. S. Jundz. Opis. rośl. 155. 1811, sine auct.; Juz. in Fl. URSS **10**: 160. 1941; Enari et al. Kodumaa taimestik 184. 1943; Galenieks in Latv. fl. **3**: 86. 1957; Ball, Pawł. et Walters in Fl. Europ. **2**: 42. 1968; Natk.-Ivanausk. in Liet. fl. **4**: 171. 1971. – *P. acutiloba* Gilib. Fl. Lith. **5**: 253. 1782. – Püstmaran; taisnais retējs; stačioji sidabražolė; лапчатка прямая.

♃. (20) 30-70 cm.

VI, VII.

VII A 3, 4; B 3, 4; на сухих склонах; on dry slopes.

На территории региона очень редко.
Very rare in the region.
1a, e; 2; 12c; 14c; 29c; 31a.

★ 15. ***Potentilla goldbachii*** Rupr. Fl. Ingr. **1**: 310. 1860; Juz. in Fl. URSS **10**: 182. 1941; Eichw. in Eesti fl. **2**: 333. 1956 et in ed. 2. **2**: 336. 1962. – *P. thuringiaca* auct.: Enari et al. Kodumaa taimestik 184. 1943; Ball, Pawł. et Walters in Fl. Europ. **2**: 43. 1968, p.p.; Gudžinskas et Leht in Ekologija (Vilnius) **1**: 107. 1991. – Tõusev maran; Goldbaha retējs; Goldbacho sidabražolė; лапчатка Голдбаха.
♃. 20-30 cm.
VI-VIII.
VII A 2, 4, 5; B 3, 4, 6c.
Довольно редко в регионе.
Rather rare in the region.
1a, b, e; 2; 5d; 6; 9a; 10a; 11; 14b, c; 15; 19a; 20a, c; 22a; 26b; 28b; 30.

5. subgenus *Potentilla*. – *Dynamidium* (Fourr.) Juz.

16. ***Potentilla crantzii*** (Crantz) G. Beck ex Fritsch, Excursionsfl. Österr. 295. 1897; Vilbaste, Taimemääraja 36. 1936; Juz. in Fl. URSS **10**: 202. 1941; Bickis et Rasiņš in Bickis, Latv. augu not. 189. 1946; Eichw. in Eesti fl. **2**: 335. 1956 et in ed. 2. **2**: 337. 1962; Galenieks in Latv. fl. **3**: 83. 1957; Ball, Pawł. et Walters in Fl. Europ. **2**: 44. 1968. – *P. alpestris* Hall. fil. in Ser. Mus. Helv. **1**: 53. 1818; Klinge, Fl. Est-, Liv- u. Curl. 571. 1882. – *P. verna* L. Sp. Pl. 498. 1753, p.p.; Fischer, Naturgesch. Livl. 244. 1778, sine auct., p.p.; Wied. et Weber, Beschr. phan. Gew. Esth-, Liv- u. Curl. 273. 1852, p.p. – *Fragaria crantzii* Crantz, Inst. rei herb. **2**: 178. 1766. – Mägimaran; Kranca retējs; –; лапчатка Кранца.
♃. (7) 10-20 (30) cm.
E, La: VI-VIII.
II A 1a, b, 2. IV C. V 1. VI Fa. VII A 3; B 3, 4, 6b, c, d.
В Эстонии нередко, преимущественно в западной части. В Латвии очень редко, единственное местонахождение в одном из западных районов. В Литве не обнаружен.
In Estonia rather frequent in the western part. Very rare in Latvia. Absent in Lithuania.
1a, b, d; 2; 4; 5a, c, d; 6; 8a; 12d.

17. ***Potentilla tabernaemontani*** Aschers. in Verh. Bot. Ver. Brandenb. **32**: 156. 1891; Enari et al. Kodumaa taimestik 184. 1943; Eichw. in Eesti fl. **2**: 336. 1956 et in ed. 2. **2**: 340. 1962; Ball, Pawl. et Walters in Fl. Europ. **2**: 44. 1968. – *P. verna* L. Sp. Pl. 498. 1753, p.p.; Fischer, Naturgesch. Livl. 244. 1778, sine auct., p.p.; Wied. et Weber, Beschr. phan. Gew. Esth-, Liv- u. Curl. 273. 1852, p.p. – *P. aurea*: Luce, Prodr. fl. Osil. 177. 1823, sine auct. – Kevadmaran; –; –; лапчатка Табернемонтана.
♃. (3) 5-10 (15) cm.
E: V, VI.
II A 2. IV B 2, 3; C. V 1a. VI Fa. VII B 3, 4, 6b, c, d, 9.
Только в Эстонии, довольно редко, преимущественно в западной части республики.
Only in Estonia, rather rare, more frequent in the western part.
1a, b, c, d; 2; 5d; 8a.

18. ***Potentilla arenaria*** Borkh. Fl. obern Grafsch. Catz. 1796; Bitzky, Latw. augu not. **1**: 105. 1920; Kuprev. et al. Vadovas 124. 1934; Juz. in Fl. URSS **10**: 208. 1941; Galenieks in Latv. fl. **3**: 81. 1957; Natk.-Ivanausk. in Liet. fl. **4**: 180. 1971. – *P. cinerea* auct.: Fleischer et Lindem. in Fleischer, Fl. Esth-, Liv- u. Kurl. 184. 1839; Wied. et Weber, Beschr. phan. Gew. Esth-, Liv- u. Curl. 273. 1852; Schmalh. Фл. Ср. и Южн. Росс. **1**: 333. 1895; Ball, Pawł. et Walters in Fl. Europ. **2**: 45. 1968, p.p. – *P. maculata* Gilib. Fl. Lith. **5**: 252. 1782. – –; smiltāju retējs; smiltyninė sidabražolė; лапчатка песчаная.

♃. 5-15 cm.

La, Li: IV-VI (VIII).

I A 5. II A 1. IV C 1. V 3. VI Ba. VII A 2; B 3, 4, 6c; C 2, 3.

В Латвии изредка, преимущественно на побережье Рижского залива и в районах средней части республики. В Литве часто в южных и восточных районах. В Эстонии не встречается.

In Latvia rather rare, mainly in coastal and central districts of the country. In Lithuania frequent in southern and eastern districts. Absent in Estonia.

1e, f, g, h; 10a; 11; 14c; 18; 19a; 20-23; 26a; 27-31.

19. ***Potentilla* × *subarenaria*** Borb. ex Zimmet. Gatt. Potent. 21. 1884; Vilberg, Eesti taimestik ed. 2. 134. 1925; Bickis et Rasiņš in Bickis, Latv. augu not. 189. 1946; Eichw. in Eesti fl. **2**: 339. 1956 et in ed. 2. **2**: 341. 1962; Galenieks in Latv. fl. **3**: 82. 1957. – *P. arenaria* auct.: Vilberg, Eesti taimestik ed. 2. 134. 1925. – *P. arenaria* Borkh. × *P. tabernaemontani* Aschers. – Värdmaran; pasmilts retējs; –; лапчатка полупесчаная.

♃. 5-15 cm.

E, La: (IV) V, VI.

I A 2, 5. IV C. V 1a, 3. VII A 3; B 3, 4, 6.

В Эстонии довольно часто в западных районах. В Латвии очень редко. В Литве не обнаружен.

Rather frequent in West Estonia. Very rare in Latvia. Absent in Lithuania.

1a, b, d; 2; 5d; 11; 12d.

20. ***Potentilla erecta*** (L.) Räusch. Nomencl. bot. ed. 3. 152. 1797; Vilbaste, Taimemääraja 36. 1936; Juz. in Fl. URSS **10**: 218. 1941; Bickis et Rasiņš in Bickis, Latv. augu not. 188. 1946; Eichw. in Eesti fl. **2**: 340. 1956 et in ed. 2. **2**: 342. 1962; Galenieks in Latv. fl. **3**: 82. 1957; Ball, Pawł. et Walters in Fl. Europ. **2**: 45. 1968; Snarskis, Vadovas 258. 1968; Natk.-Ivanausk. in Liet. fl. **4**: 181. 1971. – *P. silvestris* Neck. Del. Gallo-Belg. **1**: 222. 1768; Klinge, Fl. Est-, Liv- u. Curl. 569. 1882; Snarskis, Vadovas 434. 1954. – *P. tormentilla* (Crantz) Neck. in Hist. Comment. Acad. Elect. Theod.-Palat. **2**: 491. 1770; J. Jundz. Opis. rośl. 201. 1830, sine auct.; Ledeb. Fl. Ross. **2**: 51. 1843. – *Tormentilla erecta* L. Sp. Pl. 500. 1753; Fischer, Naturgesch. Livl. 245. 1778, sine auct.; B. S. Jundz. Opis. rośl. 272. 1791; Wied. et Weber, Beschr. phan. Gew. Esth-, Liv- u. Curl. 276. 1852. – *Fragaria tormentilla* Crantz, Stirp. Austr. **2**: 23. 1763. – Tedremaran; stāvais retējs; miškinė sidabražolė; лапчатка прямостоящая.

♃. (5) 15-40 (50) cm.

VI-VIII (IX).

I A 2, 5; B. II A; B; C; D. III B. V 1, 3, 4. VII A 1; B 10; C.

По всему региону, часто.

Common throughout the region.

21. ***Potentilla anglica*** Laich. Veg. Europ. **1**: 475. 1790; Bickis et Rasiņš in Bickis, Latv. augu not. 188. 1946; Ball, Pawł. et Walters in Fl. Europ. **2**: 45. 1968; Pēters. et

Birkm. Latv. augu not. ed. 2. 210. 1980. – *P. procumbens* Sibth. Fl. Oxon. 162. 1794; Klinge, Fl. Est-, Liv- u. Curl. 569. 1882; Bitzky, Latw. augu not. **1**: 105. 1920; Galenieks in Latv. fl. **3**: 89. 1957. – *Tormentilla reptans* L. Sp. Pl. 500. 1753; Fischer, Naturgesch. Livl. 245. 1778, sine auct.; Wied. et Weber, Beschr. phan. Gew. Esth-, Liv- u. Curl. 277. 1852. – –; pazvilu retējs; –; –.

♃. (15) 20-70 cm.

La: VI, VII.

I A 5.

Только в Латвии, очень редко.

Very rare, only in Latvia.

1e; 12c.

Примечание. В литературе (Ledebour, 1843; Vilberg, 1925) имеются данные, не подтвержденные гербарными сборами, о нахождении этого вида в Эстонии и Литве.

Comment. In literature (Ledebour, 1843; Vilberg, 1925) there are data on the occurrence of the species in Estonia and Lithuania but they are not verified by herbarium specimens.

22. ***Potentilla reptans*** L. Sp. Pl. 499. 1753; B. S. Jundz. Opis. rośl. 276. 1791; Fischer, Zusätze Naturgesch. Livl. 120. 1784, sine auct.; Wied. et Weber, Beschr. phan. Gew. Esth-, Liv- u. Curl. 272. 1852; Juz. in Fl. URSS **10**: 219. 1941; Eichw. in Eesti fl. **2**: 342. 1956 et in ed. 2. **2**: 345. 1962; Galenieks in Latv. fl. **3**: 83. 1957; Ball, Pawł. et Walters in Fl. Europ. **2**: 45. 1968; Natk.-Ivanausk. in Liet. fl. **4**: 183. 1971. – Roomav maran; ložņu retējs; penkiapirštė sidabražolė; лапчатка ползучая.

♃. 5-10 cm.

VI-VIII.

II A 1, 2; B 1; C; D 2. IV B 2, 3; C 1. V 1a, 2, 3. VI Aa; Ba; Ea; Fa. VII A 1, 2, 4; B 3, 4, 6c, 9, 10; C 3.

На всей территории региона, довольно часто. В Эстонии преимущественно в западных районах (не обнаружен в 3a; 5a, c; 6; 7). .

Rather frequent in the region. In Estonia mainly in western districts (not observed in 3a; 5a, c; 6; 7).

Дополнения и примечания к *Potentilla* L.
Addenda and comments to *Potentilla* L.

★ *Potentilla longifolia* Willd.

Обнаружен в 1989 г. в Литве (29b).

Reported from Lithuania (29b) in 1989.

★ *Potentilla multifida* L.

Обнаружен в 1988 г. в Литве (19a).

Recorded from Lithuania (19a) in 1988.

По старым литературным данным, не подтвержденным гербарными сборами, на территории региона указываются следующие виды.

In literature there are data on the occurrence of the following species in the Baltic territory; their presence has not been confirmed.

Potentilla alba L. – в Литве; in Lithuania.

Potentilla collina Wibel (*P. wibeliana* T. Wolf) – в Эстонии и Латвии; in Estonia and Latvia.

Potentilla heptaphylla L. (*P. opaca* L.) – в Латвии и Литве; in Latvia and Lithuania.

Potentilla sterilis (L.) Garcke (*P. fragariastrum* Pers.; *Fragaria sterilis* L.) – в Литве; in Lithuania.

Potentilla wiemanniana Günth. et Schumm. – в Латвии; in Latvia.

12. ***Fragaria*** L.* Sp. Pl. 494. 1753.
Maasikas; zemene; žemuogė; земляника.

1. ***Fragaria vesca*** L. Sp. Pl. 494. 1753; Fischer, Naturgesch. Livl. 243. 1778, sine auct.; B. S. Jundz. Opis. rośl. 273. 1791; Wied. et Weber, Beschr. phan. Gew. Esth-, Liv- u. Curl. 269. 1852; Juz. in Fl. URSS **10**: 59. 1941; Eichw. in Eesti fl. **2**: 306. 1956 et in ed. 2. **2**: 308. 1962; Galenieks in Latv. fl. **3**: 71. 1957; Tutin in Fl. Europ. **2**: 47. 1968; Natk.-Ivanausk. in Liet. fl. **4**: 188. 1971. – *F. succulenta* Gilib. Fl. Lith. **5**: 247. 1782. – Metsmaasikas; meža zemene; paprastoji žemuogė; земляника лесная.
♃. 5-20 cm.
V, VI.
I A 1, 2, 3, 5, 6; B 4, 5. II A 1, 2; C. IV A 3; B 3; C. V 1, 2, 3. VI Aa; Ba; Fa. VII A 2, 4, 5; B 3, 4, 6; C.
На всей территории региона, часто.
Frequent throughout the region.

Гибриды. Hybrids.

F. moschata × *F. vesca* – очень редко; very rare.

F. vesca × *F. viridis* – редко; rare.

2. ***Fragaria moschata*** Duch. Hist. nat. Frais. 145. 1766; Klinge, Fl. Est-, Liv- u. Curl. 565. 1882; Juz. in Fl. URSS **10**: 60. 1941; Eichw. in Eesti fl. **2**: 309. 1956 et in ed. 2. **2**: 311. 1962; Galenieks in Latv. fl. **3**: 72. 1957; Tutin in Fl. Europ. **2**: 47. 1968; Snarskis, Vadovas 432. 1954; Natk.-Ivanausk. in Liet. fl. **4**: 189. 1971. – *F. elatior* Ehrh. Beitr. Naturk. **7**: 23. 1792; J. Jundz. Opis. rośl. 200. 1830, sine auct.; Fleischer et Lindem. in Fleischer, Fl. Esth-, Liv- u. Kurl. 182. 1839; Wied. et Weber, Beschr. phan. Gew. Esth-, Liv- u. Curl. 269. 1852; Kuprev. et al. Vadovas 122. 1934. – Kõrge maasikas; smaržīgā zemene; miškinė žemuogė; земляника мускусная.
♃. 15-40 (45) cm.
V, VI.
I A 2, 3, 6. II A 1a, b; C. V 1, 2a, b, 3. VII A 5; B 3, 4; C 1,3.
В Эстонии и Латвии довольно редко и неравномерно. В Литве редко.
Rather rare in Estonia and Latvia. Rare in Lithuania.
1a, b, d, f; 2; 3b; 4-9a; 11; 13b; 14c; 17; 18; 20b; 22a; 26b.

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V

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10. ***Comarum*** L.* Sp. Pl. 502. 1753.
Soopihl; vārnkāja; sūdras; сабельник.

1. ***Comarum palustre*** L. Sp. Pl. 718. 1753; Fischer, Naturgesch. Livl. 246. 1778, sine auct.; B. S. Jundz. Opis. rośl. 277. 1791; Wied. et Weber, Beschr. phan. Gew. Esth-, Liv- u. Curl. 270. 1852; Juz. in Fl. URSS **10**: 74. 1941; Eichw. in Eesti fl. **2**: 314. 1956 et in ed. 2. **2**: 316. 1962; Galenieks in Latv. fl. **3**: 75. 1957; Natk.-Ivanausk. in Liet. fl. **4**: 157. 1971. – *C. rubrum* Gilib. Fl. Lith. **5**: 255. 1782. – *Potentilla palustris* (L.) Scop. Fl. Carn. ed. 2. **1**: 359. 1772; J. Jundz. Opis. rośl. 203. 1830, sine auct.; Ball, Pawł. et Walters in Fl. Europ. **2**: 39. 1968. – Harilik soopihl; purva vārnkāja; pelkinis sūdras; сабельник болотный.

♃. 20-50 cm.

VI-VIII.

I B 1, 2, 3. II A 1d, 2, 3, 5; B; C. III A 1, 2, 3, 4, 5; B; C. VI Aa; Ba; Ca; Ea; Fa.

На всей территории региона, часто.

Frequent in the whole region.

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CLADISTIC ANALYSIS OF THE DATA PUBLISHED IN "MONOGRAPHIE DER GATTUNG *POTENTILLA*" BY T. WOLF

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Abstract. The present work is an attempt at comparing classical vs. cladistic treatment using the same set of characters and data. The polymorphic and taxonomically troublesome genus *Potentilla* L. is analysed with cladistic methods (PAUP ver. 3.1.1.), using the same morphological characters as Wolf (1908) did in his species descriptions in the "Monographie der Gattung *Potentilla*"(*Bibl. Bot.*, Vol. 71). The subgenera created by Wolf did not come out as monophyletic groups, while most of the sections did. The contradiction between the results of the cladistic analysis and the empiric subgeneric grouping made by Wolf may partly reflect parallel evolution of morphological characters in the genus as well as differential weights attached to them by Wolf (he weighted style characters more highly).

Key words: *Potentilla* L., taxonomy, cladistics, monophyletic groups.

INTRODUCTION

Taxonomic history. Karl Linné in his "Species Plantarum" (1753) described 26 species of cinquefoils belonging now to the genus *Potentilla*: 22 taxa in the genus *Potentilla*, 2 in *Tormentilla*, 1 in *Comarum*, and 1 in *Fragaria.*

The following years added more species to the genus: Willdenow (1800) recognized 45 species; Nestler (1816) described 68 species, 59 of which were later called "good species" by Wolf (1908); Lehmann (1856) included 201 species with 158 "good" ones; Zimmeter (1889) described 256 species of which only 80 were recognized by later taxonomists. The researchers mentioned dealt with all taxa known at the time, mainly of European origin. Rydberg (1898) recognized in his "A Monograph of North-American Potentilleae" 215 species of cinquefoils (many now used only as varieties or subspecies); but his system was based only on American taxa and was therefore not applicable when Wolf tried to complete it with taxa from the Old World. The last taxonomist to deal with the whole genus was Theodore Wolf, whose "Monographie der Gattung *Potentilla*" (1908) was based on about a hundred studies of earlier researchers; he recognized 305 species with 336 varieties and 294 forms. In his system the genus is subdivided into subsections (subgenera) mostly on the basis of style characters.

As currently understood, the genus *Potentilla* with its 400–500 species is one of the largest in the family Rosaceae. Its centre of variation is considered to be in the mountains of Central Asia (Shah et al., 1992) whence it has spread over the whole northern hemisphere, with *P. anserina* reaching Australia as well (Meusel et al., 1965).

Reproduction, hybridization, apomixis. The representatives of the genus *Potentilla* are highly polymorphic taxa as the genus is subject not only to phenotypic variation but also to interspecific hybridization. Several species were suspected to be of hybrid origin by earlier researchers (Ascherson & Graebner, 1900–1905; Wolf, 1908). Wolf mentioned 80 spontaneous hybrids, all of European origin. However, before 1908 nobody had written anything about American or Asian hybrids; even in *Flora URSS* Yuzepchuk (Юзепчук, 1941) mentioned only about ten hybrids.

By now it has become clear that interspecific hybridization and apomixis are common in the genus *Potentilla* (Ball et al., 1968). Occurrence of apospory (apomixis) was first mentioned in this genus by Forenbacher (1914) on *P. erecta*. Experimentally the phenomenon was first demonstrated by Müntzing (1928), who tried to synthesize *P. collina* crossing *P. argentea* and *P. tabernaemontani*, but obtained only maternal progeny.

The propagation possibilities present in *Potentilla* are very diverse. In addition to sexually reproducing plants and facultative apomicts, obligate apomicts of hybrid origin are represented in the genus. Some species, amphimictic in the central parts of the range, may be apomictic at their periphery (Müntzing, 1958). There are also species propagating both vegetatively with runners and generatively with seeds. In facultative apomicts, the choice between sexual and alternate reproductive behaviour depends on pollen: pollen from distant relatives increases the level of apomixis. However, ploidization or hybridization of apomicts can lead back to sexual reproduction (Richards, 1994). Diploid apomicts are rare, but in *Potentilla* they are quite common (Müntzing & Müntzing, 1945; Asker, 1986; Czapik, 1988).

As the latest world-wide analysis of the genus, Wolf's monograph has formed the basis for most subsequent research on the genus, including attempts to evaluate or analyse his taxonomic system. Bate-Smith (1961) studied the species chromatographically for flavonoids and found *P. anserina* to be very different, and *P. montana*, *P. erecta*, *P. reptans*, and *P. procumbens* to be quite different from the other species of the genus. Sojak (1985a), focusing on the morphology of anthers, concluded that taxa with one theca (*Fragaria*-type) and taxa with two thecas (*Potentilla*-type) should belong to different evolutionary lines. However, Esau (1980) stated that such ontogenetic secondary modifications may not be of diagnostic value.

In this paper the polymorphic and taxonomically troublesome genus was analysed with cladistic methods using the same characters as Wolf did, to compare the results with Wolf's system (1908), which is, with several modifications and updated nomenclature, still in use today.

MATERIAL AND METHODS

Out of every smaller section (*grex* in Wolf's terminology) at least one species and out of larger sections up to five species were selected for the analyses. Sixty-three species of *Potentilla* and three species of *Fragaria* (outgroup) were used (Table). *Fragaria* was chosen as an outgroup because this genus is obviously very closely related to *Potentilla* and has even been treated by some taxonomists as belonging to the genus *Potentilla* (Ascherson & Graebner, 1900–1905; Rydberg, 1898).

The scientific names of the subgenera and sections in the list are as used by Wolf.

The characters employed in the study (see the list), 64 in all, were scored from the species descriptions of Wolf (1908). All characters were used as unordered in the analysis. Character states of quantitative characters were distinguished according to gaps in the ranges of measurements of quantitative characters in Wolf's descriptions of species.

The cladistic analysis was made using PAUP ver. 3.1.1. (Swofford, 1993). The computing scheme was as follows: heuristic search, random addition sequence, 50 replicates, not more than 10 trees saved, MULPARS ON, tree bisection–reconnection (TBR) branch swapping. The retained trees were used as starting point for the next heuristic search with a simple addition sequence and TBR swapping (MULPARS ON, MAXTREES = 2500). After computing strict and 95%-majority rule consensus trees, the characters were reweighted according to the rescaled consistency index (best fit), and the scheme described above was used iteratively. Branch support was estimated by the method of Bremer (1988, 1994).

The species studied

Subgenus	Section	Species
Rhopalostylae	*Fruticosae*	*P. fruticosa* L.
	Bifurcae	*P. bifurca* L.
Nematostylae	*Xylorrhizae*	*P. lignosa* Willd.
	Biflorae	*P. biflora* Willd.
	Palusteres	*P. palustris* L.
	Tridentatae	*P. tridendata* Sol
	Eriocarpae	*P. elatior* Schlecht
	Speciosae	*P. speciosa* Willd.
	Nitidae	*P. nitida* L.
	Curvisetae	*P. colletiana* Aitch.
	Crassinerviae	*P. valderia* L.
		P. brachypetala Fisch. & Mey
	Caulescentes	*P. caulescens* L.
	Fragariastra	*P. alba* L.
		P. micrantha Ram.
Closterostylae	*Rupestres*	*P. rupestris* L.
		P. tianschanica Th. W.
		P. geoides Bieb.
Conostylae	*Multifidae*	*P. multifida* L
		P. pulchella R. Br.
		P. sericea L.
		P. eversmanniana Fisch.
	Graciles	*P. effusa* Dougl.
	Haematochroae	*P. pulcherrima* Lehm.
		P. ehrenbergiana Schlecht
	Niveae	*P. nivea* L.
		P. villosa Pall.
		P. vahliana Lehm.
		P. evestitia Th. W.
	Argenteae	*P. argentea* L.
		P. dealbata Bge.
		P. canescens Bess.
		P. leucopolitana P. J. Müll.
		P. thyrsiflora (Hüls.) Zimm.
	Tanacetifoliae	*P. tanacetifolia* Willd.
		P. viscosa Don.
		P. sanguisorba Willd.
	Rectae	*P. recta* L.
		P. taurica Willd.
		P. nurensis Boiss. et Haskn
	Rivales	*P. supina* L.
		P. intermedia L.
		P. norvegica L.
		P. asperrima Turcz.
	Persicae	*P. flabellata* Reg. et Schn.
		P. komaroviana Th. W.
		P. ruprechtii Boiss.
	Grandiflorae	*P. umbrosa* Stev.
		P. chrysantha Trev.
	Chrysanthae	*P. thuringiaca* Bernh.
		P. szovitsii Th. W.
		P. sericata Th. W.
		P. multijuga Lehm.
	Multijugae	*P. fragariformis* Will.
	Ranunculoides	*P. tabernaemontani* Asch.
Gomphostylae	*Aureae*	*P. crantzii* (Crantz.) Beck.
		P. arenaria Borkh.
		P. gelida C. A. Mey
	Fragarioides	*P. fragarioides* L.
	Tormentillae	*P. erecta* Räusch.
		P. reptans L.
		P. flagellaris Willd.
Leptostylae		*P. anserina* L.
Outgroup		*Fragaria moschata* Duch.
		F. vesca L.
		F. viridis L.

List of characters scored from the species descriptions of Wolf (1908)

1. Stem: herbaceous (0), woody at base (1), woody throughout (2)
2. Rhizome: unbranched (0), branched (1)
3. Rhizome: herbaceous (0), woody (1)
4. Rhizome: thin (0), thick (1)
5. Rhizome covered with withered stipules: stipules absent (0), sparsely (1), densely (2)
6. Flowering stems: creeping (0), erect (1), ascendent (2), procumbent (3)
7. Flowering stems: not rooting (0), rooting at the nodes (1)
8. Height: up to 20 cm (0), 21–50 cm (1), 51 cm or more (2)
9. Flowering stems: without leaves (0), few leaves (1), many leaves (2)
10. Flowering stems: branching at the base (0), middle (1), top (1), unbranched (3)
11. Stems: glabrous (0), simple hairs (1), stellate hairs (2)
12. Simple hairs: tomentose (0), villous (1), straight (2)
13. Straight hairs: adpressed (0), spreading (1)
14. Leaves: pinnate (0), digitate (1), ternate (2), abruptly pinnate (3)
15. Basal leaves: absent (0), present (1)
16. Petioles of basal leaves: absent (0), short (1), long (2)
17. Leaflets of basal leaves: 1 (0), 3 (1), 5–7 (2), 9–11 (3), 13 or more (4)
18. Leaflets of cauline leaves: reduced (0), 3 (1), 5 (2)
19. Leaflets in inflorescence: 1 (0), 3 (1)
20. Petiole of cauline leaves: absent (0), short (1), long (2)
21. Stipules of lower leaves: green (0), brown (1)
22. Auricles of stipules of lower leaves: short (0), long (1), absent (2)
23. Stipules of cauline leaves: entire (0), dentate (1), densely serrate (2)
24. Stipules: obovate (0), oblong (1), ovate (2), elliptical (3)
25. Length of lower leaflets: up to 15 mm (0), 16–30 mm (1), 31–40 mm (2), 41 mm or more (3)
26. Width of lower leaflets: up to 10 mm (0), 11–20 mm (1), 21 mm or more (2)
27. Teeth: irregular (0), regular (1)
28. Number of teeth: 4–10 (0), 12–18 (1), 20 and more (2)
29. Edges of leaves: curved down (0), flat (1)
30. Size of leaflets: unequal (0), equal (1)
31. Leaflet shape: angular (0), oblong (1), ovate (2), lanceolate (3), linear (4), suborbicular (5)
32. Leaflet apex: entire (0), notched (1)
33. Leaflet upper side: glabrous (0), sparsely hairy (1), densely hairy (2)
34. Leaflet upper side: yellowish (0), grey (1), white (2), green (3)
35. Leaflet underside: glabrous (0), sparsely hairy (1), densely hairy (2)
36. Leaflet underside: yellow (0), grey (1), white (2), green (3)
37. Stellate trichomes on leaves: absent (0), present (1)
38. Hairs beneath: erect (0), tomentose (1), patent (2)
39. Petioles: glabrous (0), pubescent (1)
40. Flower diameter: up to 15 mm (0), 16–20 mm (1), 21–25 mm (2), 26 mm or more (3)
41. Flowers: solitary (0), in inflorescences (1)
42. Pedicels: glabrous (0), pubescent (1)
43. Calyx hairs: tomentous (0), long straight (1), short straight (2), short and long straight (3)
44. Long hairs: patent (0), erect (1)
45. Calyx: yellow (0), green (1), red (2), white (3)
46. Calyx and epicalyx: unequal (0), equal (1)
47. Epicalyx segments: acute (0), obtuse (1), bifurcate (2)
48. Calyx segments: acute (0), obtuse (1), bifurcate (2)
49. Petals: shorter than sepals (0), equal (1), longer (2)
50. Petals: obovate (0), roundish (1), suborbicular (2), obcordate (3), elliptic (4)
51. Corolla: white (0), yellow (1), red (2), pink (3)
52. Number of stamens: 15–20 (0), 21–25 (1), 26–30 (2)
53. Anther: reniform (0), elliptic (1), ovate (2), rounded (3), disk-like (4)
54. Receptacle: glabrous (0), hairy (1)
55. Seed: smooth (0), furrowed (1), hairy (2), hairs at base (3)
56. Seed: with a keel (0), without (1)
57. Style shape: spindle (0), conical (1), fusiform (2), stick (3), clavate (4), filiform (5)
58. Style: shorter than ovary (0), equal (1), longer (2)
59. Stigma: unexpanded (0), expanded (1)
60. Basal leaves in flowering: absent (0), present (1)

61. Fleshy receptacle: absent (0), elliptic (1), roundish (2)
62. Sepals in fruit: apressed to friut (0), reflexed (1)
63. Runners: absent (0), present (1)
64. Texture of leaves: herbaceous (0), fleshy (1), thin (2), leathery (3)

RESULTS AND DISCUSSION

With PAUP, 72 equally parsimonious trees were found with the length 893 steps, the consistency index 0.380, homoplasy index 0.845, and retention index 0.460. Since strict and 95%-majority consensus trees of these were identical and moderately resolved, reweighting of the characters was undertaken. After reweighting the characters only one tree was retained with the length of 146 044 steps, homoplasy index 0.840, retention index 0.546, and consistency index 0.510. Since the result of the reweighting (one tree) was but seemingly good being so much longer (926 steps when characters were reweighted with "1"), only the strict consensus tree will be analysed (Fig.).

The subgenera recognized by Wolf did not come out as monophyletic groups. The species of Wolf's subgenera *Nematostylae* and *Gomphostylae* are divided mostly between two monophyletic groups; the species of *Conostylae*, the largest subgenus, appear in even more groupings. The only representative of the subgenus *Leptostylae*, *P. anserina*, is grouped with *P. reptans* and *P. flagellaris* of *Gomphostylae*. Species of the subgenus *Rhopalostylae*, *P. fruticosa* and *P. bifurca*, fall into a small monophyletic group together with *P. biflora* of *Nematostylae* and *P. ruprestris* and *P. tianschanica* of *Closterostylae*. The third species in *Closterostylae*, *P. geoides*, is in an entirely different cluster, so even this small subgenus with only one section is not monophyletic.

On the other hand, several of Wolf's sections are supported as being monophyletic; e.g., the section *Aurea* of *Gomphostylae*, which comprises *P. crantzii, P. arenaria, P. tabernaemontani,* and *P. gelida*, appears as a distinct clade with the last species being the furtherest. According to Sojak (1985b), *P. gelida* can be considered the primitive ancestor of the others. The representatives of the other two sections of *Gomphostylae* belong to different clades.

The sections *Argenteae*, *Graciles*, *Rectae*, and *Niveae* in *Conostylae* also appear as monophyletic in the consensus tree.

One species from the section *Argenteae*, *P. canescens*, is connected with *P. recta* and falls into the same clade with other members of the section *Rectae*. This is in accordance with my previous placement of *P. canescence* (Leht, 1987). Two members of the section *Chrysanthae*, the closely related taxa *P. chrysantha* and *P. thuringiaca*, are connected with another species from the section *Rectae*, *P. nurensis*, and also belong to the group mentioned above. Since two other taxa of the section *Chrysanthae*, *P. szovitsii* and *P. sericata*, stand quite separately, this section does not seem to be monophyletic. The situation is similar with the

Strict consensus of 72 parsimonious trees. Length 893, consistency index 0.380, homoplasy index 0. 845, retention index 0.460. 1, 2, 3 – Bremer support.

sections *Rivales* and *Persicae*, whose representatives belong to very different clades. Two species from the section *Tormentillae*, *P. reptans* and *P. flagellata*, belong together, whilst the third member of the section stands in a separate clade. Species from the section *Tanacetifoliae* occur on the cladogram in a monophyletic group containing representatives of three other sections, too.

Nothing can be said about the monophyletic status of smaller sections, for which only one representative was used.

Bremer support was not high, mostly 1 or 2, only for some clades its value was 3. In most cases the branch support is higher for clades consisting of representatives of one and the same section (except in the case of *P. anserina* & *P. reptans*, and *P. erecta* & *P. supina*, which belong to different subgenera).

When using all the morphological characters used by Wolf for describing species, his subgenera based on style characters (shape and position) turn out to be largely polyphyletic. Based on the cladistic analysis, Wolf's sections are more natural groupings as they are mostly monophyletic. The same conclusions were achieved by Sojak (pers. comm., 1995) on the basis of comparative morphology of anthers and styles in the tribe *Potentilleae*. Sojak (1987) also suggests that in Wolf's group *Potentillae trichocarpae* (comprised of *Rhopalostylae* and *Nematostylae*) it is not necessary to retain the category of subgenus between the genus and its sections.

The subgenera recognized in *Flora Europaea* (Ball et al., 1968) are likewise not all monophyletic on the basis of characters used by Wolf. The subgenus *Potentilla* is certainly polyphyletic. The subgenera *Trichothalamus* (*P. fruticosa*) and *Schistophyllidium* (*P. bifurca*) seem to belong to one and the same group. Only the subgenus *Fragariastrum* (Wolf's species *P. speciosa, P. nitida P. valderia, P. caulescens, P. alba, P. micrantha* occur in *Flora Europaea*) is more or less clearly monophyletic.

The contradiction between the results of the cladistic analysis and the subgeneral groupings proposed by Wolf is without doubt partly the result of polygenic nature and parallel variation of morphological characters as well as of differential weights given to the characters by Wolf (style characters are weighted more highly). Wolf performed the grouping of the species on the basis of overall morphological similarity, with an emphasis on the style characters.

The characters described by Wolf were those that allow ready identification of herbarium material. Now more phylogenetically informative characters are to be found from anatomy, palynology (Лехт, 1989, 1990), and biochemistry, not to mention molecular characters etc. that can be used in the taxonomic and cladistic analysis of the genus.

This work was an example of comparing classical vs. cladistic treatments using the same set of characters. For further cladistic analysis, not only morphologic but all phylogenetically informative characters are needed, and certainly it would be better to use data of all species.

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T. WOLFI TEOSES "MONOGRAPHIE DER GATTUNG *POTENTILLA*" AVALDATUD ANDMETE KLADISTILINE ANALÜÜS

Malle LEHT

Käesolev töö on katse võrrelda nn. klassikalist ja kladistilist lähenemist taksonoomias kasutades samu tunnuseid ja andmeid.

Polümorfset ja taksonoomiliselt keerukat marana (*Potentilla* L.) perekonda on analüüsitud kladistiliste meetoditega (PAUP ver. 3.1.1.) lähtudes samadest morfoloogilistest tunnustest, millele tugines Wolf (1908) oma monograafia liigikirjeldustes. On vaadeldud 63 liiki, välisgrupiks oli kolm maasika (*Fragaria* L.) liiki, tunnuseid oli analüüsis 64.

Wolfi püstitatud alamperekonnad ei osutunud monofüleetilisteks, küll aga olid seda tema sektsioonid. Vastuolu kladistilise analüüsi tulemuste ja Wolfi poolt empiiriliselt loodud taksonoomiliste üksuste vahel peegeldab tõenäoliselt morfoloogiliste tunnuste paralleelset evolutsiooni perekonnas, aga ka tunnustele erineva kaalu andmist (näit. Wolf pidas emakakaela tunnuseid teistest olulisemaks).

VII

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of the Baltic taxa of the genus *Potentilla* L. — Bothanica Lithuanica.
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DISTRIBUTION AND NOMENCLATURE PROBLEMS OF THE BALTIC TAXA OF THE GENUS *POTENTILLA* L.

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Abstract
Genus *Potentilla* L. (*Rosaceae*) is represented by 24 species in the three Baltic countries. Seven of them are rare adventives, nine native species grow on the borders of their areals and only eight taxa lie in the central part of their distribution area here. Differences in distribution of the genus *Potentilla* among the three Baltic countries is analysed and problems connected with their synonyms and nomenclature are discussed.

Keywords: *Potentilla*, distribution, nomenclature, Estonia, Latvia, Lithuania.

INTRODUCTION

Genus *Potentilla* L. (*Rosaceae*) is represented by 24 species in the three Baltic countries: 18 in Estonia, 22 in Latvia and 19 in Lithuania; 60 % of them reach the borders of their geographical distribution here. Since high variability is usual in taxa living on the edges of their areas, an increase in taxonomical diversity and related problems are to be expected in such regions.

DISTRIBUTION

Seven species of Baltic cinquefoils are quite rare adventives, with different distribution patterns in all three countries (Fig. 1). The most recent newcomers, *P. multifida* and *P. longifolia*, were found in Lithuania in 1988 and 1989 respectively (GUDŽINSKAS & LEHT, 1991). *P. bifurca* and *P. supina* currently grow in several places in Latvia and Lithuania, but only old data and specimens from the 1930s are available in Estonian herbaria. *P. goldbachii* has been known for many years in Estonia and Latvia, while in Lithuania it was first found only in 1989. *P. recta* is an old, rare adventive which is now expanding in all three Baltic countries. The most confusing adventive species in the Baltics, *P. canescens*, reached Estonia and Latvia in the 1950s but is still absent (or not yet found) in Lithuania.

Of spontaneous species, the most common in very different habitats (Table 1) is *P. anserina*. *P. argentea* and *P. impolita* can be found growing abundantly on dry mineral soils in the whole territory. A very common species on both wet mineral and peaty soils is *P. erecta*, and a quite common one is *P. norvegica*. *P. palustris* occurs nearly everywhere on swampy soils. *P. reptans*, growing in very different habitats, is frequent in western Estonia, but quite rare in the eastern part, and rare in Latvia and Lithuania. *P. heidenreichii* is found in all three republics on meadows, grasslands, roadsides and in ruderal places, whereas its close relative *P. intermedia* L. s. str., which grows in similar habitats, occurs in only very few localities.

The most interesting distribution pattern among Baltic cinquefoils is that of the *P. verna* group (Fig. 2), all the representatives of which populate open habitats on poor soils, mostly alvars. *P. crantzii* is quite common in Estonia, very rare in Latvia and absent from Lithuania. *P. tabernaemontani* occurs only in western and northwestern Estonia. *P. subarenaria* occurs in western and northwestern Estonia and Central Latvia, but is not found in Lithuania. *P. arenaria*, which is not found in Estonia, grows abundantly in central Latvia on the sandy banks of the River Daugava and even more abundantly in Lithuania in similar habitats. *P. subarenaria* is a species of hybrid origin (*P. arenaria* Borb. × *P. tabernaemontani* Asch.), which does not occur together with both of its parents anywhere in the Baltic countries: in Estonia it sometimes grows close together with *P. tabernaemontani*, and its only two Latvian localities lie near the habitats of *P. arenaria*.

The only Baltic representatives of the *P. collina* group, *P. silesiaca*, *P. thyrsiflora* and *P. leucopolitana*, are found in very few localities in Latvia and Lithuania, while in Estonia they have not yet been encountered. These species are inhabitants of dry, poor, mostly sandy soils (Fig. 3).

P. anglica was rediscovered, after nearly one hundred years, in Latvia in 1988 near Riga. Very old literature documents its occurrence in Estonia as well but, with no herbarial material available, these data cannot be accepted.

Table 1.

Numbers of synonyms and habitats of Baltic cinquefoils (*Potentilla*).

Species	Number of synonyms	Number of synonyms in Baltic literature	First mention in Baltic literature	Habitats in the Baltic countries
P. anglica Laich.	14	2	1778	Ia
P. anserina L.	14	1	1778	IIa, IIb, IV, VI, VII
P. arenaria Borkh.	21	2	1860	Ia, IIa, IV, VI, VII
P. argentea L. s. l	35	2	1782	IIa, IV, V, VI, VII
P. bifurca L.	11	1	1943	VII
P. canescens Bess.	20	3	1844	IIa, VII
P. collina s. l.	34	2	1957	Ia, IIa, VII
P. crantzii (Crantz) Beck.	24	4	1844	Ia, IV, V, VI, VII
P. erecta (L.) Räusch.	31	4	1778	Ia, Ib, IIa, IIb, II, V, VII
P. fruticosa L.	17	2	1803	IIa
P. goldbachii Rupr.	46	2	1943	VII
P. heidenreichii Zimm.	10	4	1844	IIa, V, VII
P. impolita Wahl.	8	2	1954	IIa, IV, V, VI, VII
P. intermedia s.l.	18	1	1810	IIa, V, VII
P. longifolia	3	.	1991	VII
P. multifida	8	.	1991	VII
P. norvegica L.	20	2	1782	Ib, VII
P. palustris L.	8	1	1778	III
P. recta L.	38	2	1787	VII
P. reptans L.	8	1	1784	IIa, IV, V, VI, VII
P. subarenaria Borb.	9	2	1903	V, VII
P. supina L.	16	1	1778	VI, VII
P. tabernaemontani Asch.	26	2	1844	IIa, IV, V, VI, VII
P. verna Crantz	18	.	1778	.

Abbreviations of habitats: I - forest and forest margins, II - meadows and wooded meadows, III - mires, IV - seashores and sandy areas, V - juniper shrubs, VI - banks of waterbodies, VII - anthropogenous biotopes, a - mineral soils, b - swampy soils

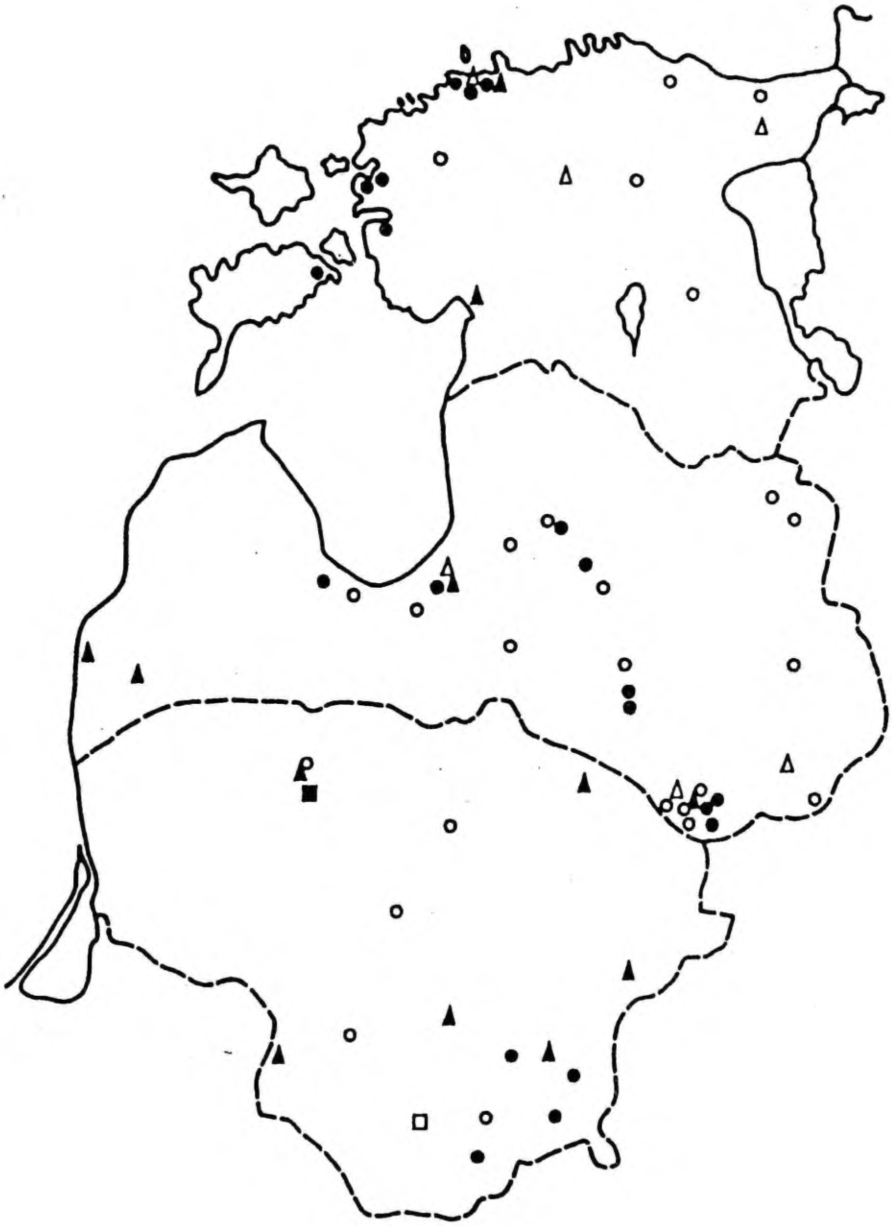

Fig. 1. Distribution of *Potentilla canescens* (Δ), *P. recta* (●), *P. goldbachii* (○), *P. bifurca* (⊗), *P. supina* (▲), *P. multifida* (■), and *P. longifolia* (□) in the Baltic states.

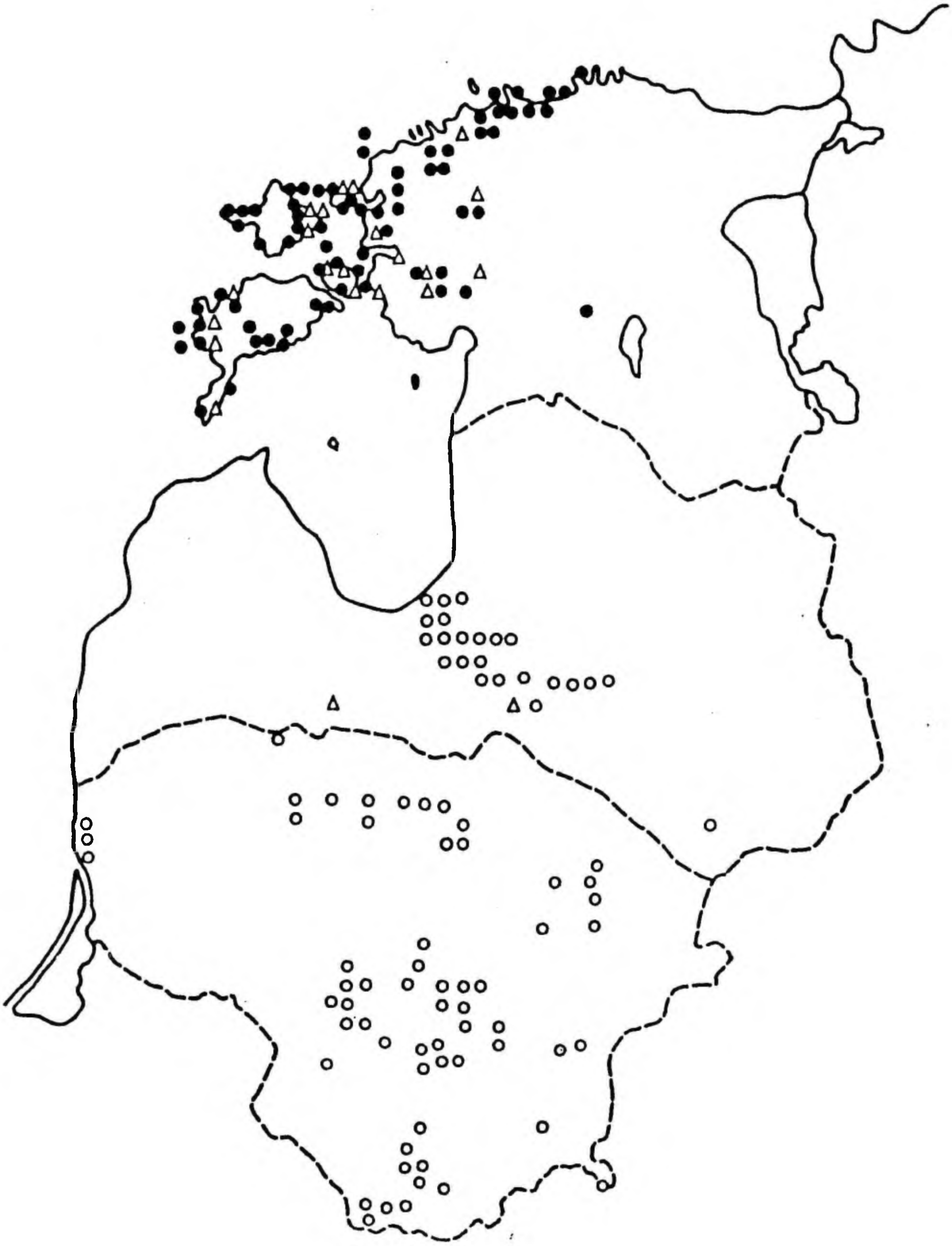

Fig. 2. Distribution of *Potentilla tabernaemontani* (●), *P. arenaria* (○), and *P. subarenaria* (Δ) in the Baltic states.

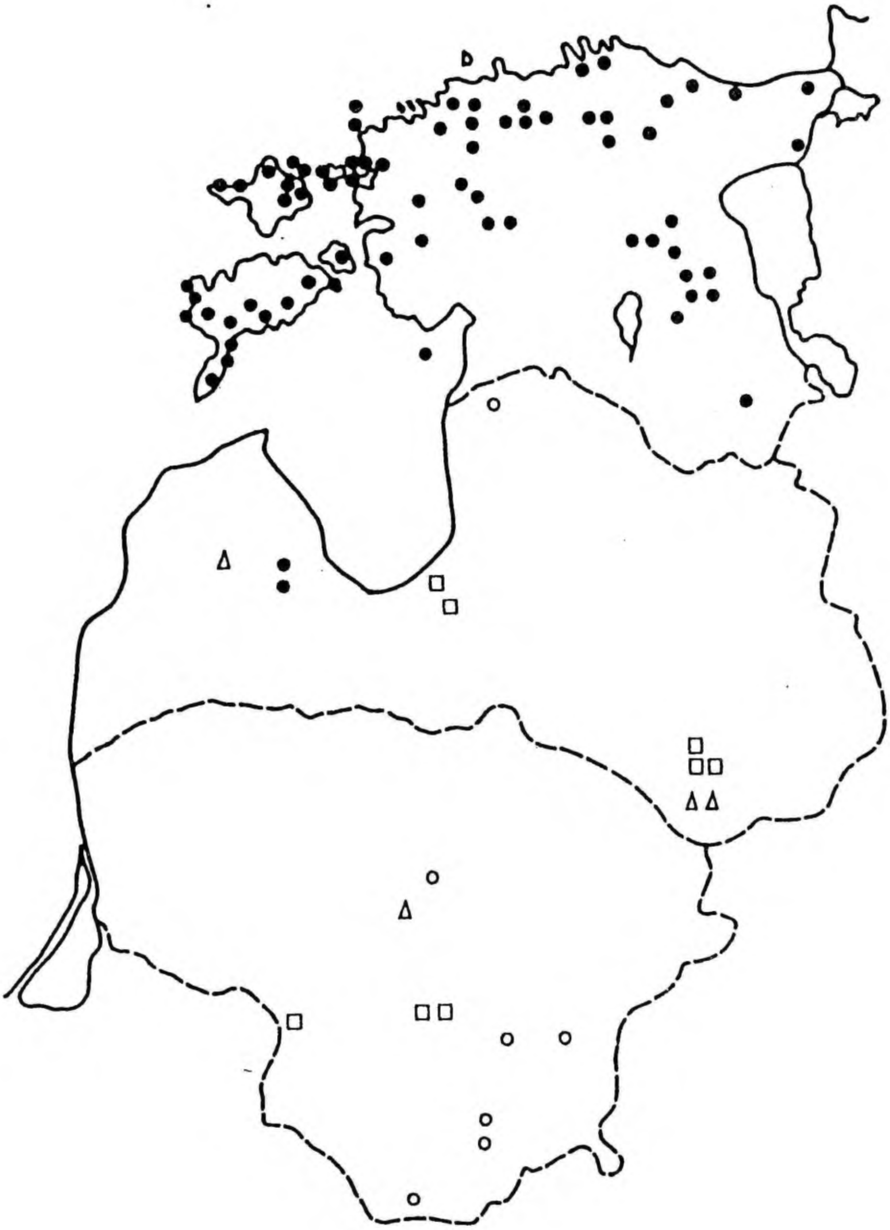

Fig. 3. Distribution of *Potentilla crantzii* (●), *P. leucopolitana* (○), *P. silesiaca* (□), and *P. thyrsiflora* (Δ) in the Baltic states.

P. fruticosa is the only shrubby *Potentilla* in the Baltic area. It grows in northwestern Estonia and in central Latvia on poor soils on alvars and in juniper shrubs.

As shown, differences between the *Potentilla* floras of Estonia, Latvia and Lithuania are quite considerable, especially when taking into account the relative proximity of these countries.

Besides *Potentilla,* many other species reach their area boundaries in the Baltic states. In Estonia there are 71 species on the northern margin of their distribution area, 131 species on their eastern, southeastern and northeastern boundaries, 89 species on their western, northwestern and southwestern boundaries, and eight on southern boundary (KASK, LAASIMER, 1987).

Nine native species out of the 24 representatives of the genus *Potentilla* growing in the Baltic states reach their area boundaries here. And, as may be expected, most of the alien species here grow quite far from their main distribution area.

The northernmost localities of *P. anglica* are in Latvia and in southwestern Finland, while its main distribution area is located in Central Europe. *P. arenaria, P. thyrsiflora, P. silesiaca* and *P. leucopolitana* reach their northern area borders in Latvia. Estonian localities on the distribution map of *P. arenaria* in E. HULTÉN (1950) and H. MEUSEL (1965) seem to be mistakes. The main area of *P. arenaria* lies in Central Europe, as does that of *P. thyrsiflora, P. silesiaca* and *P. leucopolitana. P. subarenaria* seems to be on its northern distribution borderline in Estonia and southwestern Finland. However, since its distribution in Eastern Europe is unclear, it may turn out that also the eastern boundary of *P. subarenaria* lies in Estonia. Latvian localities of *P. crantzii* are on the southern boundary of its main area (in southern Europe it has several small, disjunct areas). The mostly European species *P. tabernaemontani* grows on its eastern boundary in Estonia. Also, the continuous area of *P. reptans* reaches its eastern boundary in the Baltic countries (in the Leningrad district there exist several small separate localities); its northern margin lies in southern Finland and southern Sweden.

The main area of *P. multifida* lies in Central Asia, its northernmost localities being in Finland and Lithuania. Another casual immigrant species coming from Asia, *P. longifolia*, probably has its westernmost locality in Lithuania. The Baltic localities of *P. canescens* also seem to be the westernmost and northwesternmost for the species. Some other southern species, *P. goldbachii, P. recta, P. heidenrichii* and *P. intermedia*, reach their northern boundaries in Finland and Sweden (Table 2).

Table 2.

Distribution in the neighbouring regions of *Potentilla* species that are rare in the Baltic states (on the basis of local floras).

Species	Finland	Sweden	Lenin-grad region	Pskov region	Kalinin-grad region	Poland	Belarus
P. anglica	x	xx	.	.	.	xx	x
P. arenaria	.	x	.	.	.	x	x
P. bifurca	x	x	x	.	.	x	.
P. canescens	.	.	xx	xx	x	x	x
P. crantzii	xxx	xxx	x	x	.	x	.
P. fruticosa	.	x	.	.	0	x	.
P. goldbachii	xx	xx	xx	x	xx	xxx	xx
P. heidenreichii	xxx	xxx	xxx	xxx	xxx	xxx	x
P. intermedia	x	?	xx	xxx	xxx	xx	x
P. leucopolitana	.	.	.	.	.	x	.
P. longifolia	.	.	.	.	.	.	.
P. multifida	x	x	.	.	.	x	.
P. recta	xx	xxx	x	x	x	x	xx
P. silesiaca	.	?	.	.	.	x	.
P. subarenaria	x	?	.	.	.	.	?
P. supina	.	.	.	.	.	x	x
P. tabernaemontani	x	xx	.	.	.	x	.
P. thyrsiflora	.	.	.	x	.	x	x

x - very rare; xx - rare; xxx - not rare; 0 - escape; ? - doubtful data.

P. fruticosa has its continuous area in Asia and North America, with several discontinuous localities in Europe, while the Estonian locality is the farthest northwestern reach of the species.

Thus only six of the *Potentilla* species registered in the Baltic countries grow here in the central part of their distribution area. They are *P. argentea, P. impolita, P. erecta, P. anserina, P. norvegica, P. palustris.*

When comparing the distribution pattern of *Potentilla* and that of some other larger genera of the Estonian flora (*Carex, Taraxacum, Salix, Juncus, Alchemilla*), it appears that the percentage of the species on their distribution margins in Estonia in these genera is about 20-25 %, just as is the case with the Estonian flora as a whole, of which about 20 % of the species are so-called "margin" species. In the genus *Potentilla* the percentage is larger, over 40 %, and for all three Baltic countries it is even larger, about 60 %.

In the Baltic region cinquefoils are quite far from their center of primary diversity (which is considered to be in the mountains of Central Asia (SHAH et al., 1992)) occurring in more or less extreme conditions, which is indicated also by the great number of "margin" species. The reproductive behavior of "margin" species is very often different from that of plants inhabiting the central parts of their area, and taxonomical diversity is likely to increase in such margin areas giving rise to greater variability, as compared to central parts.

NOMENCLATURE PROBLEMS

Among *Potentilla* species growing in Estonia, Latvia and Lithuania, the most confusing ones for local botanists have been *P. intermedia* L., *P. heidenreichii* Zimm. (sect. *Rivales*) and *P. canescens* Besser (sect. *Argentea*).

P. intermedia and *P. heidenreichii* are considered to be separate species by several authors (JUZEPCZUK, 1941; STANKOV & TALIEV, 1949; GALENIEKS, 1957; EICHWALD, 1962; SERGIEVSKAJA, 1981; NATKEVIČAITĖ-IVANAUSKIENĖ, 1971; KOBELEVA, 1976, etc.) while others do not recognise *P. heidenreichii* as a taxon at all (BALL & al., 1968; GARCKE, 1972; ROTHMAHLER, 1976, etc.). *P. heidenreichii* has also been treated as a subspecies or a variety of *P. intermedia* (RUPRECHT, 1860; WOLF, 1908; SYREISČIKOV, 1907; HEGI, 1922-1923; HIITONEN, 1934; MAEVSKIJ, 1954; RACIBORSKI & al., 1955, etc.).

The variety of taxonomical viewpoints concerning *P. intermedia* and *P. heidenreichii* is accompanied by difficulties in distinguishing between *P. heidenreichii* and *P. canescens*, as well as by errors in their nomenclature - mostly mistakes in the use of synonyms (LEHT, 1987). Starting with G. Besser, who described *P. canescens* Besser, there have been mistakes in identifying *P. canescens* and *P. heidenreichii*. The herbarium of the Botanical Institute in St. Petersburg includes a specimen identified by G. Besser as *P. canescens* Besser with a remark by T. WOLF (1908) (the author of the last monograph on the genus *Potentilla*) about Besser having mixed up his own species with *P. heidenreichii* Zimm. In 1860 Ruprecht, after having seen Ledebour's *Potentilla* materials, accuses the latter in his *Flora Ingrica* of confusing

P. inclinata Vill. with *P. intermedia β. canescens* Rupr. (*P. heidenreichii* Zimm.).

The two best-known synonyms of *P. canescens* are *P. inclinata* Vill. and *P. adscendens* Walst. et Kit. However, not all taxonomists regard them as full synonyms (ZIMMETER, 1884; JUZEPCZUK, 1941; CZEREPANOV, 1973; DOSTÁL, 1982). All three of these names can be found in older Baltic floristic literature but in the sense of *P. heidenreichii* (GLEHN, 1860; GRUNER, 1864; LEHMANN, 1895; VILBERG, 1925, etc.): the descriptions added to their floristic lists correspond to *P. heidenreichii*. Also, in the older parts of the Estonian herbaria there exist several specimens of *P. heidenreichii* labelled as *P. inclinata* or *P. adscendens*.

Although *P. inclinata* and *P. adscendens* are older synonyms, it is better to use the name *P. canescens* Besser, in order to avoid confusion. It seems that the real *P. canescens* reached Estonia and Latvia in the 1950s, herbarium specimens are available from at least that time.

P. canescens is a Eurasian forest-steppe plant which was described from western Ukraine and now occurs also in regions neighbouring the Baltic countries: in Belarus and Poland, in the Pskov, Leningrad and Kaliningrad regions, and as a recent immigrant in Karelia (RAMENSKAJA & ANDREEVA, 1982). As yet no findings have been reported in Finland, Sweden, the Murmansk region or Lithuania.

P. intermedia and *P. heidenreichii* are European boreal species which are distributed in Russia in the plant geographical regions of Ladoga-Ilmen, Upper-Dnieper, Volga-Kama and Volga-Don. In Scandinavia and Central Europe they are adventives (BALL & al., 1968); some authors (EICHWALD, 1962) also consider them to be adventives in the Baltic countries.

When comparing the distribution of *P. intermedia* and *P. heidenreichii* with the "distribution of botanists", it can be seen that taxonomists working with sufficient material in the main distribution area of these species tend to regard *P. heidenreichii* and *P. intermedia* as separate species.

The wide scale of propagation possibilities in the genus – sexual reproduction, apomixis, hybridization, vegetative propagation (MÜNZING, 1958; ASKER, 1986) – is the main reason for different taxonomical treatments and problems which, in turn, give rise to numerous synonyms.

The most drastic example among Baltic cinquefoils in terms of varying taxonomical treatments is the *P. collina* group, which consists of between one and 28 taxa, depending on the author. In addition, *P. argentea* s. l. has been reported to consist of one to twelve taxa and *P. intermedia* s. l. of one to four taxa (LEHT, 1984). Table 1 illustrates the multitude of synonyms of Baltic cinquefoils. The richness of names used for *Potentilla* taxa originates with C. von Linnaeus who described 26 species now belonging to the genus *Potentilla*: 22 under the name *Potentilla*, two *Tormentilla*, one *Fragaria* and one *Comarum*. The last monograph dealing with the whole genus was published in 1908 by Theodore Wolf and contained 305 species, 336 varieties and 294 forms. Since then only local *Potentilla* floras and taxonomical groups have been studied,. and the number of species in the genus is estimated to be 350-500.

CONCLUSIONS

About 60 % of the Baltic representatives of the genus *Potentilla* are on the margins of their distribution areas or nearly so. Only in the case of six species do Baltic localities lie in the central part of their main distribution area. Seven species on the list are adventives, some of which are very well established here (*P. recta*, *P. goldbachii*).

P. heidenreichii which, together with *P. intermedia* and *P. canescens*, has caused much confusion, seems to be a very old and very well-established casual, often even considered to belong to our native flora. It is widespread in the Baltic countries, while its closest relative, *P. intermedia* L. s. str. has only a few localities here, and *P. canescens*, a rare adventive, is found only in Estonia and Latvia. Synonyms of *P. canescens*, *P. inclinata* and *P. adscendens* have often been used erroneously to indicate *P. heidenreichii*, and the name *P. canescens* Besser should be preferred. *P. canescens* reached the Baltics in the 1950s, and references to the occurrence of this species in older publications are mistakes: in fact, *P. heidenreichii* was intended.

For the *P. verna* group, the Baltic region is a kind of junction point: *P. tabernaemontani* occurs only in Estonia, *P. subarenaria* and *P. crantzii* are common in Estonia and occur in some localities in Latvia, *P. arenaria* grows in Latvia and Lithuania but is absent from Estonia.

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Variation in *Potentilla* sect. *Aureae* Wolf in the Baltic states

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Abstract

Morphological variation of four Baltic representatives of the genus *Potentilla* L. section *Aurea* Wolf — *P. neumanniana* Reich., *P. arenaria* Borkh., *P. subarenaria* Borb. and *P. crantzii* (Crantz) Beck was studied with multivariate methods. Altogether 41 characters were used.

The most important characters for the phenetical classification are those of the epidermis: characters of stellate and glandular hairs and numbers of cells. Macromorphological characters are less important; the most useful are the length of sepals and stipules and the number of teeth of the central leaflet.

All four species are significantly distinct. Even *P. subarenaria*, a putative hybrid of *P. arenaria* and *P. neumanniana*, is clearly separated. At the same time the species are morphologically quite variable, and within *P. neumanniana*, *P. subarenaria* and *P. crantzii* it is possible to distinguish subclusters (morphotypes) which are statistically distinct also. The varieties described by Wolf (1908) in *P. tabernaemontani* (*P. neumanniana*) do not agree well with our material, however, with some concessions it may be stated that var. *typica* and var. *neumanniana* are prevalent, and var. *pseudo-incisa* and var. *incisa* also occur; only var. *longifolia* can be delimited quite clearly.

Introduction

All four Baltic representatives of the genus *Potentilla* L. section *Aurea* Wolf — *P. neumanniana* Reich. (*P. tabernaemontani* Asch.), *P. arenaria* Borkh., *P. subarenaria* Borb. and *P. crantzii* (Crantz.) Beck — are quite widely distributed in Europe. *P. arenaria* extends north to the Baltic countries, *P. neumanniana* also to Central Sweden (Mascher 1990). *P. neumanniana* has a western distribution, *P. arenaria* a more eastern one. In some areas, e.g. on Gotland (Johansson 1905), in Denmark (Pedersen 1964), in Swizerland (Rutishauser 1943, 1948), *P. subarenaria*, held to be of hybrid origin between these two, also occurs (Asker 1986). The distribution area of *P. crantzii* consists of two parts with the smaller one in the mountains of southern Europe and the main one in North Europe and eastern North America (Hultén & Fries 1986).

These taxa all have distribution limits in the Baltic countries. *P. crantzii* is quite common in Estonia but very rare in Latvia where it reaches the southern boundary of its main area; *P. arenaria*, common in Lithuania, attains its northern limit in Central Latvia; *P. neumanniana* and *P. subarenaria* are common in western Estonia but absent in eastern Estonia, Latvia and Lithuania (Fig. 1). The species prefer open habitats on alvars or heathy meadows, mostly on dry calcareous rendzinas and sandy soils; *P. crantzii* can be found also growing on fresh and moist meadows on gleyed and gley-brown soils (Leht & al. 1996).

All four species are morphologically as well as cytologically quite polymorphic. Wolf (1908), using only macromorphological characters, divided *P. crantzii* into 15 varieties and 6 forms, *P. neumanniana* into 10 varieties and 27 forms and *P. arenaria* into 12 forms. Smith (1971), studying British material, stated that *P. crantzii* is relatively homogeneous but contains both hexaploids and heptaploids, while *P. neumanniana* is both cytologically and morphologically more variable.

According to Asker (1986), *P. crantzii* is very variable in Sweden, and there may be distinct morphological differences even between adjacent sites. *P. neumanniana* is extremely variable on Gotland (Asker 1985), from where Johansson (1905) has described five different taxa, while in the neighbouring parts of Sweden its variation is smaller.

As far as known, *P. neumanniana, P. crantzii* and *P. arenaria* are apomictic in the Nordic countries (Asker 1986), but in Central Europe sexual populations of all three species have been found (Müntzing 1958, Czapik 1962).

In the Baltic countries these species have been insufficiently studied. Previously (Vilberg 1925, Enari & al. 1943) *P. arenaria* was even misunderstood or erraneously identified, as it was stated to occur in Estonia. This incorrect data has also reached the maps of Hultén (1950) and Hultén & Fries (1986).

In the present study taxonomic structure of the four *Potentilla* species in the Baltic region is analyzed by the means of multivariate methods, to answer the following questions:

(i) How variable are these taxa morphologically?
(ii) How well can the species be distinguished?
(iii) Is it possible to establish infraspecific taxa?
(iv) What are the most important morphological variables characterising different taxa?

Material and methods

41 morphological characters (Table 1) were used for studying 45 specimens of *P. crantzii* (35 localities), 9 *P. arenaria* (9 localities), 66 *P. neumanniana* (40 localities) and 31 *P. subarenaria* (17 localities). Material of *P. neumanniana* and *P. subarenaria* originates from western Estonia, *P. crantzii* from western and central Estonia and *P. arenaria* from the banks of river Daugava in Latvia and from northeastern Lithuania. Material was collected mostly in 1983 and 1988 but also herbarium material from the Herbarium of the Estonian Institute of Zoology and Botany (TAA) was used.

Characters 1–10, 28, 35–41 were measured on air dry herbarium material using a binocular microscope MBS-2 and a ruler; three central leaflets of fully developed rosette leaves and three flowers from every specimen were measured and the means were used for further calculations.

For studying the epidermis herbarium material or material fixed in the field with the coagulative fixative FAA (formalin, alcohol, acetic acid, 2:10:1) was used. Leaflets were first macerated in concentrated HNO_3 adding some drops of $HClO_4$, then in 10% NH_3OH. The epidermis was peeled from the central part of the central leaflet, stained with Heidenhein hematoxylin and mounted into glycerin-jelly. 5–10 cells, stomas and hairs from each specimen were measured and average values used for calculations. Numbers of cells and stomas were counted per field of vision and recalculated per 1 mm^2.

Data processing

First, to get a overview of the potentially existing cluster structer of the sample, for standardized data the average linkage method (UPGMA) with Manhattan distance as a resemblance measure was utilized for specimen classification. Then, using that result as the initial group membership vector, further optimization of classification by k-means clustering was used. The last method works iteratively: during each step of the analysis it is examined if the relocation of any object from one cluster to another provides decrease of the sum of squares. The specimens for which maximum decrease may be achived is moved to a new cluster. Iteration is stopped if no further reduction is possible (Podani 1994). Cluster analysis was done with the SYN-TAX 5.0 program package (Podani 1993).

Principal components analysis of ln (1+C) transformed data was exploited for ordination (CANOCO package, version 3.1; ter Braak, 1990, and CANODRAW package, version 3.0; Smilauer 1992).

The SAS program package (SAS Institute Inc. 1994) was used for calculating means and standard errors as well as for estimation of the importance of characters within clusters on the basis of the analysis of. variance (ANOVA).

Estimation of adjacency

By taxonomic continuum we usually do not mean that all possible transitions between different clusters exist, but rather that there are such relationships between some of the clusters which are adjacent in the character space. Thus, the number of clusters to which an operational taxonomic unit (OTU) with intermediate characteristics can belong is smaller than the total number of clusters. Numerical analysis requires a formal criterion for deciding whether the clusters should be regarded as adjacent.

One can postulate that the j-th cluster is treated as adjacent to the i-th cluster if the distance between at least one of the OTUs of the i-th cluster and the centroid of the j-th cluster is smaller than the distance to the centroids of all other clusters (Paal & Kolodyazhnyi 1983, Paal 1994). According to such a criterion the distance of all OTUs from all centroids (except the cluster to which the OTU belongs) can be calculated and the adjacent clusters estimated. The results will be presented in the form of the so-called adjacency matrix. This definition of adjacency is non-symmetric: if the j-th cluster is adjacent to the i-th cluster, the latter will not necessarily be adjacent to the OTUs belonging to cluster j.

Testing of clusters' distinctness

In order to measure the degree of distinctness the α-criterion (Duda & Hart 1976) was used.

To acquire a better interpretation of the estimates, it is more convenient to apply the corresponding probabilities as coefficients of indistinctness (CI) instead of the direct values (Paal 1987, 1994):

$$CI = 100 / \sqrt{2\pi} \int_{\alpha}^{\infty} \exp(-x^2 / 2)\, dx \tag{1}$$

To visualize the distribution of OTUs located between the centroids of two adjacent clusters in the character space the split window method (Parzen 1962) appears appropriate. The density of the OTUs projection probability distribution on a straight line passing through the centroids of both clusters can be calculated as

$$p(x) = 1/n \, \Sigma^{n}_{i=1} \, (1/h) \, \Phi \, [(x-x_i) / h], \tag{2}$$

where p(x) is the distribution density p(x) at point x, Φ — the window function, h — the smoothing parameter, or the window breadth, n — the number of OTUs in the cluster, x_i — the projection of the i-th OTU on the line. The density of the normal distribution was regarded as the window function.

The smoothing parameter h was determined according to the formula:

$$h = 2s \, (0.05 + 1 / \sqrt{n}), \tag{3}$$

where s is the standard error of projections. The density of the projection probability for OTUs of either cluster was calculated for the line segment ±3s for every 0.1 unit of the standard error. Normalization to the standard error makes it possible to estimate the expression of the distinctness independently of the number of OTUs in the cluster.

Results

Relations of clusters

At first the significance of conventionally established species-clusters was tested. All four empirically estimated species were well separated with coefficients of indistinctness (CI) lower than 0.001.

The dendrogram (Fig. 2) received by UPGMA branches on a quite high level into three clusters and within a short distancance the largest of them branches into two clusters (four in all). Some OTUs occurring on the right side of the dendrogram as very small clusters or singletons, are artefacts characteristic to UPGMA method and in the first stage of the analysis can be merged with the nearest cluster (*P. crantzii*). Cluster A is the smallest, containing 9 specimens, all identified as *P. arenaria*. Cluster B includes 31 specimens of *P. subarenaria* and 11 specimens of *P. neumanniana*. Cluster C contains 50 specimens of *P. neumanniana*. 45 specimens of *P. crantzii* and 3 of *P. neumanniana* (at least one of them may be a hybrid with *P. crantzii*) belong to cluster D. The UPGMA classification corresponds roughly to the conventional identification of specimens and we can name cluster A as *P. arenaria*, cluster B as *P. subarenaria*, cluster C as *P. neumanniana* and cluster D as *P. crantzii*. All the clusters are mutually significantly separated, having CIs close to zero.

The only neighbour in the character space for *P. arenaria* specimens is *P. subarenaria* (adjacency 100%, Table 2). For *P. subarenaria* the main neighbour is *P. neumanniana* (81%), but to some extent its within-group variation is directed also towards *P. arenaria*. Although for *P. neumanniana* the main neighbour is *P. crantzii* (65.4%), more than a quarter of its specimens have some similarity with *P. subarenaria*, too. *P. crantzii* is mostly neighbouring to *P. neumanniana* (93.8%). Thus, the adjacency matrix indicates asymmetrical relations between the clusters, i.e. there is only one pair of clusters (C and D) whose within-group variation is directed mainly towards the centroid of the other counterpart, while the within-group variation in clusters A and B is more or less unilateral.

Optimization of the UPGMA classification by k-means procedure established clusters whose mutual distinctness is highly significant, but now the correspondence with empirical classification is somewhat weaker than with the UPGMA results. Three more (14 in all) specimens of *P. neumanniana* have been shifted to the *P. subarenaria* cluster and 3 specimens of *P. subarenaria* to the *P. neumanniana* cluster, showing existance of close connections between these species. Also, one *P. neumanniana* and one *P. crantzii* specimen have exchanged positions.

Irrespective of the changes mentioned above, adjacency relationships between the clusters obtained with the k-means algorithm show little change compared to the relationships between UPGMA clusters (Table 2).

Ordination analysis demonstrates (Fig. 3) that the whole sample consists of three obviously separated subsets, where the first one corresponds to *P. arenaria* and the second to *P. subarenaria*. The third subset represents *P. neumanniana* and *P. crantzii* specimens, occupying rather close areas in the character space. On the ordination plot the polygons of the three last clusters overlap to some extent despite a high significance of distinctness between the clusters. We must consider that owing to the reduction of dimensionality all ordination plots represent simplifications of the existing relations between objects and contain errors causing distortions of real distances (Paal & al. 1989). However, for the case studied the two dimensional solution of PCA is acceptable since the first axis accounts for 61.5% of the total variation and the second axis for 14.0%. And although PCA is a more rough method than k-means, it is useful for visualization of the results.

The UPGMA dendrogram (Fig. 2) shows that the species-clusters, except *P. arenaria*, are split further into rather large subclusters possibly representing particular morphotypes (morphs) of respective species. *P. subarenaria* and *P. crantzii* can be divided into at least two subclusters and *P. neumanniana* into three. Testing validity of the subclusters confirms that they are almost all significantly distinct (CI ≈ 0), except the *P. crantzii* subclusters, having CI = 34.8.

Using the results of UPGMA classification as the initial group membership vector, k-means procedure was employed again. This time only one *P. neumanniana*, three *P. subarenaria* and one *P. crantzii* specimen were relocated.

The *P. arenaria* cluster is adjacent to only one morph of *P. subarenaria* (Table 3). The first morph of *P. subarenaria* (cluster 2) has as neighbours the two morphs of *P. neumanniana* and also the other subcluster of *P. subarenaria*. The second morph of *P. subarenaria* (cluster 3) is adjacent mainly to the other morph of the same species (cluster 2). The first morph of *P. neumanniana* (cluster 4) is adjacent to the other two morphs of that same species. The second morph of *P. neumanniana* (cluster 5) is intermediate between the first morph of *P. neumanniana* (cluster 4) and the second morph of *P. subarenaria* (cluster 2), while the specimens of the third morph of *P. neumanniana* (cluster 6) are adjacent to the second morph of that species (cluster 4). The two morphs of *P. crantzii* (clusters 7 and 8) are adjacent mainly to each other. As on the species level, not all the morph-clusters obtained are symmetrically connected, the connections are even slightly more asymmetrical than in the case of species-clusters.

Low discrepancy between the results obtained by UPGMA as well as by k-means algorithms indicates that now the classification well reflects the real structure of the data. Reorganizing the clusters with k-means procedure increases their distinctness so that all CIs are very close to zero.

Relations of characters

According to the F-criterion values, found with the analysis of variance (ANOVA) the most important characters for all compared classifications are the same (Table 4). It is obvious that the micromorphological characters studied: width and length of glandular hair's head, number and diameter of branches and diameter of central branch of stellate hairs in the lower epidermis, as well as number of cells in the lower epidermis and number of branches of stellate hairs in the upper epidermis, are much more important in the separation of specimens into clusters than the macromorphological ones. Of the macromorphological characters, number of teeth of the central leaflet, also length of sepals and stipules are to some extent useful for classification, while length and width of the central leaflet, abundance of rosette leaves, number of branches of the shoot, and length of the petiole are the less important ones in the ranking of variables. For empirically established clusters the relative importance of characters decreases rather smoothly, while in the case of numerical classifications a remarkably rapid decrease in F values appears after the first two characters.

The top characters in the ranking list constitute three correlation groups. The first one includes width and length of glandular hair's head, with Spearman's rank correlation coefficient $r_{Glaw,Glal} = 0.87$ between them. The second group is formed by the characters of stellate hairs in the lower epidermis: $r_{Stnl,Stcl} = 0.96$, $r_{Stnl,Stbl} = 0.95$, $r_{Stcl,Stbl} = 0.98$, respectively. The third group includes variables characterizing stellate hairs in the upper epidermis: $r_{Stnu,Stbu} = 0.98$, $r_{Stnu,Stcu} = 0.98$, $r_{Stbu,Stcu} = 0.99$, respectively.

On the ordination scheme (Fig. 4) we can follow the mutual relationships of nearly all the characters, except those positioned too near the center (Tow, Sepw) to avoid overloading of the figure. As for standardized PCA the cosine of the angle between the arrows of the variables only approximates the linear correlation between variables (Jongman & al. 1987), that result can not be absolutely concordant with the matrix of Spearman's rank correlation coefficients. Still, the groups of correlated characters mentioned above form more or less compact bunches of arrows. The opposite position of the characters of glandular hairs and epidermal cells to stellate hair characteristics is obvious. Naturally, length and width of leaflets (Spearman's $r_{Lfl,\ Lfw} = 0.73$), length and width of teeth ($r_{Tol,Tow} = 0.79$), length and width of petals ($r_{Lpet,Wpet} = 0.80$), and length and width of sepals ($r_{Sepl,\ Sepw} = 0.69$) are related quite closely.

According to the ordination the diameter of hairs in the upper and lower epidermis also appear to be rather important characters.

Characterization of clusters

Potentilla arenaria

In comparison with other species studied, *P. arenaria* does not have simple hairs and has stomas only in the lower epidermis. Values of the following characters (Table 5) are larger than those of the other species: width and length of the central leaflet and number of its teeth, number of cells in the upper and lower epidermis, number of branches of stellate hairs and length and width of petals. At the same time length and width of cells both in the upper and lower epidermis, length and width of stomas, length and width of glandular hairs' heads, stomatal index and number of branches of the shoot are the smallest.

Potentilla subarenaria

In the upper epidermis representatives of this cluster mostly have simple hairs and sometimes also some stellate ones; in the lower epidermis both stellate and simple hairs occur. Stellate trichomes have much fewer branches than in *P. arenaria.* Plants of this species have less flowers than the others, their leaves have many small teeth and their stipules are the smallest. In the upper epidermis, cells are the smallest and their number is the largest. The heads of glandular hairs are the smallest and simple hairs are finer than in other species (Table 5).

Morphs of *Potentilla subarenaria*

Specimens of the first morph have stellate hairs only in the lower epidermis, those of the second morph also some few-branceh stellate hairs in the upper epidermis. Stellate hairs in the first morph are less branched than in the second, and branches are smaller in diameter, and there are less stomas in the lower epidermis (Table 6). The diameter of simple hairs in the lower epidermis is larger in the second morph, in the upper epidermis it is equal in both morphs. Cells in the upper epidermis of the first morph are a bit larger and their number is smaller. Leaves are slightly longer than in the first morph, the width being the same. In thr first morph the number of flowers is the smallest of all the morphs studied. Dimensions of flowers are the same in both morphs (Table 6).

Potentilla neumanniana

P. neumanniana specimens have no stellate hairs, their leaves are the same size as those of *P. subarenaria* but have less teeth (Table 5). Stipules and teeth are a bit longer than in *P. subarenaria*, flowers are of the same size. Stomas and the diameter of simple hairs are slightly larger than in other species.

Morphs of *Potentilla neumanniana*

Flowers are of nearly the same size in all three morphs; neither do the dimensions of the stipules differ much (Table 6). Characters of the first morph are to some extent intermediate between the two other morphs. Nevertheless, plants of this morph are slightly more hairy than in the other morphs.

Specimens of the second morph have few flowers, thin hairs and leaflets with several small teeth (Table 6). Stomas and cells are small and the number of cells is nearly two times as great than as in the third morph.

The third morph is statistically the most distinct of the three. It has many more flowers, the topmost teeth of its central leaflets are larger and there is usually only 2–3 teeth on each side of the leaflet. Cells and stomas are larger, but smaller in number in comparison with other morphs. The number of rosette leaves is equal to that of the first morph.

Potentilla crantzii
Specimens of this species have only few simple hairs and no stellate hairs (Table 5), and, therefore, appeare glabrous. They have many flowers which are larger than in *P. subarenaria* and *P. neumanniana.* Plants have many branches and long petioles. The heads of glandular hairs are largest in this species, and, as their length is smaller than their width, also of a different shape.

Morphs of *Potentilla crantzii*
The first morph differs from the second one in having slightly larger leaflets, larger teeth, longer petals, more flowers, larger stomas and cells and slender hairs (Table 6). In the first morph the width and length of the stoma is also larger and the numbers of them smaller both in the upper and lower epidermis.

Discussion

All four Baltic representatives of the genus *Potentilla* section *Aurea* — *P. neumanniana, P. arenaria, P. subarenaria* and *P. crantzii* — are well separated from the statistical point of view. *P. subarenaria,* a putative hybrid of *P. arenaria* and *P. neumanniana,* is clearly separated from both these species.

However, some overlapping of the clusters of *P. neumanniana* and *P. subarenaria* indicates closer connections between these taxa. This can also be seen on the adjacency matrix where *P. subarenaria* is more adjacent to *P. neumanniana* than to *P. arenaria* (Tables 2 and 3).

Ordination shows (Fig. 3) that variation of the morphs of *P. subarenaria* is parallely directed in the character space and that they are mutually clearly separated. According to hairiness characters (Table 6) the first morph resembles *P. neumanniana,* the second morph more closely the other parent species, *P. arenaria* (Table 3). These relations as well as the intermediate nature of their trichomes and adjacency of *P. subarenaria* with both *P. neumanniana* and *P. arenaria* clearly indicate the hybrid origin of *P. subarenaria.*

The morph is quite variable and according to Wolf's (1908) key three varieties are represented: var. *typica,* var. *neumanniana* and var. *pseudo-incisa.* Specimens of the second morph of *P. neumanniana* are closer to *P. subarenaria.* All plants identified as var. *longifolia* belong to this morph, but also some representatives of var. *typica* and var. *incisa.* Leaflets of var. *longifolia* are 2–3 times longer than wide and have 6–9 teeth on both sides extending nearly to the base of the leaflet (Wolf 1908). It seems that var. *longifolia* is the only variety among those described by Wolf which can be more or less clearly delimited in our material.

The third morph of *P. neumanniana* agrees most closely with Wolf's var. *pseudo-incisa,* but several medium-sized representatives of var. *typica* with few teeth also appear here. Although theis morph is statistically rather different from other morphs, again it was not possible to associate it with only one variety.

The pattern of variation of *P. neumanniana* in the Baltic states is thus rather complicated and Wolf's infraspecific classification, created for Central Europe, does not work well. In some populations specimens of several morphotypes grow intermixed. *P. neumanniana* is the most varying species of the four but not as varying as in Gotland. Morphs of *P. neumanniana* surely need more detailed study in order to decide their taxonomic rank, since the use of morphological characters alone seems to be insufficient.

P. crantzii and *P. neumanniana* are phenotypically well separable but appear closer to each other than the morphologically less different *P. neumanniana* and *P. subarenaria* when micromorphological characters are considered; this is indicated by *P. neumanniana* being much more adjacent to *P. crantzii* than to *P. subarenaria* (Table 3). The morphological closeness of *P. neumanniana* and *P. crantzii* is further demonstrated by the existence of some specimens macromorphologically clearly identified as *P. neumanniana* or *P. crantzii* with intermediate in some extent characters clustered into the "wrong" clusters in the conventional sense (some of these specimens may be hybrids). But since both morphs of *P. crantzii* are principal neighbours only to each other and since it was only possible to obtain distinct clusters after using k-means clustering, the subclusters being distinguished mainly on the basis of numbers and dimensions of cells and stomas, *P. crantzii* is surely a morphologically well distinguished taxon among the four species studied.

Smith (1971) mentioned that it is not always possible to assign material confidently to *P. crantzii* or to *P. neumanniana*. Smith finds that the best characters for distinguishing these species are size and shape of the stipules. According to our material the most useful characters for identifying the species are those of the rootstock. The rootstock of *P. neumanniana* is black, roundish, covered with few short dark (black) spirallely arranged withered stipules, which have straight white hairs on their edges. The rootstock of *P. crantzii* seems flat due to several brown wider and longer withered glabrous brown stipules placed in two rows. As the features of the rootstock does not vary within the species, they were not included in the list of characters analysed.

In this work the clusters (species and morphs) were distinguished mainly on the basis of epidermal characters; the macromorphological characters did not contribute significantly. Measuring micromorphological characters is quite time-consuming but, since several characters are highly correlated, in further studies of these species not all characters need be measured. Instead just one from each group of correlated characters may be used — e.g. either number or diameter of the branches of stellate hairs, either number or length or width of stomas and cells etc.

Until now chromosome numbers have been counted for one population of *P. crantzii* and for one population of *P. neumanniana*, both from Osmussaar (West Estonia) and only 2n=42 has been found, which indicates the possible occurrence of apomixis here, too. This makes it even more complicated to decide the taxonomic rank of the morphs.

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Table 1. Characters measured.

No	Notation	Character
1	LFL	length of the middle leaflet (mm)
2	LFW	width of the middle leaflet (mm)
3	TEETH	number of teeth of the middle leaflet
4	STPL	length of the stipule (mm)
5	STPW	width of the stipule (mm)
6	FLWS	number of flowers
7	TOL	length of the middle tooth (mm)
8	TOW	width of the middle tooth (mm)
9	SEPL	length of the sepal (mm)
10	SEPW	width of the sepal (mm)
11	STOLU	length of stoma in upper epidermis (µm)
12	STOWU	width of stoma in upper epidermis (µm)
13	STONU	number of stomas in upper epidermis
14	CELNU	number of cells in upper epidermis
15	CELLU	length of cell in upper epidermis (µm)
16	CELWU	width of cell in upper epidermis (µm)
17	GLAL	length of glandular hair's head (µm)
18	GLAW	width of glandular hair's head (µm)
19	HAIRU	diameter of hair in upper epidermis (µm)
20	STOLL	length of stoma in lower epidermis (µm)
21	STOWL	width of stoma in lower epidermis (µm)
22	STONL	number of stomas in lower epidermis
23	CELNL	number of cells in lower epidermis
24	CELLL	length of cell in lower epidermis (µm)
25	CELWL	width of cell in lower epidermis (µm)
26	HDL	diameter of hair in lower epidermis (µm)
27	INDX	stomatal index
28	LFN	number of leaflets
29	STNL	number of branches of stellate hair in lower epidermis
30	STBL	diameter of lateral branches of stellate hairs in lower epidermis (µm)
31	STCL	diameter of central branch of stellate hair in lower epidermis (µm)
32	STNU	number of branches of stellate hair in upper epidermis
33	STCU	diameter of central branch of stellate hair in upper epidermis (µm)
34	STBU	diameter of lateral branches of stellate hairs in upper epidermis (µm)
35	BRCH	number of branches of the shoot
36	PETIOL	length of petiole (mm)
37	LPET	length of petal (mm)
38	WPET	width of petal (mm)
39	HU	hairiness of upper side of leaflet (classes: 1, 2, 3)
40	HL	hairiness of lower side of leaflet (classes: 1, 2, 3, 4)
41	RLVS	number of rosette leaves (classes: 1, 2, 3)

Table 2. Adjacency (%) of species-level clusters. are — *P. arenaria*, sub — *P. subarenaria*, neu — *P. neumanniana*, cra — *P. crantzii*. In the upper row data considering clusters obtained by UPGMA, in the lower row data for clusters obtained with k-means procedure.

Cluster	1 are	2 sub	3 neu	4 cra
1 are	–	100	–	–
	–	100	–	–
2 sub	19.1	–	81.0	–
	21.4	–	76.2	–
3 neu	–	34.6	–	65.4
	–	36.4	–	63.6
4 cra	–	6.3	93.8	–
	–	13.3	86.7	–

Table 3. Adjacency (%) of morph-level clusters obtained with k-means procedure. Cluster names as in Table 2, numbers correspond to the morphs.

Cluster	1	2	3	4	5	6	7	8
	P. are	P. sub-1	P. sub-2	P. neu-1	P. neu-2	P. neu-3	P. cra	1 P. cra-2
1	–	–	100	–	–	–	–	–
2	–	–	25.0	33.3	41.7	–	–	–
3	–	93.8	–	–	6.3	–	–	–
4	–	–	–	–	50.0	45.2	–	–
5	–	53.3	–	46.7	–	–	–	–
6	–	–	–	100	–	–	–	–
7	–	–	–	10.7	7.1	–	–	82.1
8	–	–	–	5.9	–	–	94.1	–

Table 4. Importance of characters (according to the F-criterion of ANOVA) in the clustering of specimens using different methods. Below the name of the method stands the number of clusters. The 10 highest ranking characters and the 5 lowest ranking ones are shown. Denotation of characters (C) as in Table 1.

Empirical clustering		UPGMA		k-means		UPGMA		k-means	
4		4		4		8		8	
C	F	C	F	C	F	C	F	C	F
STNL	377.5	GLAW	366.5	GLAW	375.7	GLAW	317.8	GLAW	371.9
GLAW	333.8	GLAL	291.9	GLAL	274.8	GLAL	194.8	GLAL	231.6
STCL	333.7	STNL	216.3	STNL	156.4	STCL	117.2	STNL	166.1
GLAL	263.9	STCL	193.5	CELNL	129.1	STNL	111.5	STCL	165.9
STBL	261.2	STBL	169.6	STCL	122.2	CELNL	110.1	STBL	145.3
STNU	143.4	CELNL	136.1	STBL	102.6	STBL	103.9	HL	74.4
STBU	126.2	STNU	102.9	STNU	...94.6	STPL	67.2	CELNL	73.1
STCU	108.5	STBU	90.5	HL	85.1	SEPL	62.0	STNU	69.5
HDL	107.2	HAIRU	86.5	HAIRU	79.6	CELWL	56.4	SEPL	69.3
HL	104.9	HDL	83.3	HDL	79.0	HL	52.7	STPL	63.0
STONL	2.5	PETIOL	5.9	PETIOL	4.1	LFW	3.9	STONL	0.8
BRCH	1.9	LFW	2.6	LFL	1.9	STOWL	3.6	LFW	0.5
LFL	1.5	BRCH	2.3	BRCH	1.9	BRCH	1.4	BRCH	0.002
RLVS	0.5	LFL	0.3	LFW	0.4	RLVS	0.7	RLVS	0.001
LFW	0.2	RLVS	0.1	RLVS	0.2	LFL	0.0	LFL	0.001

Table 5. Mean ± standard error of characters for species-clusters obtained with k-means clustering. Characters denotations as in Table 1.

Character	Cluster (Species)			
	P. are	P. sub	P. neu	P.cra
LFL	20.7±3.10	9.8±0.36	9.9±0.35	11.7±0.47
LFW	8.6±0.88	5.5±0.17	5.7±0.16	6.7±0.23
TEETH	10.7±0.96	8.9±0.28	7.4±0.21	6.7±0.15
STPL	7.8±0.69	5.0±0.17	5.3±0.21	10.6±0.39
STPW	1.0±0.00	1.0±0.02	1.2±0.05	2.0±0.24
FLWS	11.6±2.86	7.6±1.14	11.9±1.54	14.0±1.59
TOL	1.6±0.16	1.3±0.07	1.6±0.05	1.7±0.07
TOW	1.3±0.12	0.8±0.04	1.1±0.04	1.3±0.05
SEPL	3.6±0.18	3.3±0.10	3.4±0.06	4.6±0.12
SEPW	2.1±0.13	1.9±0.07	1.9±0.05	2.3±0.06
STOLU	–	25.0±0.33	26.2±0.28	25.5±0.26
STOWU	–	19.7±0.30	21.2±0.20	19.3±0.24
STONU	–	3.0±0.29	3.7±0.23	4.5±0.26
CELNU	80.4±4.64	67.0±2.60	54.5±1.60	56.9±1.30
CELLU	36.1±2.11	39.8±1.05	45.9±1.06	5.0±0.79
CELWU	27.8±1.56	30.7±0.85	34.6±0.71	32.3±0.57
GLAL	25.4±0.62	33.0±0.44	35.8±0.53	47.7±0.91
GLAW	21.6±0.40	27.4±0.46	29.5±0.58	54.0±0.98
HAIRU	–	18.3±0.60	24.3±0.74	24.2±0.71
STOLL	21.4±0.73	23.5±0.41	25.5±0.26	24.7±0.27
STOWL	16.8±0.47	18.7±0.38	20.5±0.19	19.1±0.26
STONL	25.5±0.98	23.6±0.92	20.9±0.71	22.5±0.75
CELNL	114.4±2.10	98.0±3.60	74.4±2.30	68.8±1.20
CELLL	27.8±0.70	32.0±1.08	39.1±0.90	40.0±1.34
CELWL	20.4±0.62	23.7±0.80	27.4±0.62	28.3±0.65
HDL	–	14.8±0.74	24.1±0.72	21.0±0.54
INDX	17.6±0.40	19.7±0.46	21.7±0.37	24.4±0.41
LFN	5.0	5.0	5.0	5.0
STNL	19.2±1.34	6.1±0.48	–	–
STBL	11.2±0.55	18.3±0.57	–	–
STCL	8.5±0.22	8.9±0.13	–	–
STNU	13.7±1.92	8.1±0.42	–	–
STCU	13.4±0.63	11.8±2.13	–	–
STBU	8.2±0.21	5.0±0.88	–	–
BRCH	3.2±0.22	3.7±0.31	4.0±0.19	4.1±0.3
PETIOL	4.7±0.72	2.8±0.26	2.5±0.18	4.5±0.3
LPET	5.8±0.13	3.9±0.1	4.5±0.07	5.4±0.1
WPET	5.5±0.22	3.1±0.07	3.7±0.07	4.6±0.1
HU	3.1	1.2	1.3	1.2
HL	4.0	2.5	2.2	1.9
RLVS	1.1	1.5	1.4	1.5

Table 6. Mean ± standard error of characters for morph-clusters obtained with k-means clustering. Character denotations as in Table 1. Cluster names as in Table 2, numbers correspond to the morphs.

Character	Cluster (Morph)						
	P. sub-1	P. sub-2	P. neu-1	P. neu-2	P. neu-3	P. cra-1	P. cra-2
LFL	10.6±0.31	9.3±0.62	9.6±0.35	10.3±0.84	9.8±1.15	12.4±0.55	10.6±0.67
LFW	5.6±0.15	5.4±0.30	5.7±0.17	5.0±0.25	6.6±0.50	7.1±0.26	6.0±0.33
TEETH	9.5±0.37	8.3±0.42	7.5±0.26	8.2±0.42	6.2±0.35	6.8±0.19	6.5±0.20
STPL	5.3±0.26	4.8±0.26	5.1±0.20	5.2±0.31	5.8±0.81	10.9±0.47	10.3±0.65
STPW	1.0±0.02	1.0±0.03	1.2±0.06	1.1±0.09	1.3±0.17	1.9±0.28	2.1±0.46
FLWS	6.3±0.95	7.8±2.00	10.0±1.04	8.2±1.17	23.2±6.80	15.3±2.20	11.9±2.13
TOL	1.4±0.09	1.3±0.11	1.6±0.06	1.3±0.06	2.0±0.11	1.7±0.10	1.5±0.07
TOW	0.8±0.05	0.9±0.06	1.0±0.04	0.8±0.04	1.4±0.10	1.3±0.06	1.2±0.06
SEPL	3.2±0.15	3.4±0.15	3.4±0.07	3.4±0.07	3.6±0.15	4.6±0.15	4.5±0.19
SEPW	1.9±0.10	1.9±0.08	1.8±0.05	1.9±0.07	2.0±0.09	2.4±0.09	2.4±0.11
STOLU	24.5±0.34	25.1±0.51	26.5±0.28	23.8±0.31	28.2±0.65	26.2±0.32	4.5±0.36
STOWU	19.7±0.35	19.3±0.4	21.4±0.22	19.6±0.38	22.4±0.27	19.9±0.26	18.3±0.37
STONU	2.6±0.37	3.4±0.43	3.8±0.09	4.0±0.62	3.0±0.38	4.1±0.30	5.0±0.44
CELNU	66.9±3.33	71.0±3.67	52.0±0.90	72.2±2.83	8.4±1.45	52.1±1.01	65.5±1.53
CELLU	40.7±0.97	37.2±1.12	46.3±0.75	36.9±0.95	57.5±2.60	47.7±0.74	40.0±1.06
CELWU	30.8±0.64	28.9±1.04	35.0±0.60	28.7±0.76	41.9±1.60	34.1±0.65	29.0±0.45
GLAL	33.7±0.71	32.5±0.65	36.0±0.42	34.1±0.88	53.8±1.80	47.0±0.80	49.6±1.90
GLAW	28.6±0.91	26.4±0.48	29.4±0.53	27.6±0.65	30.5±0.75	54.3±1.12	54.6±1.70
HAIRU	18.6±0.83	18.6±0.88	24.2±1.02	21.1±1.04	26.5±1.56	23.0±0.93	26.2±0.93
STOLL	23.2±0.48	23.3±0.64	25.7±0.21	23.2±0.35	27.9±0.53	25.2±0.26	23.8±0.47
STOWL	19.0±0.52	17.9±0.44	20.9±0.20	19.0±0.38	21.5±0.42	19.7±0.22	18.1±0.51
STONL	22.8±1.40	24.8±1.30	19.7±0.59	27.9±1.35	16.3±0.89	20.4±0.75	25.6±1.27
CELNL	101.7±5.2	100.0±5.0	70.9±1.30	100.8±4.0	54.8±3.70	66.4±1.30	72.4±2.10
CELLL	32.4±1.62	29.9±1.31	39.6±0.54	30.3±1.08	48.2±2.23	42.6±1.87	36.1±1.18
CELWL	23.4±0.95	22.5±1.07	27.7±0.42	22.2±0.67	33.4±1.85	30.4±0.70	25.2±0.79
HDL	14.0±1.48	15.2±0.93	23.6±1.0	21.1±1.16	27.2±1.22	20.7±0.6	21.7±1.02
INDX	18.8±0.74	20.0±0.63	21.4±0.38	21.5±1.04	23.1±0.89	23.7±0.45	25.2±0.75
LFN	5.0	5.0	5.0	5.0	5.0	5.0	5.0
STNL	5.9±0.93	6.5±0.58	–	–	–	–	–
STBL	17.8±0.87	19.1±0.79	–	–	–	–	–
STCL	8.6±0.21	9.0±0.18	–	–	–	–	–
STNU	–	4.1±0.39	–	–	–	–	–
STCU	–	22.9±0.75	–	–	–	–	–
STBU	–	9.6±0.21	–	–	–	–	–
BRCH	3.7±0.37	3.9±0.53	4.0±0.25	3.6±0.32	4.3±0.42	4.1±0.33	3.9±0.57
PETIOL	2.8±0.50	3.0±0.32	2.3±0.19	2.8±0.40	2.4±0.40	4.8±0.38	4.2±0.43
LPET	3.9±0.20	3.8±0.10	4.5±0.07	4.6±0.21	4.5±0.10	5.4±0.11	5.3±0.21
WPET	3.2±0.06	3.1±0.12	3.7±0.09	3.7±0.11	3.7±0.10	4.5±0.14	4.5±0.22
HU	1.3	1.2	1.4	1.3	1.2	1.2	1.3
HL	2.3	2.6	2.3	2.2	2.1	1.9	1.9
RLVS	1.5	1.4	1.3	1.5	1.3	1.4	1.5

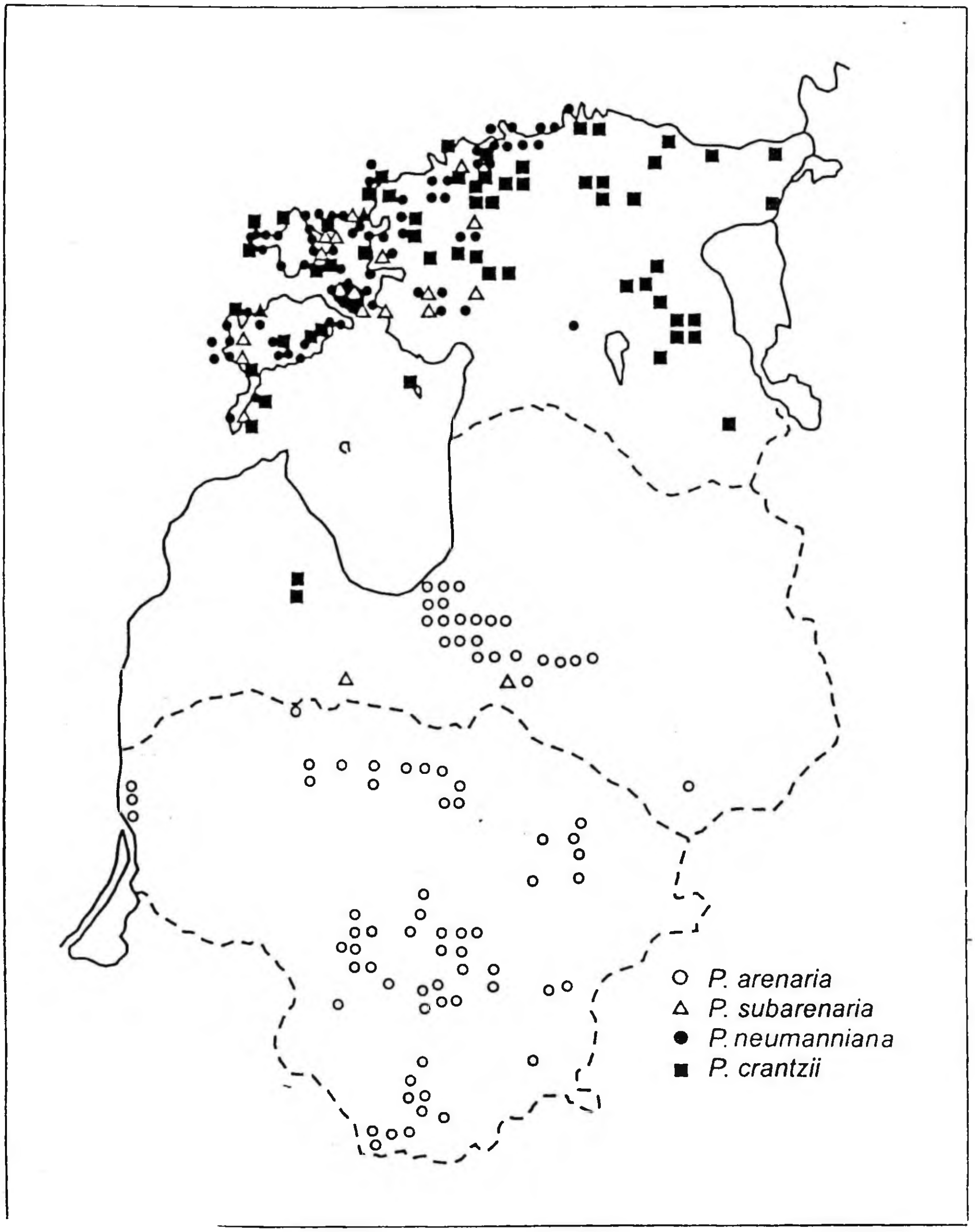

Figure 1. Distribution of *P. arenaria, P. subarenaria, P. neumanniana* and *P. crantzii* in Estonia, Latvia and Lithuania on the bases of field notes and herbarium specimens. Each symbol indicates occurrence of the species in a 10 × 10 km quadrat.

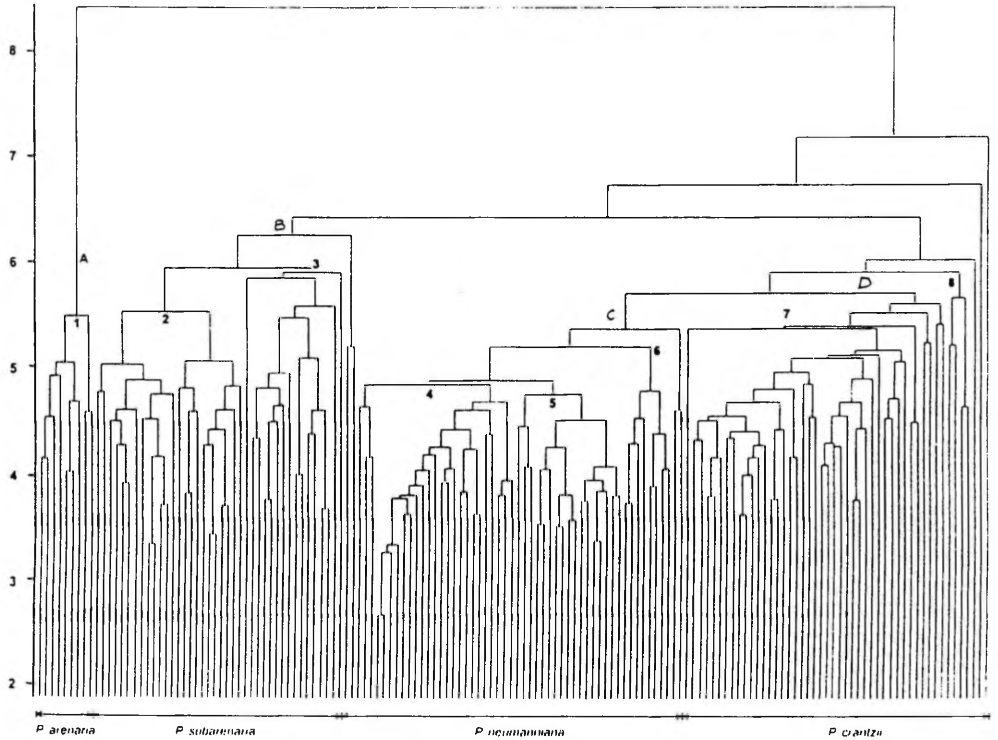

Figure 2. UPGMA dendrogram (Manhattan distance, data standardized) of studied specimens. Species-clusters are marked with arrows under the dendrogram. Morph-clusters are denoted with numbers: 1 — *P. arenaria,* 2 — first morph of *P. subarenaria,* 3 — second morph of *P. subarenaria,* 4 — first morph of *P. neumanniana,* 5 — second morph of *P. neumanniana,* 6 — third morph of *P. neumanniana,* 7 — first morph of *P. crantzii,* 8 — second morph of *P. crantzii.*

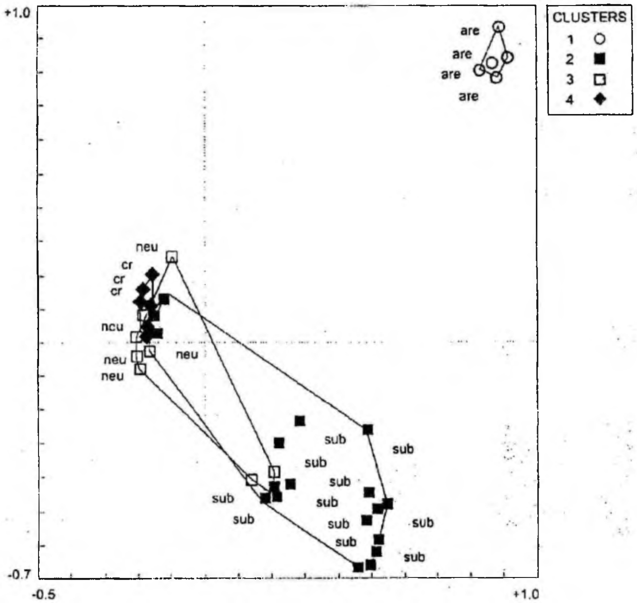

Figure 3. Ordination of species-clusters obtained by k-means procedure. 1 — *P. arenaria*, 2 — *P. subarenaria*, 3 — *P. neumanniana*, 4 — *P. crantzii.*

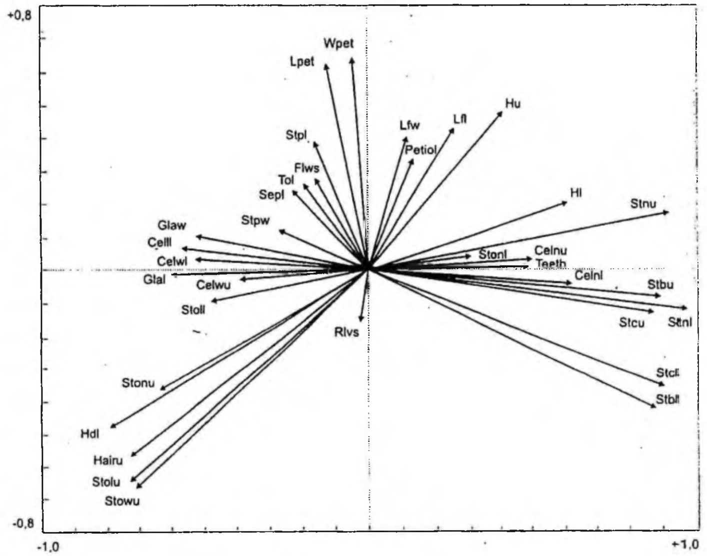

Figure 4. Ordination of characters. Denotations as in Table 1.

IX

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Variation of *Potentilla erecta* (Rosaceae) in Estonia

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Infraspecific variation of Estonian *Potentilla erecta* (L.) Räusch. was studied with different morphometrical methods. Both *P. erecta* ssp. *erecta* and ssp. *strictissima* (Zimm.) A. J. Richards were identified with ssp. *strictissima* prevailing; however, several specimens are morphologically of an intermediate type. Representatives of the two taxa have no geographical or ecological preference in Estonia, and since it was not possible to statistically delimit them, we preferred to treat these taxa as varieties: *P. erecta* var. *erecta* and *P. erecta* var. *strictissima* (Zimm.) Hegi.

Key words: Estonia, infraspecific taxonomy, multivariate methods, *Potentilla erecta*

INTRODUCTION

Potentilla erecta (L.) Räusch. (sect. *Tormentillae* Rydb.) is widespread in Estonia and quite common in Latvia and Lithuania on moderately moist and moist mineral soils and peat (Leht *et al.* 1996). Being a genetically and phenotypically widely variable taxon, it has been treated rather differently: Hegi (1922) has summarized its infraspecific taxonomy and listed 19 taxa of different ranks and taxonomic significance (excluding synonyms) that can be joined under the name *P. erecta.* Also, the multitude of synonyms, more than 30 (Leht 1984), points to its variability.

Variation of *Potentilla erecta* has been thoroughly studied by Vasari (1968) in Finland and by Richards (1973) in Great Britain. They established three different races (subspecies): two in Great Britain and three in Finland (Richards 1973). On the British Isles, the most common is the race growing on lowlands, identified as *P. erecta* ssp. *erecta.* The race of higher altitudes (500 m a.s.l.), *P. erecta* ssp. *strictissima* (Zimm.) A. J. Richards, is rarer. In Finland, *P. erecta* ssp. *strictissima* dominates, and *P. erecta* ssp. *erecta* occurs mostly in the SW part of the country (Richards 1973). The race growing on a thick peat layer in North Finland represents a subspecies which Vasari has not yet described. According to Vasari (1968), the border between the northern race and the other two subspecies coincides roughly with the border between the Southern Boreal and Mid-Boreal vegetation zones (Ahti *et al.* 1964).

According to Richards (1973), *Potentilla erecta* ssp. *strictissima* is found, as a relic from colder climatic periods, in uplands and in northern regions of Europe, where it is able to survive only in conditions resembling those of the period during which it evolved. Vasari (1968) suggests that the northern race is an old constituent of the Finnish flora, while his southern race (*P. erecta* ssp. *erecta* and *P. erecta* ssp. *strictissima* together) is likely to have migrated from the south during the post-glacial climatic optimum.

Since Estonia is the nearest southern neighbouring territory to Finland, it seemed interesting to attempt to confirm Vasari's (1968) approach as well as to find answers to the following questions:

— How variable is *Potentilla erecta* in Estonia?
— Is it possible to identify *P. erecta* ssp. *erecta* and *P. erecta* ssp. *strictissima* on the basis of Estonian material?
— Is it statistically justified to divide *P. erecta* into subtaxa?

MATERIAL AND METHODS

The material studied was mostly collected in 1988 and 1996; and herbarium specimens from the Herbarium of the Institute of Zoology and Botany (TAA), located in Tartu, were also used.

Eighteen macromorphological characters (Table 1) were measured with a binocular microscope MBS-2 or with a ruler. To reduce the effects of individual variability, characters 2–6, 8–11, 13 and 14 were measured three times, and the corresponding average values were used for further calculations. A total of 180 specimens were studied.

The distribution patterns of the subspecies of *Potentilla erecta* in adjacent sites were studied in transitional (mixotrophic) mire and transitional mire-forest habitats in the Alam-Pedja Nature Reserve (Central Estonia) on two transects (300 m and 800 m), where all flowering specimens of *P. erecta*, 60 altogether, were collected. The length of their branches was measured to compare the height of the two subspecies; in cluster analysis this character was not used.

The distribution of the subspecies in Estonia was investigated on the herbarium material of both TAA and the Herbarium of the University of Tartu (TU); over 300 specimens were studied.

The material collected is preserved in TAA.

Data processing

For standardized data, Ward's clustering method with the Manhattan distance as a resemblance measure was employed. Then, using the result as the initial group membership vector, further optimization of classification by k-means procedure was carried out. Ward's clustering was performed by SAS (SAS Institute Inc. 1994), k-means clustering, by SYN-TAX 5.0 program (Podani 1993) packages.

Principal components analysis was used for the ordination of ln-transformed data (CANOCO package, version 3.1; Ter Braak 1990, and CANODRAW package, version 3.0; Smilauer 1992). To calculate means and standard errors as well as to evaluate characters' importance within clusters by ANOVA, the SAS program package was used.

To estimate adjacency of clusters, the distances of all specimens, or operational taxonomic units (OTUs), from all centroids (except for the cluster to which the OTU belongs) were calculated according to the postulate that the j-

Table 1. Morphological characters of measured *Potentilla erecta* (L.) Räusch. specimens.

No.	Notation	Characters
1	NOD	Number of nods under the first branch
2	LFL	Length of the central leaflet (mm)
3	LFW	Width of the central leaflet (mm)
4	TEETH	Number of teeth of the central leaflet
5	STPL	Length of the stipule (mm)
6	STPW	Width of the stipule (mm)
7	FLWS	Number of flowers
8	TOL	Length of the central tooth (mm)
9	TOW	Width of the central tooth (mm)
10	SEPL	Length of the sepal (mm)
11	SEPW	Width of the sepal (mm)
12	BRCH	Number of branches on the shoot
13	LPET	Length of the petal (mm)
14	WPET	Width of the petal (mm)
15	HU	Hairiness of the upper side of the leaflet (1 = glabrous, 2 = hairy)
16	HL	Hairiness of the lower side of the leaflet (1 = glabrous, 2 = hairy)
17	DSTP	Division depth of the stipule (1 = to the base, 2 = 3/4 of the way, 3 = 1/2 of the way, 4 = 1/4 of the way)
18	DLF	Length of the dentated part of the leaflet (1 = to the base, 2 = 3/4 of the way, 3 = 1/2 of the way, 4 = 1/4 of the way)

th cluster is interpreted as adjacent to the i-th cluster if the distance between at least one of the OTUs of the i-th cluster and the centroid of the j-th cluster is shorter than the distance to the centroids of all other clusters (Paal & Kolodyazhnyi 1983, Paal 1994).

In order to measure the degree of distinctness of clusters, the α-criterion (Duda & Hart 1976) was used. To acquire a better interpretation of estimates, it is more convenient to apply the corresponding probabilities as coefficients of indistinctness (*I*) instead of direct values (Paal 1987, 1994).

The last two analyses were made by the original SYNCONT 3.0 program.

RESULTS

Clusters

Using Richards' (1973) characters, 101 specimens were identified as *Potentilla erecta* ssp. *strictissima* and 45 as *P. erecta* ssp. *erecta*, 34 appeared intermediate.

Potentilla erecta ssp. *strictissima* has larger leaflets with more teeth, larger stipules and more flowers; the dentated part of its leaves is longer, and stipules are divided deeper (the other characters do not reveal any difference (Table 2)). According to ANOVA *F*-criterion (Table 3), it is these characters that are important in distinguishing the subspecies, with the length of the dentated part of the leaflet and the depth of division of the stipule being the most important ones.

The dendrogram showing the results of the classification by Ward's algorithm (Fig. 1) is split, at a comparatively high level (level I), into two significantly distinct (*I* = 0.0) clusters, the first (cluster I_1) consisting of 61 and the second (I_2) of 119 specimens. The ratio of ssp. *erecta* to ssp. *strictissima* in the clusters is 1:5 and 1:1.5, respectively.

After reorganizing the obtained classification by k-means procedure, the clusters contain 89 and 91 specimens, and ratios of ssp. *erecta* to ssp. *strictissima* are 1:4 and 1:2, respectively. The coefficient of distinctness of the clusters is in this case also close to zero, despite their partial overlapping in the character space (Fig. 2). The most important characters in determining the clusters at level I are the length of the stipule, the length and width of the leaflet and the length and width of the central tooth (Table 3).

Plants belonging to cluster I_1 have larger leaflets and stipules, their stipules are not deeply divided, their flowers are larger and more numerous. Plants in cluster I_2 are smaller, and have more

Table 2. Mean ± *S.E.* of the characters of *Potentilla erecta* (L.) Rausch. ssp. *erecta* and *P. erecta* ssp. *strictissima* (Zimm.) A. J. Richards and two clusters obtained by k-means. Denotation of characters as in Table 1.

Character	Conventional estimation		Clustering by k-means algorithm	
	ssp. *erecta*	ssp. *strictissima*	Cluster I_1	Cluster I_2
	n = 45	*n* = 101	*n* = 89	*n* = 90
NOD	2.42 ± 0.20	2.19 ± 0.16	2.07 ± 0.12	2.43 ± 0.17
LFL	21.24 ± 0.68	24.23 ± 0.65	27.11 ± 0.62	19.94 ± 0.37
LFW	7.24 ± 0.32	7.56 ± 0.20	8.86 ± 0.22	6.42 ± 0.15
TEETH	8.60 ± 0.30	10.27 ± 0.88	10.97 ± 1.00	8.36 ± 0.17
STPL	11.36 ± 0.40	12.69 ± 0.35	14.56 ± 0.32	10.28 ± 0.21
STPW	8.42 ± 0.42	9.69 ± 0.34	11.23 ± 0.37	7.63 ± 0.20
FLWS	8.87 ± 0.97	11.26 ± 0.94	11.67 ± 1.01	9.16 ± 0.72
TOL	2.46 ± 0.09	2.61 ± 0.08	2.74 ± 0.09	2.39 ± 0.07
TOW	1.25 ± 0.06	1.21 ± 0.03	1.32 ± 0.03	1.14 ± 0.03
SEPL	2.96 ± 0.06	3.18 ± 0.05	3.32 ± 0.05	2.93 ± 0.05
SEPW	1.47 ± 0.03	1.47 ± 0.02	1.59 ± 0.02	1.37 ± 0.02
BRCH	1.98 ± 0.02	1.97 ± 0.07	1.93 ± 0.04	1.98 ± 0.07
LPET	3.83 ± 0.11	3.70 ± 0.08	4.03 ± 0.08	3.52 ± 0.07
WPET	3.49 ± 0.13	3.40 ± 0.08	3.69 ± 0.09	3.24 ± 0.08
HU	2.00 ± 0.00	1.95 ± 0.02	1.96 ± 0.02	1.98 ± 0.02
HL	1.98 ± 0.02	1.98 ± 0.01	1.99 ± 0.01	1.97 ± 0.02
DSTP	2.71 ± 0.11	2.38 ± 0.08	2.60 ± 0.08	2.31 ± 0.08
DLF	2.62 ± 0.10	2.48 ± 0.06	2.53 ± 0.08	2.56 ± 0.06

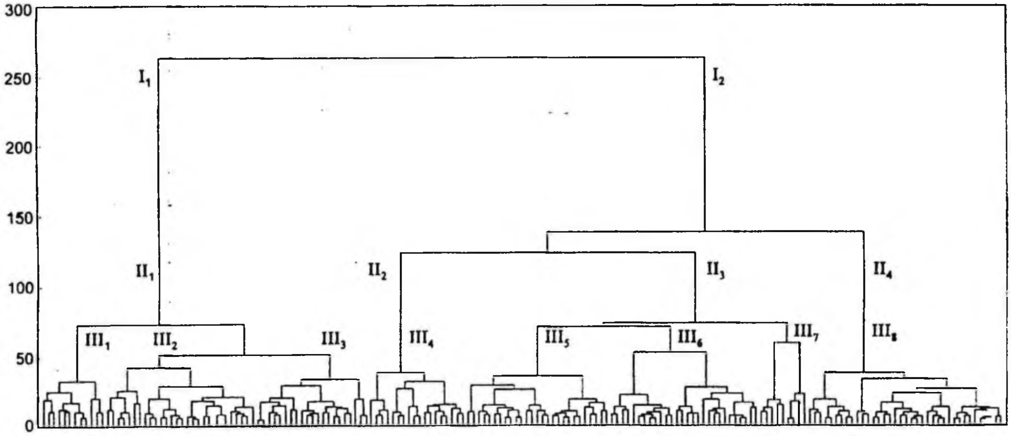

Fig. 1. Dendrogram of clustering *Potentilla erecta* (L.) Räusch. specimens according to Ward's algorithm, Manhattan distance.

nods. No difference is observed in the branching of plants, in the hairiness of leaflets or in the length of the dentated part of the leaflet.

In the dendrogram (Fig. 1) cluster I_2 is clearly divided at the level of the linkage distance of 120–140 units (level II), into three smaller clusters (II_2, II_3, II_4), whereas cluster I_1 remained unsplit at this level. Two cluster pairs have the coefficients of indistinctness higher than 5% ($I_{II_2,II_3} = 46.9$, $I_{II_2,II_4} = 8.0\%$) and, are thus insignificantly separated. After reorganizing the clusters by k-means procedure, their size remains nearly the same, and

Table 3. Importance of morphological characters (C) of *Potentilla erecta* (L.) Räusch. in delimiting infraspecies-clusters according to ANOVA *F*-criterion (*F*). Denotation of characters as in Table 1. Subspecies = specimens with intermediate characters excluded; KM-2 = clusters obtained by k-means procedure at the two-cluster level; KM-4 = clusters obtained by k-means procedure at the four-cluster level; KM-8 = clusters obtained by k-means procedure at the eight-cluster level.

Subspecies		KM-2		KM-4		KM-8	
C	F	C	F	C	F	C	F
LFL	8.08	STPL	134.43	STPL	126.36	STPL	173.19
DSTP	6.04	LFL	117.04	LFL	84.41	LFL	121.01
SEPL	4.85	LFW	64.16	STPW	83.32	TOW	102.36
STPL	4.58	STPW	59.51	LFW	56.35	STPW	75.93
STPW	3.69	SEPW	43.04	TOW	51.74	LFW	67.54
TEETH	3.29	SEPL	33.62	TOL	30.22	TOL	62.23
FLWS	2.62	LPET	22.28	TEETH	12.76	TEETH	15.63
HU	2.31	TOW	15.63	FLWS	5.70	DLF	6.38
DLF	1.49	TEETH	15.51	DLF	5.15	FLWS	4.81
LPET	1.11	WPET	14.22	SEPL	1.77	HL	3.78
NOD	0.91	TOL	10.00	SEPW	1.41	HU	2.18
TOL	0.84	DSTP	6.57	NOD	1.40	LPET	1.10
LFW	0.73	FLWS	4.31	LPET	1.19	SEPL	1.03
BRCH	0.32	NOD	2.78	HL	0.95	SEPW	0.83
WPET	0.22	HL	0.99	BRCH	0.88	BRCH	0.82
TOW	0.17	HU	0.71	HU	0.71	DSTP	0.57
SEPW	0.01	DLF	0.20	WPET	0.28	WPET	0.50
HL	0.01	BRCH	0.04	DSTP	0.10	NOD	0.00

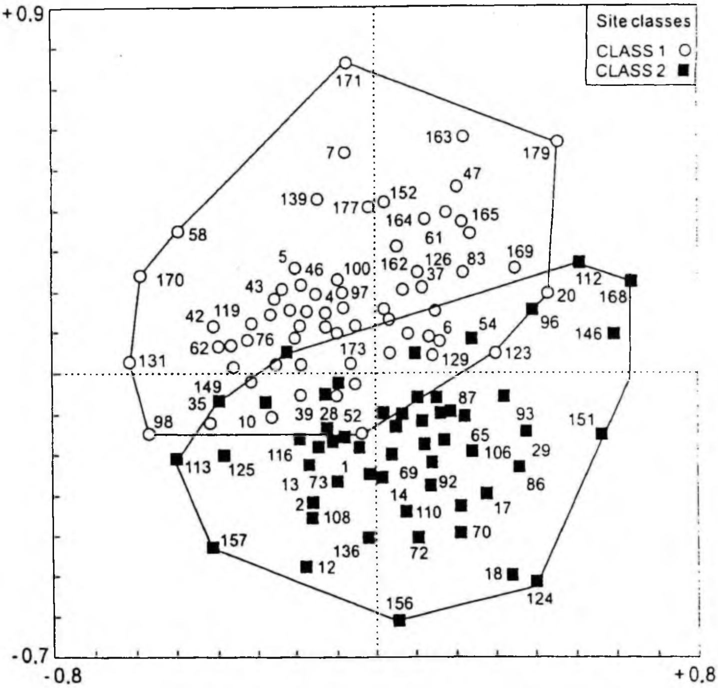

Fig. 2. Classification polygons superimposed onto a PCA scatterplot. Clusters obtained at the two-cluster level by k-means procedure.

the same cluster pairs are indistinct (Fig. 3); however, the coefficients of indistinctness are now lower, I_{II_2,II_3} = 20% and I_{II_2,II_4} = 5.5%, respectively. None of the clusters contain representa-

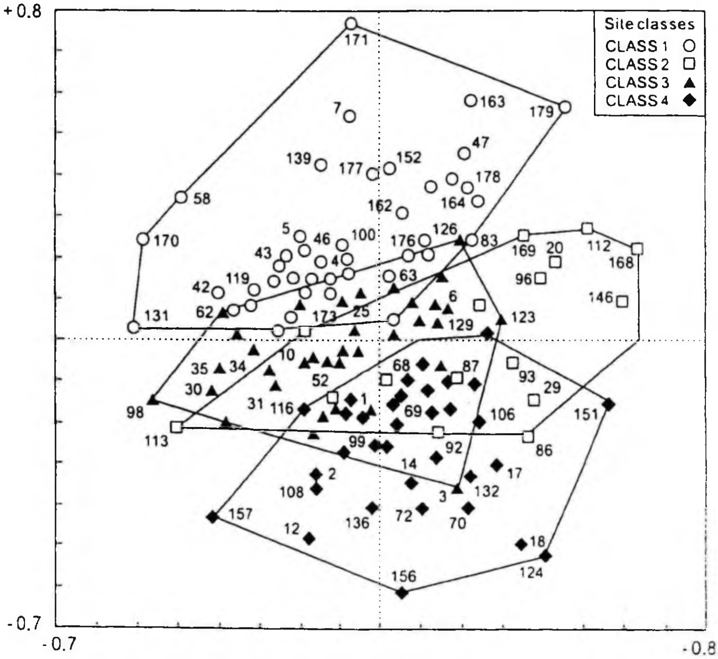

Fig. 3. Classification polygons superimposed onto a PCA scatterplot. Clusters obtained at the four-cluster level by k-means procedure.

tives of only one of the putative subspecies: the ratios of ssp. *erecta* to ssp. *strictissima* are 1:4, 1:2.5, 1:2 and 1:1.

The characters that are important for the separation of specimens at level II are mostly the same as at level I, except that the length and width of the central tooth are now much more important than the length and width of the sepal (Table 3). The division depth of the stipule appears unimportant, whereas the length of the dentated part of the leaflet matters to some extent.

In the dendrogram (Fig. 1), clusters II_1 and II_3 are both divided further into 3 pronounced subclusters, which yields 8 clusters in all (III_1–III_8). After using k-means procedure, most cluster pairs (except III_3 & III_7, III_5 & III_7, III_6 & III_7) become distinct. Nevertheless, all clusters are mixed, consisting of both subspecies and intermediates; only cluster III_8 consists predominantly of ssp. *erecta*.

The characters that are most important for distinguishing clusters at level III are the same as those involved in the case of four clusters (level II), whereas their order is somewhat different (Table 3).

Clusters III_1–III_7 differ mostly in metric characters, while the length of the dentated part of the leaflet and the division depth of the stipule do not reveal any clear pattern here. Cluster III_8 (44 specimens) in which *Potentilla erecta* ssp. *erecta* prevails consists of plants with small leaflets, few teeth, small stipules and few nods (1.85 ± 0.2). Their leaves are dentated 1/4–3/4 of the way and the stipules about 3/4 of the way. Cluster III_8 is adjacent to three clusters (III_4, III_5, III_6) which contain relatively more ssp. *erecta* specimens (ratios 1:2, 1:2.5, 1:3). At the same time, this cluster is convincingly separated from clusters where ssp. *strictissima* prevails: it is distinct from these clusters without any adjacency to them.

The second largest cluster (III_3, 25 specimens) consists predominantly of ssp. *strictissima* (ratio 1:11) but is adjacent to clusters III_5 and III_7 and indistinct from cluster III_7, which all contain relatively more specimens of ssp. *erecta*. Therefore, it is quite complicated to delimit ssp. *erecta* and *strictissima* even at the level of comparatively small clusters; the only different group seems to be cluster III_8 which corresponds more or less also to cluster II_4.

Characters

Correlation between the characters is not very strong; Spearman's rank correlation coefficients exceeding the arbitrary level of 0.60 occurred only between the length and width of the leaflet (0.74), between the length of the leaflet and length of the stipule (0.85), between the length of the leaflet and width of the stipule (0.62), between the length of the stipule and width of the leaflet (0.70). and between the length and width of the central tooth (0.73). This can also be observed on the character vector plot (Fig. 4) where the above characters form a compact bunch of vectors. The opposite positions on the ordination plot are occupied by the number of flowers and branches, and the number of nods. In case of more strongly correlated characters, the length of their vectors on the plot corresponds well to their importance in distinguishing clusters according to the F-criterion (Table 3).

It is remarkable, however, that the length of the dentated part of the leaflet and the division depth of the stipule, which were considered by Richards important characters for delimiting ssp. *erecta* and ssp. *strictissima*. are rather weakly correlated ($r = 0.23$). According to the diagnosis, plants of ssp. *strictissima* must have stipules divided nearly to the base and leaflets dentated nearly to the base; in ssp. *erecta* stipules are divided less than half way and leaflets dentated only in the upper part.

Habitat preferences

When considering habitat preferences of plants in different clusters, either on mineral soil or peat, no correlations were found; all clusters contained plants from both habitats.

Among the studied herbarium specimens of TAA and in TU, ssp. *strictissima* was more common; several intermediates were also found. The plants of the two subspecies and their intermediates had been growing on a large variety of soils from gley–podzols and gley soils to peaty and peat soils.

Sixteen out of the 60 plants collected to estimate the distribution of subspecies in adjacent localities were identified as ssp. *erecta*, 25 as ssp.

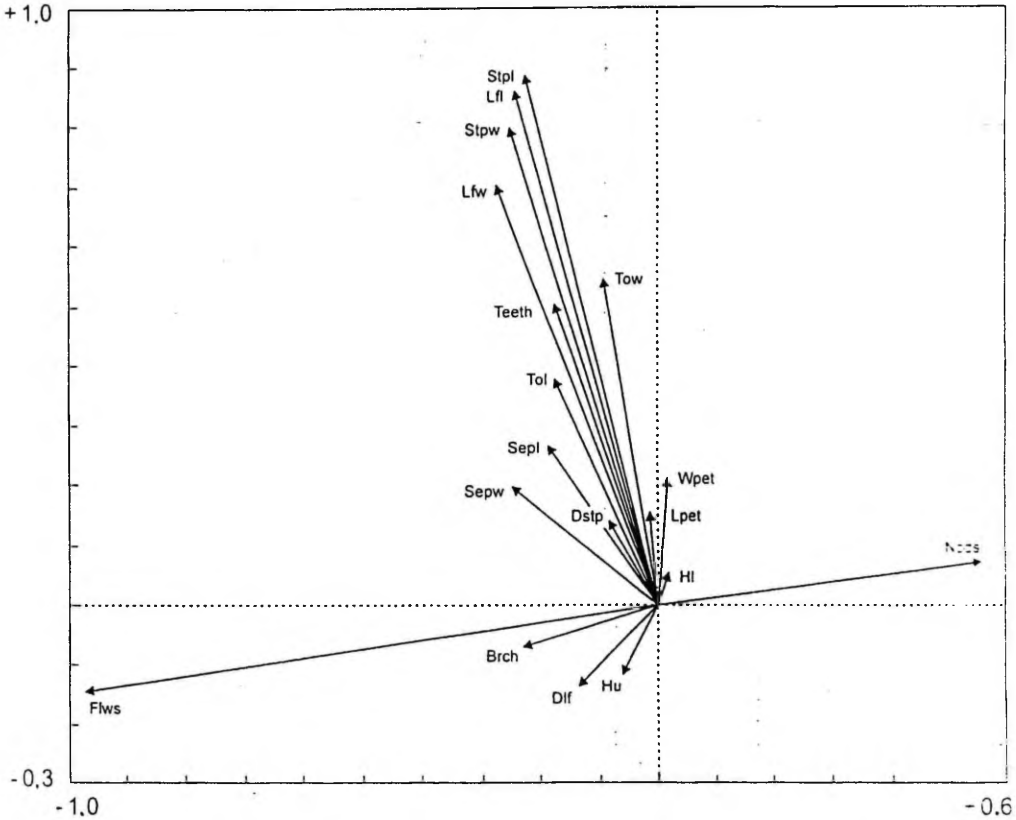

Fig. 4. PCA ordination of morphometrical characters of *Potentilla erecta* (L.) Räusch. specimens. Abbreviations as in Table 1.

strictissima and 19 appeared to be intermediates. Hence, no differences could be seen in the distribution of subspecies on peaty soil.

The height of *Potentilla erecta* ssp. *erecta* specimens collected from transects was 20–65 cm and that of ssp. *strictissima*, 30–80 cm.

DISCUSSION

Vasari (1968) did not consider the dentation of leaflets and stipules, i.e. the characters used by Richards (1973), and found it possible to separate the two subspecies in his southern race only after discussion with Richards (Richards 1973). In the Estonian material these characters occurred quite often in an unexpected way: stipules were divided nearly to the base and leaflets were dentated only in the upper 1/4 or 1/2, or vice versa.

The division depth of the stipule (DSTP) and the length of the dentated part of the leaflet (DLF) were weakly correlated ($r = 0.23$), and only the division depth of the stipule was important in distinguishing subspecies (Table 3). When clustering the material into four or eight clusters. DSTP had almost no importance at all, DLF being slightly more important. In the case of two clusters, DSTP and DLF had swapped positions (Table 3). Therefore, these characters do not seem to be discriminative enough in the nordic material but are more useful in the case of material from other parts of the areal.

According to Richards (1973), *Potentilla erecta* ssp. *erecta* has more and larger flowers than ssp. *strictissima*, the teeth of its leaflets should not exceed 1.5 mm and the leaflets 20 mm in length and the length of its stems should be up to 150 mm.

Considering the Estonian material, it seems that *Potentilla erecta* ssp. *erecta* does not meet these criteria in all respects. Our plants tended to be taller (e.g. on transects in Alam-Pedja the branch length of ssp. *erecta* specimens was 20–65 cm, that of ssp. *strictissima* 30–80 cm), and the difference in the size of flowers, if any, was very slight. Leaflets and their teeth were often larger, and it was ssp. *strictissima* that tended to have more flowers than ssp. *erecta* (Table 2). When analysis was based only on specimens identified as ssp. *strictissima* and ssp. *erecta*, the most important characters for distinguishing the taxa appeared to be the length of the leaflet, length of the sepal, length and width of the stipule, and the number of teeth and flowers (Table 3). When, however, intermediates were included, the corresponding *F*-criterion value of all characters was very low, indicating that the separation power of the characters was low too, which makes discrimination between the groups very difficult.

The two subspecies have been observed to occur together in only one locality on the British Isles where a few intermediates have also been found (Richards 1973). Zimmeter (1884) noted that ssp. *erecta* and ssp. *strictissima* sometimes occur together in Central Europe, and Hegi (1922) has recorded intermediates from the same area. In Finland, intermediates between all the three subspecies occasionally occur. Richards (1973) suggests that although each of these races originated in isolation, they meet in geographically and ecologically intermediate localities in Finland.

Since Estonia is a low-lying country (maximum elevation 318 m), ssp. *strictissima* grows here in habitats different from those it favours on the British Isles and in Central Europe. *Potentilla erecta* ssp. *strictissima* and ssp. *erecta* have no ecological or geographical preference in Estonia: they both grow on various soils, in rather wet places and in moderately moist habitats. Intermediates can be found everywhere.

TAXONOMIC CONCLUSIONS

In Estonia, both *Potentilla erecta* ssp. *erecta* and ssp. *strictissima* occur, ssp. *strictissima* being more common. Therefore, the theory of their migration from the south to Finland (Vasari 1968) seems to be plausible.

Often *Potentilla erecta* ssp. *erecta* and ssp. *strictissima* grow together, and their intermediates seem to be common. However, it was not possible to delimit the two subspecies even at the level of small clusters; all the clusters obtained were mixed ones.

Already Wolf (1908), when characterizing his varieties of *Potentilla erecta* (he recorded six), mentioned that four of them (incl. var. *strictissima* and var. *typica*) are sometimes difficult to distinguish and that intermediate forms exist.

According to our material, these taxa are much more variable and transitional in Estonia than on the British Isles. Hence, they are not worthy of the rank of the subspecies but should rather be referred to as varieties, since the rank of the subspecies (race) is used for taxa that have their own geographical areal and/or established ecological preference.

As the material appeared to be morphologically quite varying and the clusters obtained distinct, the infraspecific taxonomy of the species needs further investigation over a more extensive area of distribution with the use of more elaborated methods (DNA and/or isozyme analysis etc.).

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Potentilla L. sect. *Rivales* Wolf and the nearest taxa in the Baltic states

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Abstract

Morphological variation of *P. norvegica* L., *P. heidenreichii* Zimm. and *P. supina* L. from section *Rivales* Wolf, *P. recta* L. from section *Rectae* Wolf, *P. canescens* Bess., *P. argentea* s.l., *P. collina* Wib. from *Argenteae* Wolf and *P. goldbachii* from *Chrysanthae* Wolf was studied using multivariate statistical methods. According to k-means analyses, *P. canescens* stands nearer to *P. heidenreichii* than to *P. argentea*. *P. collina*, the other representative of sect. *Argenteae*, is not connected with *P. canescens* at all. At the same time, *P. canescens* is adjacent mainly to *P. heidenreichii* from sect. *Rivales*. Therefore, *P. canescens* belongs to sect. *Rivales* not to sect. *Argenteae*.

In *P. argentea* s.l. material *P. impolita*, *P. argentea* var. *typica*, var. *decumbens*, var. *demissa*, var. *grandiceps* and var. *tenerrima* were identified. *P. impolita* specimens did not cluster out into a separate cluster as did the "good" species *P. collina*, *P. canescens* and *P. heidenreichii*, but formed mixed clusters with different varities of *P. argentea*. Therefore, *P. impolita* is not worthy of the rank of species and evidently even not that of subspecies, not even on the basis of morphological characters, and should be referred to as a variety of *P. argentea*.

Keywords: multivariate methods, morphology, taxonomy, sect. *Argenteae* Wolf.

Introduction

Potentilla L. section *Rivales* Wolf is represented in the Baltic states with four species, *P. supina* L., *P. norvegica* L., *P. intermedia* L. and *P. heidenreichii* Zimm. The first is a very rare adventive here, the other three are either old adventive (Eichwald 1962) or native species (Ball et al. 1968, Leht et al. 1996).

Taxonomically, the nearest species to sect. *Rivales* in the Baltic states are rare adventives *P. canescens* Bess. (sect. *Argenteae* Wolf), *P. recta* L. (sect. *Rectae* Wolf) and *P. goldbachii* (sect. *Chrysanthae* Wolf), and two native species, *P. argentea* L. s.l. and *P. collina* Wib. from section *Argenteae* Wolf. *P. collina* is a very rare taxon growing only in Latvia and Lithuania.

P. heidenreichii and *P. intermedia* have been treated taxonomically in various ways (as separate species, subspecies or varieties) by different taxonomists (Juzepczuk 1941, Ball et al. 1968, Garcke 1972, Raciborski et al. 1955, etc.). This divergence in taxonomical viewpoints is accompanied by problems in distinguishing between *P. heidenreichii* and *P. canescens* and mistakes in the use of their synonyms (Leht 1987).

P. intermedia s.l. is supposed to be a stable hybrid of *P. argentea* s.l. (2n=28, 42) and *P. norvegica* (2n=70) (Janchen 1957). Skalinska and Czapik (1958), after establishing 2n=56 for *P. intermedia* s.l., found it possible that *P. intermedia* s.l. has arisen only with part of hexaploid *P. argentea*. Hence, polyploids are in general apomictic in the genus *Potentilla*, just as appeared in *P. norvegica* (Asker 1970a, b). And it is difficult to explain the origin of tetraploid *P. intermedia* (2n=28) from *P. norvegica* because of its high chromosome number. Asker (1970a) suggests that *P. intermedia* consists of apomictic biotypes, which have resulted from crosses between *P. argentea* and *P. norvegica*, or perhaps even other members of the sections *Argenteae* and *Rivales*; the origin of *P. intermedia* s.l. is still to be tested experimentally.

P. canescens Bess. belongs to the sect. *Argenteae* in Wolf's system (1908), but when the characters from Wolf's descriptions were used for cladistic analysis (Leht 1996), *P. canescens* was placed much closer to the representatives of sect. *Rivales*.

For botanists in the Baltic states *P. canescens* has been the most troublesome species in the genus *Potentilla* already since the beginning of the century (Leht 1987), having been confused with *P. intermedia*, *P. heidenreichii* and probably also with *P. recta*. As *P. canescens* is also thought to have a hybrid origin, of *P. argentea* × *P. recta* or related species (Juzeptchuk 1941, Ball et al. 1968), it seemed useful to analyze all these closely connected taxa, incl. *P. goldbachii* and *P. collina*, together, to answer the questions:

— Does *P. canescens* belong to section *Rivales* or *Argenteae*?
— How well can these species be distinguished from the statistical point of view?
— How variable morphologically are *P. heidenreichii* Zimm., *P. norvegica* L. and *P. argentea* in Estonia?

Material and methods

Morphological variation of *P. norvegica* L. (98 specimens), *P. heidenreichii* Zimm. (55) and *P. supina* L. (10) from section *Rivales* Wolf, *P. recta* L. (50) from section *Rectae* Wolf, *P. canescens* Bess. (28), *P. argentea* s.l. (231), *P. collina* Wib. (21) from *Argenteae* Wolf and *P. goldbachii* (48) from *Chrysanthae* Wolf was studied using multivariate statistical methods. Material was collected mostly in 1988. However, as four of these species are quite rare or absent in Estonia, herbarial material from the herbarium of the Institute of Zoology and Botany (TAA) and the University of Helsinki was also used.

Collected material is preserved in TAA.

19 macromorphological characters (Table 1, 1–19) most often used in diagnoses of *Potentilla* species were measured with a binocular microscope MBS-2 and a ruler. To reduce the effects of individual variability, characters 2–6, 8–11, 13 and 14 were measured three times and average values used for further calculations.

In accordance with the possibilities offered by software packages the whole data matrix (543 specimens) was used only for the evaluation of the taxonomic continuum between conventionally estimated species, for further analysis three smaller data sets were formed: (i) *P. argentea*, *P. collina*, *P. heidenreichii* and *P. canescens* (300 specimens), (ii) *P. heidenreichii*, *P. recta*, *P. goldbachii*, *P. supina*, *P. norvegica* and *P. canescens* (290 specimens) and (iii) *P. heidenreichii* (55 specimens), *P. goldbachii* (7) and *P. norvegica* (23), 85 specimens in all. The first and the second data set enable the study of the relationship between *P. canescens* and other taxa. The third set, where micromorphological characters (Table 1, 20–36) were added, was used for studying the variability of *P. heidenreichii* and *P. norvegica* in comparison with *P. goldbachii*.

Micromorphological characters were measured under a light microscope Ergaval (16x40). Herbarial material or material fixed in the field with FAA (formalin, alcohol, acetic acid) was macerated at first in HNO_3 adding $HClO_4$, then in NH_3OH. The epidermis was peeled from the central part of the leaflet, stained with Heidenhein hematoxylin and mounted into glycerin-jelly. 5–10 cells, stomas and hairs from each specimen were measured and average values used for calculations. Numbers of cells and stomas were counted per field of vision and recalculated for 1 mm^2.

Chromosome numbers were counted from buds and root tips fixed in Farmer fixative. Buds were stained using the Snow method at 60°C for one hour or more, anthers were squashed in 45% acetic acid. Root tips were pre-treated with 8-hydroxyquinolin and macerated in 1N HCl at 60°C for 20 min and stained in acetoorcein or carmin and squashed.

Data processing

At first, for standardized data the Ward's clustering method with Manhattan distance as a resemblance measure was used. Then, using that result as the initial group membership vector, further optimization of classification was achieved by k-means procedure. Cluster analysis was realized by SAS (SAS Institute Inc. 1994) and SYN-TAX 5.0 program packages (Podani 1993). For calculating means and standard errors and for the evaluation of the importance of characters within clusters the SAS program package was used.

Ordination of log-transformed data was carried out with principal components analysis (CANOCO package, version 3.1; Ter Braak, 1990, and CANODRAW package, version 3.0; Smilauer, 1992).

For the estimation of clusters' adjacency the distances of all specimens, or operational taxonomic units (OTUs), from all centroids (exept the cluster to which the OTU belongs) were calculated according to the postulate that the j-th cluster is interpreted as being adjacent to the i-th cluster if the distance between at least one of the OTUs of the i-th cluster and the centroid of the j-th cluster is smaller than the distance to the centroids of all the other clusters (Paal & Kolodyazhnyi 1983; Paal 1994).

In order to measure the degree of distinctness of the clusters the α-criterion (Duda & Hart 1976) was used. To acquire a better interpretation of the estimates, it is more convenient to apply the corresponding probabilities as coefficients of indistinctness (CI) instead of the direct values (Paal 1987, 1994).

The last two analyses were performed using the SYNCONT 3.0 program.

Results

Species-clusters

Of the conventionally established species-clusters two pairs appeared indistinct — cluster 3 (*P. canescens*) and cluster 5 (*P. heidenreichii*), cluster 3 and cluster 6 (*P. norvegica*), with coefficients of indistinctness $CI_{3,5}=5.0$ and $CI_{3,6}=69.0$, respectively. The Euclidean distances (ED) between the centroids of these clusters in the similarity matrix are also the shortest. In the adjacency matrix *P. heidenreichii* and *P. canescens* are also mutually each other's principal neighbours (Table 2), but the adjacency between *P. norvegica* and *P. canescens* is asymmetric: the *P. norvegica* cluster is not adjacent for any specimens of *P. canescens*, while *P. canescens* is adjacent for 22.5% of *P. norvegica* specimens. The *P. norvegica* cluster varies in the same extent towards *P. recta* (cluster 2), as it is adjacent for 22.5% of *P. norvegica* specimens. Towards *P. goldbachii* (cluster 1) adjacency of the *P. norvegica* cluster is 31.6%.

Rather remarkable is the asymmetry of relationships between taxonomically close taxa, *P. argentea* (cluster 7) and *P. collina* (cluster 8): *P. collina* is the principal neighbour for *P. argentea* specimens (47.2%), while only 15% of *P. collina* specimens are adjacent to *P. argentea*. The main neighbour in the character space for *P. collina* is *P. supina* (55.0%). Euclidean distances between *P. argentea* and *P. collina* ($ED_{7,8}=$ 0.215) and *P. argentea* and *P. canescens* ($ED_{7,3}=$ 0.183) are of medium length. In the distance matrix *P. recta* stands most apart from all the other species.

According to the F criterion in ANOVA the most important characters for distinguishing the species are hairiness of leaflets, width of stipules, width of middle tooth and hairiness of upper size of the leaflet, while petal and sepal characters are unimportant (Table 3).

The first data set

Ward's algorithm clustered the first data set (*P. argentea* s.l., *P. collina*, *P. heidenreichii* and *P. canescens*) into ten obvious clusters, which are nearly all distinct, but mostly consist of specimens from different species. After reorganization these clusters using k-means procedure, the clusters are in much better accordance with empirical species identifications (Fig. 1). *P. canescens* specimens form a separate cluster (cluster 1), *P. argentea* specimens are divided into six clusters (clusters 2–7). *P. heidenreichii* specimens are split into two clusters (8 and 9), one of them also contains three *P. argentea* and two *P. canescens* specimens. *P. collina* specimens belong to cluster 10 together with three *P. argentea* specimens.

Using Wolf's (1908) descriptions six taxa were identified within *P. argentea* s.l. material — *P. impolita* Wahl., *P. argentea* var. *typica*, var. *decumbens* (Jord.) Lehm., var. *demissa* (Jord.) Lehm., var. *grandiceps* (Zimm.) Roy & Cam. and var. *tenerrima* (Vel.) Wolf. All *P. argentea* s.l. clusters contain *P. impolita* specimens, but they do not dominate in any of the clusters. Each cluster consists of 3–5 taxa. Hence, in each cluster one variety of *P. argentea* is more or less prevalent: *P. argentea* var. *typica* in clusters 2 and 3, var. *decumbens* in cluster 5, var. *demissa* in cluster 6 and var. *grandiceps* in cluster 7. Only in cluster 4 are var. *typica* and var. *decumbens* equally represented.

The main neighbours of *P. canescens* in the character space are the two *P. heidenreichii* clusters. *P. argentea* clusters are adjacent mostly with each other and with *P. col-*

lina, except for cluster 4 which is most adjacent with one of the *P. heidenreichii* clusters (61.5%).

Several pairs of clusters are indistinct. *P. canescens* (cluster 1) is indistinct from the smallest *P. argentea* cluster (cluster 7, $CI_{1,7}$=14.2), and even more so from both *P. heidenreichii* clusters ($CI_{1,8}$=18.1 and $CI_{1,9}$=22.2). *P. argentea* clusters are distinct from each other, except clusters 5 and 6 ($CI_{5,6}$=34.7) and clusters 3 and 7 ($CI_{3,7}$=18.9). Cluster 2 (*P. argentea*) and cluster 8 (*P. heidenreichii*) form the most indistinct pair with $CI_{2,8}$=56.3. *P. collina* is nonsignificantly separated from two clusters of *P. argentea*: $CI_{10,5}$=6.9 and $CI_{10,6}$=14.7.

Euclidean distances between *P. canescens* and *P. argentea* clusters are longer ($ED_{1,2}$=0.180, $ED_{1,3}$=0.217, $ED_{1,4}$=0.395, $ED_{1,5}$=0.284, $ED_{1,6}$=0.328, $ED_{1,7}$=0.174) than between the *P. canescens* cluster and clusters of *P. heidenreichii* ($ED_{1,8}$=0.134, $ED_{1,9}$= 0.160). The smallest *P. argentea* cluster (7) is the most different of the *P. argentea* clusters, and stands quite far from all the clusters (ED=0.276–0.647). Distances between *P. collina* and *P. argentea* clusters are variable (0.647, 0.410, 0.328, 0.223, 0.088, 0.066).

The most important characters for distinguishing the clusters according to the F-criterion are the number of rosette leaves and the number of branches, and the length and number of teeth of the central leaflet. Petal and sepal widths, and leaflet and petiol lengths have no importance (Table 3).

The second data set

Clustering the second set (*P. heidenreichii, P. goldbachii, P. recta, P. canescens, P. supina, P. norvegica*) with Ward's algorithm led to the formation of six clusters. Cluster 1 consists of *P. goldbachii* specimens, cluster 2 of *P. recta* (with few *P. goldbachii* specimens), clusters 3-6 are mixtures of all other species. All clusters are mutually distinct. The clusters received with k-means procedure using Ward's classification as an initial group membership vector are again in better accordance with empirical identifications (Fig. 2). Now cluster 1 consists only of *P. goldbachii* specimens and cluster 2 only of *P. recta*. Specimens of *P. norvegica* are divided between clusters 3 and 4; cluster 3 also includes some specimens of *P. supina* and *P. canescens,* while cluster 4 includes only specimens of *P. norvegica*. Clusters 5 and 6 are still mixed clusters with *P. heidenreichii* specimens prevalent. *P. supina* and *P. canescens* are divided more or less equally between two clusters: *P. supina* specimens from Lithuania belong to cluster 3 and those from Finland to cluster 5, *P. canescens* is distributed between clusters 5 and 6. All clusters are distinct.

Euclidean distances between mixed clusters are vary greatly (ED=0.129–0.469). *P. recta* stands quite far from all other clusters (ED=0.257–0.492), while the distances between *P. goldbachii* and other clusters are again very different (ED=0.132–0.562).

According to F-criterion the clusters are separated mostly by length and width of sepals, number of teeth of the leaflet and width and length of petals. The numbers of branches and rosette leaves are least important (Table 3).

The third data set

Several authors have shown that micromorphological characters serve as useful criteria for the identification of species belonging to the same genus (Stace 1965, Wallis 1967, Inamdar & Rao 1981, etc.). Therefore for better separation of mixed clusters micromorphological characters (Table 1, 20–36) were added to the analysis for *P. heidenreichii* and *P. norvegica*, and also for Baltic *P. goldbachii* (85 specimens in all). Unfortunately *P. canescens* and *P. supina* are so rare in the Baltic states that not enough material was available for micromorphological study.

When studying the data set with micromorphological characters, Ward's method splits the material clearly into three clusters which correspond to *P. goldbachii, P. norvegica* and *P. heidenreichii*, the last two are both further divided into two subclusters. All the clusters are distinct.

After k-means procedure *P. goldbachii* forms a separate cluster as before. But all the *P. norvegica* specimens are placed into one cluster and *P. heidenreichii* split into three (Fig. 3), and again the clusters are statistically distinct. *P. goldbachii* is most adjacent to the smallest *P. heidenreichii* cluster and *P. norvegica* to two clusters of *P. heidenreichii.* All three *P. heidenreichii* subclusters are neighbouring only with each other. Euclidean distances are the longest between *P. goldbachii* and all other clusters (ED=0.485–0.648), a little shorter between *P. norvegica* and *P. heidenreichii* (ED=0.408–0.550) and the shortest, as expected, between *P. heidenreichii* clusters.

According to the F-criterion nearly all micromorphological characters are more important than macromorphological characters in distinguishing specimens into clusters. The most useful characters are the number of cells in upper and lower epidermis, length and width of stomas in the upper epidermis, number of stomas in the lower epidermis and diameter of hairs in the lower epidermis. Of the macromorphological characters, width of the stipule and number of flowers are the most important ones, followed by the less important micromorphological characters: length and width of stomas in the lower epidermis and diameter of hairs in the upper epidermis.

Correlation of characters

When only 19 characters are used, the highest correlations (p=0.005) appear between length and width of petals (0.91), length and width of teeth (0.88) and length and width of sepals (0.86), as could be expected, and also between width of leaflet and width of tooth (0.79), length of leaflet and length of stipule (0.76), width of leaflet and width of stipule (0.6), width of leaflet and length of tooth (0.67), width of tooth and number of leaflets ()0.65), number of leaflets and nods (0.68) (Fig.4).

Among micromorpholocical characters length and width of cells and stomas are highly correlated (0.93–0.88), also dimensions of stomas with numbers of stomas in the upper epidermis (0.71, 0.69) and dimensions of cells and number of cells in the lower epidermis (0.83, 0.84), number of stomas and length and width of cells in the lower epidermis (0.8, 0.79). Micro- and macromorphological characters are not correlated with each other, except number of leaflets and number of cells (0.68) and number of leaflets and length of stoma in the upper epidermis (0.65).

Discussion

When following connections between *P. argentea*, *P. heidenreichii* and *P. canescens*, according to k-means analysis, *P. canescens* stands nearer to *P. heidenreichii* than to *P. argentea*. *P. canescens* appeared adjacent and indistinct with only one small *P. ar-*

gentea subcluster. *P. collina*, the other representative of sect. *Argenteae*, is not connected with *P. canescens* at all. At the same time, *P. canescens* is adjacent mainly to *P. heidenreichii* from sect. *Rivales*. Also, Euclidean distances are longer between clusters of *P. argentea* and *P. canescens* than between *P. canescens*, *P. heidenreichii* and *P. norvegica*. Therefore it may be stressed that *P. canescens* stands morphologically too far from representatives of sect. *Argentea* to be placed into that section.

P. canescens, which in Wolf's (1908) system belongs to a different section than *P. heidenreichii*, *P. norvegica* and *P. supina*, is much nearer to these species than are *P. recta* and *P. goldbachii*, since *P. canescens* specimens do not form a separate cluster as *P. recta* and *P. goldbachii* do, but belong to mixed clusters together with specimens of *P. heidenreichii*, *P. norvegica* and *P. supina*. Therefore, *P. canescens* can not be placed taxonomically as far from *P. heidenreichii*, *P. norvegica* and *P. supina* as *P. recta* and *P. goldbachii* are situated (that means into a separate section). More likely, *P. canescens* belongs to the same section (sect. *Rivales*) with these three species. The closeness of *P. canescens* to that section is also well demonstrated by the indistinctness of its species-cluster with *P. heidenreichii* and *P. norvegica* as well as by its adjacency with these clusters. Euclidean distance, which is longer between the centroids of *P. canescens* and *P. argentea* than between centroids of *P. canescens* — *P. norvegica* and *P. canescens* — *P. heidenreichii*, also supports the closeness of *P. canescens* to sect. *Rivales*.

If micromorphological characters are considered, *P. goldbachii* forms its own cluster as before, and *P. heidenreichii* and *P. norvegica* stand separately, with no overlapping. *P. heidenreichii* varyies more than *P. norvegica*, since it is split into three subclusters while *P. norvegica* is not divided into subgroups.

As for distinguishing the subclusters of *P. heidenreichii*, micromorphological characters are the most important and no correlations between micro- and macromorphological characters were found. It is quite complicated to describe these subclusters using macromorphological variables. The largest subcluster consists of typical *P. heidenreichii* specimens, while the smallest slightly resembles *P. intermedia* s.str. with larger and less hairy leaves. Also the only two *P. intermedia* s.str. specimens in the data set belong to that subcluster. As we had so little material of *P. intermedia*, we can only say that the multidimensional distance between *P. heidenreichii* and *P. intermedia* s.str. is quite small and they are rather similar.

No differences were found in habitat preferences between the clusters, they all grow on dry roadsides, field edges and sandy ruderal places. So far chromosomes have been counted from few localities, and only 2n=28 has been found.

Specimens of *P. supina* from Finland and Lithuania appeared different enough to be placed into separate clusters (but mixed clusters), indicating the geographical variability of the species in the region or, more probably, that this adventive has reached Lithuania and Finland from different parts of its area.

In *P. argentea* s.l. material *P. impolita*, *P. argentea* var. *typica*, var. *decumbens*, var. *demissa*, var. *grandiceps* and var. *tenerrima* were identified. Hence, differences between these taxa are very small, and all six clusters are mixed clusters containing specimens of 3–5 varieties. Specimens of *P. collina*, which is a very close relative of *P. argentea* s.l., stand in a separate cluster, indicating a greater difference between *P. collina* and *P. argentea* than between varieties of *P. argentea*.

Müntzing & Műntzing (1941) have attributed diploids to *P. argentea* s.str. and hexaploids to *P. impolita* Wahl., and consider tetraploids as hybrids between diploids and hexaploids. But *P. argentea* s.str. and *P. impolita* often grow closely together and are morphologically difficult to separate since intermediate forms exist. This was faced also by Holm (1996) when trying to sample only diploid *P. argenta.*

P. impolita specimens did not cluster out into a separate cluster as did the "good" species *P. collina*, *P. canescens* and *P. heidenreichii*, but formed mixed clusters with different varities of *P. argentea.* Therefore, *P. impolita* is not worthy of the rank of species and evidently even not that of subspecies, not even on the basis of morphological characters, and should be referred to as a variety of *P. argentea.*

Asker (1986) suggests that the diploid chromosomal type (*P. argentea* s.str.) is more common to the north and the hexaploid (*P. impolita*) to the south and that the two types come into contact in the southern part of the Scandinavian Peninsula. No strict correlation has been found between ploidy level and morphological characters in *P. argentea* s.l. (Holm 1996). Very few chromosome counts have so far been made on Estonian material, and still different numbers (2n=14, 28, 42) have been received. When identified only on the basis of morphological characters, *P. argentea* s.str. is more common in Estonia, Latvia and Lithuania, but intermediates occur and often mixed populations exist. Therefore the "contact territory" of diploids and hexaploids is not confined to southern Scandinavia but extends also to Estonia, Latvia and Lithuania.

In such a complicated group as g. *Potentilla*, it is impossible to indicate only some characters useful for identification. Different macromorphological characters appeared to be important in different data sets, e.g. length and width of sepals were the most useful characters for clustering *P. argentea*, *P. canescens*, *P. collina* and *P. heidenreichii* with k-means procedure in the first data set, but were unimportant when all the empirically identified species were studied.

Micromorphological characters appeared very useful for distinguishing species in the genus *Potentilla*, just as it has been in *Solanum* (Edmonds 1982), *Jatropa* (Dehgan 1980), *Ipomoea* (Srivastava 1983), etc. With the help of micromorphological characters it is also possible to study within)species variation as demonstrated in *P. heidenreichii* and *P. norvegica.*

Acknowledgements

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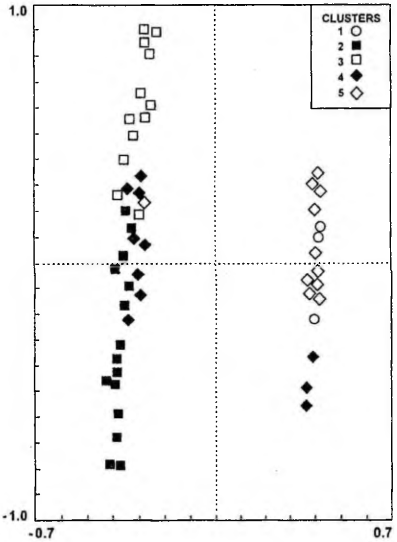

Figure 1. Ordination of clusters of the first data set obtained by k-means procedure. 1 — *P. canescens*, 2–7 — *P. argentea*, 8, 9 — *P. heidenreichii*, 10 — *P. collina*

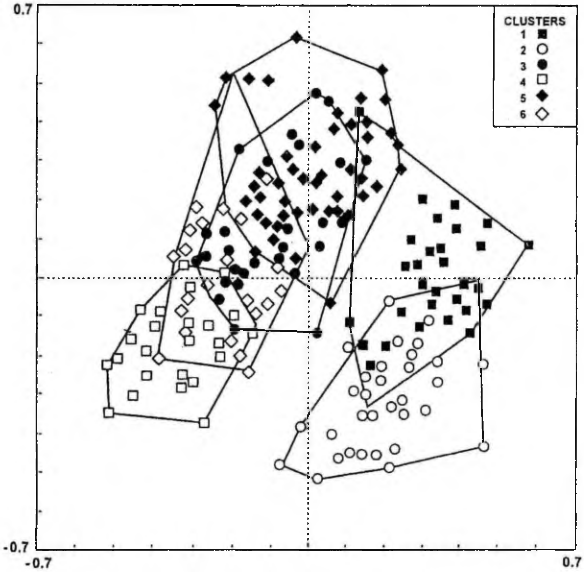

Figure 2. Ordination of clusters of the second data set obtained by k-means procedure. 1 — *P. goldbachii*, 2 — *P. recta*, 3 — *P. norvegica* and *P. supina*, 4 — *P. norvegica*, 5, 6 — mixed clusters of *P. heidenreichii, P. canescens* and *P. supina*.

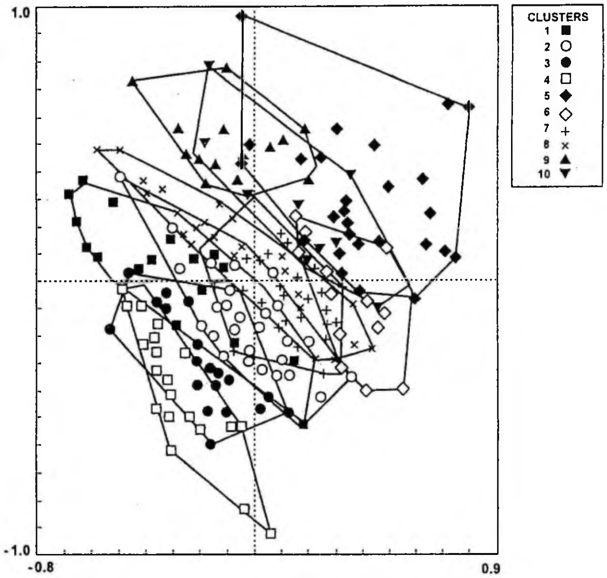

Figure 3. Ordination of clusters of the third data set (micromorphological characters incl.) obtained by k-means procedure.
1 — *P. goldbachii*, 2 — *P. norvegica*, 3–5 — *P. heidenreichii*

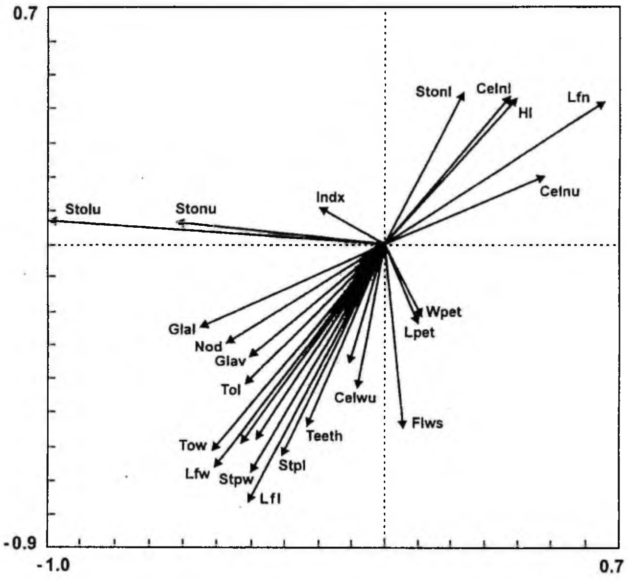

Figure 4. Ordination of characters. Denotions as in Table 1.

Leht, M. & Reier, Ü. Chromosome numbers and sexual type of *Potentilla fruticosa* L.
in Estonia and Latvia. — (Manuscript)

Chromosome number and sexual type of Potentilla fruticosa in Estonia and Latvia

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Abstract

Potentilla fruticosa was found to be dioecious tetraploid (2n=28) in the Harku-Keila-Vääna locations, Ohukotsu, Enge and Kandava i.e. in all three Estonian and the only Latvian native populations. According to this, it may be confirmed that Estonian and Latvian shrubby cinquefoils belong to *P. fruticosa* L. s. str. We are of the opinion that *P. fruticosa* is not a naturalized species in Estonia, as has earlier been proposed by some Estonian authors, but a relic. In favourable conditions Estonian and Latvian populations of *P. fruticosa* have sufficient potential for generative reproduction, however vegetative renewal is prevalent in all locations.

Introduction

The shrubby cinquefoil *Potentilla fruticosa* L. is a nice, 0.2–1.5 m high shrub with yellow or white (rarely pink) flowers. It has a wide distribution area in the northern hemisphere: boreal-montane in Europe and arctic-subarctic and boreal-montane in Asia and N America (Hultén & Fries 1986).

P. fruticosa is often grown as an ornamental plant as well, which is running wild in Lithuania (Leht *et al.* 1996) and Finland (Hämet-Ahti *et al.* 1986). In Norway (Lid 1987), Germany and Austria (Hegi 1922–1923) it has become naturalized.

The primary distribution center of *P. fruticosa* is considered to be in the mountains of Central Asia (Gorchakovski 1960, Shah *et al.* 1992). In the Baltic region it achieves the NW boundary of its European scattered areal.

The range of variation of the morphological characters of *P. fruticosa* is rather large, the variation of leaf shape and size, height of plants and size of flowers is particularly great (Klackenberg 1983). This has lead to different taxonomic treatments of the taxon (Rydberg 1898, Juzepczuk 1941, Löve 1954, Soják 1969, etc.).

P. fruticosa can be either a hermaphroditic diploid (2n=14) or a dioecious tetraploid (2n=28). According to the breeding system and ploidy level Elkington (1969) proposed to divide *P. fruticosa* s.l. into two subspecies. Klackenberg (1983) supported these taxa on the species rank: *P. fruticosa* L. s.str. and *P. floribunda* Pursh, which are considered to have different geographical distributions as well. According to Klackenberg (1983) *P. fruticosa* L. s.str. is a dioecious tetraploid species growing in N Europe and Siberia, *P. floribunda* Pursh a hermaphroditic diploid occurring in N America, S Europe and Siberia.

Consequently it may be supposed that Estonian and Latvian shrubby cinquefoils are also dioecious tetraploids. However, Eichwald (1956) declares in "The Estonian Flora" that *P. fruticosa* is diploid and hermaphroditic. Vilbaste (1953), the author of the only study on Estonian *P. fruticosa*, says nothing about its ploidy level or its sexual type. Klackenberg (1983) mentions that dioecious populations are found on the Baltic Sea islands and the surrounding areas but says nothing specifically about Estonia or Latvia, indeed Latvian locality is not even marked on the maps (Klackenberg 1983, Hultén & Fries 1986).

As far as we know, no investigations of the chromosome number of plants from Estonia and Latvia have been made. All karyological investigations conducted so far show that tetraploidy is linked to dioecism (Klackenberg 1983). Hence our first task was to identify sexual type in the Estonian and Latvian populations and afterwards to gather material with the identified sexual type for karyological investigations.

The taxon's origin in Estonia and Latvia — relic or a newcomer — also needed revision. *P. fruticosa* was first recorded in Estonia "near Tallinn" by Grindel (1803). In Latvia the species was first mentioned by Seiler in 1847 at Kandava in the only natural habitat known today (Tabaka & Klavina 1981). Vilbaste (1953), Eichwald (1956) and Laasimer (1965) have proposed that *P. fruticosa* is an old naturalized introducent in Estonia. Other researchers consider it to be a relic of boreal times in the Baltic region (Gorchakovskii 1960, Eilart & Eilart 1974). Klackenberg (1983) supposed that *P. fruticosa* has a relic origin in N-Europe, but this does not include, for example, Norway where the species has been naturalized.

In this paper we present our preliminary data about the sexual structure and reproductive mode of the populations of *P. fruticosa* in Estonia and Latvia.

Distribution of *Potentilla fruticosa* in Estonia and Latvia

In Estonia *P. fruticosa* grows on alvars in the NW part of the territory — a large, vigorous and dense population between Harku, Keila and Vääna and two smaller separate populations at Enge and Ohukotsu (Fig. 1), where *P. fruticosa*, being intolerant to shading, seems to be declining as a result of overgrowing by trees. In the Latvian locality, which lies on dolomite in the Abava River valley near Kandava (Čuzupurvs Botanical Reserve), *P. fruticosa* is also viable and abundant.

Material and methods

The sexual type of flowers was preliminarily investigated on herbarium material in the Herbarium of the Institute of Zoology and Botany (TAA), Herbarium of University of Tartu (TU) and Herbarium of University of Helsinki (H).

From 1994 to 1996 *P. fruticosa* was studied in eight localities: Niitvälja (1), Kulna (2), Vääna (3), Vääna-Posti (4), Türisalu (5), Ohukotsu (6), Enge (7) in Estonia and Kandava (8) in Latvia (Fig. 1). Flowerbuds were collected from all localities, seeds from localities 1, 2, 3 and 6. In all localities the sexual type of flowers and the reproductive mode of plants were studied.

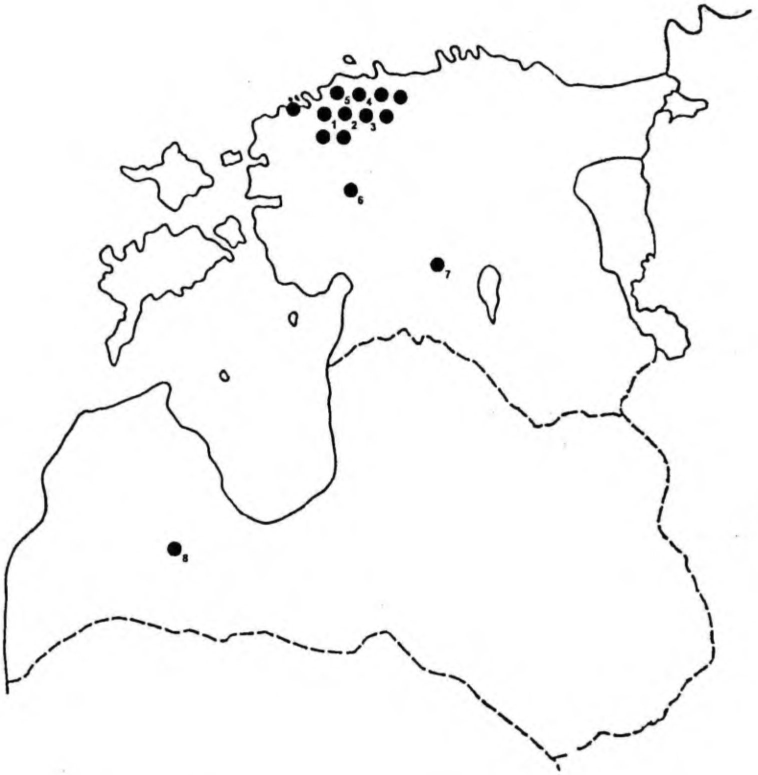

Figure 1. Distribution of *Potentilla fruticosa* in Estonia and Latvia: Niitvälja (1), Kulna (2), Vääna (3), Vääna-Posti (4), Türisalu (5), Ohukotsu (6), Enge (7) and Kandava (8).

Chromosome counts were made from young flowerbuds and from the root-tips of seedlings under a Standard 20 Microscope (Zeiss).

Flower buds were fixed in Carnoy fixative and stained according to Snow (1963) at 60°C overnight, anthers were squashed in 40% acetic acid with glycerin. For permanent slides the fixed buds were embedded into parafin, sectioned at 10m and stained with Heidenhein's hematoxylin.

Root-tips were fixed in Carnoy fixative, macerated in 0.1N HCl at 60°C and stained with Feulgen. As Feulgen dye alone did not give good results, the stained tips were smeared in acetic carmine.

10 fruits each from 10 bushes at not less than 3 m intervals were picked from the localities 1, 2, 3 and 6 in 1994. Seeds and undeveloped (unpollinated) pistils in the composed fruits where counted using a binocular microscope (8×4). After pre-treatment in a fridge at ca +4°C for 45 days, seeds were germinated on moistened filter paper in Petri dishes in a growing chamber at +28°C in 1995. Germinating seeds were counted every third day during the first two weeks and once a week during the following two months.

The sexual structure of the populations was studied on five 6×6 m plots placed along a transect with 10 m intervals (locations 1, 2, 3 and 5). All flowering male and female shrubs were counted. In Enge (7) we counted all flowering shrubs along three transects of 150 m across the whole population. We encountered serious difficulties in distinguishing ramets and genets in dense populations (locations 1, 2, 3 and 5). After gaining some experience and digging up some connections between the bushes on the plots we felt able to present our preliminary results as the sex ratios of genets. The sex ratio was not determined in the scattered population of Ohukotsu (location 6) and due to time limitations at Kandava (location 8).

RESULTS

In all the eight localities all the plants studied were dioecious.

Evidently, all hermaphroditic herbarium specimens that have been previously collected in Estonia come from cultivated plants or from cultivated plants that have run wild. Specimens with hermaphroditic flowers have never been found within the natural populations of Harku—Keila—Vääna, Ohukotsu and Enge.

In spite of the technical problems with staining it was possible to determine the ploidy level from the root-tip mitoses of several seedlings from Ohukotsu, Vääna and Niitvälja as well as the exact meiotic number from some buds from Vääna-Posti, Enge and Kandava (Fig. 2). The chromosome number obtained from all samples was 2n=28. The only hermafroditic sample was collected from the park at Pärnu-Jaagupi and it had a chromosome number of 2n=14.

Tabel 1. Sexual structure of genets in Estonian populations of *Potentilla fruticosa*

Locality (No)	Flowering genets	Female (%)
Kulna (2)	63	44.6
Vääna (3)	138	49.5
Vääna-Posti (4)	164	56.3
Türisalu (5)	85	54.6
Enge (7)	147	58

The sexual structure of Estonian populations does not show significant deviation from 1:1 ratio (table 1).

Table 2. Mean seed set and fruiting percentage per flower of *Potentilla fruticosa* in Estonia in 1994.

Locality (No)	Number of fruits	Pistils per flower	Seed set per flower	Fruiting % per flower
Niitvälja (1)	100	78±2.30	25±1.34	30.8±1.16
Kulna (2)	100	53±2.04	30±1.38	33.5±1.13
Vääna (3)	100	71±2.04	22±1.23	30.5±1.27
Ohukotsu (6)	50	54±1.78	15±1.14	26.8±1.73

The average number of pistils per flower varied from 53 to 78 according to the locality (Table 2). The smallest numbers of pistils were counted at Niitvälja and Ohukotsu, 22 and

23 respectively. The largest numbers of pistils were: 120 from Niitvälja and 121 from Vääna.

Seed set per flower varied between and within the localities: the average value being from 15 (Ohukotsu) to 30 (Kulna) seeds per flower (Table 2). The smallest number was 1 seed per fruit from Kulna and Vääna, and the largest were: 61 seeds per fruit from Niitvälja, 60 from Vääna and 58 from Kulna. The fruits of a single shrub from Vääna had from 8 to 53 seeds.

The average fruiting percentage was 30.5% (Tab. 2). The maximum percentage was 61% from Niitvälja and 63% from Ohukotsu.

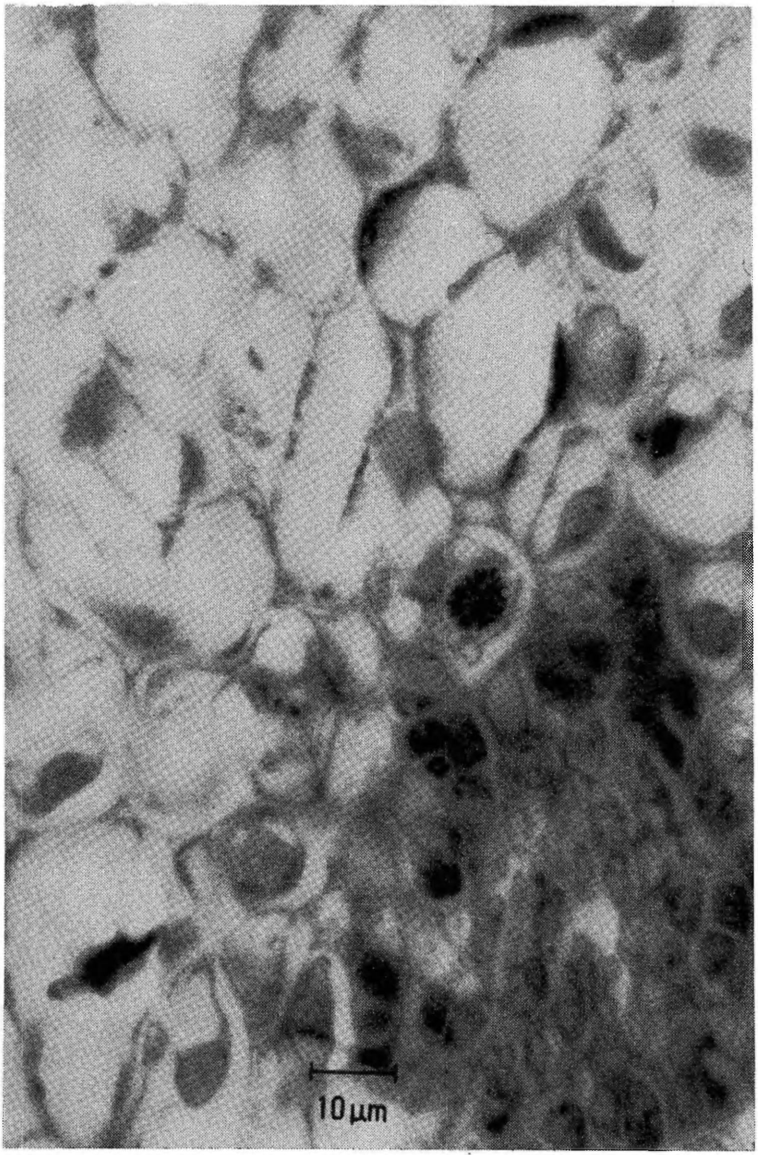

Figure 2. Metaphase in young petal of Potentilla fruticosa from Ohukotsu (2n=28).

Table 3. Germination of seeds of *P. fruticosa*.

Locality (No)	Number of seeds	Germination %
Niitvälja (1)	670	40.9
Kulna (2)	814	28.1
Vääna (3)	816	27.3
Ohukotsu (6)	465	28.4

The germination maximum was achieved in 18 days, during the next 2 months only a few more seedlings emerged. The germination percentage varied between 27.3 and 40.9 (Table 3).

In natural habitats seedlings were not found in Ohukotsu and Enge, in other localities they grew only on open soil. A particularly large number of seedlings were found in the Latvian population, where we counted 12 and 14 seedlings on 1 dm². We did not find generatively reproduced offspring: all small shoots which seemed to be separate plants, actually were found to be connected to the nearest specimen by shoots or originate (prevailingly) from creeping branches covered with mosses and litter.

DISCUSSION

As all the plants studied were dioecious and tetraploid (2n=28), we can conclude that shrubby cinquefoils in Estonia and Latvia belong to *Potentilla fruticosa* L. s. str. Hermaphroditic plants were found only among ornamentals. The only chromosome number counted from hermapfroditic material from Pärnu-Jaagupi park was diploid (2n=14).

The sexual structure of Estonian populations does not show any significant deviation from 1:1 ratio (Table 1). Male : female sex ratios from 2:1 up to 1:2 are known from England and Öland (Elkington & Woodell, 1963), where cultivation experiments on single parent progenies resulted in sex ratios not significantly different from 1:1. Richards (1975) and Grewal and Ellis (1972) obtained 66% and 71% females in the cultivation experiments, respectively. *P. fruticosa* is strictly dioecious in the natural populations of N Europe and the female sex is heterogametic (Grewal & Ellis 1972). Richards (1975) proposes that if male plants are superior colonizers, an excess of female seedlings might help to restore the balance. We think that the sexual structure of the Estonian native populations needs further investigation. According to our preliminary results the sexual structure of the Estonian populations seems to be favourable for successful generative reproduction.

Our results concernning the seed set correspond quite well with the results of other researchers (Table 2). According to Raudi's (1979) unpublished data from four localities around Keila (near our localities 1–4), average seed sets of 27, 19, 34, 21 were attained; the largest variation within one sample of 20 fruits was 9–44 seeds per fruit. Elkington and Woodell (1963) report average numbers of 18 up to 77 seeds per flower. Our results, from 15 to 30 seeds per flower, compare well with those of Raudi, but are quit low in comparison to the results of Elkington & Woodell (1963). Still, we think that the germination percentage in Estonia is sufficient to allow generative renewal, since one shrub may have over 1000 flowers as reported from England (Elkington & Woodell 1963).

The percentage of pistils that had developed into seeds ranged from 26.8% to 33.5% which is not a large number either (Table 2). We have no data from other researchers concerning the number of pistils or the fruiting percentage per flower.

The results of the germination experiments based on the Estonian material are also comparable with the results from other regions: 22% from Teesdale (Elkington & Woodell 1963); Davidson and Lenz (1989) describe results of 22,2% to 63.55% from outcrossed European parents of *P. fruticosa*, whereas the tetraploid samples had germination percentages of 22,2% and 32,4%. Richards (1975) obtained 80% germination without any pretreatment or dormancy period and 55% germination when pretreated for a week at 0°C in the dark. Germination experiments with seeds from 6 populations in Altai (Siberia), stored dry at *ca* 20°C for six months and germinated at the same temperature, also prooved high germination percentages (56–80%), although some samples from lower altitudes gave only 30% and even 7% (Tril 1985).

Consequently, it seems that unstratified seeds produce a higher germination percentage. In our experiments, we still, howerver, preferred stratification, since it more exactly reproduces natural conditions in Estonia. We can not comment on the higher germination percentages from Altai by Tril (1985), because the author does not give any information about the sexual type of the flowers of *P. fruticosa* in Altai and so the results may concern *P. floribunda* Pursh. The high percentage given by Richards (1975) may have been determined by his use of only a single fruit of 64 seeds.

The potential for generative propagation of the species is fairly good since the sexual structure of the population is almost balanced, the seed set is stable and the germination percentage is relatively high. However, in nature seedlings were found only in a few places and only on open soil; young plants of certain generative origin were not found. The soil on which the seedlings were growing was very thin, and disturbed by freezing and flooding which makes survival for young plants very difficult. Therefore, propagation by seeds cannot be important in Estonian and Latvian natural populations.

Vegetative reproduction seems to prevaile. Vegetative spread occurs via creeping stems, lying directly below the soil surface, in some cases the plant is thus capable of covering a large area (Elkington & Woodell, 1963). In Estonian localities vegetative spread or, in this case, rather renewal takes place namely in such a way. In suitable conditions *P. fruticosa* can also be a colonizing species in Estonia. This was noted by Vilbaste (1953) as occurring on the banks of trenches after the World War I and on abandoned fields after WW II.

In the Harku—Vääna—Keila area *P. fruticosa* stands are in some places very dense, in others moderately so. The population seems is viable, it flowers abundantly here and the seedset is in the normal range. Nevertheless it is not extending its area here, as has also been noted by Raudi (1979, unpublished) in his undergarduate project.

In Ohukotsu and Enge, where the population is declining due to the expansion of forest canopy, no seedlings were found. The shrubs were smaller with several dried branches here.

P. fruticosa in Estonia and Latvia, thus, is not enlarging its population area, in some places (Ohukotsu) its area is even diminishing. The main population in the Harku—Keila—Vääna area has been known in its present location for almost 200 years. Therefore, one can agree with Eilart & Eilart (1974) that *P. fruticosa* is a relic and not an introducent in Estonia and Latvia as well. There was no actual reason for Vilbaste to doubte in the natural origin of *P. fruticosa* in Estonia; and his opinion seems to be the basis for latter similar considerations by Eichwald (1956) and Laasimer (1965) as well.

CONCLUSIONS

Estonian *Potentilla fruticosa* populations, as well as the only population in Latvia, consist of dioecious tetraploids (2n=28). Hence, they are *Potentilla fruticosa* s.str.

Diploid hermaphroditic specimens are also found both in Estonia and Latvia, but these are single specimens of cultivated origin that have run wild. No hermaphroditic flowers were found in the natural populations.

The sexual structure of the populations was not easy to determine due to the possible vegetative origin of the shrubs. The results of counting bushes that had reched the generative phase (had flowers at the time of counting) did not show a significant deviation from the 1:1 ratio.

Potentilla fruticosa can spread vegetatively as well as generatively. Generative organs were fully developed, the average seed set consisted of up to 30% of the pistils. After stratification up to 40.9% of seeds germinated. Hence, *Potentilla fruticosa* has sufficient potential for generative renewal but this is seldom realized. Seedlings were found only on open soil. We could not find any young shrubs of generative origin, it seems they do not survive to the second vegetation period.

The populations in Estonia and Latvia seem to be rather stable and are threatened only by radical changing in its habitat conditions brought on by man. On the other hand it seems that *Potentilla fruticosa* is intolerant to shading and a permanently high water level as well.

In Estonia and Latvia *Potentilla fruticosa* s. str. probably has the same origin as in England and Gotland, being a part of the species' former larger distribution area. Hence we do not share the opinion of some earlier authors who deem the populations of *Potentilla fruticosa* to be a naturalized in Estonia, but consider them a relic.

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Education

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Professional employment

1977–	Institute of Zoology and Botany
1990–	University of Tartu, part-time teaching
1992–1995	University of Agriculture, part-time teaching

Scientific work

Fields of research: plant taxonomy (especially *Rosaceae*), anatomy, cytology and floristics. Main projects I have participated: Flora of the Baltic Countries, Estonian Red Data Book, Red Data Book of the Baltic Region, Key-book of Estonian vascular plants and Cytotaxonomy and breeding systems in some neoendemic plant taxa in the Baltic Region.

Results have been presented at international conferences in Finland, Czeck Republic, Lithuania, Estonia and Hungary.

Number of scientific publications: 31.

Organizational activities

1979–	Member of the Estonian Naturalist' Society
1983–1992	Secretary of the Section of Botany of the Estonian Naturalists' Society
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Teadustegevus

Uurimisvaldkonnad: taksonoomia (eriti roosõielised), anatoomia, tsütoloogia ja floristika. Peamised projektid, milles olen osalenud: Baltimaade floora, Eesti "Punase raamatu", Läänemeremaade "Punase raamatu" ja Eesti soontaimede määraja koostamine ning Läänemere regiooni mõnede taimeliikide tsütotaksonoomia ja paljunemisbioloogia.

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