

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
<i>Rhopalostylae</i>	<i>Fruticosae</i>	<i>P. fruticosa</i> L.
	<i>Bifurcae</i>	<i>P. bifurca</i> L.
<i>Nematostylae</i>	<i>Xylorrhizae</i>	<i>P. lignosa</i> Willd.
	<i>Biflorae</i>	<i>P. biflora</i> Willd.
	<i>Palustreres</i>	<i>P. palustris</i> L.
	<i>Tridentatae</i>	<i>P. tridentata</i> Sol
	<i>Eriocarphae</i>	<i>P. elatior</i> Schlecht
	<i>Speciosae</i>	<i>P. speciosa</i> Willd.
	<i>Nitidae</i>	<i>P. nitida</i> L.
	<i>Curvisetae</i>	<i>P. colletiana</i> Aitch.
	<i>Crassinerviae</i>	<i>P. valderia</i> L.
		<i>P. brachypetalata</i> Fisch. & Mey
	<i>Caulescentes</i>	<i>P. caulescens</i> L.
	<i>Fragariastra</i>	<i>P. alba</i> L.
		<i>P. micrantha</i> Ram.
<i>Closterostylae</i>	<i>Rupestres</i>	<i>P. rupestris</i> L.
		<i>P. tianschanica</i> Th. W.
		<i>P. geoides</i> Bieb.
<i>Conostylae</i>	<i>Multifidae</i>	<i>P. multifida</i> L.
		<i>P. pulchella</i> R. Br.
		<i>P. sericea</i> L.
		<i>P. eversmanniana</i> Fisch.
	<i>Graciles</i>	<i>P. effusa</i> Dougl.
	<i>Haematochroae</i>	<i>P. pulcherrima</i> Lehm.
		<i>P. ehrenbergiana</i> Schlecht
	<i>Niveae</i>	<i>P. nivea</i> L.
		<i>P. villosa</i> Pall.
		<i>P. vahliana</i> Lehm.
		<i>P. evestitia</i> Th. W.
	<i>Argenteae</i>	<i>P. argentea</i> L.
		<i>P. dealbata</i> Bge.
		<i>P. canescens</i> Bess.
		<i>P. leucopolitana</i> P. J. Müll.
		<i>P. thyrsoflora</i> (Hüls.) Zimm.
	<i>Tanacetifoliae</i>	<i>P. tanacetifolia</i> Willd.
		<i>P. viscosa</i> Don.
		<i>P. sanguisorba</i> Willd.
	<i>Rectae</i>	<i>P. recta</i> L.
		<i>P. taurica</i> Willd.
		<i>P. nurensis</i> Boiss. et Haskn
	<i>Rivales</i>	<i>P. supina</i> L.
		<i>P. intermedia</i> L.
		<i>P. norvegica</i> L.
		<i>P. asperima</i> Turcz.
	<i>Persicae</i>	<i>P. flabellata</i> Reg. et Schn.
		<i>P. komaroviana</i> Th. W.
		<i>P. ruprechtii</i> Boiss.
	<i>Grandiflorae</i>	<i>P. umbrosa</i> Stev.
		<i>P. chrysantha</i> Trev.
	<i>Chrysanthae</i>	<i>P. thuringiaca</i> Bernh.
		<i>P. szovitsii</i> Th. W.
		<i>P. sericata</i> Th. W.
		<i>P. multijuga</i> Lehm.
	<i>Multijugae</i>	<i>P. fragariformis</i> Will.
	<i>Ranunculoides</i>	<i>P. tabernaemontani</i> Asch.
<i>Gomphostylae</i>	<i>Aureae</i>	<i>P. crantzii</i> (Crantz.) Beck.
		<i>P. arenaria</i> Borkh.
		<i>P. gelida</i> C. A. Mey
	<i>Fragarioides</i>	<i>P. fragarioides</i> L.
	<i>Tormentillae</i>	<i>P. erecta</i> Rausch.
		<i>P. reptans</i> L.
		<i>P. flagellaris</i> Willd.
<i>Leptostylae</i>		<i>P. anserina</i> L.
Outgroup		<i>Fragaria moschata</i> Duch.
		<i>F. vesca</i> L.
		<i>F. viridis</i> 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: appressed to fruit (0), reflexed (1)
 63. Runners: absent (0), present (1)
 64. Texture of leaves: herbaceous (0), fleshy (1), thin (2), leathery (3)

RESULTS AND DISCUSSION

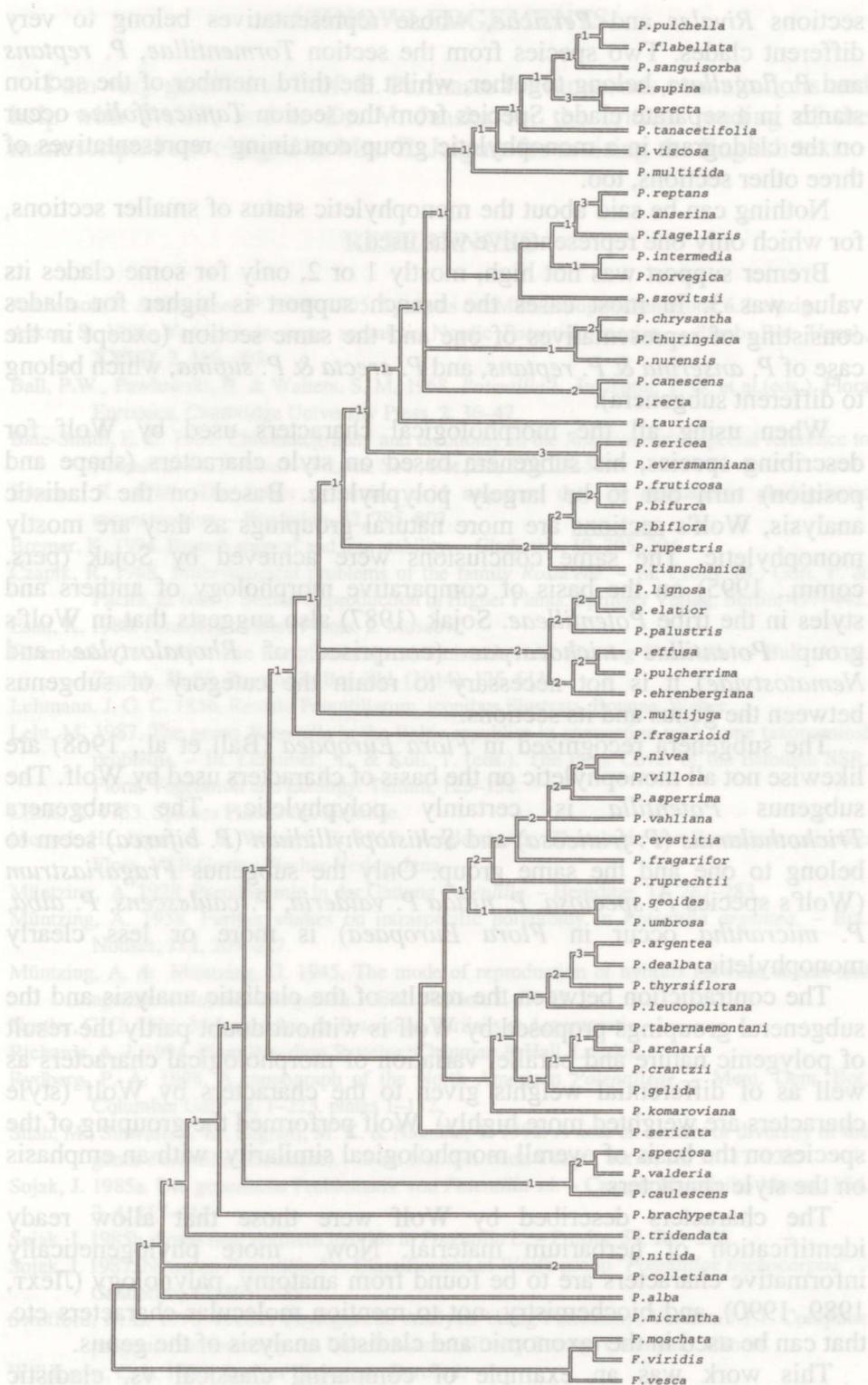
With PAUP, 72 equally parsimonious trees were found with the length 893 steps, the consistency index 0.380, homoplasy index 0.845, and retention index 0.460. Since strict and 95%-majority consensus trees of these were identical and moderately resolved, reweighting of the characters was undertaken. After 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 furthestest. 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. canescens* (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 (Jętek, 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 TEOSE "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 seksioonid. Vastuolu kladistilise analüüsi tulemuste ja Wolfi poolt empiirilisel loodud taksonoomiliste üksuste vahel peegeldab tõenäoliselt morfoloogiliste tunnuste paralleelset evolutsiooni perekonnas, aga ka tunnustele erineva kaalu andmist (näit. Wolf pidas emakakaela tunnuseid teistest olulisemaks).