

Phylogenetic analysis of *Potentilla* using DNA sequences of nuclear ribosomal internal transcribed spacers (ITS), and implications for the classification of *Rosoideae* (*Rosaceae*)

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Abstract: The circumscription of *Potentilla* has varied widely. To investigate the monophyly of *Potentilla* and the phylogenetic relationships of associated genera we used nuclear ribosomal internal transcribed spacer (ITS) DNA sequences. Fourteen species of *Potentilla* (sensu WOLF 1908) were included, some of which represent proposed segregate genera (such as *Argentina*, *Comarum*, *Drymocallis*, *Duchesnea*, *Pentaphylloides*, and *Sibbaldiopsis*), and 17 other genera of *Rosoideae*, using *Prunus* as outgroup. Our most parsimonious tree strongly implies that *Potentilla* is not monophyletic. Forcing the monophyly of *Potentilla* yields distinctly longer trees. Several morphological features appear to have evolved several times independently, including the swollen receptacle (“strawberry”) and ternate leaves. In order to minimise nomenclatural change and to name only well supported clades, *Potentilla* should be split into several genera, while other previously recognised genera such as *Duchesnea*, *Horkelia*, and *Ivesia* are best included in *Potentilla*. We suggest, however, that a phylogenetic nomenclature (sensu DE QUEIROZ & GAUTHIER 1994) might be a better solution.

Potentilla L. is a rather large genus (c. 200–500 species) of herbaceous or somewhat woody perennials distributed mainly in the Northern Hemisphere. Species diversity is highest in northern Eurasia. A few species are grown as ornamentals and some are found in temperate areas of the Southern Hemisphere. While the genus is regarded as easy to recognise, morphological synapomorphies have not been identified and some taxonomic treatments have resorted to circumscribing the genus by simply listing its species.

Potentilla and its presumed relatives are generally placed in subfam. *Rosoideae* of the *Rosaceae*. Phylogenetic analyses of *rbcL* sequences by MORGAN & al. (1994) showed the *Rosaceae* to be monophyletic when certain groups (*Chrysobalanaceae*, *Neuradaceae*, *Quillaja* and relatives) were removed. The *Rosoideae* as traditionally delimited appears to be polyphyletic, but the analyses by MORGAN & al. (1994)

strongly support the monophyly of a somewhat more narrowly circumscribed *Rosoideae*. In this paper we present analyses of *Rosoideae*, and especially of the *Potentilleae*, with the aim of identifying well supported monophyletic groups. Our main concern is the circumscription of *Potentilla* itself.

Background information. Since WOLF's (1908) influential monograph, *Potentilla* has usually been circumscribed rather broadly, but this has not always been the case. At times several more or less well defined segregates have been "split off" only to be "lumped" again into a more inclusive *Potentilla*. Splitting by different authors has sometimes led to the recognition of rather different entities. Since our present taxonomic system lacks criteria for assigning Linnaean ranks, such complex histories of classification are commonplace (DE QUEIROZ & GAUTHIER 1994). However, we suspect that *Potentilla* is among the more complicated cases in angiosperms. What follows is a brief synopsis (cf. Table 1).

Table 1. Annotated list of genera previously considered close to or congeneric with *Potentilla*; some synonyms shown in square brackets. Genera sampled in this analysis are marked with an asterisk.

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- * *Alchemilla* L. – A large group of 60 mainly northern temperate species or up to 250 if "micro species" are considered. Always kept separate from *Potentilla*; sometimes split into three or four genera: *Alchemilla*, *Aphanes*, *Lachemilla*, and *Zygalthemilla*. Until recently mostly classified in the tribe *Poterieae* or a similar group.
 - * *Aphanes* L. – Annual plants (c. 20 spp.) similar to certain *Alchemilla*; sometimes included in *Alchemilla*, but often treated as a separate genus, especially in local floras.
 - * *Argentina* HILL – Described for *Potentilla anserina*; LAMARCK (1778) widened its scope but RYDBERG (1898) treated it as comprising *P. anserina* and close relatives. HUTCHINSON (1964) estimates the number of species to 12 of temperate northern hemisphere, but SOJÁK (1994) treats *P. anserina* in a group of 54 species mainly from eastern Asia.
 - [*Boottia* BIGELOW – See *Drymocallis*.]
 - Callionia* GREENE – A segregate of one (or three) American species of *Potentilla*, erected in an offhand way (GREENE 1906) apparently on account of them being pleasant to look at. Not accepted by modern authors.
 - Chamaephyton* FOURR. – Erected for one species, *Potentilla supina*, which was classified by WOLF (1908) close to *P. norvegica* (sampled in this analysis). Included in *Potentilla* by modern authors.
 - * *Chamaerhodos* BUNGE – Five East Asian and North American species; usually separate from *Potentilla*, but considered closely related (Focke 1894, RYDBERG 1898, WOLF 1908, HUTCHINSON 1964, KALKMAN 1988); lacks epicalyx, and has only five stamens.
 - Chionice* BUNGE ex LEDEB. – Erected [instantly becoming a synonym of *Dryadanthe* (LEDEBOUR 1844)] for one East Asian species identical to *Sibbaldia tetrandra* (also see HOOKER & JACKSON 1895, WOLF 1908, DIXIT & PANIGRAHI 1981). It is classified in *Potentilla* by some authors (HOOKER 1878, HUTCHINSON 1964). *Chionice* is not used by modern authors.
 - [*Coelas* DULAC – Synonym of *Sibbaldia*.]
 - Comarella* RYDB. – A segregate of two species from North America; generally accepted as a separate genus in the *Potentilleae*.
 - * *Comarum* L. – Described for *C. palustre*, but now considered to include c. 5 northern temperate species (HUTCHINSON 1964); variously regarded as congeneric with *Potentilla* or separate from it.

Table 1 (continued)

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- [*Comocarpa* (TORR. & A. GRAY) RYDB. – See *Pentaphylloides* and *Trichothalamus*.]
 [Dactylophyllum SPENN. – Described for species of *Potentilla* s. l. with digitate leaves (including the type of *Potentilla*), along with *Fragaria*, *Sibbaldia*, and *Duchesnea*; not accepted by any modern authors.]
 [Dasiphora RAF. – See *Pentaphylloides*.]
Dryadanthe BUNGE – See *Sibbaldia*.
 * *Drymocallis* FOURR. ex RYDB. – Segregate of c. 30 pinnate-leaved northern temperate herbs; accepted by RYDBERG (1898, 1908) and HUTCHINSON (1964), but rarely by others (includes the type of *Bootia* BIGELOW, an invalid name).
 * *Duchesnea* SM. – A group of up to six East Asian and North American weedy species; strawberry-like in habit and by having bright red swollen toruses. Mostly classified as a separate genus, while some (WOLF 1908, BATE-SMITH 1961, KALKMAN 1968, PANIGRAHI & DIKSHIT 1987, KALKMAN 1988) include them in *Potentilla* or *Fragaria* (BENTHAM & HOOKER 1865).
 [Dynamidium FOURR. – Synonym of *Potentilla* (includes its type).]
 [Fraga LAPEYR. – Species of *Potentilla* s. l. similar to *Fragaria* but lacking “strawberries”. See *Fragariastrum*.]
 * *Fragaria* L. – Comprises c. 8–12 species found in the temperate part of the northern hemisphere and in parts of South America. Generally separated since LINNAEUS (1753), based on the strawberry “fruit”; several authors note similarities with parts of *Potentilla* and join the two (CRANTZ, 1762, 1769; SCOPOLI, 1772). WOLF (1908) and KALKMAN (1968) questioned the logic of keeping *Fragaria* separate from *Potentilla* when including some other segregates.
 * *Fragariastrum* HEIST. ex FABR. – Originally erected for *Fragaria sterilis* (FABRICIUS 1759) but later described anew (CANDOLLE 1858) for a small collection of white-flowered *Potentilla* species, *P. sterilis* among them. Often treated at subgeneric level in *Potentilla* (e.g. BALL & al. 1968).
 * *Horkelia* CHAM. & SCHLTDL. – C. 12 to 17 North American species, sometimes including *Ivesia* (RYDBERG 1898). Generally accepted by modern authors but included in *Potentilla* by some (e.g. JEPSON 1925, KERNEY & PEEBLES 1942).
Horkeliella RYDB. – Segregate of three species from *Horkelia*.
Hypargyrium FOURR. – A selection of (French) species from *Potentilla* s. l., probably based on indumentum characters (FOURREAU did not supply a description, only a list of species). Not accepted by modern authors but has occasionally been used at subgeneric level within *Potentilla* (e.g. SHAH & WILCOCK 1993).
 * *Ivesia* TORR. & A. GRAY – Generally separated from *Horkelia* and from *Potentilla*, despite RYDBERG'S (1898) view that the distinguishing characters intergrade. Contains c. 20–35 North American species.
 [*Jussiea* L. ex SM. – Erected posthumously from a Linnean manuscript. The description of this genus was made “as a matter of curiosity to the learned botanist” (SMITH 1811), and it instantly became a synonym of *Sibbaldia*. *Jussiea* is not used by modern authors, but for some reason treated as a synonym of *Potentilla* by some (HOOKER & JACKSON 1895, HUTCHINSON 1964).]
 [*Lehmanna* TRATT. – Synonym of *Trichothalamus*.]
 [*Pancovia* HEIST. ex FABR. (nom. rej.) – Synonym of *Comarum*.]
 * *Pentaphylloides* DUHAMEL – Used for the circumpolar shrub *Potentilla fruticosa* and its three close relatives (RYDBERG 1898, YUZEPCHUK 1941, HUTCHINSON 1964, SOJÁK 1969, also see KLACKENBERG 1983). More often treated as a subgenus within *Potentilla* (e.g. LEHMANN 1856, WOLF 1908, BALL, & al. 1968, PANIGRAHI & DIKSHIT 1987, KALKMAN 1988).

Table 1 (continued)

[*Pentaphyllum* HILL – Superfluous name for *Potentilla*.]

Potaninia MAXIM. – Comprising only one Mongolian species included in the *Potentillinae* by FOCKE (1894); classified by HUTCHINSON (1964) and KALKMAN (1988) with *Cercocarpus*, i.e. outside the *Rosoideae* s. str.

Potentillopsis OPIZ – A segregate of a single North American *Potentilla* species (*P. pentandra*) based on the presence of only five stamens, like in some *Sibbaldia*, in *Purpusia* and *Chamaerhodos*. Usually included in *Potentilla*.

Purpusia BRANDEGEE – A segregate of three species of *Potentilla* s. l. from western North America included in the *Potentilleae* by HUTCHINSON (1964) and KALKMAN (1988). Lacks an epicalyx and has only five stamens.

* *Quinquefolium* ADANS. – Described for species of *Potentilla* s. l. with digitate leaves, excluding *Fragaria* and *Sibbaldia*; not accepted by modern authors.

* *Sibbaldia* L. – A group of c. 20 species found in the northern hemisphere and in alpine regions. Commonly separated from *Potentilla* based on the lower number of stamens, though this feature also occurs in *Potentilla* s. l. *Sibbaldia* was treated as separate by SOJÁK who nevertheless identified close relatives within *Potentilla*: “I am convinced that *P. coriandrifolia* and the red-flowered species of *Sibbaldia* have a common ancestor in spite of the different number of stamens and the different shape of leaflets” (SOJÁK 1994: 12). It is sometimes used within *Potentilla* at subgeneric level (HOOKER 1865, JEPSON 1925, KERNEY & PEEBLES 1960). Some authors split off a number of genera such as *Dryadanthe* and *Sibbaldianthe* from *Sibbaldia* (e.g. YUZEPCHEV 1941, but see DIXIT & PANIGRAHI 1981).

Sibbaldianthe JUZ. – See *Sibbaldia*

* *Sibbaldiopsis* RYDB. – Segregated from *Potentilla* s. l. based on trifoliate leaves and hairy achenes; included by SPRENGEL (1818) in *Trichothalamus*. Comprises a single North American species.

Stellariopsis RYDB. – Erected for one Californian species of *Potentilla* s. l. by RYDBERG (1898) based on its peculiar habit, anthers opening by pores, and being “intermediate between *Potentilla* and *Horkelia* (*Ivesia*)”. Recognition varies.

* *Tormentilla* L. – Described for a small number of four-merous species of *Potentilla* s. l.; accepted by many earlier authors but not by modern workers. WOLF (1908) placed it in his *Tormentillae* with *P. reptans*, the type of *Potentilla*, and *P. indica* (usually classified as *Duchesnea*).

* *Trichothalamus* SPRENG. – Erected for species of *Potentilla* s. l. with hairy achenes; not accepted by modern authors but used by some for a subgenus in *Potentilla* (e.g. HOOKER 1865, WOLF 1908, BALL, & al. 1968, SHAH & WILCOCK 1993). The same set of species has been recognised under the name *Comocarpa*.

* *Tridophyllum* NECK. – Created for species of *Potentilla* s. l. with ternate leaves but excluding *Fragaria*; not accepted by modern authors.

[*Tylosperma* Botsch. – Substitute name for *Lehmannia*, a synonym of *Trichothalamus* (FARR & al. 1979).]

LINNAEUS (1753) described five genera relevant to the *Potentilla* problem, namely *Potentilla* itself, *Comarum*, *Fragaria*, *Sibbaldia*, and *Tormentilla*. ADANSON (1763) put the species of *Potentilla* with digitate leaves (but not *Tormentilla*) into his *Quinquefolium*, while keeping those with pinnate leaves in *Potentilla*.

He kept *Comarum* (as *Pancovia*), *Fragaria*, and *Sibbaldia* separate. GAERTNER (1788) preferred the pre-Linnaean name *Pentaphyllum* for *Potentilla*, but he also maintained *Comarum*, *Fragaria*, and *Sibbaldia*. NECKER (1790), also stressing leaf characteristics, created the genus *Tridophyllum* for the species with ternate leaves, while placing those with pentafoolate leaves in *Tormentilla*. Like ADANSON (1763) he put species with pinnate leaves in *Potentilla*, and kept *Fragaria* and *Comarum* separate. CRANTZ (1762, 1769) submerged *Potentilla*, *Comarum*, and *Tormentilla* within *Fragaria*, while SCOPOLI (1772) lumped all these genera into *Potentilla*. LAMARCK (1778) used the genus *Argentina* for *Potentilla* species with pinnate leaves. He treated *Fragaria* similarly to LINNAEUS and included several white flowered species with ternate leaves now generally classified in *Potentilla*, while placing those with more than three leaflets in *Potentilla*.

A variety of other segregate genera were recognised by later authors. SMITH (1810) described *Duchesnea* for a species which has false fruits similar to strawberries. The characteristics of this species have justified its inclusion in both *Potentilla* and *Fragaria* (HOOKER 1865, WOLF 1908). LAPEYROUSE (1813) moved those species of LINNAEUS' *Fragaria* without strawberries into a new genus *Fraga*. SPRENGEL (1818) created *Trichothalamus* for those species in *Potentilla* with hairy achenes. BIGELOW (1824) erected the genus *Bootia* based on stamen position, but the name was invalid. Later, FOURREAU (1868) put forward the genus *Drymocallis* for closely related species. The small shrub *Potentilla fruticosa* was disengaged by DUHAMEL DU MONCEAU (1755) as the genus *Pentaphylloides*. Several later authors have accepted such a genus under various names (RAFINESQUE 1838; RYDBERG 1898, 1908; HUTCHINSON 1964; SOJÁK 1969) but it is still included in *Potentilla* by most authors (e.g. HOOKER 1865, FOCKE 1894, WOLF 1908, SCHULZE-MENZ 1964, BALL & al. 1968, ROBERTSON 1974, KALKMAN 1988). During the exploration of North America several other new genera were described, such as *Horkelia* (CHAMISSE & SCHLECHTENDAL 1827), *Ivesia* (TORREY & GRAY 1857), *Purpusia* (BRANDEGEE 1899), and *Potentillopsis* (OPIZ 1857). Each of these has at times been included in *Potentilla*.

NESTLER (1816) set the stage for a broad circumscription of *Potentilla*. He lumped *Potentilla* (including *Pentaphylloides* and *Quinquefolium*), *Comarum*, some species of *Fragaria* (in the sense of LINNAEUS), and *Tormentilla*, into *Potentilla*. He maintained *Sibbaldia* and *Fragaria* as separate genera, however. NESTLER's delimitation of *Potentilla* was followed closely by several authors (e.g. CANDOLLE 1825, SERINGE 1825, LEHMANN 1856, HOOKER 1865, WOLF 1908), with minor differences involving the recognition of genera such as *Duchesnea*. Nevertheless, alternatives continued to emerge. Thus, SPENNER (1829: 1084) suggested the transfer of all species with digitate leaves previously placed in *Potentilla*, *Tormentilla*, *Fragaria*, and *Sibbaldia* into his *Dactylophyllum*. FOURREAU (1868) did not accept the broad generic concept of NESTLER (1816) and again split *Potentilla* of southern France into eight genera: *Fraga*, *Trichothalamus*, *Dynamidium*, *Tormentilla*, *Chamaephyton*, *Drymocallis*, *Hypargyrium*, and *Potentilla* sensu stricto. In his revision of *Potentilla* WOLF (1908: 9) indignantly asked "Wie viele Gattungen hätte dieser Florist wohl aufstellen müssen, wenn er alle Potentillen der Erde zu bearbeiten gehabt hätte?"

RYDBERG (1898, 1908) accepted most segregates and described some of his own. Thus, he accepted *Argentina*, *Chamaerhodos*, *Comarella*, *Comarum*, *Dasiphora*, *Drymocallis*, *Duchesnea*, *Fragaria*, *Horkelia* (including *Ivesia*), *Sibbaldia*, *Sibbaldiopsis*, and *Stellariopsis*, in addition to *Potentilla* (including *Tormentilla*). RYDBERG's classification was to some extent accepted by WOLF (1908), but in relation to *Potentilla* he adopted a broad concept. In particular, WOLF included *Argentina*, *Comarum*, *Dasiphora*, *Drymocallis*, *Duchesnea*, and *Sibbaldiopsis* within *Potentilla*, though he accepted some of these at a subgeneric level. He worried, in fact, about not including other genera, especially *Fragaria* and *Sibbaldia* (WOLF 1908: 15, also see KALKMAN 1968).

More recently, HUTCHINSON (1964) followed RYDBERG (1898, 1908) quite closely, although he accepted *Horkelia* and *Ivesia* as separate genera, and considered *Pentaphylloides* to be the valid generic name for *Potentilla fruticosa*, rather than RYDBERG's *Dasiphora*. Altogether, HUTCHINSON included 16 genera within his tribe Potentilleae. SCHULZE-MENTZ (1964), on the other hand, did not follow RYDBERG's example. In his classification only *Comarum*, *Fragaria*, *Duchesnea*, *Horkelia*, and *Ivesia* were separated from *Potentilla*. It is noteworthy that this may have been the first classification to associate *Alchemilla* closely with *Potentilla*.

ROBERTSON (1974) returned to a classification even more similar to that of WOLF (1908), differing only in maintaining *Duchesnea* as a separate genus. KALKMAN (1988) listed ten genera in the Potentilleae: *Chamaerhodos*, *Comarella*, *Drymocallis*, *Fragaria*, *Horkelia*, *Horkeliella*, *Ivesia*, *Potentilla*, *Purpusia*, and *Sibbaldia*, thereby including *Comarum*, *Tormentilla*, *Duchesnea*, *Pentaphylloides*, and *Argentina* in *Potentilla*. Most modern floras adhere to WOLF's (1908) classification (e.g. FERNALD 1950, GLEASON & CRONQUIST 1963, HUBER 1964, VALENTINE & CHATER 1968, POLUNIN 1969, STEERE 1970, HITCHCOCK & CRONQUIST 1973, MUNZ 1974, STACE 1991, MOSSBERG & al. 1992, KROK & ALMQUIST 1994, LID & LID 1994) and only rarely to something similar to RYDBERG's (1898, 1908) system (RYDBERG 1906, YUZEPCHUK 1941). *Duchesnea* is the one segregate more or less consistently recognised. In some floras the view of *Potentilla* is expanded beyond that of WOLF (1908) to include genera such as *Horkelia*, *Horkeliella*, *Ivesia*, *Comarella*, and *Stellariopsis* (e.g. JEPSON 1925, KERNEY & PEEBLES 1942, KERNEY & PEEBLES 1960).

A phylogenetic analysis of *Potentilla* and its immediate relatives has not been attempted before. KALKMAN (1988) tried to elucidate relationships among proposed monophyletic groups within the *Rosaceae* as a whole, but owing to limited data his analysis was not very satisfying. Our re-analysis of KALKMAN's (1988) data using a more powerful computer program (SWOFFORD 1993) failed to find any well supported resolution of relationships. A full investigation of morphological characters is under way (VRETBLAD & al. 1996; M. HIBBS and T. ERIKSSON, unpubl.).

The *rbcL* analysis of MORGAN & al. (1994) strongly supported a monophyletic *Rosoideae* sensu stricto, and showed *Filipendula* to be sister group to the rest of the genera. MORGAN & al. (1994) also showed some resolution within the *Rosoideae*, but as their aim was to investigate the family as a whole sampling within the *Rosoideae* was quite limited.

Materials and methods

Selection of taxa. In order to test the monophyly of *Potentilla* we selected 14 species placed in *Potentilla* by WOLF (1908), and one representative of 17 additional genera of *Rosoideae* sensu stricto (Table 3). The *Potentilla* species were chosen so as to sample the main groups in WOLF's classification (Table 2). Among the *Potentilla* species were several which have been recognised as separate genera (*Comarum*, *Argentina*, *Drymocallis*, *Sibbaldiopsis*, *Pentaphylloides*, *Duchesnea*). Other genera were selected mainly from the *Potentilleae*, but also from other tribes that have at times been considered closely related to *Potentilla* (*Poterieae*, *Dryadeae*, *Ulmariaceae*, sensu HUTCHINSON 1964). One of WOLF's groups, the *Tormentillae*, is sampled more than the others in order to investigate the position of *P. indica*, which is often treated in the genus *Duchesnea*. Representatives of several other genera were included to achieve a better sampling of the *Rosoideae* and to test the phylogeny presented by MORGAN & al. (1994). We also included *Dryas octopetala*, which their analysis suggested should be removed from the *Rosoideae* sensu stricto. A previously obtained sequence of *Prunus* (CAMPBELL & al. 1995) was included for rooting purposes, and an additional sequence of *Fragaria* (*F. ananassa*) was acquired from Genbank.

The sequences used in our analyses are listed in Table 3. In the specimens sequenced in this study, DNA's were extracted from herbarium leaf material except in two cases, *Potentilla norvegica* (extracted from frozen fresh leaves) and *Hagenia abyssinica* (collected and extracted by E. KNOX). Herbarium material from A, GH, LD, and S (HOLMGREN & al. 1990) were used. In most cases the collections were made and/or determined by the first author, but in several cases we relied upon herbarium sheet determinations.

Molecular methods. Extractions were carried out using a scaled-down version of the CTAB extraction method described by DOYLE & DOYLE (1990; R. JANSEN, pers. comm.), with 1% PVP (polyvinylpyrrolidone) added to the extraction buffer. Approximately 15–40 mg of leaf tissue was rehydrated in water for c. 15–30 min prior to grinding in either liquid nitrogen or in CTAB buffer.

The ITS region was PCR amplified using a Perkin-Elmer 9600 thermal cycler. The primers used for amplification were "ITS4" and "ITS5" (WHITE & al. 1990). In most cases we used a Perkin-Elmer GeneAmpTM kit with AmpliTaqTM DNA polymerase, but in a few cases a Gibco BRL PCR reagent kit was used. The PCR reactions (25 µl) contained 12.5 µl of a reagent mix [2.5 µl 10× buffer with 1 mg/ml gelatine added, 2.5 µl 50% glycerol, 3.03 µl H₂O, 0.625 µl of each of the dNTPs, 1.25 µl of each of the primers (10 µM dilutions), 0.1 µl polymerase (0.5 units) for each sample, mixed in that order] and 12.5 µl of diluted template DNA. Each DNA sample was diluted 1:10, 1:100, and 1:1000. Amplification started with 2 min denaturation at 94 °C or, with DNA's extracted from fresh material, at 97 °C. Then 40 cycles were performed of 30 s denaturation at 94 °C, 30 s. annealing at 48 °C, and 90 s extension at 72 °C. A 7 min additional extension time at 72 °C followed the completion of the 40 thermal cycles.

Amplified DNA samples were cleaned using GeneClean IITM (Bio 101) and sequenced using cycle sequencing reactions. For sequencing, 10 µl reactions were used, containing 4.75 µl of Taq DyeDeoxyTM fluorescent terminator cycle sequencing premix, 2–5.05 µl of template DNA, and water and primer added to a final primer concentration of 1.6–2 µM. Primers used for sequencing were "ITS2", "ITS4", and "ITS5" (WHITE & al. 1990), and "ITS3B" (BAUM & al. 1994). Centri-Sep (Princeton Separations, Inc.) columns were used to remove the remaining dye terminators prior to sequencing. The reactions were re-suspended in 2.5 µl of loading buffer containing 5 parts de-ionised formamide and one part 50 mM EDTA and loaded onto a Sequagel-6 Polyacrylamide gel (National Diagnostics).

Table 2. WOLF's (1908) classification of *Potentilla*, with indication of species included in the present study (cf. Table 1). Segregate genera to which these species have been assigned are noted within brackets. The number of species assigned by WOLF (1908) to his numbered groups (greges) are indicated within square brackets. In total, WOLF treated 305 species in *Potentilla*

I. <i>Potentillae trichocarpae</i>	
A. <i>Rhopalostylae</i>	
1. <i>Fruticosae</i> [2]	<i>P. fruticosa</i> (<i>Pentaphylloides</i>)
2. <i>Bifurcae</i> [1]	<i>P. bifurca</i>
B. <i>Nematostylae</i>	
a. <i>Suffruticulosae</i>	
3. <i>Xylorrhizae</i> [2]	
4. <i>Biflorae</i> [2]	
5. <i>Palustres</i> [2]	<i>P. palustris</i> (<i>Comarum</i>)
6. <i>Tridentatae</i> [3]	<i>P. tridentata</i> (<i>Sibbaldiopsis</i>)
7. <i>Eriocarpae</i> [4]	<i>P. dickensii</i>
b. <i>Herbaceae</i>	
8. <i>Speciosae</i> [5]	
9. <i>Nitidae</i> [3]	
10. <i>Curvisetae</i> [3]	
11. <i>Crassinerviae</i> [7]	
12. <i>Caulescentes</i> [2]	
13. <i>Fragariastra</i> [4]	<i>P. micrantha</i> (<i>Fraga</i> , <i>Fragariastrum</i>)
II. <i>Potentillae gymnocarpae</i>	
A. <i>Closterostylae</i>	
14. <i>Rupestres</i> [11]	<i>P. arguta</i> (<i>Drymocallis</i>)
B. <i>Conostylae</i>	
a. <i>Eriotrichae</i>	
15. <i>Multifidae</i> [27]	
16. <i>Graciles</i> [24]	
17. <i>Haematochroae</i> [10]	
18. <i>Niveae</i> [12]	<i>P. nivea</i>
19. <i>Argenteae</i> [9]	
19a. <i>Collinae</i> [16]	
b. <i>Orthotrichae</i>	
20. <i>Tanacetifoliae</i> [15]	
21. <i>Rectae</i> [9]	
22. <i>Rivales</i> [21]	<i>P. norvegica</i>
23. <i>Persicae</i> [19]	
24. <i>Grandiflorae</i> [6]	
25. <i>Chrysanthae</i> [13]	
26. <i>Multijugae</i> [12]	
27. <i>Ranunculoides</i> [16]	
C. <i>Gomphostylae</i>	
28. <i>Aureae</i> [28]	
29. <i>Fragarioides</i> [2]	<i>P. fragarioides</i>
30. <i>Tormentillae</i> [8]	<i>P. erecta</i> , <i>P. reptans</i> , <i>P. indica</i> (<i>Duchesnea</i>)
D. <i>Leptostylae</i>	
31. <i>Anserinae</i> [7]	<i>P. anserina</i> (<i>Argentina</i>)

Table 3. List of species used in this study, with voucher specimen information, geographical origin, ploidy level, and GenBank accession numbers; names of the *Potentilla* species follow WOLF (1908). The sequence of *Fragaria ananassa* was obtained from Genbank. There was no indication of a voucher specimen for this accession. Chromosome number information was compiled from the literature (LID 1974; ROBERTSON 1974; GOLDBLATT 1981, 1984, 1985, 1988; KLACKENBERG 1983; GOLDBLATT & JOHNSON 1990; LID & LID 1994). Additional ploidy levels have been reported for the species with asterisk-marked entries

Species	Voucher and geographical origin	Ploidy level	Accession no.
<i>Agrimonia eupatoria</i>	T. ERIKSSON 654 (GH, S) Uppland, Sweden, July 1993	tetraploid	U90798
<i>Alchemilla alpina</i>	R. ERIKSSON s.n. (GH, S) Lapland, Sweden, Aug. 1993	polyploid (17–22-ploid)	U90816, U90817
<i>Aphanes arvensis</i>	RYDBERG s.n. (S) Gotland, Sweden, June 1989	hexaploid	U90818, U90819
<i>Aremonia agrimonioides</i>	KARLSSON 94076 (LD) Skåne, Sweden, Sept. 1994	hexaploid	U90799
<i>Chamaerhodos erecta</i>	LACKSCHEWITZ 11453 (GH) Montana, USA, June 1988	diploid	U90794
<i>Dryas octopetala</i>	ARONSSON s.n. (S) Lapland, Sweden, July 1994	diploid	U90804
<i>Fallugia paradoxa</i>	HILL 14684 (GH) New Mexico, USA, July 1984	tetraploid	U90805
<i>Filipendula ulmaria</i>	T. ERIKSSON 643 (GH, S) Värmland, Sweden, June 1993	diploid	U90783
<i>Fragaria vesca</i>	T. ERIKSSON 647 (GH, S) Värmland, Sweden, June 1993	diploid	U90793
<i>F. ananassa</i>	obtained from GenBank SIMOVIC & al., 1989, unpubl.	octaploid	X15589
<i>Geum urbanum</i>	T. ERIKSSON 655 (GH, S) Uppland, Sweden, July 1993	hexaploid	U90802
<i>Hagenia abyssinica</i>	KNOX 2532 (GH) Mt. Kenya, Kenya, 1994	not available	U90800
<i>Horkelia fusca</i> subsp. <i>pseudocapitata</i>	BARTHOLOMEW & ANDERSON 4901 (GH), California, USA, June 1989	not available	U90795
<i>Ivesia gordonii</i>	HIGGINS & GOODRICH 14745 (GH) Utah, USA, Aug. 1984	not available	U90796
<i>P. anserina</i>	T. ERIKSSON 644 (GH, S) Värmland, Sweden, June 1993	tetraploid hexaploid	U90788
<i>P. arguta</i>	LAFFERRIÈRE 2357 (A) Washington, USA, June 1992	diploid	U90787
<i>P. bifurca</i>	KARIS 412 (S) Uppland, Sweden, July 1991	octaploid	U90786
<i>P. dickinsii</i>	SUN, BYUNG YUN s.n. (A) Kwangwon Do, Korea, July 1989	diploid	U90785
<i>P. erecta</i>	T. ERIKSSON 648 (GH, S) Värmland, Sweden, June 1993	tetraploid*	U90810, U90811
<i>P. fragarioides</i>	BOUFFORD & al. 25327 (A) Toyama, Japan, May 1990	diploid	U90806, U90807
<i>P. fruticosa</i>	KARLSSON 94074 (LD) land, Sweden, Sept. 1994	tetraploid*	U90808, U90809
<i>P. indica</i>	T. ERIKSSON s.n. (GH, S) Cult. Sweden, Aug. 1993	dodecaploid	U90792

Table 3 (continued)

<i>P. micrantha</i>	KARLSSON 94075 (LD) Skåne, Sweden, Sept. 1994	diploid	U90812, U90813
<i>P. nivea</i>	ARONSSON s.n. (S) Lappland, Sweden, July 1994	di-, tetra-*	U90814, U90815
<i>P. norvegica</i>	T. ERIKSSON 674 (GH) Massachusetts, USA, Aug. 1994	decaploid*	U90790
<i>P. palustris</i>	T. ERIKSSON 659 (GH, S) Uppland, Sweden, July 1993	hexaploid*	U90789
<i>P. reptans</i>	T. ERIKSSON 650 (GH, S) Uppland, Sweden, July 1993	tetraploid	U90784
<i>P. tridentata</i>	HILL 17146 (A) New Hampshire, USA, Aug. 1986	tetraploid	U90791
<i>Prunus cerasifera</i>	see CAMPBELL & al. (1995)	diploid	U16200
<i>Rosa majalis</i>	T. ERIKSSON 641 (GH, S) Värmland, Sweden, June 1993	diploid*	U90801
<i>Rubus chamaemorus</i>	R. ERIKSSON s.n. (GH, S) Lapland, Sweden, Aug. 1993	octaploid	U90803
<i>Sanguisorba parviflora</i>	T. ERIKSSON s.n. (GH, S) Cult. (ex Siberia), Aug. 1993	tetraploid	U90797
<i>Sibbaldia procumbens</i>	ARONSSON s.n. (S) Lapland, Sweden, July 1994	diploid	U90820
<i>Waldsteinia fragarioides</i>	HILL & SOBLO 21384 (GH) S. Carolina, USA, April 1990	diploid triploid	U90822, U90823

Sequences were obtained using an Applied Biosystems 370A automated fluorescent DNA sequencer. For data collection, base calling, proof-reading and editing we used Apple MacintoshTM computers with Applied Biosystems software (Data Collection 1.1.1, Analysis 1.1.1., SeqEd 1.0.3). Both strands of nucleotides were sequenced in all species except one, *Aphanes arvensis*, where the ITS2 sequence is mainly based on one strand only. The two internal primers ("ITS2" and "ITS3B") are reverse complements of each other and in order to get sequences of the primer region it is necessary to get good results from the external primers. In several accessions this proved difficult (*Potentilla fragarioides*, *P. fruticosa*, *P. erecta*, *P. micrantha*, *P. nivea*, *Alchemilla*, *Aphanes*, *Sibbaldia*, *Fallugia*, and *Waldsteinia*) and "blank" areas of the 5.8S gene were coded as "missing data" ("?").

Alignment. Sequences were submitted to Clustal W 1.5 (HIGGINS & al. 1992, THOMPSON & al. 1994) in "Pearson/FASTA" format and a multiple alignment performed. Clustal was run on a Power MacintoshTM computer using the pre-set parameters, and several adjustments were made following inspection. The ITS data set has been submitted to TreeBASE (SANDERSON & al. 1994) and can be downloaded (accession number: M165c2 × 14 × 97c16c15c05) from the TreeBASE world wide web site (<http://phylogeny.harvard.edu/treebase/>). The boundaries of the ITS spacer regions and the 5.8S gene were estimated in comparison with previously published sequences (YOKOTA & al. 1989).

Phylogenetic analyses. Parsimony analyses were conducted using PAUP 3.1.1 (SWOFFORD 1993). All characters were unordered and weighted equally except in a few cases where transition/transversion weighting biases were tried (0:1, 1:2, and 1:5). Gaps were coded with hyphens (—) and treated as uncertain in the PAUP analyses. In proof-reading the sequences several ambiguous base-callings were encountered and these were coded using IUPAC (International Union of Pure and Applied Chemistry) ambiguity codes.

Heuristic searches were conducted with MULPARS and TBR branch swapping. Starting trees were constructed using 1,000 replicates of random addition sequence. Consensus trees were computed using the strict consensus option. In order to assess node support, bootstrap analyses (FELSENSTEIN 1985, HILLIS & BULL 1993) were performed, as well as decay analyses (BREMER 1988, DONOGHUE & al. 1992) using the reverse constraint option in PAUP and AutoDecay 2.9.5 (a freeware program designed to obtain decay indices for all nodes in a tree using PAUP; ERIKSSON 1996). In the bootstrap runs PAUP was set to run 500 bootstrap replicates with TBR branch swapping and MULPARS. In the reverse constraint runs for the Decay analyses PAUP was set to run 100 random addition sequence trees.

Alternative phylogenetic arrangements were tested using constraints in PAUP and also using MacClade 3.05 (MADDISON & MADDISON 1992). MacClade was also used to explore implications for the evolution of particular morphological characters. Trees were output using TreeView 1.3 (PAGE 1996) or MacClade, and PAUP (SWOFFORD 1993) was used to calculate the amount of change along branches, the consistency and retention index values, and pairwise mean distances.

Results

The ITS1 spacer was found to vary in length from 220 to 266 base pairs (average 247, median 251), and the ITS2 spacer between 201 and 221 (average 207, median 206). The longest in both cases was *Agrimonia*. The shortest ITS1 was *Aremonia* while the shortest ITS2 was *Potentilla fragarioides*. In all cases where the entire 5.8S gene could be sequenced it was uniformly 164 base pairs long, in keeping with other angiosperms (BALDWIN & al. 1995). The G + C content is 60%. Pairwise sequence divergences range from 1.7% (*Horkelia* – *Ivesia*) to 24.6% (*Prunus* – *Agrimonia*). Within *Potentilla* sensu WOLF (1908) they range from 2.4% (*P. reptans* – *P. erecta*) to 15.4% (*P. anserina* – *P. palustris*).

There are 728 aligned ITS nucleotide positions in this data set, of which 256 appear to be potentially informative, and 217 are constant. The ITS region is quite variable in terms of length and since a number of distantly related species and genera were included in the analysis the alignment contains numerous gaps. Most gaps are uninformative because only a single species differs from the rest, and other gaps are ambiguous, especially in regions which were hard to align. A few possible informative gaps were considered for inclusion in our analyses, but in all cases but two (see Discussion) they join only pairs of species which always form well supported clades based on nucleotide changes alone. Hence, *Sibbaldia* and *P. tridentata* are joined by one gap (positions 152–165), *Geum* and *Waldsteinia* by one gap (positions 150–165), and *Aremonia* and *Hagenia* by two gaps (positions 109–169 and 233–234). If included, these gaps add to the support of those groups, but do not change the topology. The total amount of uncertainty in the data set is 17%, when gaps and unsequenced parts of the 5.8S gene are considered. Uncertain base callings (coded as polymorphisms) amount to 1.1% of the data.

Analysis of the ITS data set resulted in a single tree of 1141 steps (CI = 0.44 excluding, and 0.51 including, uninformative characters; RI = 0.59). This tree is shown in Fig. 1, along with bootstrap and decay indices (d). Figure 2 shows those clades with decay indices of 3 or more; several of these are labelled to facilitate discussion. Branch lengths are shown in Fig. 3.

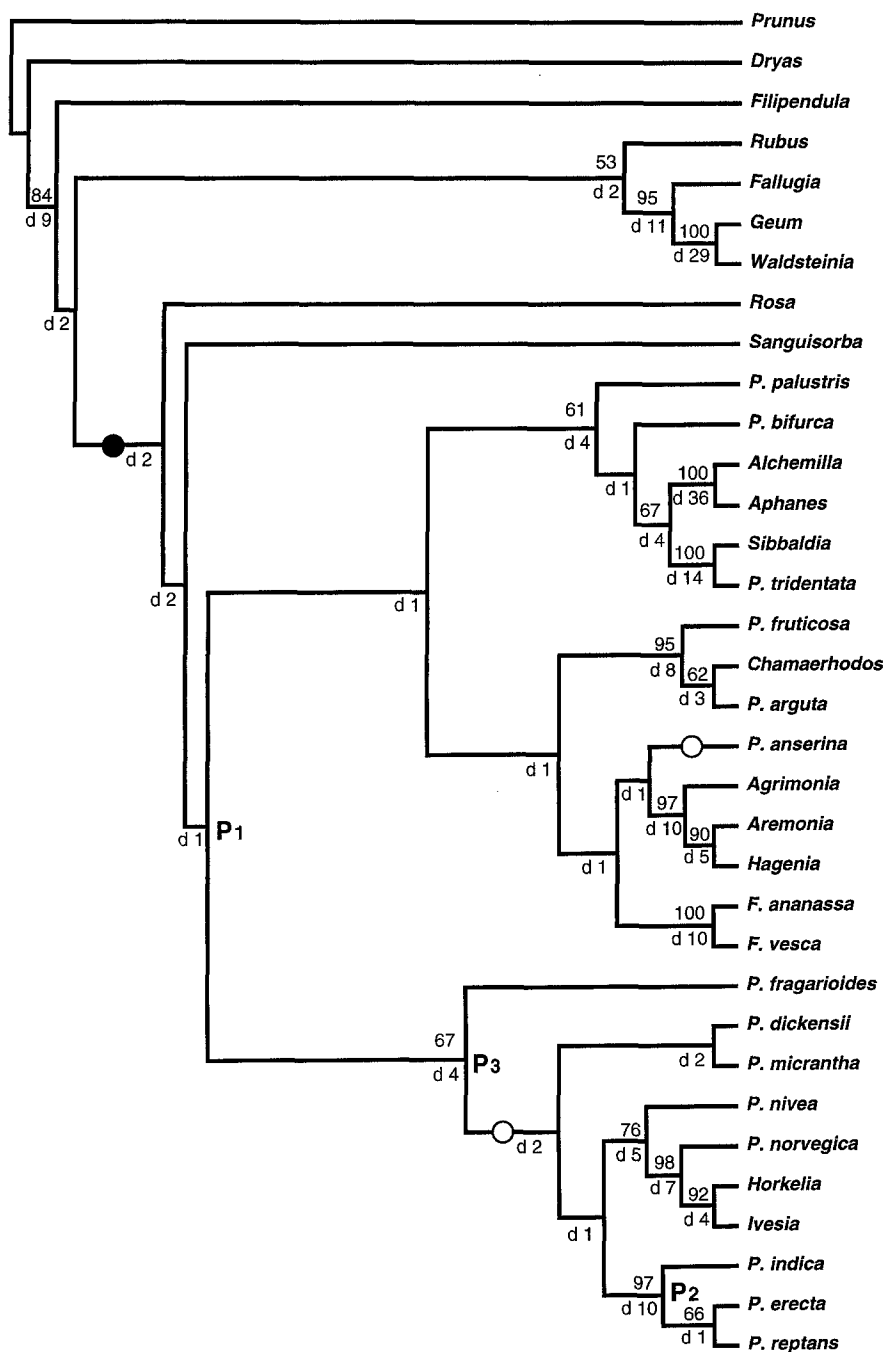


Fig. 1. Most parsimonious tree obtained from analysis of the ITS data set, showing decay index (d) and bootstrap values higher than 50% for appropriate branches; length = 1141 steps, CI = 0.44, RI = 0.59. The circles indicate the two gap characters (● at positions 186–188, and ○ at positions 655–656). The three nodes labelled (P1–P3) are possible candidates for the name *Potentilla*

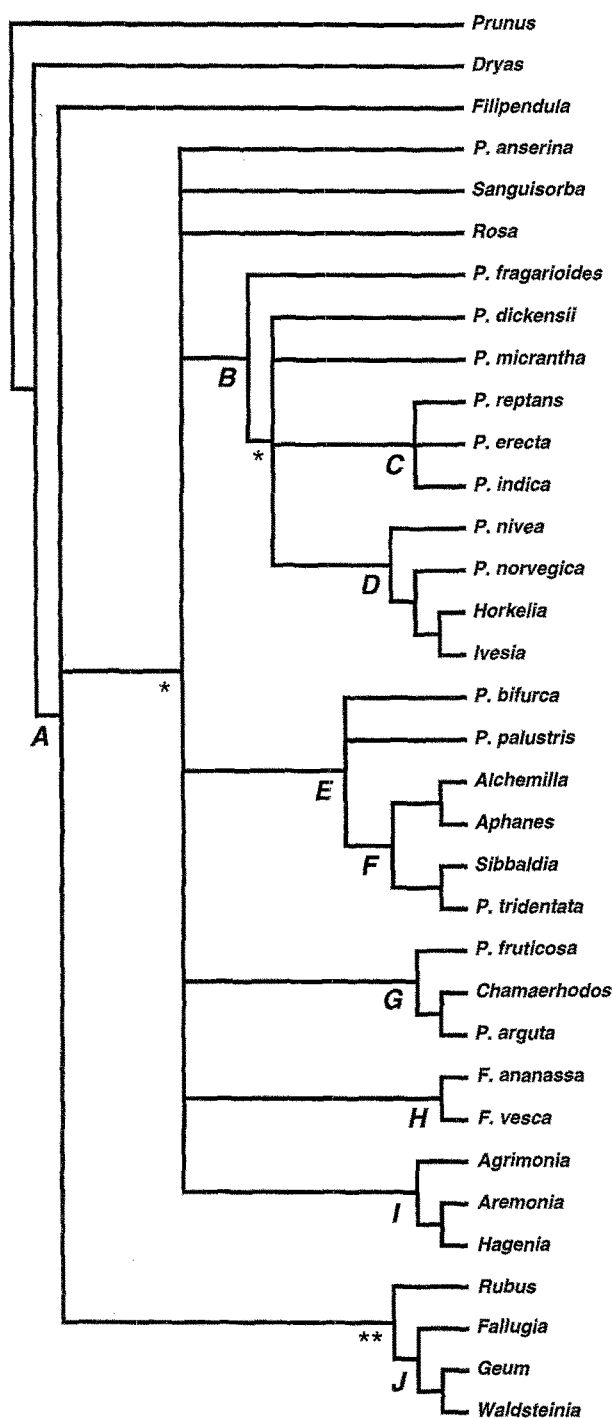


Fig. 2. The tree shown in Fig. 1 collapsed to show only those nodes with a decay index of three or greater, thus indicating an arbitrary level of stability; nodes discussed in the text are indicated by capital letters. The three nodes marked with asterisks have a decay index of two but are included here because they have a decay index of three when * the two gap characters mentioned in Fig. 1 are added, or ** when additional sequences of *Rubus* are added

The clade including everything except *Prunus* and *Dryas* (node A, Fig. 2) has a decay index of nine and delimits subfam. *Rosoideae* sensu stricto. This node is congruent with the result of MORGAN & al. (1994). They reported strong support in *rbcL* for this node ($d > 6$, our re-analysis of their sequences yielded $d = 11$). MORGAN & al. (1994) also discussed several cytological and chemical characters in

support of their re-definition of this subfamily. Two of those, the base chromosome number ($x=7$) and the presence of ellagic acid in the *Rosoideae* sensu stricto, yield additional support for this node.

The clade consisting of *Fallugia*, *Geum*, and *Waldsteinia* also agrees with the *rbcL* result of MORGAN & al. (1994), as does the position of this clade as the sister group of the rest of the genera of *Rosoideae* (see below).

Within the *Rosoideae* several branches are supported by relatively high decay indices (>3) and bootstrap percentages ($>70\%$). Most importantly, *Potentilla* species (sensu WOLF 1908) are spread among these clades and it is evident from this that the genus is not monophyletic. Of the well supported clades just one (node C, Fig. 2) contains only *Potentilla* species. This strongly supported clade ($d=10$) joins *P. reptans* (the type species of *Potentilla*) and *P. erecta* with *P. indica*, upon which the genus *Duchesnea* is based. According to WOLF (1908), this group (*Tormentilleae*) is distinguished by cymose bostryx inflorescences with exceptionally long petioles. This is especially notable in stoloniferous species where the stolons are seemingly unbranched with lateral flowers opposite the leaves, and continuous apical growth. It is uncertain if this character is present in all species, however, and we know of no other morphological synapomorphies for this clade.

All other well supported clades consist of a mix of *Potentilla* species and various segregate genera. It is notable that in several instances *Potentilla* species are seen to be basal and paraphyletic in clades with segregate genera nested within (see Fig. 1). This implies that parts of *Potentilla* constitute “leftovers,” perhaps recognised only on the absence of the apomorphic states of the segregate genera. A prime example of this pattern is provided by the clade including *Horkelia* and *Ivesia* (node B, Fig. 2). These two genera are linked within a well supported clade including *P. norvegica* and *P. nivea* (node D, Fig. 2). The union of *Horkelia* and *Ivesia* is potentially supported by the characteristics that has suggested their removal from *Potentilla*, namely a campanulate calyx tube, the low number of stamens, flattened stamen filaments, and the more distant insertion of the stamens. Variation has been reported in these characters, however (e.g. GREENE 1887, RYDBERG 1898), and it is probable that they will not all appear at this node in an analysis of all species of these genera.

Similarly, *Alchemilla* is very strongly linked with *Aphanes* within the clade including *P. bifurca* and *P. palustris* (node E, Fig. 2). This result supports the view of some authors (SCHULZE-MENZ 1964, DAHLGREN & al. 1981, KALKMAN 1988, MORGAN & al. 1994) that *Alchemilla* is more closely related to *Potentilla* than it is to members of the *Poterieae*, where it has usually been placed. It is noteworthy that *Sibbaldia* and *P. tridentata*, which was treated as the genus *Sibbaldiopsis* by RYDBERG (1898) and others, are also very strongly united by ITS characters. These join the *Alchemilla* branch in our analysis (node F, Fig. 2), but firmer conclusions will require better sampling in this part of the phylogeny. *Chamaerhodos* joins *P. arguta* and *P. fruticosa* (node G, Fig. 2), which is a connection that appears not to have been proposed before. *Potentilla arguta* and *P. fruticosa* share “festooned” stamen arrangement (RYDBERG 1898), and *P. fruticosa* and *Chamaerhodos* share membranaceous stipules. The well supported connection of *Agrimonia*, *Aremonia*, and *Hagenia* (node I, Fig. 2), is discussed below.

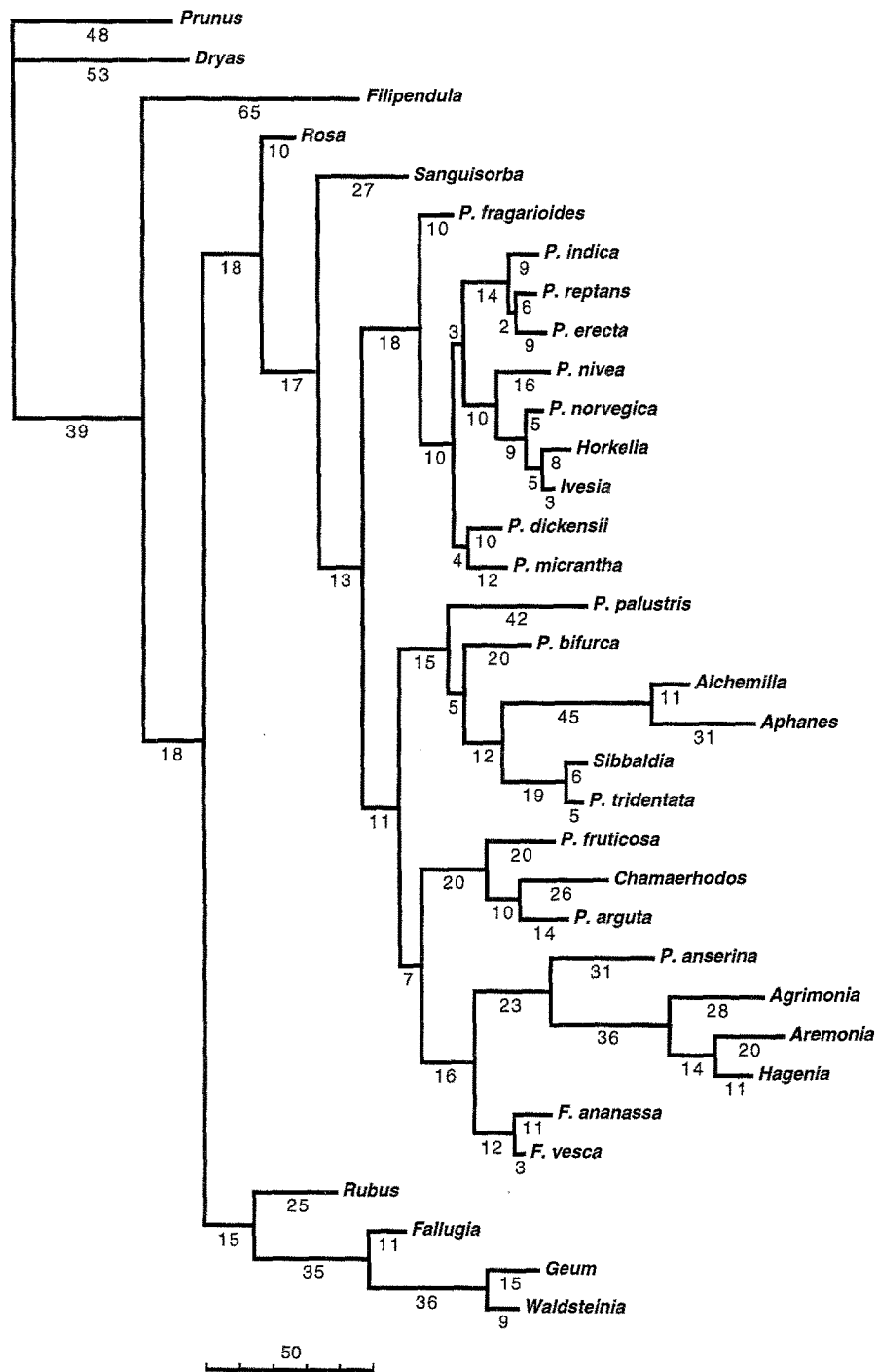


Fig. 3. The tree shown in Fig. 1 with branches drawn proportional in length to the number of character changes occurring under ACCTRAN optimisation in PAUP. The number of changes is noted for each branch; scale bar corresponds to 50 changes

The ITS data clearly indicate that *Potentilla*, as it is usually delimited, cannot be maintained in a monophyletic system of classification. If *Potentilla* sensu WOLF (1908) is forced to be monophyletic, 91 steps are added to the length of the shortest tree. Forcing the monophyly of *Potentilla* as delimited by HUTCHINSON (1964) adds 56 steps.

Discussion

Our results are largely congruent with those presented by MORGAN & al. (1994) based on *rbcL* sequences. Some apparent differences are not well supported in their tree and/or in ours, and, owing to differences in taxon sampling, the cause of these discrepancies is unclear. In our analysis *Dryas* is situated at the base of the tree. This does not contradict MORGAN & al.'s removal of *Cercocarpus* and *Purshia* from the *Rosoideae*, which share several chemical, cytological and morphological characters with *Dryas*. Although our analysis is limited in the sample of taxa from this portion of the *Rosoideae*, the tribe *Dryadeae* in the traditional sense does appear to be polyphyletic. Also in agreement with their analysis, *Filipendula* is seen to be the sister group of the rest of the *Rosoideae*, and *Fallugia*, *Geum*, and *Waldsteinia* form a well supported clade which falls outside of the clade including the rest of the genera. It should be noted, however, that the clade containing the remaining genera is not strongly supported in our tree ($d = 2$, Fig. 1), although the presence of a gap at positions 186–188 also supports this node. If this gap is used as a separate character and analysed with the sequence data it adds one step to the length of the tree and increases the decay index for this node to three (marked by an asterisk above A in Fig. 2). The addition of preliminary morphological data also seems to increase the support for this node ($d = 6$, VRETBLAD & al. 1996). MORGAN & al. (1994) reported solid support for this node and discussed the presence of operculate pollen as a character supporting the “alliance of *Potentilleae*, *Sanguisorbeae*, and *Roseae*”, which corresponds to the node discussed above. However, this character seems to vary within this group (REITSMA 1966).

Another gap, at positions 655–656, joins the species of the node marked by an asterisk above B in Fig. 2 (node P3, Fig. 1 except *P. fragarioides*), and appears to have originated independently in *P. anserina*. This node has relatively low support ($d = 2$) but when the gap is added to the sequence data the decay index increases to three. This gap supports the presence of *Horkelia* and *Ivesia* as well as *Duchesnea* within the P3 clade (see below).

Our tree does differ in some ways from the tree presented by MORGAN & al. (1994). *Rubus* is linked in our tree with the *Fallugia-Geum-Waldsteinia* clade (marked by asterisks below J, Fig. 2), while in their tree *Rubus* is basal to the remainder of the genera. While this is not a strongly supported node in their tree ($d = 1$) or in ours ($d = 2$), support for our result is somewhat strengthened ($d = 3$) when additional *Rubus* ITS sequences are added (L. ALICE & C. CAMPBELL, unpubl. data). In the MORGAN & al. (1994) tree *Agrimonia* is placed outside of a well supported clade (the “*Alchemilla* clade”) comprised of *Alchemilla*, *Fragaria*, and *P. fruticosa*. They reported a decay index for this clade of greater than six, which in our re-analysis of their sequences turned out to be eight. In contrast, in our tree *Agrimonia*, *Aremonia*, and *Hagenia* (the “*Agrimonia* clade”) are positioned within

the clade that corresponds to their *Alchemilla* clade, as the sister group of *P. anserina*. Our *Agrimonia* clade is well supported by nucleotide characters ($d = 10$; 97% bootstrap), and these genera have almost always been classified in the *Poterieae*, with *Sanguisorba*. In fact, if the *Agrimonia* clade is constrained to fall outside of the MORGAN & al. *Alchemilla* clade, it is inevitably linked to *Sanguisorba*. This more traditional position is only one step longer than our shortest tree, whereas other positions of the *Agrimonia* clade yield distinctly longer trees. Applying weighting schemes such as transversion parsimony or transition/transversion bias weighting (see SWOFFORD & OLSEN 1990) yields trees which are identical to our tree except for the position of *Sanguisorba* and the *Agrimonia* clade. In the weighted trees they are found together as a monophyletic group or as a basal (paraphyletic) grade below a clade containing *Fragaria*, *P. anserina*, *P. fruticosa*, *P. arguta* and *Chamaerhodos*. Furthermore, morphological data (VRETBLAD & al. 1996; M. HIBBS & T. ERIKSSON, unpubl.) appear to tip the balance in favour of the traditional position of the *Agrimonia* clade with *Sanguisorba* (supported in preliminary analyses of ITS data in combination with preliminary morphology by a decay index of four). The distribution of one morphological character in particular, the position of the style on the ovary (used as a major character by WOLF 1908), supports the removal of the *Agrimonia* clade to the vicinity of *Sanguisorba*. In view of the *rbcL* results, the effect of morphological characters, and the apparent instability of the *Agrimonia* clade, its position in our ITS tree may be a spurious result, possibly due to limited taxon sampling within the *Poterieae*.

The main conclusion of our analysis is that prior circumscriptions of *Potentilla* are incompatible with our understanding of phylogenetic relationships based on ITS sequences. This is true whether one considers broader circumscriptions (e.g. WOLF 1908) or narrower ones (e.g. HUTCHINSON 1964). The main reason for this incompatibility is the recognition of several segregate genera that now appear to be nested well within *Potentilla*, such as *Duchesnea*, *Horkelia*, and *Ivesia*. In addition, the ITS data strongly indicate homoplasy in some of the characters that have been used to circumscribe taxa in previous classifications. For example, hairy achenes, stolons, and the epicalyx each appears to have evolved and/or been lost several times independently. A particularly striking example of homoplasy is provided by the swollen receptacle (Fig. 4A). The wide separation of *Fragaria* from *Duchesnea* indicates that the “strawberry” (i.e. swollen, red coloured, receptacles) evolved twice, and a similar swollen condition is also found in *P. palustris*. Forcing the monophyly of *Duchesnea* with *Fragaria* as suggested by the classifications of some authors (ANDREWS 1807, HOOKER 1865) yields trees 39 steps longer than our shortest tree.

Leaf form (especially the dissection of the blade) has figured prominently in previous classifications of the *Rosoideae*. Taxa recognised on the basis of pinnate leaf morphology are suspect because this condition is most likely plesiomorphic in the *Rosoideae*. It appears, however, that this character has had an even more complex history than one might have imagined (Fig. 4B). Ternate leaves seem to have evolved at least three times in the *Rosoideae*, digitate leaves (with five or more leaflets) probably evolved independently several times, and pinnate leaves may have re-evolved in the ancestor of *Horkelia* and *Ivesia* (contra SOJÁK 1986: 146). The sampling in this part of the tree, however, is limited in our analysis, and

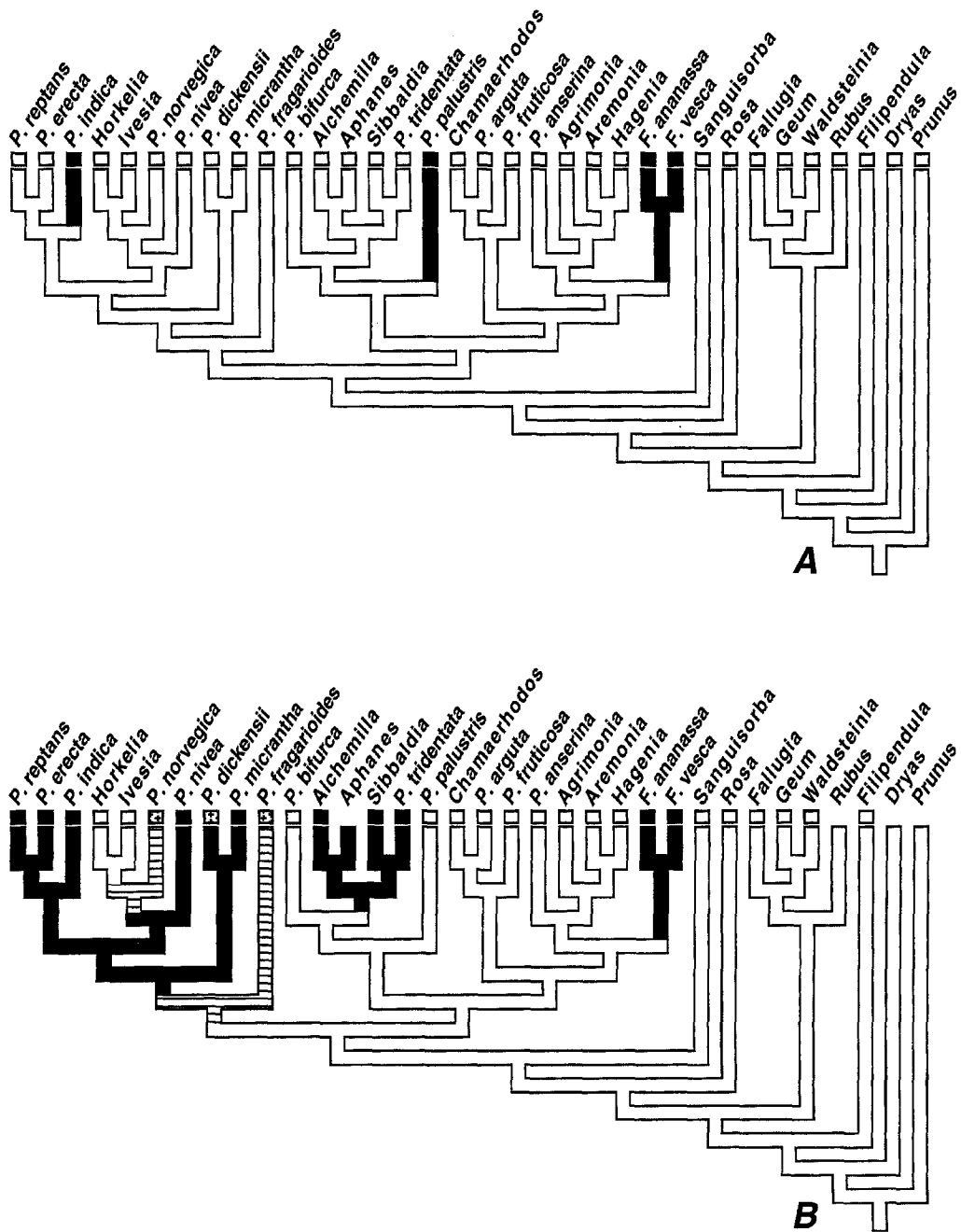


Fig. 4. Parsimony optimisation of two morphological characters on the most parsimonious ITS tree (Fig. 1), drawn using MacClade (MADDISON & MADDISON 1992). *A* Black branches indicate the presence of a distinctly swollen receptacle at maturity. *B* White branches indicate presence of pinnate leaves, black branches indicate digitate leaves (ternate or pentafoliate), striped branches indicate more than one equally parsimonious character optimization (due to polymorphisms in terminal taxa, indicated as stippled boxes)

the addition of other species of *Potentilla* to the analysis, especially those with pinnate leaves, should further clarify the evolution of leaf form. For example, species such as *P. multifida*, *P. pennsylvanica*, or *P. saxosa* may turn out to be related to *Horkelia*, which would imply that their pinnate leaves are homologous. A more detailed analysis of the leaves themselves is also needed, with special attention to instances of polymorphism and the presence of rudimentary leaflets in some species (e.g. *P. fragarioides*). In any case, it is clear from our analysis that several genera containing only pinnate-leafed species are not monophyletic; e.g. *Argentina* sensu FOURREAU (1868), or *Potentilla* sensu ADANSON (1763) and NECKER (1790). Indeed, our tree implies that taxa based solely on leaf form will fail to accurately reflect phylogenetic relationships; e.g. *Quinquefolium* sensu ADANSON (1763), *Fragaria* sensu LINNAEUS (1753), *Tridophyllum* and *Tormentilla* sensu NECKER (1790), or *Dactylophyllum* sensu SPENNER (1829).

It is premature to propose a phylogenetic nomenclature for the *Rosoideae*. Our sample of taxa is still limited, and it will need to be expanded to adequately test the phylogenetic hypotheses put forward here. For example, the monophyly of most of the segregate genera has not been tested, since only one representative has been included (except in the case of *Fragaria*, with two strongly united species; node H, Fig. 2). Even more importantly, additional datasets are needed to test the relationships suggested by the ITS sequences, especially in view of processes that may result in differences among gene and species trees (e.g. see DOYLE 1992, MADDISON 1995, WENDEL & al. 1995, CAMPBELL & al. 1997). The combination of data from different sources may also provide a more robust estimate of relationships (DE QUEIROZ & al. 1995), especially among major lines, than can the ITS alone (BALDWIN & al. 1995). Nevertheless, we are confident that *Potentilla*, in any standard sense, is not monophyletic, and that current nomenclature will have to be changed to reflect this understanding. For this reason we briefly consider several possible solutions.

One strategy would be to attach the name *Potentilla* to the least inclusive node that includes all species previously assigned to *Potentilla*. In our case this is the node/clade labelled P1 in Fig. 1, which corresponds to the entire tribe *Potentilleae* sensu HUTCHINSON (1964). This solution would entail sinking a large number of genera into *Potentilla*: *Fragaria*, *Chamaerhodos*, *Sibbaldiopsis*, *Sibbaldia*, *Aphanes*, *Alchemilla*, *Ivesia*, *Horkelia* and *Duchesnea*, and probably others that have not been included in our analysis (though possibly not *Hagenia*, *Aremonia*, and *Agrimonia*). Under current rules of nomenclature this would require that hundreds of species be renamed in *Fragaria* (which has priority), and many more if the micro-species of *Alchemilla* are also considered. Leaving these practical considerations aside, this solution is questionable on the grounds that this particular node is not strongly supported by ITS sequence characters ($d=1$; 19% bootstrap). There seems to be additional morphological support for this node, however. The presence of lateral (sub-apical to sub-basal) styles used by RYDBERG (1898) and WOLF (1908) supports this node, especially if the *Agrimonia* clade is moved to *Sanguisorba*. These species are also joined by having an epicalyx (in parallel with the *Geum* group), and by having comparatively short stamen filaments.

Another solution would be to select a less inclusive, but well supported, clade that includes the type species of *Potentilla*, *P. reptans*. There are two such clades in

our analysis, labelled P2 and P3 in Fig. 1 (nodes C and B, respectively, in Fig. 2). Clade P2, which includes only three species in our analysis, *P. reptans*, *P. erecta* and *P. indica* (*Duchesnea*), is marked by a decay index of 10 and a bootstrap value of 97%. This circumscription of *Potentilla* would entail the description of quite a number of separate genera for clades containing some species of *Potentilla* (in the traditional sense) and their associated segregate genera. Clade P3 is not as well supported ($d = 4$, 67% bootstrap), but may be the better choice. Attaching the name *Potentilla* to this node would make it necessary to submerge at least *Duchesnea*, *Horkelia*, and *Ivesia*, but most of those species have been placed in *Potentilla* at some time in the past. Furthermore, most *Potentilla* species that fall outside of the P3 clade in our analysis (except *P. bifurca*) have already been assigned to separate genera at some time, so few new names and combinations would be needed. Thus, *Potentilla anserina* (here linked with the *Agrimonia* clade) has been treated as the genus *Argentina*; *P. fruticosa* has been called *Pentaphylloides*; *P. arguta* has sometimes been classified with *Drymocallis*; and *P. palustris* is commonly treated as *Comarum palustre*.

While attaching the name *Potentilla* to node P3 may minimise name changes under the traditional rank-based taxonomic system, we think that a better solution would be to abandon ranks altogether and devise a phylogenetic nomenclature (sensu DE QUEIROZ & GAUTHIER 1994). There are two reasons why a phylogenetic nomenclature is appealing. First, the assignment of taxonomic rank (genus, family, etc.) is arbitrary and the use of such ranks in subsequent evolutionary studies leads to confusion (DOYLE & DONOGHUE 1993). Second, centering the rules of nomenclature on arbitrary decisions about taxonomic rank (as we do now), often requires the changing of names when knowledge of phylogenetic relationships has not changed (DE QUEIROZ & GAUTHIER 1994).

As emphasised above, the issue of name changes is certainly an important consideration in the case of *Potentilla* and other *Rosoideae*. For example, if we chose to attach the generic name *Potentilla* to clade P1, the traditional system requires, under the rank-based rules of priority, that this clade be referred to as *Fragaria*. Furthermore, all species previously referred to *Potentilla*, *Alchemilla*, *Horkelia*, *Ivesia*, etc., must be renamed as species of *Fragaria*. In contrast, in a phylogenetic nomenclature, such name changes would be unnecessary; *Potentilla*, defined phylogenetically, would simply refer to a clade (P1) that happens to include other clades named *Fragaria*, *Alchemilla*, *Horkelia*, *Ivesia*, etc. (assuming these are each monophyletic). *Fragaria*, for example, would be circumscribed as it has been in the past, and hundreds of name changes would be avoided. The consequence of such a taxonomic system is that users would have to adjust to the fact that something they had once learned as a “genus” (e.g. *Fragaria*) might end up nested within another clade that they also had learned as a “genus” (e.g. *Potentilla*). To the extent that this mental adjustment serves to emphasise the arbitrary nature of taxonomic ranks, we view this consequence as a benefit rather than a cost. In any case, the *Potentilla/Rosoideae* case highlights, perhaps more than any other comparable problem in angiosperms, the implications of adopting different taxonomic systems, and we hope that it will help focus attention on the possible advantages of a phylogenetic nomenclature.

Notes added in proof. Recent work on “Flora Nordica” (JONSELL & al., in progress) has unearthed a number of nomenclatural problems in the *Potentilla* group, two of which (T. KARLSSON, pers. comm.) are related to the present paper.

1. The preferred name for *Potentilla fruticosa* if treated as a genus appears to be *Dasiphora* RAF., rather than *Pentaphylloides* DUHAMEL. This is because DUHAMEL in 1755 cited *Potentilla* as a synonym. Hence, the species name should be changed to *Dasiphora fruticosa* (L.) RYDB.
2. The name for *Potentilla bifurca* if treated as a separate genus should be *Schistophyllidium bifurcum* (L.) IKONN.

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