

SYSTEMATICS OF THE GENUS *POTENTILLA* L. — (ROSACEAE JUSS.) — ITS INFRAGENERIC CLASSIFICATION AND EVOLUTIONARY TRENDS

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ABSTRACT

The genera *Argentina* J. Hill, *Pentaphylloides* Duhamel, *nom. illeg.* (= *Dasiphora* Rafin.) and *Duchesnea* Smith are treated as congeneric synonyms of *Potentilla* L. *sens. stricto*; nine subgenera are recognised with keys to their identification and nomenclatural set up. The origin of the genus *Potentilla* L. is discussed and evolutionary trends within the subgenera hypothesized.

INTRODUCTION

Linnaeus (1753, 1754) described the genus *Potentilla* L. (accredited with 22 species), and together with two other related genera, *Comarum* L. (with 1 species) and *Fragaria* L. (with 3 spp.), attributed them to his class "Icosandria Polygynia". Simultaneously, he assigned another related genus *Sibbaldia* L. (with 2 spp.) to his class "Pentandria Pentagynia". These genera are assigned to-day to the family Rosaceae Juss. (1789), subfam. Rosoideae, tribe Potentilleae Juss., subtrib. Potentillinae. Rydberg (1908) and Hutchinson (1964) recognised 16 genera within the tribe Potentilleae, of which species belonging to eight genera, viz. *Argentina* J. Hill, *Chamaerhodos* Ledeb., *Comarum* L., *Duchesnea* J. E. Smith, *Fragaria* L., *Pentaphylloides* Duhamel *nom. illeg. superfl.* (= *Dasiphora* Rafin.), *Potentilla* L. and *Sibbaldia* L., occur in India. While we treat *Sibbaldia* L., as generically distinct (Dikshit and Panigrahi, 1981b), we reduce *Argentina* J. Hill, *Pentaphylloides* Duhamel, and *Duchesnea* J. E. Smith as congeneric with and synonymous to *Potentilla* L., for reasons as discussed hereunder :

ARGENTINA J. Hill vis-a-vis POTENTILLA L.

Rydberg (1906, 1908), followed by Hutchinson (1964) treat *Argentina* J. Hill (as 'Lam.'), lectotypified by the perennial herbaceous species *A. anserina* (L.) Rydberg (*Potentilla anserina* L.) as generically distinct from *Potentilla* L.

The discovery of primitive phenolic constituents (both elagitannins and the trihydroxy phenolics pyricetin and leucodelphinidin) in *Potentilla anserina* L. (Bate-Smith, 1962) led Challice (1973) to visualise *P. anserina* as the most primitive member of the subfam. Rosoideae in terms of chemical characters. Wolf (1908) also considered his *grex* Anserinae Wolf (with *P. anserina*, amongst other taxa) as an old group from its circumpolar distribution extending way back to the Tertiary period. These may justify segregation of *Argentina* J. Hill as a distinct genus based on *A. anserina* (L.) Rydberg.

But in terms of comparative morphological characters such as primitive versus advanced characters, *Potentilla anserina* L., with its herbaceous habit, rod-shaped styles, glabrous achenes coupled with its higher polyploid cytomes (2n=28, 35, 42) and apomictic nature, must be treated as an evolutionary advanced group within the genus *Potentilla* L.

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As a member of the subgenus *Chenopotentilla* (Focke) Juzepczuk, *P. anserina* L., has affinity with *P. leuconota* and *P. coriandrifolia*, amongst others, in its perennial herbaceous habit, imparipinnate leaves, rod-shaped styles and glabrous achenes ; and with *P. indica*, in its perennial herbaceous creeping habit, rod-shaped styles and glabrous achenes.

DASIPHORA Rafin. vis-a-vis POTENTILLA L.

Schwarz (1949), Löve (1954), Hutchinson (1964) and Sojak (1969) considered *Pentaphylloides* Duhamel (1755) as a genus distinct from *Potentilla* L. and made several combinations at species rank. But the genus has to be rejected as a superfluous illegitimate name, in as much as Duhamel (l.c.), (although he referred only to the woody species of *Potentilla* L., under *Pentaphylloides* Duhamel) included *Potentilla* L. (not *Potentilla* L. p.p.) as an obligate synonym. (Art. 7. 11 ; Art. 63. 1, ICBN 1983). In the circumstances, *Dasiphora* Rafin. (1838) typified with *D. riparia* Rafin., nom. illeg., is the next available correct name at generic rank, if one were to consider the genus as distinct from *Potentilla* L. *sens. stricto*.

Schwarz (l.c.), Love (l.c.), Hutchinson (l.c.) and Sojak (l.c.), as stated above, considered the shrubby *Potentilla* species with woolly hairy receptacles and hairy achenes as constituting a separate genus, *Pentaphylloides* Duhamel (= **Dasiphora** Rafin.) on morphological, anatomical, chemical, cytological evidence and on geographical distribution. Löve (l.c.), who follows Schwarz (l.c.), observed that "taxonomically the *Fruticosae* group doubtlessly deserves the rank of a separate genus, distinct from *Potentilla* even in its wider sense...." and that of all sections of *Potentilla*, the most distinct, both morphologically and anatomically, is the group *Fruticosae* which includes perennial shrubs, pinnately leaved with

entire leaflets and hairy fruits...." and that "these shrubs are completely unable to cross with any other section...." This group is isolated from other taxa of *Potentilla* for a long time and the present distribution of the taxa indicates that they are old well-established types. Sojak (1969) supported the idea of treating the shrubby species of *Potentilla* as a distinct genus, because they possess alternate cotyledonary leaves, the primary leaves are never rosette and the stipules are ochreate, whereas, in other species of *Potentilla* L., they first form rosettes and the stipules are not ochreate.

However, the genus *Dasiphora* Rafin., shares its (i) shrubby habit and absence of rosette leaves with *Potentilla palustre* (L.) Scop., *P. salesoviana* Stephan, *P. sericophylla* Parker and *P. xylorhiza* Boiss. & Hohen., but the leaflets of *P. palustre* and *P. salesoviana* are serrate ; (ii) its entire leaflets with *P. biflora* and *P. armerioides* ; (iii) its hairy achenes with *P. salesoviana*, *P. sericophylla*, *P. cuneifolia*, *P. eriocarpa*, *P. curveseta*, *P. pteropoda* and *P. collettiana* and in *P. biflora*, *P. palustre* and *P. armerioides* the achenes are glabrous ; (iv) its basic chromosome number $x=7$ ($2n=14, 28$) with all species of *Potentilla* L., studied to-date.

The geographical distribution of various species of *Dasiphora* Rafin., is no more discontinuous than some other species of *Potentilla*, such as *P. biflora* L., which occurs in Europe, Asia and North America.

We, therefore, opt here to follow Wolf (1908) in treating the *Fruticosae* *Potentillas* as belonging to the genus *Potentilla* L., but segregate the species involved into two subgenera, viz. subg. *Dasiphora* and subg. *Trichothalamus*.

DUCHESNEA J. E. Smith vis-a-vis POTENTILLA L.

Wolf (1908), Bate-Smith (1961), Kalkman (1968) and Acharya Goswami (1972) adduce

morphological, plant-chemical and genetical evidence in support of reduction of *Duchesnea* J. E. Smith (1811) as congeneric with *Potentilla* L. (1753), because :

(i) The morphological difference between the two genera concerns only the character of the torus : torus subcarnose and more or less edible—*Duchesnea* ; torus not very much enlarged and not edible—*Potentilla*. However, such a difference in the dimension of the torus attained only after anthesis in *Duchesnea*, is merely quantitative in nature.

(ii) Chromatographically, Bate-Smith (1961) grouped *Duchesnea indica* with many other species of *Potentilla* L., because he did not find any consistent differences between the two genera.

(iii) Genetically, *Potentilla* and *Duchesnea* belong to one comparium (Wolf, 1908 ; Acharya Goswami, 1972) ; when *Duchesnea indica* (male) was artificially crossed with *Potentilla reptans* (female), the F_1 plants, although remained infertile and reproduced only vegetatively, had very luxurious growth and flowered extensively.

In view of such evidence, we treat *Duchesnea* Smith as a subgenus of *Potentilla* L.

SIBBALDIA L. vis-a-vis POTENTILLA L.

Linnaeus (1753, 1754), Wolf (1908), Rydberg (1908), Juzepczuk (1941) and Hutchinson (1964) treat *Sibbaldia* L., as generically distinct from *Potentilla* L. and differentiate them on the number of stamens : 4, 5 or 10 stamens—*Sibbaldia*, whereas 20-30 stamens—*Potentilla* L. Except the number of stamens, no other consistent difference can be discerned between the two genera. However, *Sibbaldia* L., is only herbaceous, sexually-reproducing and shows no enlargement of torus after anthesis. In *Potentilla*, some species are fruticose, are obligate apomicts and exhibit torus enlargement after anthesis.

The Indian species of *Potentilla* sensu

J. D. Hooker (1878) which conform with all the above characters are segregated and treated as *Sibbaldia* L. (Dixit and Panigrahi, 1981b).

INFRAGENERIC CLASSIFICATION OF *POTENTILLA* L. SENSU STRICTO

After a review of literature and critical study of specimens we have formulated the following classification of *Potentilla* L. sens. stricto, which recognises 9 subgenera and a number of sections to include the 80 Indian taxa dealt with within the systematic account of the genus :

1. Subg. *DASIPHORA* (Rafin.) Panigr. et Dikshit, comb. nov., et stat. nov. *Dasiphora* Rafin. in Aut. Bot. : 167. 1838 ; Rydberg in N. Amer. Fl. 22(4). 366. 1908 ; Juzepczuk, in Komarov's Fl. URSS 10 : 52. 1941 (Eng. edn. : 68. 1971). Lectotype sp. : *Dasiphora riparia* Rafin. nom. illeg. [selected by Rydberg, 1908 ; = ***Potentilla fruticosa*** L. ; = *Dasiphora fruticosa* (L.) Rydberg].
2. Subg. *TRICHOThALAMUS* (Lehm.) Reich., Consp. Regn. Veget. : 167. 1828. *Trichothalamus* [Spreng. Anleit. ed. 2, 2 : 864. 1818] Lehm. in Nova Acta Acad. Leop.-Carol. 10 : 585. 1821. Type species : *Trichothalamus lignosus* (Willd. ex Schlecht.) Lehm. (= *Potentilla lignosa* Willd. ex Schlecht.).
Potentilla L. subg. *Lasiocarpa* Dixit et Panigrahi in Journ. Sc. Club 33-34 : 39. 1983. Type species : *P. salesoviana* Stephan.
3. Subg. *FRAGARIASTRUM* (Heist. ex Fabr.) Reich, op. cit. : 167. 1828 ; Ball et al., Fl. Europ. 2 : 45. 1968.
Fragariastrum Heist. ex Fabr., Enum. Method. Pl. 64. 1759. Lectotype species : *F. sterilis* (L.) Schur. *Fragaria sterilis* L. (selected by Panigrahi and Dikshit, Taxon 35 : 350. 1986).

Sect. **Tridentatae** Dikshit et Panigrahi in J. Orissa Bot. Soc. 3(1) : 13. 1981.

Potentilla L. sect. *Trichocarpae* Wolf subsect. *Nematostylae* Wolf grex *Tridentatae* Wolf, Bibl. Bot. Heft 71, Band 16 : 46, 77. 1908, *nom. invalid.* (Art. 4, Art. 5. 1, ICBN, 1983). LT : *Potentilla tridentata* Sol. (selected here).

Sect. **Eriocarpae** Juzepczuk, in Komarov, Fl. URSS 10 : 88. 1941 (Eng. ed. : 1971) ; Grossan. Fl. Kawkass 5 : 68. 1952.

Potentilla L. Sect. *Trichocarpae* Wolf subsect. *Nematostylae* Wolf ser. *Suffruticulosae* Wolf grex *Eriocarpae* Wolf, *op. cit.* : 46, 79. 1908, *nom. invalid.* (Art. 4. 1 ; Art. 5. 1, ICBN, 1983).

Lectotype species : *Potentilla eriocarpa* Wall. ex Lehm. (selected here).

Sect. **Curvisetae** Schiman-Czeika in K. H. Rechinger, Fl. Iranica 66 : 87. 1969.

Potentilla L. sect. *Trichocarpae* Wolf subsect. *Nematostylae* Wolf ser. *Herbaceae* Wolf grex *Curvisetae* Wolf, *op. cit.* : 47. 1908, *nom. invalid.* (Art. 4.1 ; Art. 5.1, ICBN, 1983).

Lectotype species : *Potentilla curviseta* J. D. Hooker (selected here).

Subg. **SCHISTOPHYLLIDIUM** Juzepczuk, *op. cit.* : 81. (1941) (Engl. ed. : 61. 1971) Ball *et al.*, *op. cit.* : 39. 1968.

Lectotype species : *Potentilla bifurca* L. (selected here).

Subg. **MICROPOGON** (Bunge) Juzepczuk, *op. cit.* : 84. 1941 (Eng. ed. : 64. 1971).

Micropogon Bunge, Suppl. Fl. Alt. : 40. 1836.

Type species : *Potentilla biflora* Willd. ex Schlecht.

Potentilla L. sect. *Trichocarpae* Wolf subsect. *Nematostylae* Wolf grex *Biflorae* (Rydberg) Wolf, *op. cit.* : 46, 70. 1908, p. p., *comb. invalid.* (Art. 4.1 ; Art. 5.1, ICBN, 1983).

Subg. **CLOSTEROSTYLIS** (Torrey & Gray) Juzepczuk, *op. cit.* : 93. 1941 (Engl. ed. : 71. 1971).

Potentilla L. sect. *Closterostylis* Torrey & Gray, *op. cit.* : 445. 1840 ; Janchen, Cat. Fl. Austr. Tiel. 1 Pteridophytes and Anthrophytes 178. 1957.

Lectotype species : *Potentilla arguta* Pursch (selected here).

Subg. **CHENOPOTENTILLA** (Focke) Juzepczuk, *op. cit.* : 164. 1941 (Engl. ed. 220. 1971).

Potentilla L. sect. *Chenopotentilla* Focke, *op. cit.* : 415. 1899.

Type species : *Potentilla anserina* L.

Sect. **Chenopotentilla** Focke Type Species : *Potentilla anserina* L.

Argentina J. Hill, *op. cit.* : 6. 1756 ; Lamarck, *op. cit.* : 118. 1778, p.p. ; Hutchinson, *op. cit.* : 198. 1964.

Lectotype species : *Argentina anserina* (L.) Rydberg ($\equiv$ *Potentilla anserina* L.).

Potentilla L. sect. *Gymnocarpae* Wolf subsect. *Leptostylae* Wolf grex *Anserinae* (Lehm.) Wolf, *op. cit.* : 52, 667. 1908, p.p.

Potentilla L. sect. *Herbaceae* Lehm. ser. *Anserinae* Lehm. *op. cit.* : 8, 188. 1856.

Potentilla L. sect. *Anserinae* (Lehm.) Grossh. *op. cit.* : 82. 1952.

Sect. **Leuconotae** Dikshit & Panigrahi, J. Orissa Bot. Soc. 3(1) : 33. 1981.

Type species : *Potentilla leuconota* D. Don.

Potentilla L. sect. *Gymnocarpae* Wolf subsect. *Nematostylae* Wolf grex *Anserinae* Wolf, *op. cit.* : 52, 667. 1908, p.p., excl. *P. anserina* L. *nom. invalid* Art 4.1, 5.1, ICBN 1983.

Sect. **Dumosae** Sojak in Preslia 41 : 349. 1969.

Type species : *Potentilla dumosa* (Franch.) Hand.-Mazz.

Potentilla L. sect. *Gymnocarpae* Wolf subsect. *Conostylae* Wolf ser. *Orthotrichae*

Wolf grex *Tanacetifoliae* (Lehm.) Wolf, *op. cit.* : 670, 743. 1908, p.p.

Subg. *POTENTILLA* Syme in Smith & Sowerby, English Botany, ed. 3, 3 : 143. 1864. Lectotype species : *Potentilla reptans* L. (selected by Rydberg, 1908).

Potentilla L. sect. *Gymnocarpae* Wolf subsect. *Gomphostylae* Wolf *op. cit.* : 671, 786. 1904, et *op. cit.* : 52, 641. 1908. *Potentilla* L. subg. *Dynamidium* Juz., *op. cit.* : 194. 1941 (Engl. ed. : 144. 1971).

Sect. **Potentilla** Lectotype sp. : *Potentilla reptans* L. *Potentilla* L. sect. *Tormentilla* Focke, *op. cit.* : 415. 1889 ; Schiman-Czeika, *op. cit.* : 111. 1969.

Sect. **Duchesneae** (J. E. Smith) Dikshit et Panigrahi, comb. nov.

Duchesnea J. E. Smith in Trans. Linn. Soc. London 10 : 372. 1811 ; Valentine in Tutin *et al.*, Fl. Europ. 2 : 36. 1968.

Type species : *Duchesnea fragiformis* J. E. Smith, *nom. illegit.* [= *Potentilla indica* (Andrews) Wolf].

Fragaria sensu J. D. Hooker, *op. cit.* : 343. 1878, p.p., incl. *F. indica* Andrews, non L. (1753).

Potentilla L. sect. *Gymnocarpae* Wolf subsect. *Gomphostylae* Wolf grex *Tormentillae* (Lehm.) Wolf, *op. cit.* : 52, 641. 1908, p.p. incl. *Potentilla indica* (Andrews) Wolf.

Sect. **Aureae** Juzepczuk, *op. cit.* : 197. 1941 (Eng. ed. : 147) [as '(Lehm.) Juz.'].
Lectotype species : *Potentilla aurea* L. (selected here).

Potentilla L. sect. *Herbaceae* Lehm, ser. *Digitatae* Lehm. tribe *Aureae* Lehm., *op. cit.* : 6 : 112. 1856, p.p., *nom. invalid.* (Art. 4.1 ; Art. 5.1, ICBN, 1983).

Potentilla L. sect. *Gymnocarpae* Wolf subsect. *Gomphostylae* Wolf grex *Aureae* Wolf, *op. cit.* : 787. 1904, *op. cit.* : 523. 1908. *nom. invalid.* (Art. 4.1 ; Art. 5.1, ICBN, 1983).

Subg. *HYPARGYRIUM* Juzepczuk, *op. cit.* : 101. 1941 (Engl. ed. : 76. 1971).

Lectotype species : *Potentilla argentea* L. (selected here).

Potentilla L. sect. *Fragariastrum* Ser. ex DC. Prodr. 2 : 583. 1825 p.p. incl. *P. ieschenaultiana* Ser.

Hypargyrium Fourr. Ann. Soc. Linn. Lyon 2, 16 : 371. 1888, *nom. invalid.* (Art. 36.1, ICBN, 1983).

Sect. **Multifidae** Juzepczuk, *op. cit.* : 113. 1941 (Engl. ed. : 85. 1971) ; Schiman-Czeika, *op. cit.* : 68. 1969, [as '(Rydberg)'].

Lectotype species : *Potentilla multifida* L. (selected here).

Potentilla L. group *Multifidae* Rydberg in Bull. Torr. Bot. Club 23 : 262. 1896, *nom. invalid.* (Art. 4.1, Art. 5.1).

Sect. **Haematochroae** Schiman-Czeika, *op. cit.* : 91. 1969.

Lectotype species : *Potentilla atrisanguinea* Lodd, (selected here).

Potentilla L. sect. *Gymnocarpae* Wolf subsect. *Conostylae* Wolf ser. *Eriotrichae* Wolf grex *Haematochroae* Wolf, *op. cit.* : 49, 219. 1908, *nom. invalid.* (Art. 4.1 ; Art. 5.1, ICBN, 1983).

Sect. **Hypargyrium**

Potentilla L. sect. *Herbaceae* Lehm. ser. *Digitatae* Lehm. tribe *Multiflorae* Lehm. subtribe *Argenteae* Lehm., *op. cit.* : 6, 93. 1856 *nom. invalid.* (Art. 4.1 ; Art. 5.1, ICBN, 1983).

Potentilla : sect. *Gymnocarpae* Wolf subsect. *Conostylae* Wolf ser. *Eriotrichae* Wolf grex *Argenteae* Wolf, *op. cit.* : 49, 252. 1908, *nom. invalid.* (Art. 4.1 ; Art. 5.1).

Potentilla L. subg. *Hypargyrium* Juz. sect. *Argenteae* Juz., *op. cit.* : 144. 1941 (Engl. ed. : 106. 1971) ; Schiman-Czeika, *op. cit.* : 92. 1969.

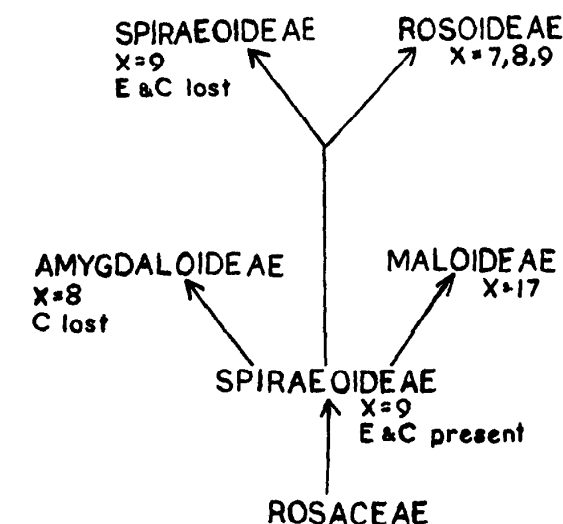
Sect. **Tanacetifoliae** Juzepczuk, *op. cit.* : 152. 1941 (Engl. ed. : 113. 1971) ;

Schiman-Czeika *op. cit.* : 94. 1969 [as '(Lehm.) Juz.].

Lectotype species : *Potentilla tenacetifoliae* Lindl. ex Lehm. (selected here).

Potentilla L. sect. *Herbaceae* Lehm. ser. *Pinnatae* Lehm. tribe *Tenacetifoliae* Lehm., *op. cit.* : 55. 1856, p.p., *nom. invalid.* (Art. 4.1).

Potentilla L. sect. *Gymnocarpae* Wolf subsect. *Conostylae* Wolf ser. *Orthotrichae* Wolf grex *Tenacetifoliae* Wolf, *op. cit.* : 670, 743. 1908, *nom. invalid.* (Art. 4.1 ; Art. 5.1, ICBN, 1983).



E=Ellagitannins

C= Flavone-c-glycosides

Hypothetical Scheme-1.

Sect. **Chrysanthae** Juzepczuk, *op. cit.* : 180. 1941 (Eng. ed. : 134. 1971) ; Schiman-Czeika, *op. cit.* : 108. 1969.

Lectotype species : *Potentilla chrysantha* Trevir ex Ledeb. (selected here).

Potentilla L. sect. *Herbaceae* Lehm. ser. *Digitatae* Lehm. tribe *Multiflorae* Lehm. subtribe *Chrysanthae* Lehm., *op. cit.* : 5. 75. 1856 *nom. invalid.* (Art. 4.1 ; Art. 5.1, ICBN, 1983).

Potentilla L. sect. *Gymnocarpae* Wolf subsect. *Conostylae* Wolf ser. *Orthotrichae* Wolf grex *Chrysanthae* Wolf, *op. cit.* : 51. 455. 1908, *nom. invalid.* (Art. 4.1 ; Art. 5.1).

Sect. **Rectae** Juzepczuk, *op. cit.* : 160. 1941 (Eng. ed. : 119. 1971) ; Schiman-Czeika, *op. cit.* : 94. 1969 [as '(Lehm.) Juz.].

Lectotype species : *Potentilla recta* L. (selected here).

Potentilla L. sect. *Herbaceae* Lehm. ser. *Digitatae* Lehm. tribe *Multiflorae* Lehm. subtribe *Rectae* Lehm., *op. cit.* : 5, 81. 1856, *nom. invalid.* (Art. 4.1 ; Art. 5.1, ICBN, 1983).

Potentilla L. sect. *Gymnocarpae* Wolf subsect. *Conostylae* Wolf ser. *Orthotrichae* Wolf grex *Rectae* Wolf, *op. cit.* : 50, 302. 1908, *nom. invalid.* (Art. 4.1 ; Art. 5.1).

Sect. **Persicae** Juzepczuk, *op. cit.* : 175. 1941 (Eng. ed. : 130. 1971) ; Grossh., *op. cit.* : 76. 1952 [as '(Wolf) Juz.].

Lectotype species : *Potentilla persica* Regel & Schmalh. (selected here).

Potentilla L. sect. *Gymnocarpae* Wolf subsect. *Conostylae* Wolf ser. *Orthotrichae* Wolf grex *Persicae* Wolf, *op. cit.* : 671, 786. 1904, et *op. cit.* : 51. 1908, *nom. invalid.* (Art. 4.1 ; Art. 5.1).

Sect. **Rivales** Juzepczuk, *op. cit.* : 165. 1941 (Engl. ed. : 123. 1971) ; Schiman-Czeika, *op. cit.* : 99. 1969 [as '(Wolf) Juz.].

Lectotype species : *Potentilla rivalis* L. (selected here).

Potentilla L. sect. *Gymnocarpae* Wolf ser. *Orthotrichae* Wolf grex *Rivales* Wolf, *op. cit.* : 670, 744. 1904, et *op. cit.* : 50, 384. 1908 *nom. invalid.* (Art. 4.1 ; Art. 5.1, ICBN, 1983).

Potentilla L. sect. *Herbaceae* Lehm. tribe *Multiflorae* Lehm. subtribe *Rectae* Lehm. *op. cit.* : 5, 81. 1856, p.p., *nom. invalid.* (Art. 4.1 ; Art. 5.1).

ECONOMIC UTILISATION

Economically, *Potentilla* are not very important to human beings, although according to the old herbals of the 16th-18th century by Fuchs, Bauhin, Book and Tabernaemontanus, the healing powers of

KEY TO THE NINE SUBGENERA OF *POTENTILLA* L.

- 1a. Receptacle after anthesis becoming densely villous ; achenes clothed with and concealed by long woolly hairs
 - 2a. Herbs ; bark not peeling off ; caudex aerial, with a rosette of radical leaves ; leaves chiefly radical, ternate ; styles lateral or subterminal .. *Fragariastrum* (6 taxa)
 - 2b. Shrubs ; bark peeling off ; caudex subterranean ; without a rosette of radical leaves ; leaves chiefly cauline, imparipinnate (except *Potentilla rigida* with ternate leaves) ; styles subbasal or lateral
 - 3a. Leaflets entire ; flowers androdynamic or gynodynamic ; petals yellow (white in same Chinese taxa) ; styles claviform, as long as ovary .. *Dasiphora* (6 taxa)
 - 3b. Leaflets finely serrulated or dented ; flowers bisexual ; petals white ; styles filiform, two (three-) four times longer than ovary .. *Trichothalamus* (3 taxa)
- 1b. Receptacles after anthesis becoming glabrous-shortly tomentose ; achenes glabrous
 - 4a. Flowers androdynamic or gynodynamic ; styles claviform .. *Schistophyllidium* (1 taxa)
 - 4b. Flowers bisexual ; styles otherwise, not claviform
 - 5a. Leaflets entire ; styles filiform (2-3 mm long) .. *Micropogon* (2 taxa)
 - 5b. Leaflets toothed/serrulated/pinnately partite ; styles otherwise, not filiform
 - 6a. Styles spindle- or rod-shaped
 - 7a. Leaves interruptedly pinnate with one or more pairs of reduced leaflets, styles spindle-form .. *Closterostylis* (3 taxa)
 - 7b. Leaves regularly pinnate without reduced leaflets (except in *P. anserina* and often in *P. leuconota*) ; styles rod-shaped .. *Chenopotentilla* (13 taxa)
 - 6b. Styles claviculiform or coniform
 - 8a. Styles claviculiform .. *Potentilla* (7 taxa)
 - 8b. Styles coniform .. *Hypargyrium* (39 taxa)

Potentilla for many human ailments were eulogised. However, *P. reptans* sometimes is applied as astringent in domestic medicines and for tanning of hide and to impart red colour for the woollen fabrics. Thick roots of *P. anserina* serve as the food stuff to poor inhabitants of Northern region. In an earlier communication (Dixit & Panigrahi, 1980) the economic utilisation of 12 species of *Potentilla* occurring in India has been exhaustively dealt with.

Apomixis and its impact on the delimitation of taxonomic categories in Potentilla

Darlington (1939) considers apomixis as an escape from sterility, because it permits perpetuation of well-adapted but sexually sterile phenotypes, resulting in a large population of genetically similar individuals for colonization. Apomixis has been reported in about 300 genera, including *Potentilla* L., belonging to about 80 families of angiosperms (Khokhlov, 1970). The highest rate of occurrence of apomixis is in the phylogenetically young and progressive taxonomic groups occupying widespread

geographical areas and showing a tendency for further spread, often occupying larger areas than their sexual relatives. Cosmopolitanism with significant intraspecific polymorphism, without much evidence for ecological localisation (*viz.* ecotypes, ecads etc.) are characteristic of larger genera of apomictic nature. Apomicts show an absence of stability in chromosome numbers : polyploid and aneuploid series are almost the rule. Yet, a relative constancy in the morphology of the apomictic progeny and even of mutants in the succeeding generations, is ensured by the absence of meiosis and fertilisation, aided by the universal presence of agamospermy and vegetative apomixis, 'While this is true for obligate apomicts, as in *Alchemilla* L., in which ca. 1000 'microspecies' are recognised (Panigrahi & Purohit, 1983), taxonomic delineation in facultatively-apomictic genera, such as *Potentilla* L. poses problems of a different, more challenging, nature. Here, in the progeny of facultatively apomictic parents, biotypes resulting from normal sexual processes, with an introgression of characters of both the parents occur simul-

taneously, with parthenogenetically produced 'uniparental' progeny, thus blurring up the originally phenotypically distinguishable parents. Recognition of 'microspecies' a taxonomic category amongst obligate apomicts or subspecies or varieties which are taxonomic entities recognised in the sexually-breeding taxa, is rather difficult, among facultatively apomictic taxa. However, apomixis is not found in relics which are at the point of extinction or represent evolutionary blind-ends.

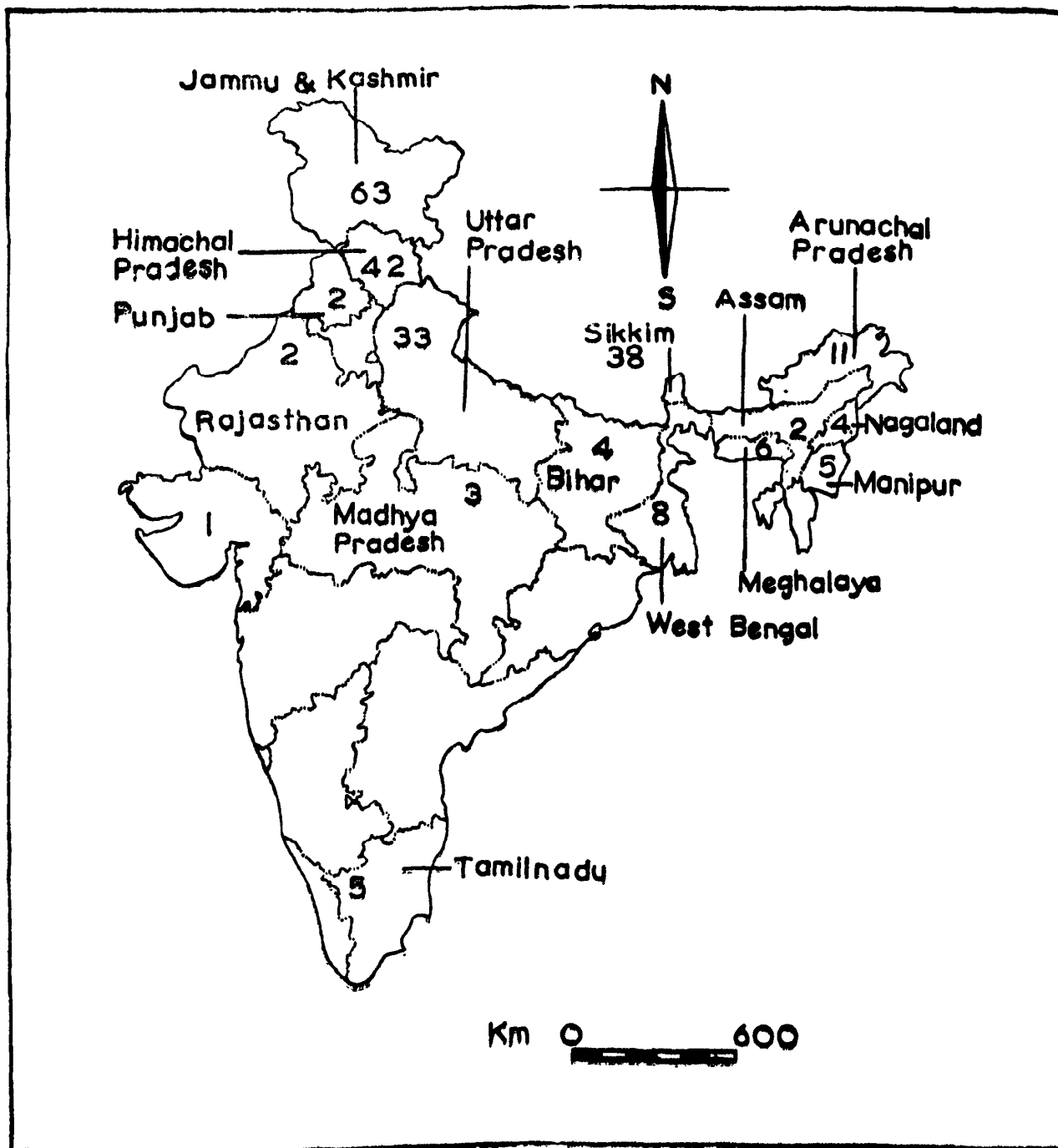
Judged in this context, amongst the nine subgenera recognised in *Potentilla*, four subgenera, viz. *Dasiphora* (6 taxa), *Schistophyllidium* (1 sp.), *Trichothalamus* (3 taxa) and *Fragariastrum* (6 taxa) and even *Micropogon* (2 sp.) and *Closterostylis* (3 taxa), which represent the basal stocks or evolutionarily blind-ends or occupy mid-points in the evolutionary grades, sharing one or more primitive traits, are strictly sexually-breeding and no evidence of apomixis in any species of the six subgenera is yet available.

Even amongst the remaining three subgenera, comprising 59 (80-21) taxa apomixis is recorded only in 10 species: subg. *Potentilla* (*P. reptans* L. with $2n=28$), subg. *Chenopotentilla* (*P. anserina* L. with $2n=28$, 35, 42) and subg. *Hypargyrium* with the remaining eight apomictic taxa, viz. *P. neglecta* Baug. ($2n=42$), *P. argyrophylla* Lehm. ($2n=14$, 56, 63), *P. atrisanguinea* Lodd. ($2n=56$, 63, 84), *P. nepalensis* W. J. Hooker ($2n=42$) and *P. nivea* L. ($2n=56$, 70), *P. multifida* L. ($2n=28$, 42), *P. recta* L. ($2n=28$, 42) and *P. supina* L. ($2n=28$). These taxa exhibit cuploid and aneuploid series based on $x=7$ and are usually considered as facultatively apomictic with pseudogamous reproduction. *P. neglecta* usually an obligate apomict with $2n=42$, produces in Europe progeny with $2n=35$ which are morphologically indistinguishable from the hexaploid parents. On the other hand,

within *P. recta* L., a collective species, four segregate species are recognised in Europe (Ball *et al.*, 1968). Of the Indian apomicts, *P. reptans* is represented by an additional variety var. *microphylla*, *P. argyrophylla* by an additional var. *leucochroa*, *P. multifida* by two additional varieties var. *glabrata* and var. *minor* and *P. supina* by an additional subsp. *paradoxa*. Since *P. neglecta*, *P. recta* and *P. nivea* are represented by less than 5 specimens in Indian herbaria, it is not possible to comment on the degree of variations amongst their Indian populations. *P. atrisanguinea*, and *P. nepalensis*, each with a number of cytotypes, represented by a large number of specimens in CAL, DD, BSD, do not contribute distinctive phenotypes sufficient to recognise any additional variety in any of them. *P. multifida*, on the other hand, with $2n=28$, 42, presents distinctive populations not sufficiently geographically isolated differing from each other in the degree of pubescence of the upper surfaces of leaflets and in the cutting of the leaflets. By and large, then, the Indian apomicts do not pose a challenge to orthodox taxonomists, but conform with the theoretical expectations that, despite genotypic variations, the facultative apomicts do not throw up distinctive phenotypes sufficient to accord them taxonomic status.

Of the sexually-breeding species, *P. arbuscula* and *P. microphylla*, etc. produce distinctive morphological types, in different ecological habitats, to enable one to recognise four-five distinct varieties, not subspecies, because of the geographical overlapping between the distinct phenotypic populations. Thus, the original apprehension that facultative apomixis in *Potentilla* would blur taxonomic judgements proves false at least amongst the Indian taxa.

Distribution : The distributional range of *Potentilla* L. lies mainly between the Tropic of Cancer and the everlasting ice of the Polar



region in the Northern Hemisphere, although the cold temperate high mountain peaks in the Southern Hemisphere harbour some species. The great Himalayan ranges in the north, serve as the gene sanctuary for the wealth of *Potentillas* in India. Airy Shaw (1973) assigns 500 species to *Potentilla* L., 20 species to *Sibbaldia* L. and one species to *Duchesnea* Smith, in the world flora. J. D. Hooker (1878) reported only 56 taxa (32 spe-

cies with 24 additional varieties) of *Potentilla* L. and seven species to *Potentilla* L. sect. *Sibbaldia* (L.) J. D. Hooker. A critical study of the tribe *Potentilleae* Jussieu in India has led us to delimit the occurrence of 80 taxa of *Potentilla sensu stricto* (Map) and 14 taxa (12 species and 2 varieties) of *Sibbaldia* L. (Dixit & Panigrahi, 1981b) with Indian distribution. Of the 80 taxa of *Potentilla*, 54 taxa are indigenous/endemic

Table 1
Potentilla Taxa Indigenous/Endemic to the Himalayas and to South India

Serial Number	Names of the taxa	I N D I A																
		Afghanistan	Pakistan	Jammu & Kashmir	Himachal Pradesh	Uttar Pradesh	Tamil Nadu	Bihar	West Bengal	Sikkim	Meghalaya	Arunachal Pradesh	Naga Land	Manipur	Nepal	Bhutan	Burma	China
Subg. DASIPHORA																		
1.	<i>Potentilla rigida</i>			+	+	+			+	+		+			+	+		+
2.	<i>P. arbuscula</i> var. <i>arbuscula</i>			+	+				+	+					+	+		+
3.*	„ var. <i>glabrata</i>									+	+							
4.	„ var. <i>pumila</i>			+	+					+					+	+		+
5.	„ var. <i>ochreate</i>				+	+									+			+
Subg. TRICHOTHALAMUS																		
6.	<i>P. sericophylla</i> var. <i>sericophylla</i>		+	+	+													
7.*	„ var. <i>longifolia</i>			+														+
Subg. FRAGARIASTRUM																		
Sect. TRIDENTATAE																		
8.	<i>P. cuneifolia</i>		+	+	+	+				+		+			+	+	+	+
Sect. ERIOCARPAE																		
9.	<i>P. eriocarpa</i> var. <i>eriocarpa</i>			+	+	+				+					+	+		+
10.	„ var. <i>tsarongensis</i>									+					+			+
Sect. CURVISETAE																		
11.	<i>P. curviseta</i>		+	+	+													
12.	<i>P. colletiana</i>	+	+	+														
13.	<i>P. pteropoda</i>		+	+														
Subg. MICROPOGON																		
14.	<i>P. armerioides</i>									+					+			+

Table 1 (Contd.)

Serial Number	Names of the taxa																	
		I	N	D	I	A												
		Afghanistan	Pakistan	Jammu & Kashmir	Himachal Pradesh	Uttar Pradesh	Tamil Nadu	Bihar	West Bengal	Sikkim	Meghalaya	Arunachal Pradesh	Naga Land	Manipur	Nepal	Bhutan	Burma	China
Subg. CLOSTEROSTYLIS																		
15.	<i>P. lineata</i> var. <i>lineata</i>			+	+	+			+	+	+	+	+	+	+	+	+	+
16.*	„ var. <i>intermedia</i>			+	+	+			+	+	+	+	+	+	+	+	+	+
Subg. CHENOPOTENTILLA																		
Sect. LEUCONOTAE																		
17.	<i>P. leuconota</i>			+	+	+			+	+					+	+	+	+
18.	<i>P. peduncularis</i> var. <i>peduncularis</i>									+		+			+	+	+	+
19.*	„ var. <i>clarkei</i>									+								
20.*	„ var. <i>obscura</i>					+												
21.	<i>P. microphylla</i> var. <i>microphylla</i>				+	+				+					+	+	+	
22.	„ var. <i>achilleifolia</i>					+				+					+			
23.	„ var. <i>glabriuscula</i>					+				+					+		+	
24.	„ var. <i>latifolia</i>			+	+	+				+					+			
25.	„ var. <i>latiloba</i>			+	+	+				+					+		+	
26.	<i>P. tatsienluensis</i>					+											+	
Sect. DUMOSAE																		
27.	<i>P. coriandrifolia</i>					+				+					+	+		+
28.	<i>P. hypargyrea</i>									+								+
Subg. POTENTILLA																		
Sect. POTENTILLA																		
29.	<i>P. hemsleyana</i>		+	+						+								+
Sect. AUREAE																		
30.*	<i>P. khasiana</i>										+	+		+				
Subg. HYPARGYRIUM																		

to the temperate-alpine regions of the Himalayas between 1830-6100 m, extending from the Baluchistan arc to the Burmese arc, enduring severe cold and frost (Table 1). They are distributed from the Northwestern to the Eastern Himalayas, through the mountain ranges of the Himachal Pradesh, Uttar Pradesh, Nepal, Darjeeling-Sikkim region, Bhutan, Arunachal Pradesh, Manipur and Burma and extending to Meghalaya-Nagaland sector, the latter belonging to earlier geological age than the Himalayas. Some of the higher hills of the Western Chhota Nagpur plateau in Bihar enjoying a mild subtropical climate congenial to the growth of *Potentillas*, harbour four taxa viz. *Potentilla bannehalensis*, *P. indica*, *P. sundaica* and *P. supina* subsp. *supina*. It is interesting to note that the latter three extend their range further South to the Nilgiri Hills, through the tropical belt of India and grow luxuriantly, together with *Potentilla leschenaultiana*, endemic to the Nilgiri Hills. Of the 53 *Potentilla* taxa endemic to the Himalays, only 15 taxa are endemic to India proper (asterisked in table 1). Of the remaining 26 taxa having a wider geographical distribution, nine extend as far west as the Western Asia, three species (viz. *P. sundaica*, *P. polyphylla* and *P. indica*), to Japan and Sri Lanka, and, 13 taxa reach as far as the cold temperate belt of Europe and Siberia. Of these 13 taxa, only five species reach as far as the North America, beyond their Asiatic range (Table 2). According to Wolf (1908), no species of *Potentilla* are common to Europe and Arctic America (including Greenland).

Only *Potentilla anserina* L. of the Northern Hemisphere occurs in the saline habitats of Chile, South America and New Zealand as *P. anserina* L. subsp. *anserinoides* (Rousi, 1965). Not a single species of *Potentilla* is reported from Australia and from Africa beyond the Mediterranean region of North Africa.

ORIGIN OF THE GENUS *POTENTILLA* L.

The epoch when the genus originated : The exact epoch for the origin of *Potentilla* L. and its close allies, cannot be stated with certainty, although the occurrence of unmistakable remnants of *Potentilla fruticosa* in Pliocene deposits, seen together with the doubtful findings of *Potentilla* L. seeds both in the Miocene and Pliocene deposits (Wolf, 1908), is a pointer to the probable origin of *Potentilla* and *Potentilla*-like ancestors earlier to the Miocene period.

Place of origin and differentiation : It is well recognised that the recent arctic and boreal flora of the Northeastern Asia has survived to a great extent up to the present-day because of their escape from complete glaciation during the Pleistocene. That the modern *Potentillas* and their allies occur preponderantly in the arctic boreal region, probably led Wolf (1908) to assume, with certainty, that the Tertiary Circumpolar land might have been the native land of earlier *Potentillas* and that its major evolution must have taken place in the temperate and cold regions of the Northern Hemisphere. One may justifiably start with the presumption that the original stock in the arctic Tertiary flora, might have already split up into many species-groups, of which some of the remnants still survive in that region.

Wolf (1908) regarded the groups, viz. the *Fruticosae* (= *Potentilla* L. subg. *Dasiphora*), the *Palustres* (= *Potentilla* subg. *Comarum*), the *Rupestres* (= *Potentilla* L. *Closterostylis*), the *Niveae* (*Potentilla* subg. *Hypargyrium* sect. *Niveae*) and the *Anserinae* (= *Potentilla* subg. *Chenopotentilla* sect. *Chenopotentilla*) distributed in all the three northern continents (Asia, Europe and North America), as very old within the genus. He (*l.c.*) believed that these groups distributed originally in the Tertiary Circumpolar region migrated southwards, differentiated and split up into the present-day northern continents. And, that, with this separation, a new phase of

Table 2

Serial Number	Names of the taxa	Europe (including N. Africa)	U.S.S.R. (including Sibi-rian re- gion)	E. Asia	W. Asia	Pakis- tan	Nepal	Bhutan	Burma	S. E. Asia	China	Sri Lanka	N. Ame- rica	S. Am- erica
1.	Subg. DASIPHORA <i>Potentilla parvifolia</i>		+		+	+					+			
2.	Subg. TRICHOTHALAMUS, <i>P. salesoviana</i>		+		+	+	+	+			+			
3.	Subg. SCHISTOPHYLLIDIUM <i>P. bifurca</i>	+	+		+	+	+	+			+			
4.	Subg. MICROPOGON <i>P. biflora</i>		+			+	+	+			+		+	+
5.	Subg. CLOSTEROSTYLIS <i>P. polyphylla</i>						+	+		+	+	+		
6.	Subg. CHENOPOTENTILLA Sect. CHENOPOTENTILLA <i>P. anserina</i> sub. sp. <i>anserina</i>	+	+		+	+					+		+	
7.	Subg. POTENTILLA Sect. DUCHESNEAE <i>P. indica</i>	+	+	+	+	+	+	+		+	+		+	
8.	Sect. POTENTILLA <i>P. reptans</i> var. <i>reptans</i>	+	+	+	+	+	+				+			
9.	„ var. <i>microphylla</i>	+					+							
10.	<i>P. flagellaris</i>		+	+							+			
11.	Sect. AUREAE <i>P. gelida</i>		+		+	+					+			
12.	Subg. HYPARGYRIUM Sect. MULTIFIDAE <i>P. multifida</i> var. <i>multifida</i>	+	+	+	+	+	+		+		+		+	
13.	„ var. <i>minor</i>		+				+				+			
14.	<i>P. baltistana</i>		+											
15.	<i>P. polyschista</i>		+		+	+								
16.	<i>P. hololeuca</i>		+		+	+								
17.	<i>P. soongorica</i>		+		+	+								
18.	<i>P. sericea</i>		+			+	+							
19.	Sect. NIVEAE <i>P. nivea</i>	+	+				+		+		+			+
20.	Sect. HYPARGYRIUM <i>P. neglecta</i>	+			+	+	+				+			
21.	Sect. RECTAE <i>P. recta</i>	+	+		+									+
22.	Sect. PERSICAE <i>P. flabellata</i>		+		+	+								
23.	Sect. RIVALES <i>P. desertorum</i>		+		+	+	+				+	+		
24.	<i>P. sundaica</i>			+			+		+		+	+	+	
25.	<i>P. supina</i> sub sp. <i>supina</i>	+	+	+	+	+	+		+	+	+	+		
26.	„ sub sp. <i>paradoxa</i>		+										+	

evolution for *Potentillas* began ; many species perished, leaving a few survivors in the Circumpolar region. And, consequent to the disappearance of original Circumpolar source and spatial separation of the three continents, further diversification and separation occurred, resulting in specific Asiatic, specific European and specific American groups of species. Despite such specificity, about 16 taxa of the European continent extend their range to the temperate Asiatic mountains through the higher mountain ranges of the Mediterranean-West Asia and Afghanistan (Wolf, 1908). However, Jiri Sojak comments (Personal communication) that Wolf's theory of the arcto-tertiary evolutionary region as the centre of *Potentilla*, is rather improbable.

Centre of differentiation

The principal centre of origin of *Potentilla* L. Wolf in India may be conjectured from the fact that as many as 54 taxa from among a total of 80 taxa (66%) are endemic to the temperate-alpine zone of the Himalayas. Critical analysis of the distributional data of these taxa suggests that within this broad centre of origin, two endemic subcentres may be recognized : (a) the North-West Himalayan subcentre with 66 taxa, of which only 13 are restricted to this region and (b) the East Himalayan subcentre with 47 taxa, of which only 10 taxa are restricted to the Sikkim-Burmese arc of Himalayas.

It is significant to note that of the 80 Indian taxa of *Potentilla* L., only 10 are known to be apomicts : three species viz. *P. nepalensis*, *P. atrisanguinea* and *P. argyrophylla*, endemic to the Himalayas ; four species presumed to have originated in the Central Europe and remaining three species, in Central-Asia-Arctic region. Of the three non-apomictic species common to India, Europe and Asia, *P. bifurca* is postulated to have originated in the Arctic region ; *P.*

salesoviana in the Central Asia and *P. biflora* in the circumpolar region. It is interesting to record that major part i.e. 75% of *Potentilla* common to North America-Europe-Siberia-Indian sector are apomictic species. While the sexually free-breeding species of *Potentilla* have in general restricted distribution, the apomictic taxa comprise a number of 'microspecies' and cover wider geographical area and present a network of morphologically intergrading forms.

Ancestral relationship of the genus Potentilla

Of the four subfamilies recognised within the family *Rosaceae* Jussieu, the *Spiraeoideae* with basic chromosome number $x=8$, 9 and the *Amygdaloideae* with $x=8$ comprising trees and shrubs represent two ancient and distinct evolutionary lines. The subfamily *Maloi-deae* with $x=17$, on the other hand, is considered as an allopolyploid arising from hybridization between the *Spiraeoideae* with $x=9$ and the *Amygdaloideae* with $x=8$, followed by chromosome doubling. According to Gajewski (1959) and Challice (1974) the present-day *Rosoideae* evolved from the *Spiraeoideae*, because : (i) the basic chromosome numbers $x=7$, 8, 9 of *Rosoideae* probably developed through one of its tribes, the *Kerrieae* ($x=9$) from the tribe *Spireae* of the subfamily *Spiraeoideae*. (ii) Ellagitannins (E) and flavone c-glycosides (c) present in the *Spiraeoideae* ancestors are also present in the *Rosoideae* genera with $x=7$ and $x=8$; (iii) the *Spiraeoideae* and the *Rosoideae* are linked by 6-o substitution of flavones ; Scutellerin 7-rhamnoside and scutellerin 7-methyl ether in *Sorbaria* of the *Spiraeoideae* vis-a-vis Scutellerin 6, 4 dimethyl ether in *Kerria* of the *Rosoideae*.

Challice (l.c.) speculates that the 6-hydroxylated flavonols came from the original rosaceous stock and that the 6-hydroxylated

flavonols did not appear until later and prior to the separation of primitive *Spiraeoideae* into present-day *Spiraeoideae* and *Rosoideae*. On the other hand, Bate-Smith (1961) considers, on the basis of plant chemistry, that the *Rosoideae* represent the oldest surviving form of the primitive *Rosaceae*. The view is countered by the argument that, although the *Rosoideae* may be primitive in respect of phenolic constituents, in comparative morphology, it is more advanced.

Within the subfamily *Rosoideae*, the ancient ancestral group comprising trees and shrubs belong to the tribe *Kerrieae*, *Dryadeae* and *Cercocarpaceae*, each with $x=9$. The majority of the genera in these tribes are monotypic with small relic geographic ranges lying primarily on both

sides of the Pacific ocean. The tribe, *Potentilleae*, comprising 16 genera, shares the basic number of chromosome ($x=7$) with a few other allied tribes, such as the *Geeae*, the *Roseae*, the *Sanguisorbeae* and the *Ulmariaceae* amongst others, and may be considered as one of the youngest evolutionary branches of the subfamily *Rosoideae* (Gajewski, 1957) and in which active evolutionary differentiation is discernible (Hypothetical scheme 1).

Evolutionary trends within the nine subgenera of Potentilla L.

In discussing the evolutionary tendencies detected in the different subfamilies or tribes or genera of the family *Rosaceae*, botanists generally consider the following traits as primitive or advanced :

Primitive Traits	Advanced Traits
1. Plants perennial	Plants annual or biennial
2. Shrubs or undershrubs without a rosette of radical leaves	Herbs with a rosette of radical leaves
3. Leaflets with entire margin	Leaflets with toothed/dented/pinnatifid margin.
4. Flowers dioecious	Flowers bisexual
5. Styles persistent, hairy and geniculate	Styles deciduous, glabrous and entire
6. Achenes hairy	Achenes glabrous
7. Receptacles saucer-shaped and becoming woolly after anthesis	Receptacles more or less enlarged after anthesis, dry or fleshy and becoming shortly pubescent or glabrous after anthesis
8. Anemochoric dissemination of seeds	Epizoochoric dissemination of seeds

Amongst the 9 subgenera of *Potentilla*, subgenus *Dasiphora* stands out as the most primitive, as much as all of its species represent shrubs with woody branches, ensuring perennation, lacking rosette leaves, entire leaflets, almost dioecious flowers, woolly receptacles, claviform styles and long-hairy achenes conducive to anemochoric dissemination. Such primitive morphological trends, seen against the palaeontological evidence of its occurrence in the pleistocene of the tertiary (Kirchheimer, 1957); its wide geographical distribution ranging from North America to Europe

and further southwardly to central Asia and Mongolia, the discovery of both diploid forms in North America-Europe and tetraploid forms in the Far East, may be a pointer to its ancestral and still evolving nature. In its southward migration to the temperate-alpine Himalayas, *Potentilla fruticosa* the most primitive species of the genus *Potentilla*, is substituted by the polymorphic species *P. arbuscula* with four varieties and *P. rigida*, both endemic to the Himalayas; whereas *P. parvifolia*, mainly distributed in the high mountains of Central Asian region of U.S.S.R., extends to the Himalayas.

In possessing serrated leaflets and bisexual flowers, the species belonging to the subgenus *Trichothalamus* exhibit evolutionarily advanced traits in relation to the species of the subgenus *Dasiphora*.

The subgenus *Fragariastrum* with its remarkable distribution in the high mountains of Central Europe and of the Alps shows that probably the ancestor of the whole group originated here and as the little known or small groups (sections), it extended to and/or developed in due course in the Himalayas. These Himalayan taxa are not only morphologically, but also genetically, nearly related to the other species within the groups or other groups (sections) of the subgenus *Fragariastrum*. The subgenus *Fragariastrum* shares its serrated leaflets, bisexual flowers, filiform styles and hairy achenes with the subgenus *Trichothalamus*. But in producing a rosette of radical leaves and herbaceous aerial branches it scores over the subgenus *Trichothalamus* as more advanced.

The subgenus *Schistophyllidium* represented by the single polymorphic species *P. bifurca*, probably originated in the upper North, and radiated eastwardly to Central Europe and to U.S.S.R. as distinct varieties/formas. But only as var. *bifurca* it has extended southwardly through Western Asia to the Himalayas. The subgenus *Schistophyllidium* shares with the subgenera *Dasiphora* and *Trichothalamus* its perennial habit and imparipinnate leaves, but it shows more affinity with the former in possessing entire leaflets, dioecious flowers, hairy ovaries, when young, claviform styles, yet, it differs from them in developing a rosette of radical leaves with 2-3-toothed leaflets and glabrous achenes. The affinity of the subgenus *Schistophyllidium* with the subgenus *Fragariastrum* appears remote despite the rosette of radical leaves common to both. In weighing the characters common to the other subgenera,

Schistophyllidium appears to have a parallel development with the subgenus *Trichothalamus* from *Dasiphora*-like ancestors.

Similarly, in the subgenus *Micropogon*, the paleotypic species *P. biflora* originating in the circumpolar land, has gradually advanced in all directions and is presently distributed over a wide range, from North America, U.S.S.R., Mongolia, Iran and to the whole of the Himalayas. However, in the Eastern Himalayas *P. armerioides* might have developed independently. Subgenus *Micropogon* (with *P. biflora* and *P. armerioides* in the Indian region) approaches the subgenus *Fragariastrum* in its perennial herbaceous habit, radical leaves (ternate or imparipinnately 5-foliolate), bisexual flowers and filiform styles, and represents a further stage in evolutionary advance in possessing glabrous achenes. Yet, the presence of entire leaflets, a primitive character met with in *Dasiphora*, shows that evolutionary development of different organs of the same plant body is not synchronous.

Subgenus *Chenopotentilla* is represented by four sections. Of this, the section *Chenopotentilla* with the centre of origin in the mountains of central Asia, comprises a single polymorphic and apomictic species, *P. anserina*, with a number of geographical races: as subspecies *anserina*, it attained most extensive range of distribution and the broadest morphological variation and occupies most of the temperate zone in the Northern Hemisphere and Southern Hemisphere due to its obligate outbreeding, combined with a vigorous vegetative reproduction, aided by frequent migrations through human agency. However, the other sections viz. *Leuconotae* and *Dumosae* are neotypic in origin and are mainly distributed in the Himalayas.

In the subgenus *Chenopotentilla*, the section *Chenopotentilla* shows its affinity with the subgenus *Micropogon* in its perennial

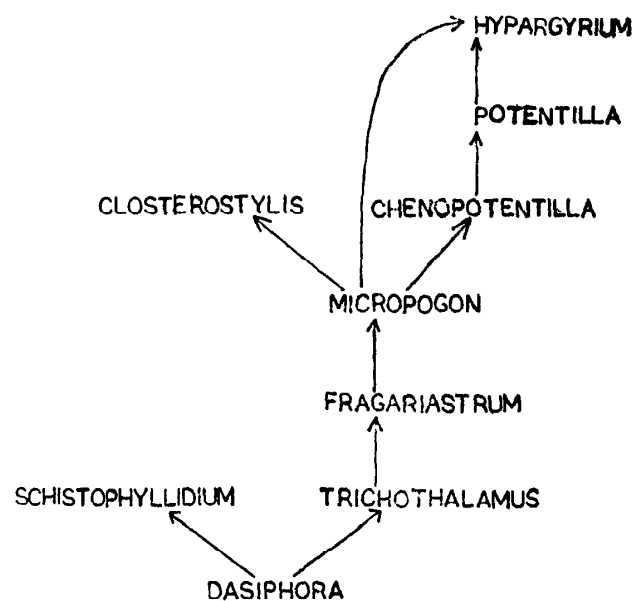
herbaceous habit, rosette of radical leaves, bisexual flowers, filiform styles and glabrous achenes, but represents a further stage of evolution in having interruptedly imparipinnate leaves, dentate or serrulated leaflets, and prostrate and creeping flowering stems. Section *Leuconotae*, in having perennial herbs with a rosette of imparipinnate leaves, reduced (in *P. leuconota*) and serrated leaflets, bisexual flowers, rod-shaped styles and glabrous achenes, approaches the section *Chenopotentilla*. But, in possessing a rosette of leaves without reduced leaflets (as in *P. penduncularis*, *P. microphylla* and *P. tatsienluensis*) and erect or ascendent flowering stems, it is less advanced than the section *Chenopotentilla*; and, in having pinnatisect leaflets (as in *P. microphylla*), it is more advanced than the section *Chenopotentilla*. Whether *Leuconotae* with rod-shaped styles is a direct offshoot from *Chenopotentilla* or is derived from *Micropogon* may only be conjectured at present.

Subgenus *Closterostylis* in having perennial herbs with a rosette of interruptedly imparipinnate radical leaves, serrated leaflets, bisexual flowers and glabrous achenes, is related to the subgenus *Chenopotentilla*. But it shows an advanced stage of development in possessing spindle-shaped styles over the subgenus *Chenopotentilla*.

Subgenus *Potentilla* with perennial herbs, rosette of radical leaves ternate or digitately 5-foliolate, bisexual flowers, subterminal styles, glabrous and smooth achenes, is nearer to the subgenus *Micropogon*, but, in its creeping flowering stems (as in section *Potentilla*) and serrated leaflets (in both the section *Potentilla* and *Aureae*), it has greater affinity with the subgenus *Chenopotentilla*.

In having leaves ternate, digitate or even imparipinnate with serrated leaflets, subg. *Hypargyrium* appears to be a synthetic group combining with the characters of subgenera *Micropogon* and *Potentilla*.

But in coniform styles, it is possible to have been derived either from the filiform styles of *Micropogon* or the rod-shaped styles of *Chenopotentilla* by the swelling of the lower basal portion of the style, since it is difficult to visualise the development of a coniform style from a claviculiform or even spindle-shaped style.



Hypothetical Scheme-2

The evolutionary tendencies within *Potentilla* L. in India, as visualised above, may be represented by a schematic diagram (Hypothetical scheme 2).

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