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# ANATOMY OF CORTEX AND SECONDARY PHLOEM OF *ROSACEAE*. 7. *ROSOIDEAE — POTENTILLEAE*

Л. И. ЛОТОВА, А. К. ТИМОНИН. АНАТОМИЯ ПЕРВИЧНОЙ И ВТОРИЧНОЙ КОРЫ *ROSACEAE*. 7. *ROSOIDEAE—POTENTILLEAE*

Cortex and phloem anatomy is described in aerial shoots, stolons, rhixomes, and perennial branches, in 8 of 13 genera (*Potentilla, Chamaerhodos, Comarum, Pentaphylloides, Drymocallis, Fragaria, Duchesnea, Sibbaldia*) of Takhtajan's (1987) tribe *Potentilleae*. The anatomy is rather uniform in all genera investigated, but phellogen arises in the outer phloem in *Pentaphylloides* and in the pericycle in others. The hypodermis structure is a uniqueness of *Potentilla bifurca* of subgenus *Schistophyllidium*. *Pentaphylloides* and, perhaps, *Schistophyllidium* should de considered as the separate genera, while other investigated members of the tribe might be easily congregated into a very diverse genus *Potentilla*.

Key words: cortex, secondary phloem, *Rosaceae*, *Potentilleae*.

The tribe *Potentilleae* of *Rosoideae* subfamily must be considered one of the most natural taxa among all rosaceous tribes. It had been mostly outlined by the end of the last century (Focko, 1894), though *Geum*, a representative of up-to-date *Dryadeae* (Takhtajan, 1987; Kalkman, 1988) or *Greeae* (Hegi, 1995; Takhtajan, 1997), and *Alchemilla*, *Aphanes* and *Potaninia*, members of modern *Poterieae* (Takhtajan, 1987) or *Alchemilleae* and *Potanineae* (Hegi, 1995; Takhtajan, 1997), were occasionally included into the tribe (Focko, 1894; Bonne, 1928; Schulze-Menz, 1964; Hanelt, 1971). Stability of its bounds and position among rosaceous[1] are in sharp contrast with highly controversial generic composition of the tribe (comp. Takhtajan, 1987; Kalkman, 1988). The resources of characters in traditional use for rosaceous taxonomy are likely to be drained. Therefore, the cortex and phloem anatomy would be applied to testing and improving tribe's taxonomy, but it is still completely neglected by taxonomists due, perhaps, to essentially herbaceous growth habit of the *Potentilleae* members.

The article is intended for bridging the gap and valuating taxonomic bearing of the bark anatomy in *Potentilleae.* We follow A. Takhtajan (1987) here in recognizing 13 constituent genera of the tribe (*Ivesia*, *Purpusia*, *Horkeliella*, *Horkelia*, *Potentilla*, *Comarum*, *Pentaphylloides*, *Duchesnea*, *Fragaria*, *Sibbaldia*, *Drymocallis*, *Chamaerhodos*, *Brachycaulos*). Of those, 8 genera (*Potentilla*, *Comarum*, *Chamaerhodos*, *Pentaphylloides*, *Drymocallis*, *Fragaria*, *Duchesnea*, and *Sibbaldia*) are under the present investigation.

## Materials and methods

Whole herbal plants, annual shoots and perennial branches of shrubby plants were gathered for present investigation. *Potentilla anserina* L., *P. argentea* L., *P. goldbachii* Rupr., *P. recta* L., *Comarum palustre* L., *Fragaria moschata* Duch., and *F. vesca* L. were collected in their natural habitats at Biological Station of Lomonosov Moscow State University (MSU) ca. 45 km west to Moscow. *Potentilla alba* L., *Fragaria* × *ananassa*

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[1] A. L. Takhtajan (1997) arranged the tribe into the subfamily *Potentilloideae* with a few former rosoid tribes.

Duch., *Duchesnea indica* (Andr.) Focke, *Pentaphylloides davurica* (Nestl.) Ikonn., *P. mandshurica* (Maxim.) Ikonn. were sampled in Botanical Garden of MSU. Dr. A. A. Kozhevnikova kindly provided the material of *Potentilla chinensis* Ser., *P. cryptotaeniae* Maxim., *P. fregarioides* L., *P. freyniana* Bornm., *P. supina* L., and *Fragaria orientalis* Losinsk. picked up in their habitats at Kedrovaya Pad'Reserve (Khasan district, Primorskiy region, Russian Far East). *P. micrantha* Ramond ex DC. was sampled by Dr. S. R. Mayorov from its natural populations in Tuapse (Krasnodar region) vicinities. The material of *Chamaerhodos erecta* (L.) Bunge was obtained from Dr. N. I. Borisova (Yakutsk, Yakutian-Sakha Republic). All samples were fixed with 70 % (v/v) ethanol. We happened to investigate voucher specimens preserved at the Herbarium of MSU (MW) of *Potentilla bifurca* L. (№ 202 «МНР, Центральный аймак, Лун. 15 км на восток от пос. Лун. Оголенные участки в зарослях на засоленной почве. 9 VII 1978, И. Губанов»), *P. tianschanica* Th. Wolf (№ 75 «Западный Тянь-Шань. Ташкентская обл., Бостандыкский р-н. Пскемский хр., верховья ущелья Баркрак-сай. На склонах близ тающего снежника в кулуаре по правому борту ущелья, в 1 км ниже конца ледника, 3200 м. 10 VIII 1959, В. Павлов»), *Sibbaldia adpressa* Bunge [*Sibbaldianthe adpressa* (Bunge) Juz.] (№ 9539 «МНР, Сухэ-Баторский аймак, 68 км на юго-юго-восток от г. Бурун-Урит по дороге в Дариганту. На пологом склоне среди степи. Обильно. 6 VII 1985, И. Губанов»), *S. procumbens* L. (№ 1037 «Тува, нагорье Сангилен, хребет Остроконечный. Танну-Ола, междуречье верх. р. Кускуннуг-Хем и р. Шурмак, выс. 2200 м. Выше границы леса, русло ручья, на галечнике. 5 VIII 1979, В. Ханминчун, В. Рожицына, Ю. Полев»), and *S. tetrandra* Bunge [*Dryadanthe tetrandra* (Bunge) Juz.] (№ 244 «Внешняя Монголия, Убсугурский аймак, северо-восток Монгольского Алтая. Хребет Хархира, гора Цаган-Дыгли в верховьях р. Хархира-гол. Морена нивального пояса. 28 VIII 1989, Г. Огуреева»). All the dried samples were softened with ethanol—water—glycerol (1 : 1 : 1) medium at 37 °C for 3—7 days.

Transverse, tangential, and radial sectiones were treated with phloroglucinol-hydrochloric acid or 5 % alcoholic iodine and embedded in glycerol for light microscopy. All the measurements were taken directly from the slides with a calibrated ocular micrometer. Camera lucida drawings were prepares.

## Results

### *Potentilla* L.
### (*P. alba*, *P. anserina*, *P. argentea*, *P. bifurca*, *P. chinensis*, *P. cryptotaeniae*, *P. fragarioides*, *P. freyniana*, *P. goldbachii*, *P. micrantha*, *P. recta*, *P. supina*)

Nearly undershrub (*P. bifurca*), rhizomatous herbs with erect leafy shoots (*P. argentea*, *P. bifurca*, *P. chinensis*, *P. cryptotaeniae*, *P. freyniana*, *P. goldbachii*, *P. recta*), rosette herbs with herbaceous ascending rhizome and scapes bearing clustered (*P. fragarioides*) or solitary (*P. micrantha*) flowers, rosette herb with herbaceous ascending rhizome, epigeous creeping stolons, and solitary flowers (*P. anserina*), rosette herb with bracteate peduncles and stout woody rhizome creeping nearly epigeously (*P. alba*), and erect or ascending annual (*P. sipuna*).

Though the investigated species considerably vary in their growth habits and designs, the general anatomy of their stems and rhizomes as well as the phloem structure is nearly uniform.

**Shoot** is conditionally considered here as erect or ascending sprout bearing foliage leaves. Then, rather bracteate flowers' and inflorescences' stalks of some *Potentilla* species were not anatomically studied at all. Specialized flower scapes of *P. anserina* which creep, root at each second node and produce a daughter rosettes are dealt with in the next section.

Epidermis (fig. 1, *A*, *E*) consists of a layer of cells whose external wall thickness varies according to a species. The outer wall is usually a bit thicker than its counterparts.

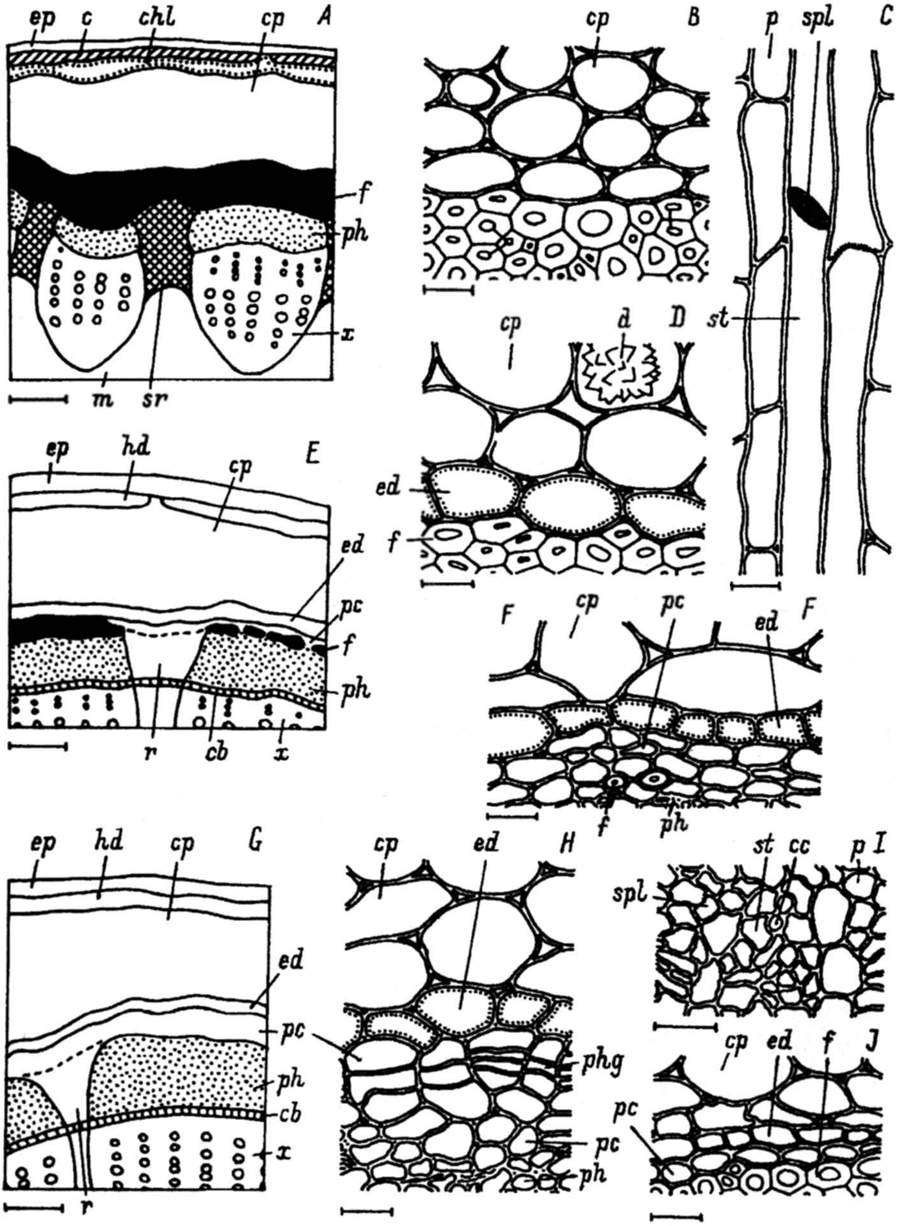

Fig. 1. Stem and rhizome of *Potentilla* species.

*A, B, D—J* — transverse sections, *C* — radal section. *A* — scheme of distal part of the stem, *B* — junction of the cortex and stele, *C* — phloem, *D* — endodermis, *E* — scheme of the basalmost part of the stem, *F* — junction of the cortex and stele, *C* — young rhizome, *H* — the first phellogen origin in the basalmost part of the stem, *I* — stem phloem, *J* — stem endodermis. *A, B, E—I* — *P. goldbachii; C, J* — *P. supina; D* — *P. recta. c* — collenchyma, *cb* — cambium, *cc* — companion cell; *chl* — chlorenchyma, *cp* — cortical parenchyma, *d* — calcium oxalate druse, *ed* — endodermis, *ep* — epidermis, *f* — protophloem fibres, *hd* — hypodermis, *m* — medulla, *p* — phloem axial parenchyma, *pc* — pericycle, *ph* — phloem, *phg* — phellogen, *r* — ray, *spl* — sieve plate, *sr* — sclerified ray, *st* — sieve tube, *x* — xylem. Bar: *A, E, G* — 0.1 mm; *B—D, F, H—J* — 0.01 mm.

It is, however, much thicker in *P. freyniana* while all the cell walls are evenly thin in *P. chinensis*. The cuticle is thin and non-ornamented in all the species but in *P. bifurca* which has longitudinally striated cuticle. The epidermis more or less dispersedly bears long unicellular trichomes. The trichome wall is usually thickened and lignified, but it is thin and hardly lignified in *P. goldbachii* and thick unlignified in *P. chinensis* and *P. freyniana*. The trichomes are elevated on big multicellular pedestals in *P. bifurca*, *P. chinensis*, and *P. cryptotaeniae*.

Three tissues are characteristically distinguishable in the cortex (fig. 1, *A*, *E*). One- to 2(3)-layered collenchyma of angular or angular-lamellar type mostly adjoins the epidermis. The collenchyma intergrades downward the stem to 1(2)-layered hypodermis (fig. 1, *E*) of small cells with evenly slightly thickened walls and a few chloroplasts. The hypodermis of *P. bifurca* is unique in characteristically thickened lignifying walls (fig. 3, *A*). There is 2—4-layered small-celled chlorenchyma inside the collenchyma in distal part of the stem (fig. 1, *A*) in all but *P. cryptotaeniae* species. The chlorenchyma is unidentifiable in the stem of the latter species and in the basalmost part of the stem in other species (fig. 1, *E*). Inner parenchyma constitutes the bulk of the cortex (fig. 1, *A*, *B*, *D—F*, *H*). It differs from the chlorenchyma in larger cells with much fewer chloroplasts and in the idioblasts with browinsh content (*P. argentea*) or calcium oxalate druse (others) (fig. 1, *D*). The cortical parenchyma usually becomes deformed or even obliterated by the end of the growing season.

The homogeneous cortical parenchyma adjoins the stele in the whole stem in *P. freyniana* or its more distal part (fig. 1, *B*) while innermost layer of the cortex develops into the endodermis in stem's basal part in other species. The structure of the endodermis varies according to a species. It differs from the cortical parenchyma only in (much) smaller cells retaining their shape with the stem ageing in *P. argentea* and *P. chinensis*. The endodermis of *P. goldbachii* (fig. 1, *F*) is a starch-storing sheath. The endodermal cells of *P. recta* (fig. 1, *D*) have evenly thin, slightly lignifying walls and store tannic acid. Casparian bands characterize the endodermis in *P. bifurca* and *P. cryptotaeniae*. The endodermis of *P. supina* shows U-shaped lignifications of evenly thin walls of its cells (fig. 1, *J*).

The stem is eustelic; collateral bundles are widely separated with primary rays (fig. 1, *A*, *E*) which is typical of dicotyledonous herbs (Dormer, 1946) in all the species but in *P. bifurca*. In the latter, continuous rings of the phloem and xylem develop. The most of the cambium soon ceases to divide, and the primary rays harden. The periphery of the eustele is mostly occupied with sclerenchymal ring of protophloem fibres' masses interconnected with the hardening parenchyma of the primary rays. The two tissues cannot be properly distinguished, however, in many samples (fig. 1, *A*). The sclerenchymal ring of the stele decreases downward the stem, fragmentizes (fig. 1, *E*, *F*), and completely disappears at last while the cambium duration increases; all the primary rays' parenchyma stays unlignified.

Detached portions of 1—3-layered pericyclic parenchyma interfere into between the cortex and stele's sclerenchyma and/or bundles' phloems (fig. 1, *E*, *F*) in the basal part of stem. The portions gradually merge with each other downward the stem. Thin-walled parenchyma of the pericycle lignifies by the middle of the growing season in *P. chinensis*, *P. cryptotaeniae*, *P. freyniana*, and *P. recta*.

The phloem does not differentiate into conducting and nonconducting zones. It is 50—170 μm in radial width depending on a species under consideration and consists of homogeneous axial parenchyma, sieve tubes and companion cells (fig. 1, *I*). Sieve tube members are 5—10 × 90—100 to 8—11 × 160—180 μm according to a species and associate each with 1 companion cell; sieve plates are simple (fig. 1, *C*), transverse to oblique.

**Stolon** of *P. anserina* is a sympodial chain of units of 2 internodes (Kusnetzova et al., 1992). Designs of the internodes are very similar and can be easily compared to the design of other potentillas' shoots. They are protected with the ordinal epidermis (fig. 2, *A*) bearing sparse subulate unicellular trichomes. The 1-layered hypodermis of rather evenly

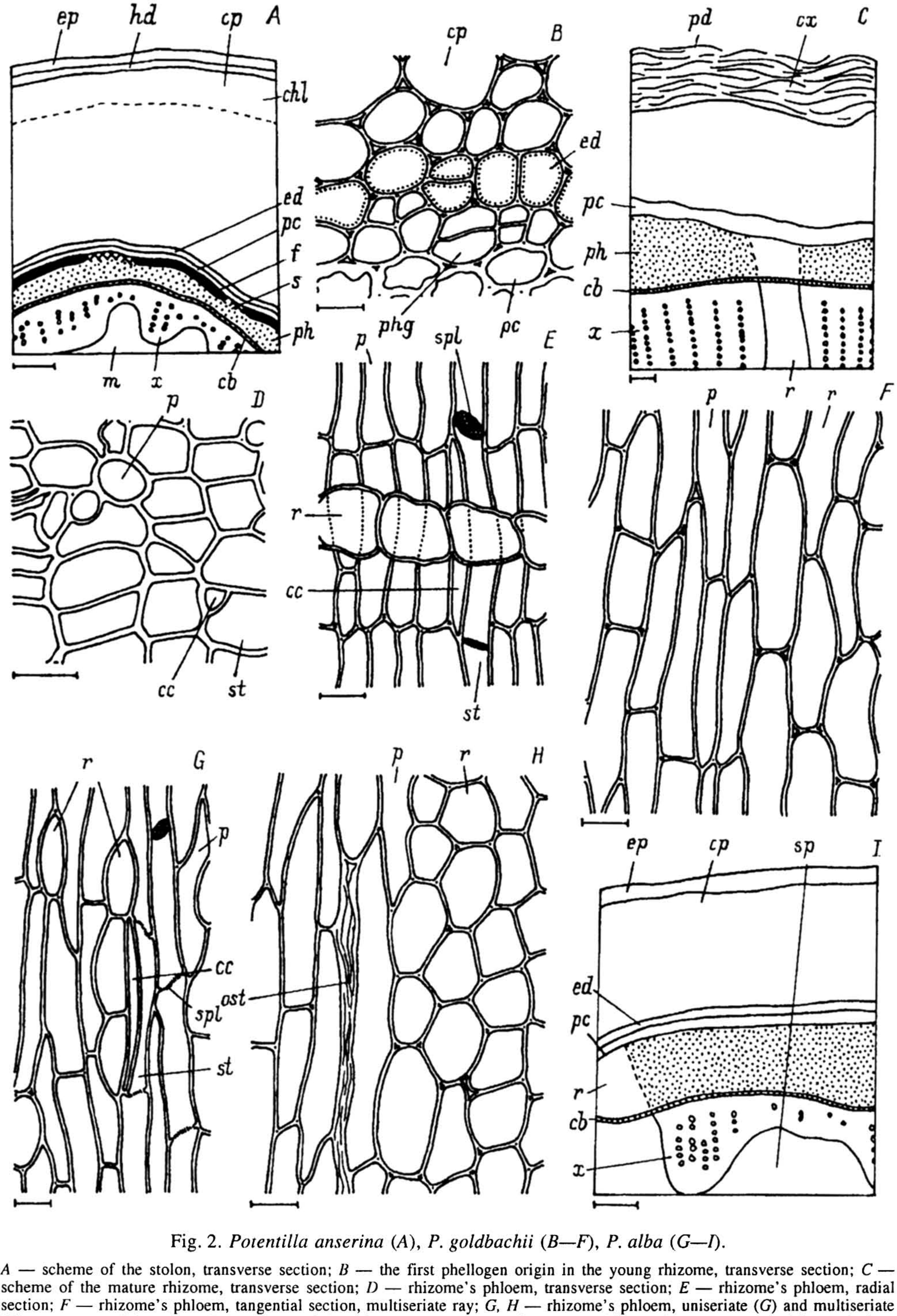

Fig. 2. *Potentilla anserina* (*A*), *P. goldbachii* (*B—F*), *P. alba* (*G—I*).

*A* — scheme of the stolon, transverse section; *B* — the first phellogen origin in the young rhizome, transverse section; *C* — scheme of the mature rhizome, transverse section; *D* — rhizome's phloem, transverse section; *E* — rhizome's phloem, radial section; *F* — rhizome's phloem, tangential section, multiseriate ray; *G, H* — rhizome's phloem, uniseriate (*G*) and multiseriate (*H*) rays, tangential section; *I* — scheme of the rhizome, transverse section. *cx* — obliterated cortex, *ost* — obliterated sieve tube(s), *pd* — periderm, *s* — sclereids, *sp* — storage parenchyma. Other signs see fig. 1. Bar: *A, C, I* — 0.1 mm; *B, D—H* — 0.01 mm.

thick-walled cells is inside the epidermis. Three- to 4-layered chlorenchyma of small cells with numerous chloroplasts adjoins the hypodermis. The inner bulk of the cortex consists of larger parenchymal cells nearly free of chloroplasts. Small scattered rexigeneous cavities are visible here and there in the bulky parenchyma. The innermost layer of the cortex is a starch-storing endodermis.

Peripheral stele's parenchyma constitutes the 3- to 4-layered pericycle (fig. 2, *A*) which slightly lignifies in the lower internodes. There is a sclerenchymal ring of alternating protophloem fibres' masses and hardened primary ray parenchyma. The stolon is originally eustelic, but cambial activity soon results in juxtapositional rings of the secondary phloem and xylem (fig. 2, *A*). The former is 45—60 μm wide and contains only soft elements: homogeneous axial parenchyma and sieve tubes with one companion cell per each of their members. The sieve tube members are 7—9 × 90—11 μm; sieve plates are simple, transverse to oblique.

**Rhizome.** Annual part of rhizome is nearly glabrous (*P. erecta*) or pubescent with unicellular subulate trichomes with thick walls. They either lignify in time or stay cellulosic (*P. goldbachii*). The epidermal cells have slightly thickened external walls covered with very thin cuticle. Homogeneous parenchyma is the only constituent of the cortex in *P. recta* and *P. anserina*. Rexigeneous cavities are scattered in the cortex of the latter species. In other species, the parenchyma is the bulky component of the cortex which the innermost cell layer is the endodermis of brownish or transparent (*P. bifurca*, *P. micrantha*) cells. It bears typical Casparian bands in *P. bifurca*. Besides, the outermost cortex of *P. goldbachii* (fig. 1, *G*) and *P. alba* could be recognized as 1-layered hypodermis though it indistinctively differs from the cortical parenchyma in the latter. The cortical parenchyma contains some starch in *P. goldbachii* and numerous idioblasts with the calcium oxalate druse in *P. fragarioides*.

The inner cortex of *P. micrantha* is worth being paid special attention to for its very distinctive design. There is a layer of starch-rich cells that looks like as if it were a typical starch-bearing sheath (=endodermis). Just inside the layer, another layer is situated which cells bear characteristic Casparian bands on their anticlinal walls.

Every rhizome has a contiguous pericycle (fig. 1, *G*) of (1)2 to 3(4) layers of parenchymal cells which never lignify. The outer pericyclic cells subsequently give rise to the phellogen (fig. 1, *H*). It produces a thin periderm of 1-layered starch-storing phelloderm and few-layered homogeneous phellem by the end of the growing season in all investigated species with herbaceous rhizomes. The cortex dies off and gradually disturbs soon after the phellogen has arisen (fig. 2, *C*) while the pericyclic parenchyma develops unevenly thickened walls and stores starch.

Surprisingly enough, the woody rhizome of *P. alba* retains its cortex for about 3 years (fig. 2, *I*) as the origin of the phellogen delays for that period. Only inner pericycle develops unevenly thickened cell walls in the species. The outermost pericycle remains thin-walled, perhaps, because it is allocated for producing the phellogen (fig. 2, *B*). However, tangential cell divisions are rarely seen in the endodermis as well (fig. 2, *B*). Therefore, the endodermis might contribute to generating the phellogen in rhizome of *P. alba*.

Large-scaled or ring rhytidome protects the rhizome in *P. bifurca*. The scale tissue consists of starch-storing phloemic parenchyma which some parts lose starch and lignify. The innermost phellem contains starch.

The stele structure hardly changes with the rhizome ageing (comp. fig. 1, *G* and 2, *C*) in all the species except for *P. bifurca*. The phloem and xylem are juxtaposed with each other as if irregular wide bandles separated with more or less wide primary rays had developed in the stele. There are complete rings of both the phloem and xylem in *P. bifurca*.

The phloem is 140—180 to 300—400 μm wide according to a species (only 30—60 μm in *P. bifurca*) and only consists of soft elements. The conducting phloem is about 30—40 μm in width and hardly distinguishable from the nonconducting one, though the latter contains masses of obliterated and compressed sieve tubes (fig. 2, *H*). The phloem's elements are clearly situated in radial files (fig. 2, *D*). The parenchymal cells greatly outnumber the sieve tubes with their companion cells. Very many parenchyma strands store starch though strands of cells containing calcium oxalate druse occur (*P. alba*) and solitary cells with a druse (*P. fragarioides*) or dispersed crystals (*P. argentea*) interpose in between the starch-storing cells of a strand. The axial parenchyma is thick-walled in *P. argentea.*

The sieve tubes are clustered and hardly recognizable in transverse sections. The sieve tube members are 8—10 × 80—100 to 11—17 × 145—150 μm depending on a species (5—6 × 60—65 μm in *P. bifurca*). They associate with 1(2) companion cell(s) per member (fig. 2, *E*, *G*). The sieve plates are mostly simple, transverse to oblique (fig. 2, *E*, *G*), but compound ones of 2(3) sieve areas do occasionally occur in *P. alba*.

The multiseriate (primary) rays are clearly visible (fig. 2, *C*, *I*) in all species but *P. bifurca*, though they cannot be undoubtfully contoured in herbaceous rhizomes due to the extreme parenchymatization of the phloem (fig. 2, *F*). They are up to 0.6 mm wide and more than 3 mm high. In woody rhizome of *P. alba* the outlines of the multiseriate rays are much more prominent in tangential sections (fig. 2, *H*) where they are maximum 1.8 mm in width and > 3.5 mm in height. The rays are homogeneous, mostly starch-storing. There are numerous cells with a calcium oxalate druse in the rays in *P. alba*.

Only uniseriate homogeneous rays 1—6-celled in height were revealed in *P. bifurca*.

The uniseriate rays are recognizable only in tangential and radial sections of rhizomes in *P. alba*, *P. chinensis*, *P. cryptotaeniae*, *P. freyniana*, and *P. goldbachii* (fig. 2, *E*, *G*). They are homogeneous, 1-celled (*P. chinensis*, *P. freyniana*) or 1—3-celled in height (*P. alba*, *P. cryptotaeniae*, *P. goldbachii*).

### *Drymocallis: Potentilla tianschanica*[2]

Rosetten perennial with bracteate flower stocks.

**Rhizome** is protected with glabrous epidermis with thick external cell walls. The homogeneous 4- to 5-layered parenchyma bulks the cortex. The innermost cortical layer is a tannin-bearing endodermis surrounding the 1(2)-layered parenchymal pericycle. It is the pericycle that generates the phellogen. The latter produces 1-layered phelloderm and rather thick phellem of thin-walled cells. Irregular masses of yellow-brownish cells are scattered through the phellem. The 3 to 4 inner layers of the phellem store starch. The periderm causes the cortex to die and abscise (fig. 3, *C*). The ringlike splitting of the phellem occurs with rhizome ageing which results in successive sloughing off the outer parts of the phellem.

Juxtapositional rings of the phloem and xylem are in the stele. No hard phloem develops in the rhizome (fig. 3, *C*). The phloem is 70—80 μm thick, all conducting. The homogeneous axial parenchyma outnumbers the clustered sieve tubes (fig. 3, *E*). The sieve tube members are 5—7 × 55—60 μm, associated each with 1 companion cell (fig. 3, *B*, *D*—*E*); the sieve plates are simple, mostly transverse (fig. 3, *B*, *D*—*E*).

The rays are hardly visible in transverse sections (fig. 3, *E*). The uniseriate ones (fig. 3, *D*, *E*) are 2—8 cells high; the multiseriate rays are 3—5 cells in width and 650 μm to more than 1.5 mm in height. All the rays are homogeneous (fig. 3, *B*).

### *Comarum palustre*

Creeping undershrub which bases of annual shoots add to the perennial system of plant's axes while the distal parts of the shoots and all their branches abscise in the winter.

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[2] *P. tianschanica* is a member of *Potentilla*'s subgenus *Closterostyles*. If a genus, the latter must be called *Drymocallis* (Juzepczuk, 1941), but only American representatives of the taxon are likely to be nomenclaturally legalized as *Drymocallis* species. The nomenclatural combinations of their Old World counterparts that we need seem to have been never published. We should rather avoid to arrange necessary combination as our results contradict to considering generic status of *Drymocallis*. Then, we have to confine ourselves with such a bit strange name of the object of research.

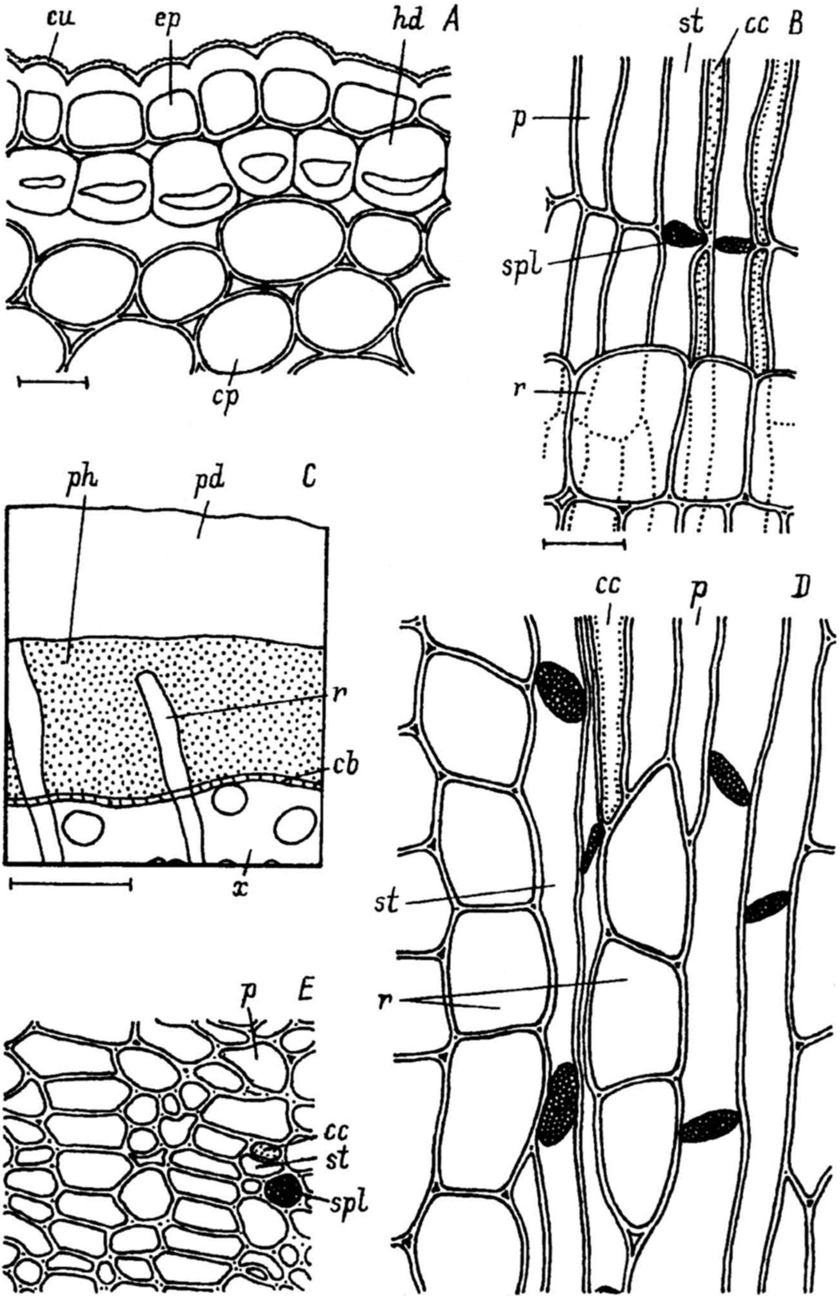

Fig. 3. Cortex and perennial rhizome structure of *Potentilla bifurca* (*A*) and *P.* (*Drymocallis*) *tianschanica* (*B—E*).

*A* — outer cortex of aerial shoot, transverse section; *B* — phloem, radial section; *C* — scheme of rhizome, transverse section; *D* — phloem, tangential section; *E* — phloem, transverse section. *cu* — cuticle. Other signs see figs. 1, 2. Bar: *A, C* — 0.1 mm; *B, D, E* — 0.01 mm.

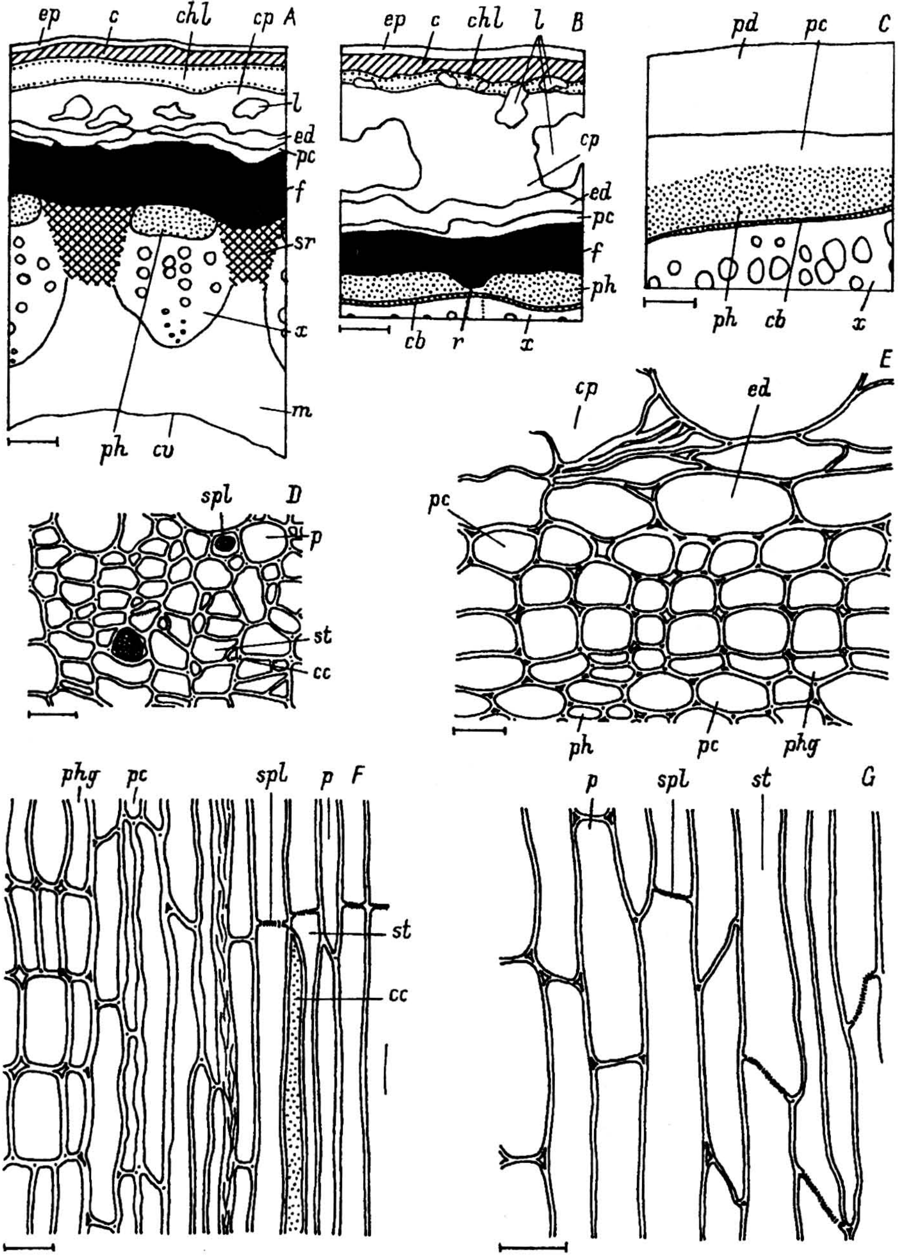

Fig. 4. Stem and phloem of *Comarum palustre*.

*A* — distal part of the annual stem, transverse section; *B* — basal part of the annual stem, transverse section; *C* — 3-year old stem, tangential section; *D* — phloem, transverse section; *E* — the first phellogen origin, transverse section; *F* — phloem, radial section; *G* — phloem, tangential section. *cv* — medullar cavity, *l* — lacuna. Other signs see figs. 1, 2. Bar: *A—C* — 0.1 mm; *D—G* — 0.01 mm.

**Annual stem.** The anatomy of the stem slightly changes in accordance to the part of the annual shoot (compare fig. 4, *A*, *B*).

The stem is pubescent with uniseriate unlignifying trichomes. Thin cuticle covers the ordinary epidermis which cells have thickened external walls. Four tissues constitute the cortex. One- to 2-layered subepidermal collenchyma is lamellar-angular or lamellar. Two-to 3-layered chlorenchyma adjoins the collenchyma and contains small schizogeneous lacunas (fig. 4, *B*). The bulk of the cortex is a cortical parenchyma with numerous rexigeneous cavities which are much larger in the base of the stem (fig. 4, *B*) than in its distal part (fig. 4, *A*). The innermost component of the cortex is an endodermis, fragmented and storing starch in the stem's distal part (fig. 4, *A*) and continuous brownish free of starch in stem's base (fig. 4, *B*, *E*).

The 1(2)-layered disconnected pericycle of thin-walled lignifying cells in the stem's distal part (fig. 4, *A*) changes downwards to the continuous few-layered zone of proliferating parenchymal cells (fig. 4, *B*, *E*). The subexternal layer of the pericyclic parenchyma generates the phellogen (fig. 4, *E*). There is a complete sclerenchymal ring of alternating protophloem fibres' masses and hardened ray parenchyma inside the pericycle. The ring decreases downwards (fig. 4, *A*, *B*) and disappears in the basalmost part of the stem which adds to the perennial system of plant's axes.

The distal part of the stem retains its original eustelic structure (fig. 4, *A*) due to intermittent cambial activity. Much more prominent functioning of the cambium in stem's base produces the juxtaposed rings of the secondary phloem and xylem intersected with primary multiseriate rays (fig. 4, *B*) and secondary uniseriate ones.

Thickness of the soft phloem increases from 18—23 to 30—40 μm downward the stem. All phloem is conducting. The sieve tubes vary from ca. 2 to 4—5 μm in width; each their member is accompanied with 1 companion cell. The sieve plates are always simple, transverse to oblique.

**Perennial stem** sometimes bears cortex remnants and intact endodermis for about 3 years. Anyway, the periderm with 8- to 9-layered phellem protects the stem (fig. 4, *C*). Some its layers are brownish and some are transparent, but all of them store starch. The parenchymal pericycle (fig. 4, *C*) grows up to 4 to 5 cell layers and stores starch, too. Its cells develop unevenly thickened unlignifying walls (fig. 4, *F*).

There is only soft phloem (fig. 4, *C*), approximately 30 μm wide, in the perennial stems. The external phloem contains compressed sieve tubes (fig. 4, *F*) and could thereof be regarded as the nonconducting phloem contrarily to the conducting inner one though the boundary between the two cannot be recognized with confidence. The sieve tube members are 5—7 × 80—90 μm, conjoint each with 1 companion cell (fig. 4, *D*, *F*). The sieve plates are invariably simple, transverse to very oblique (fig. 4, *F*, *G*). The axial parenchyma is homogeneous, thin-walled, and starch-storing.

The rays are homogeneous and uncertainly discernible in transverse sections. The multiseriate primary rays are 0.2—0.5 mm wide and more than 3 mm high and mostly consist of procumbent parenchymal cells. The uniseriate secondary rays are (1)2- to 3(4)-celled in height.

### *Chamaerhodos erecta*

Rhizomatous herb with upright aerial leafy shoots.

**Shoot** is pubescent with rather dense, long, subulate, thick-walled trichomes (fig. 5, *A*) and sparser stalked glands. The latters consist of uniseriate two-celled stalk and top unicellular gland (fig. 5, *A*). The outer epidermal cell walls are the thickest and covered with smooth moderate cuticle. The angular collenchyma of 1 to 2 cell layers adjoins the epidermis. 1- to 2-layered chlorenchyma is situated just inside the collenchyma. The interior parenchyma of more loosely packed larger cells with few chloroplasts bulks the cortex (fig. 5, *A*). The 1-layered starch-bearing endodermis is highly discontinuous.

Lignifying thin-walled parenchyma composes the fragmented pericycle (fig. 5, *A*). Its lignification decreases downward the shoot while its fragments gradually merge with each other. There is the nonlignifying pericycle that mostly gives rise to the phellogen in the basalmost part of the shoot though the endodermis does contribute to producing the phellogen in between the pericycle's fragments (fig. 5, *C*).

Nearly complete ring 5 to 6 protophloem fibres in width is situated interior the pericycle (fig. 5, *A*); the ring decreases basipetally.

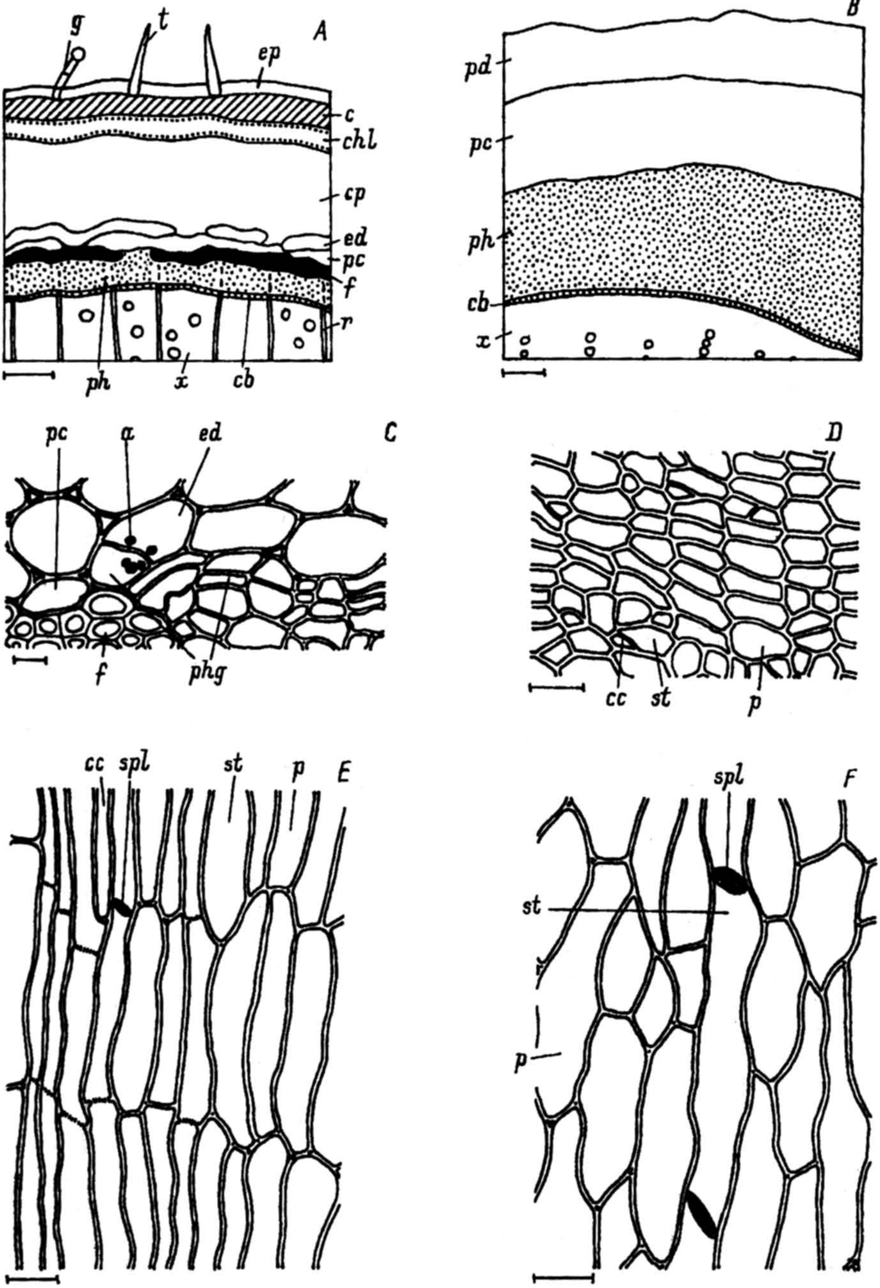

Fig. 5. *Chamaerhodos erecta.*

*A* — scheme of the stem, transverse section; *B* — scheme of the rhizome, transverse section; *C* — the first phellogen origin in the basalmost part of stem, transverse section; *D* — rhizome's phloem, transverse section; *E* — rhizome's phloem, radial section; *F* — rhizome's phloem, tangential section. *a* — amiloplast, *g* — gland, *t* — trichome. Other signs see figs. 1, 2. Bar: *A, B* — 0.1 mm; *C—F* — 0.01 mm.

The original eustele soon changes into the phloem and xylem rings in juxtaposition (fig. 5, *A*) due to cambial secondary thickening through the shoot except for its topmost part. The phloem varies from 20 to 25 μm in width. The sieve tube members are 4—5 × 110—140 μm and combine each with single compation cell; the sieve plates are simple, transverse or oblique. The axial parenchyma is homogeneous. Multiseriate primary rays and uniseriate secondary ones are hardly distinguishable in the phloem (fig. 5, *A*).

**Rhizome.** Very young rhizome bears subulate trichomes and ordinary epidermis. The bulky cortex consists of homogeneous parenchyma excepting its innermost layer which is the starch-storing endodermis. The latter participates in producing the phellogen but just the parenchymal pericycle mostly gives rise to the phellogen. The phellogen generates multilayered phellem of uniform thin-walled cells and 1-layered phelloderm. All cortex is doomed to dying and sloughing off after the periderm has developed.

Mature rhizome (fig. 5, *B*) is protected with the periderm inside of which there is proliferating parenchymal pericycle. The border between it and interior phloem is much less distinctive than that in the shoot because the protophloem fibres never form in the rhizome.

4—6 large bundles or more precisely irregular masses of phloem and xylem in juxtaposition constitute the vasculature of the rhizome.

The phloem is 60—70 μm wide and characteristic of prominent radial files of its constituents (fig. 5, *D*). It consists only of soft elements. Compressed sieve tubes are in the outer phloem but nonconducting phloem is indistinguishable from the conducting one. The sieve tube members are 6—8 × 50—70 μm and usually associated each with 2 companion cells; the sieve plates are simple (fig. 5, *E*, *F*). The axial parenchyma is homogeneous and hardly distinguishable from the primary ray parenchyma. That is why only the uniseriate rays 1—3 cells high could be contoured with confidence in tangential sections. Those are secondary rays. The multiseriate primary rays are in between the vasculature masses and up to 0.3 mm wide and > 2.2 mm high. The rays must be homogeneous.

## *Fragaris* L.

(*F.* × *ananassa*, *F. moschata*, *F. orientalis*, *F. vesca*)

Rosetten herbs with herbaceous ascending rhizome, scapes bearing clustered flowers, and epigeous stolons.

**Scape's stalk** (fig. 6, *A*) is pubescent with long unicellular lignifying trichomes situated solitary on more or less prominent pedestals. The epidermis has typically thicker external walls of its cells. Subepidermal 2(3)- (*F.* × *ananassa*) or 1-layered (other three) collenchyma is angular or angular-lamellar and discontinuous under the stomata. There is 3- to 4-layered chlorenchyma with large tangential intercellular spaces just inside the collenchyma. 6—8 indistinctive layers of cortical parenchyma adjoin the chlorenchyma. Idioblasts containing a calcium oxalate druse are scattered through the cortical parenchyma. The innermost cortex is a 1-layered endodermis (discontinuous in *F. vesca*), which cells have lignified radial and internal walls (all species) or sometimes bear only Casparian bands in radial walls.

The stalk is typically eustelic all its life (fig. 6, *A*). Each vascular bundle is armed with «cap» 5—7 protophloem fibres thick. Quite distinct primary rays harden in between the phloems of the vascular bundles. The phloem is 80—90 μm thick (up to 100 μm in *F.* × *ananassa*). The sieve tube members are 4—7 μm wide; the sieve plates are simple; the axial parenchyma is uniform. The secondary rays are unlikely to develop in the scape's stalk.

**Stolon.** Ordinary epidermis sparsely bears long unicellular trichomes with lignifying walls. The trichomes are raised on pedestals in *F.* × *ananassa*. Besides the trichomes, the uniseriate nonlignifying hairs develop on the stolons of *F. vesca*. 1(2)-layered lamellar collenchyma is inside the epidermis in *F. moschata*, *F. orientalis*, *F. vesca* (fig. 6, *B*); in *F.* × *ananassa*, the subepidermal collenchyma is 1- to 2(3)-layered lamellar in mesopodium and 4—6-layered in hypopodium where it changes inwards from lamellar to loose.

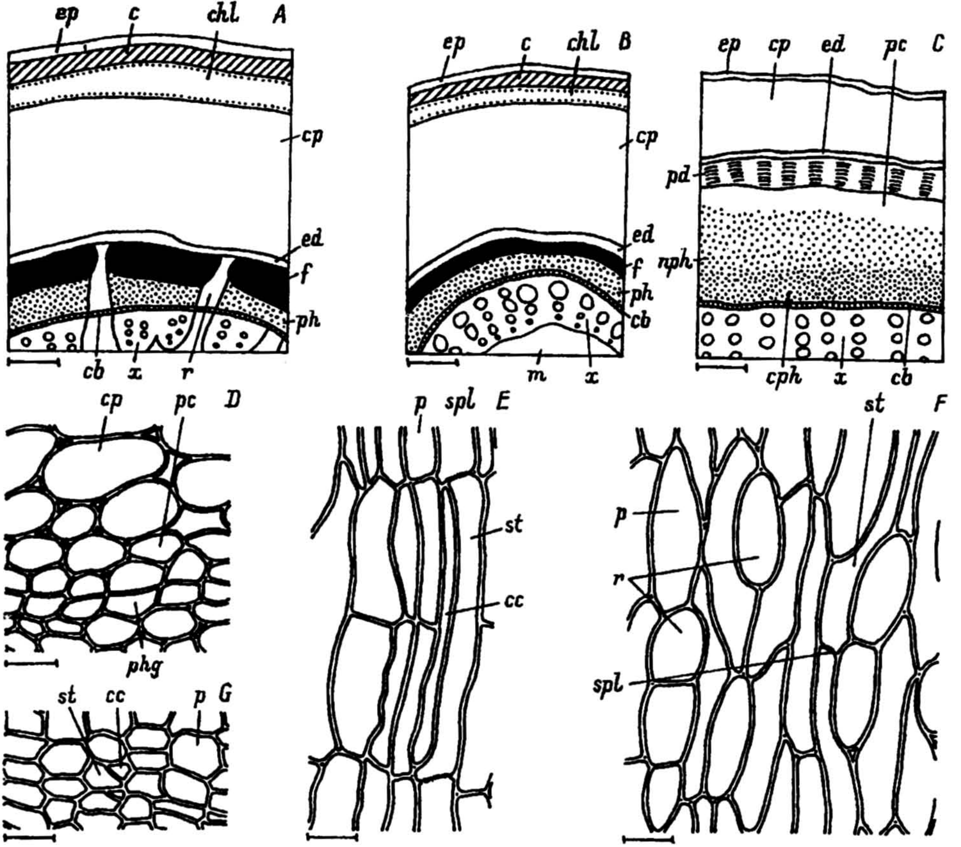

Fig. 6. *Fragaria vesca.*

*A* — flower stalk, transverse section; *B* — stolon, transverse section; *C* — rhizome, transverse section; *D* — the first phellogen origin in the rhizome, transverse section; *E* — rhizome's phloem, radial section; *F* — rhizome's phloem, tangential section; *G* — rhizome's phloem, transverse section. *cph* — conducting phloem, *nph* — nonconducting phloem. Other signs see figs. 1, 2. Bar: *A—C* — 0.1 mm; *D—G* — 0.01 mm.

1- to 3-layered chlorenchyma of rather small cells and little tangential lacunas adjoins the collenchyma (fig. 6, *B*) in all species but in hypopodium of *F.* × *ananassa*. The interior parenchyma bulks the cortex (fig. 6, *B*); it contacts with the collenchyma in *F.* × *ananassa*'s hypopodium. Typical endodermis with Casparian bands is visible in *F. moschata*, *F. orientalis*, and *F. vesca* (fig. 6, *B*), but starch-storing sheath develops in *F.* × *ananassa*.

There are complete rings of phloem and xylem in the stolon's stele due mostly to very narrow primary rays and partly to cambial activity which is more prominent than that in the scape's stalk. The stele is externally bordered with the sclerenchymal ring 3—5 cells thick in all samples (fig. 6, *B*) but hypopodia of *F.* × *ananassa* where fragmented 1- to 2(3)-layered parenchymal pericycle arises. The sclerenchymá consists of hardened protophloem fibres, thin-walled in *F. moschata*, *F. orientalis*, *F. vesca* and thick-walled in *F.* × *ananassa*.

The phloem is soft (fig. 6, *B*), 35—90 μm wide according to a species. All phloem is conducting. The sieve tubes are 5—7 μm in diameter; the axial parenchyma is uniform. Neither multiseriate rays nor uniseriate ones could be visible.

**Rhizome** is protected with nearly glabrous epidermis (fig. 6, *C*). The homogeneous parenchyma is a bulk of the cortex where idioblasts with a calcium oxalate druse are scattered. The border between the cortex and inner pericycle is originally indistinctive (fig. 6, *D*) but the endodermis of smaller cells retaining their shapes after dying off the cortex develops soon after the phellogen has appeared. The latter is generated by the first or second outermost pericycle's layer (fig. 6, *D*). It produces starch-storing phellem of alternating layers of transparent and yellow-brownish cells. The periderm causes the cortex to die but it does not slough off long after developing the periderm (fig. 6, *C*).

The parenchymal pericycle is few-layered from very beginning and slightly proliferates with rhizome ageing. It stores starch.

Large distant bundles constitute the vasculature. No hard phloem develops in the rhizome (fig. 6, *C*). Th phloem is 20—120 μm thick according to a species, the thickest in *F.* × *ananassa*. It more or less clearly differentiates into inner conducting phloem and outer wider nonconducting one (fig. 6, *C*). The starch-bearing axial parenchyma greatly outnumbers the clustered sieve tubes (fig. 6, *G*). The sieve tube members are 7—10 × 70—80 μm, associated each with 1 companion cell (fig. 6, *E*); the sieve plates are simple, mostly transverse (fig. 6, *E, F*). The sieve tubes obliterate and compress in nonconducting phloem.

The huge multiseriate primary rays are 0.1—0.8 × 1.0—1.5 mm and consist of starch-storing parenchyma. The uniseriate secondary rays 1—3 cells high are visible in tangential sections (fig. 6, *F*). All the rays are most likely to be homogeneous.

### *Duchesnea indica*

Rhizomatous rosetten herb with creeping stolons and solitary flowers. The rhizomes are rather ephemeral, bi- to three-ennial.

**Stolon.** The ordinary epidermis bears long unicellular trichomes. Subepidermal cells differentiate into 1-layered hypodermis (fig. 7, *A*) of tightly packed cells with evenly thickened walls, which discontinues under the stomata. 1- to 2-layered chlorenchyma underlies the hypodermis. Its cells are packed more loosely than the hypodermal ones. The inner larger cells compose the indistinctively 4- to 5-layered parenchyma of the cortex (fig. 7, *A*). They contain chloroplasts as well, but the latters are certainly smaller than the chloroplasts in chlorenchyma cells. 1- to 2-layered interior cells have big amiloplasts. A layer of gentle cells which radial and internal walls lignify neighbours the amiloplast-bearing cells on the inside.

Continuous 2—6-layered ring of hardened cells borders externally the stele (fig. 7, *A*). It must consist of protophloem fibres' and ray sclerenchyma's masses though the two cannot be distinguished with confidence.

The cambial activity is drastically intermittent, thereof the distant bundles retain in mature stolon (fig. 7, *A*). The primary ray parenchyma lignifies; the secondary rays do not develop. The phloem is about 50 μm wide and consists mostly of the axial parenchyma. The sieve tubes are rather rare, 7 to 8 μm in diam.; the sieve plates are simple.

**Rhizome.** The epidermis protecting the rhizome (fig. 7, *B*) is very similar with its stolon's counterpart. There is neither the hypodermis nor the chlorenchyma in the cortex though the homogeneous cortical parenchyma does contain small numerous plastids. Very many idioblasts with a calcium oxalate druse are scattered, predominantly in the inner cortex. The same idioblasts are among the starch-bearing cells which constitute fragmented interior cell layer.

2 or 3 layers of thin-walled cells are situated just inside the starch-bearing cells. The interior layer or, respectively, the middle one generates the phellogen while the exterior layer is characteristic of its tightly packed cells (fig. 7, *F*). The latters develop hardly lignifying Casparian bands in the oldest available rhizomes. The phellogen is discontinuous even in the oldest rhizomes under investigation and produces very thin periderm (fig. 7, *B*). More centripetally, there is 2—4-layered parenchymal pericycle (fig. 7, *B*) which cells resemble the collenchyma cells in having unevenly thickened walls (fig. 7, *F*).

The are few large irregular bundles in the rhizome's stele. The phloem is ca. 0.40 mm wide of which ~ 0.15 mm zone could be considered the conducting phloem because of unthickened walls of its constituents. Nevertheless, the border between the conducting phloem and nonconducting one is obscure. The phloem cells are in indistinct radial files

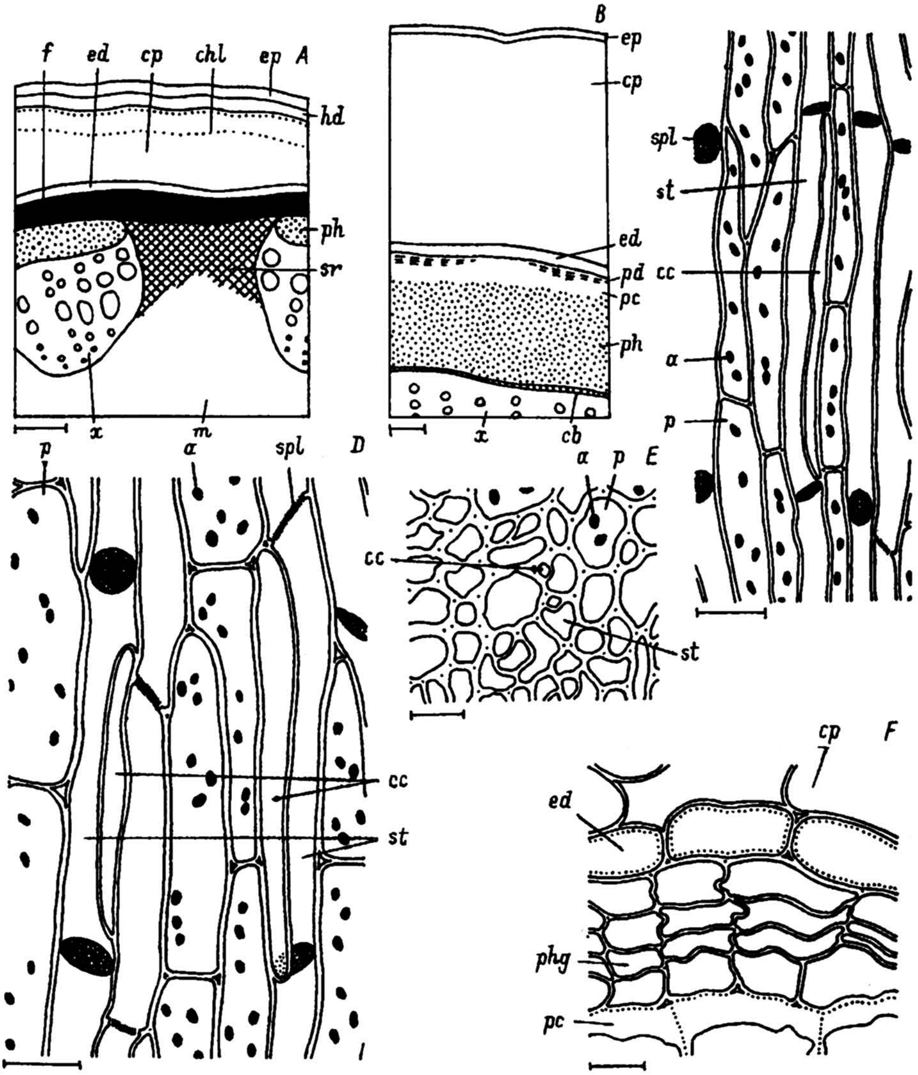

Fig. 7. *Duchesnea indica.*

*A* — creeping stem, transverse section; *B* — rhizome, transverse section; *C* — rhizome's phloem, radial section; *D* — rhizome's phloem, tangential section; *E* — rhizome's phloem, transverse section; *F* — the first phellogen origin in the rhizome. Other signs see figs. 1, 2. Bar: *A, B* — 0.1 mm; *C—F* — 0.01 mm.

(fig. 7, *E*). The sieve tube members are 8 to 12 μm wide, 100 to 113 μm long, and complicated with solitary companion cells (fig. 7, *C, D*). The axial parenchyma is starch-storing (fig. 7, *C—E*); small nodules are visible time to time in its cells' walls in radial sections of the rhizome.

Only the primary rays are recognizable in the rhizomes. They are homogeneous, parenchymal, multiseriate, up to 0.4 × 4.0 mm.

### *Pentaphylloides davurica, P. mandshurica*

Deciduous erect shrubs with perennial branches.

**Annual shoot** is pubescent with uniseriate trichomes and protected with typical epidermis (fig. 8, *A*). The chlorenchyma succeeds the (1)2—3-layered subepidermal

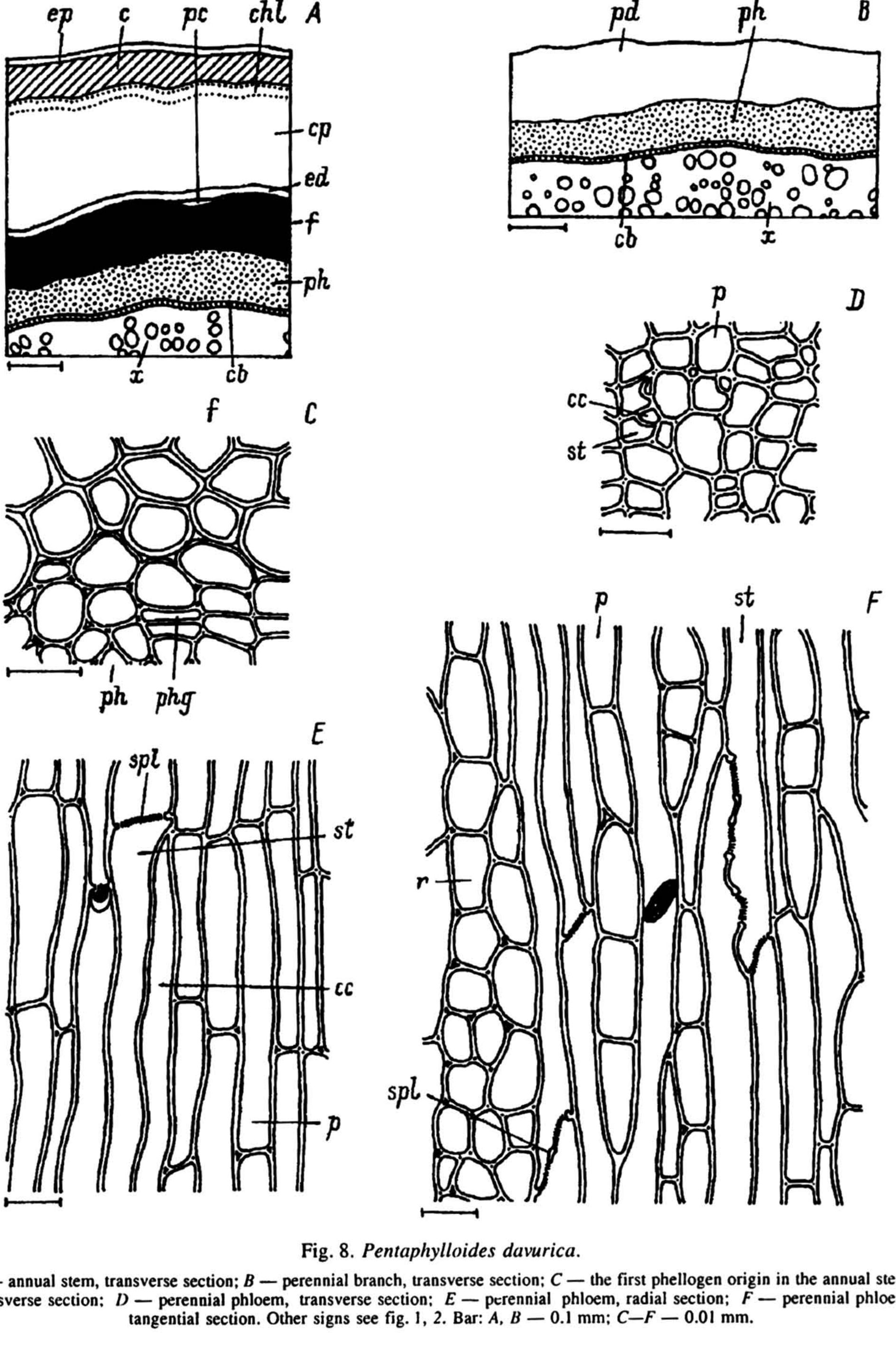

Fig. 8. *Pentaphylloides davurica*.

*A* — annual stem, transverse section; *B* — perennial branch, transverse section; *C* — the first phellogen origin in the annual stem, transverse section; *D* — perennial phloem, transverse section; *E* — perennial phloem, radial section; *F* — perennial phloem, tangential section. Other signs see fig. 1, 2. Bar: *A*, *B* — 0.1 mm; *C*–*F* — 0.01 mm.

collenchyma of angular or angular-lamellar type toward the centre of the shoot (fig. 8, *A*) in both species. It is 1-layered in *P. davurica* and 2- to 3-layered in *P. mandshurica* in which it interferes here and there in the collenchyma up to the epidermis. The bulky inner parenchyma of the cortex partly distorts to produce rexigeneous lacunas by the end of the growing season. There is starch-bearing discontinuous endodermis and tiny fragments of the parenchymal pericycle in *P. davurica*'s shoot (fig. 8, *A*).

The stele periphery is occupied with multilayered ring of thin-walled lignified fibres of the protophloem (fig. 8, *A*, *C*) with parenchymal intrusions (not shown).

Prominent cambial activity soon transforms the original eustele, typical of herbs (Dormer, 1946), into juxtaposed rings of the phloem and xylem (fig. 8, *A*), characteristic of trees and shrubs (Dormer, 1946). The phloem ring is 30—35 µm wide. It consists of sieve rubes ca. 5 µm in diam. with their companion cells and axial parenchyma outnumbering the sieve tubes. Obliterated sieve tubes are sometimes visible in the outer phloem by the end of the growing season. The rays are uni- and bi-seriate.

The first phellogen arises in the phloem parenchyma interior the protophloem fibres (fig. 8, *C*) and produces 1- to 2-layered starch-storing phelloderm and phellem of alternating zones of wider and narrower cells, respectively. Periderm developing results in abscission of the cortex.

**Perennial branch.** Ringlike rhytidome is a protective structure of the perennial branch, but its outer rings are easily caducous and never retain in preparations (fig. 8, *B*) making appearance as if the branch were protected with ordinary periderm. Contrarily to the annual shoot phellem, the phellem of perennial shoot is rather thin, homogeneous.

All phloem interior the innermost periderm is soft, conducting (fig. 8, *B*), ca. 15 µm wide in *P. davurica* and 30—35 µm in width in *P. mandshurica*. Its cells are more or less clearly in radial files (fig. 8, *D*). The axial parenchyma is homogeneous. The sieve tube members are 7—8 × 70—85 µm in *P. davurica*, 5—7 × 80—100 µm in *P. mandshurica*. Solitary companion cell develops in association with each sieve tube member. Simple sieve plates, transverse (fig. 8, *E*) or oblique (fig. 8, *F*), prevail, but compound ones do sometimes occur as well (fig. 8, *F*).

All the rays are homogeneous, starch-storing; the uniseriate rays are (1)4—6(12) cells high in *P. davurica* and 2—5 cells high in *P. mandshurica*; the bi-seriate ones are more than 20 cells in height in the former (fig. 8, *F*) and up to 12 cells in height in the latter.

The rhytidome rings' tissue lignifies in *P. mandshurica*. In *P. davurica*, most axial parenchyma of rhytidome rings barely stores starch; scanty crystalliferous parenchyma which each cell contains irregular crystal of calcium oxalate and few secondary phloem fibres form there, too. The sieve tubes collapse in the rhytidome rings in both species.

## *Sibbaldia* L.
## (*S. adpressa* (*Sibbaldianthe adpressa*), *S. procumbens*, *S. tetrandra* (*Dryadanthe tetrandra*))

Rhizomatous rosetten perennials with bracteate flower stocks.

**Annual rhizome.** *S. adpressa* and *S. procumbens* have rather ordinal rhizome morphology while in *S. tetrandra*, leaf bases merge with the internodes just like in shoots of *Sibiraea altaënsis* (Lotova, Timonin, 1998a). The rhizome is protected with glabrous epidermis (*Sibbaldia adpressa*, *S. tetrandra*) or bears sparse, unicellular, subulate trichomes with thick lignified walls (*S. procumbens*). The epidermal cells have hardly thickened external walls covered with very thin cuticle (fig. 9, *F*). The cortex is parenchymatous, 4—6-layered in *S. procumbens* and *S. tetrandra*. Very many cortical cells have thickened, slightly lignified external walls in *S. adpressa* (fig. 9, *F*).

The innermost cortical layer is an endodermis with hardly visible Casparian bands in *S. adpressa* and with slightly lignifying radial walls in *S. procumbens* (fig. 9, *C*); the inner 1-layered parenchymal pericycle produces phellogen. There is a layer of small cells that is internally underlied by 1 layer of phellogen-generating parenchyma in *S. tetrandra*. Thus, the outer layer of the two can be compared to the endodermis.

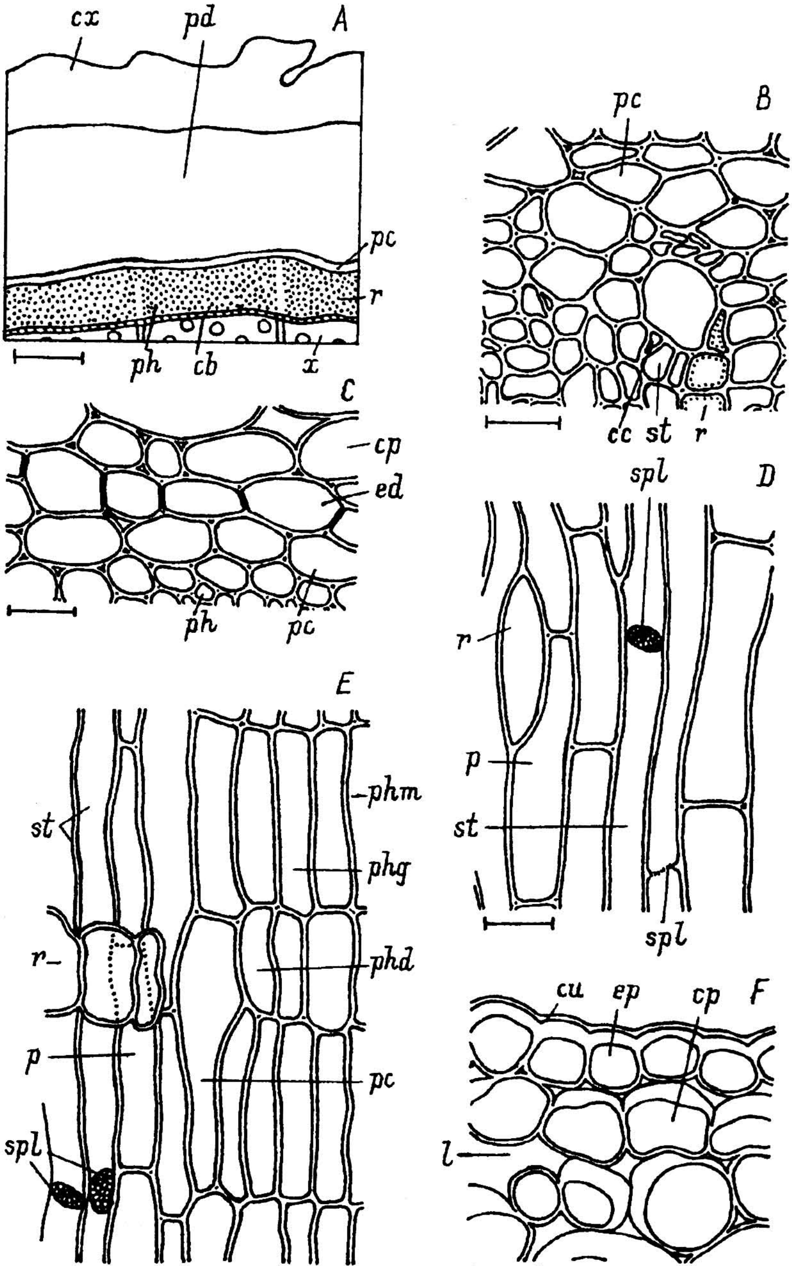

Fig. 9. Rhizome structure of *Sibbaldia procumbens* (*A—E*) and *S. adpressa* (*F*).

*A* — scheme of perennial rhizome, transverse section; *B* — phloem, transverse section; *C* — endodermis, transverse section; *D* — phloem, tangential section; *E* — phloem, radial section; *F* — outer cortex, transverse section. *phd* — phelloderm. Other signs see figs. 1, 2. Bar: *A* — 0.1 mm; *B—F* — 0.01 mm.

There are irregular masses of phloem and xylem in juxtaposition in *S. adpressa* and 4 separate collateral bundles in *S. tetrandra*. Initially multi-bandlous eustele transforms into juxtapositional rings of the phloem and xylem in *S. procumbens*. The phloem is soft, 8—11 μm thick (20—30 μm thick in *S. procumbens*); the sieve tubes are ca. 3 μm in diam. (5 μm in *S. procumbens*); the axial parenchyma is homogeneous. Uniseriate rays are present in the phloem masses in *S. adpressa* and *S. procumbens*.

**Perennial rhizome.** The periderm with brown phellem which outer parts ringlikely or scaly abscise protects the rhizome in *S. adpressa* and *S. tetrandra*, respectively. Dead deformed cortex remains on *S. procumbens*'s rhizome (fig. 9, *A*). The phellem is homogeneous in *S. adpressa*, though its 2 to 3 inner layers store starch. It consists of rather regularly alternating rings of flattened and non-flattened cells in *S. procumbens* and *S. tetrandra*. The flattened cells have slightly lignified radial walls in the former species. The phelloderms is 1-layered in the three species.

The phelloderm seems to adjoin the phloem in *S. adpressa*, but 1- to 3-layered parenchyma of thinwalled cells (*S. procumbens*) or even 6- to 7-layered parenchyma of thick-walled cells (*S. tetrandra*) occurs in between the two tissues. It must be considered the proliferating pericycle (fig. 9, *A*, *B*).

Juxtapositional rings of the phloem and xylem are in the stele of *S. adpressa* and *S. procumbens* (fig. 9, *A*); 4 collateral bundles are in that of *S. tetrandra*. The phloem is 20—30 μm (up to 60 μm in *S. tetrandra*) thick. No hard elements develop in the phloem (fig. 9, *B*, *D—E*). Unevenly thickened cell walls are typical of *S. tetrandra*'s phloem. The sieve tubes are 3—4 × 55—90 μm in *S. adpressa*, 6—7 × 60—70 μm in *S. procumbens*, and 3—4 × 60—70 μm in *S. tetrandra*. There is 1(2) companion cell(s) per sieve tube member. The sieve plates are invariably simple (fig. 9, *D*, *E*). The homogeneous axial parenchyma is starch-storing in the three species.

The homogeneous uniseriate rays 1—4 cells high are inherent in *S. adpressa* and *S. procumbens* (fig. 9, *D*, *E*). Only huge primary rays in between the 4 vascular bundles are seen in *S. tetrandra*. Anyway, the rays store starch.

## Discussion

Growth habit deeply affects the anatomy of the axial organs which reflects functional specialization of aerial shoots, stolons, and rhizomes, respectively. The comparable structures are mostly very similar, however, in all the investigated species.

The innermost cortex of annual aerial shoot is evidenced to be the most diverse structure in the tribe. It varies, according to a species, from ordinary parenchyma indistinguishable from outer cortical parenchyma (*Potentilla argentea*, *P. chinensis*, *P. freyniana*, *Sibbaldia tetrandra*) to starch-storing sheath (*Potentilla goldbachii*, *Comarum palustre*, *Chamaerhodos erecta*, *Fragaria × ananassa*, *Pentaphylloides* sp. sp.), tannic acidbearing sheath (*Potentilla recta*, *Comarum palustre*, *Drymocallis tianshanica*), to typical endodermis which cells bear either Casparian bands (*Potentilla bifurca*, *P. cryptotaeniae*, *Fragaria* sp. sp., *Sibbaldia adpressa*) or characteristically thickened and lignified walls (*Potentilla supina*, *Fragaria* sp. sp., *Duchesnea indica*, *Sibbaldia procumbens*). Every sort of specialized innermost cortex is treated here as endodermis on the base of its spatial homology. The diversity of the endodermis is, however, taxonomically unimportant, because its variety in *Potentilla* seems to cover that in whole *Potentilleae* tribe.

The innermost cortex pattern in rhizome of *Potentilla micrantha* and rhizome and stolon of *Duchesnea indica* is worth being specially commented on. It consists of inner layer of Casparian bands bearing cells or cells with characteristically lignifying walls and of outer 1(2) layer(s) of starch-storing cells. 5-layered polydermis is asserted to be typical of rosaceous' rhizomes (Kaussmann, 1963). However, polydermal cells are always in radial files while the cells of the two layers under consideration alternate. Therefore, the two do not satisfy the criterion of the polydermis. The few-layered endodermis of alternated cells develops in some species outside the *Rosaceae* family (Vekhov et al., 1980), but all its cells are identical. That is why only one layer should be interpreted as the endodermis in both species. There is the inner one that is recognized here as the real endodermis, because Casparian bands are much more specific to the tissue than storing the starch. Anyway, the additional non-endodermal starch-bearing sheath shows close relation between *Potentilla* and *Duchesnea*.

The perennial bark of rhizome demonstrates more abundant parenchyma than that of branches in shrubby *Comarum* and *Pentaphylloides*. The difference is quite typical of the Angiosperms' rhizomes and thereof insignificant to taxonomy. The rhizome's and branch's barks share a number of character, indeed. Either is protected with thin periderm of 1-layered phelloderm and homogeneous phellem (excepting that of *Drymocallis*, *Fragaria*, *Pentaphylloides*, *Sibbaldia procumbens*, and *S. tetrandra* which have the phellem of alternated zones of transparent and brownish cells). The periderm is underlaid with proliferating parenchymal pericycle in *Comarum* and rhizomatous herbs, but adjoins the phloem in *Pentaphylloides*. Both in branch and rhizome, the phloem shows neither hard elements, nor differentiation between conducting and nonconducting phloem (excepting *Fragaria*); its constituents and their arrangement are very similar in two organs, but copious axial parenchyma of rhizome's phloem makes its rays less distinct than the rays of branch's phloem. Besides, the perennial bark structure in shrubby species can be easily derived from the structure of that in the herb's aerial shoots and viewed as overdeveloping form of the latter.

The perennial branches of shrubby species and woody rhizomes of *Potentilla alba* have compound sieve plates and outnumbering simple ones, while all herbaceous rhizomes only possess the simple plates. The distinction is rather a reflection of herb's specificity than a mark of taxa's relationships (see also Esau, 1939).

The first phellogen arises in the outer phloem in *Pentaphylloides* and in the pericycle (in the endodermis in berween the pericycle fragments where the pericycle is discontinuous) in other investigated members. Thus, the pericyclic origin of the phellogen is sure to be a mark of the whole tribe (Bonne, 1928). Then, the difference should be of great taxonomical importance.

The tribe *Potentilleae* contains 3 Linnean genera, *Potentilla*, *Fragaria* and *Sibbaldia*, and a variable number of former segregates of *Potentilla* and *Fragaria* (*Duchesnea*). The generic rank of the three have been never questioned since their establishing (Linnaeus, 1957), inspite of the delimitations between them are conventional (Bonne, 1928). All controversies about the tribe's taxonomy have been due to different interpretations of its other members. Contrarily to the taxonomic routine, the present data show with confidence that *Pentaphylloides*, a segregate of Linnean *Potentilla*, sharply contrasts with other *Potentilleae* representatives by the site the first phellogen originates. The site the first phellogen arises seems to be of great taxonomical importance in *Rosaceae* family (Lotova, Timonin, 1998a, b, 1999a—c, 2000). Therefore, the difference is much more significant taxonomically than mostly quantitative differences between other members of the tribe, because it contradicts the tribe's syndrome.

The structure of the cortex and phloem in *Drymocallis* fits well that in other potentillas and therefore, it does not confirm the generic status of the taxon contrarily to Takhtajan (1987) and in accordance with very many taxonomists (see Focko, 1894; Schulze-Menz, 1964; Hanelt, 1971; Kalkman, 1988; Hegi, 1995).

Surprisingly enough, *Potentilla bifurca* of subgenus *Schistophyllidium* (Juzepczuk, 1941) sharply contrasts with all other *Potentilleae* members presented here in its very specific hypodermis. This could indicate artificially lowered taxonomic rank of the subgenus.

The cortex and stele anatomy of investigated *Sibbaldia* species shows some variety and might indicate dividing of the genus to be reasonable. However, the variety is nearly completely covered with that of extremely diverse *Potentilla*. Even the unusual thickening of cortical cells' walls in *S. adpressa* can be comparable to thickened walls of hypodermal cells in *Potentilla* (*Schistophyllidium*) *bifurca*.

If the taxonomy of the tribe had been based primarily on the bark anatomy, only two genera would have been recognized with confidence in the tribe: *Pentaphylloides* and very diverse *Potentilla*, the latter combining all other investigated genera which have been whenever described. Besides, *Schistophyllidium* might be worth being considered a genus rather than an infrageneric taxon. Anyway, the generic level of *Pentaphylloides* is much better evidenced than that of every other member of the tribe.

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Описана анатомия кортекса и флоэмы соответственно надземных побегов, столонов, корневищ и многолетних ветвей у 8 родов (*Potentilla*, *Chamaerhodos*, *Comarum*, *Drymocallis*, *Pentaphylloides*, *Fragaria*, *Duchesnea*, *Sibbaldia*) из 13, составляющих трибу *Potentilleae*, по системе А. Л. Тахтаджяна (1987). Строение этих структур в существенных чертах идентично у всех исследованных родов, но у *Pentaphylloides* феллоген закладывается в наружной флоэме, а у остальных представителей — в перицикле. Уникально строение гиподермы у *Potentilla bifurca* из подрода *Schistophyllidium*. *Pentaphylloides* и, возможно, *Schistophyllidium* заслуживают родового ранга, тогда как все остальные исследованные представители данной трибы можно было бы объединить в один полиморфный род *Potentilla*.