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ANATOMY OF CORTEX AND SECONDARY PHLOEM OF ROSACEAE. 4. ROSEAE AND ULMARIEAE (ROSOIDEAE)

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КОРЫ ROSACEAE. 4. ROSEAE И ULMARIEAE (ROSOIDEAE)

The tribes *Roseae* and *Ulmariaceae* differ in lots of characters. Whether the differences are due to different relationships of the tribes or to their dissimilar growth habits, is still not quite clear. *Rosa* and *Hulthemia* species seem to be too similar in their cortex and phloem anatomies to be segregated. *Ulmariaceae* does share some cortex and phloem characters with herbaceous members of the subfamily *Spiraeoideae*.

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

Tribes *Roseae* and *Ulmariaceae* are usually considered monotypic (consisting of *Rosa* and *Filipendula*, respectively) (Focko, 1894; Schulze-Menz, 1964; Kalkman, 1988; Hegi, 1995). Some botanists, however, are in favour of keeping apart some Middle-Asian roses lacking stipules such as the genus *Hulthemia* (Juzepczuk, 1941; Takhtajan, 1987, 1997). Anyway both tribes are likely to be rather distantly related to other rosoids. That is why A. Takhtajan (1997) has raised tribal rank of *Ulmariaceae* up to that of subfamily *Filipenduloideae* and restricted customary *Rosoideae* to former *Roseae* members. *Ulmariaceae* was even rarely placed among the tribes of subfamily *Spiraeoideae* (see Kalkman, 1988 for more detail).

The bark anatomy of a few European roses was scrutinized by J. Moeller (1882). It was demonstrated to differ from that of European *Maloideae* and *Prunoideae* in its architecture and some characters of tissue structure. We have failed to find some data on cortex and phloem anatomy in both *Hulthemia* and *Filipendula*. The anatomy of their bark is unlikely to have been thoroughly investigated. Besides, the cortex and phloem structure is still ignored by all the taxonomists. We researched the cortex and phloem anatomy in 7 species of the three genera to make a base for subsequent taxonomic speculations.

Material and methods

Annual and perennial branches of *Rosa acicularis* Lindl. and *R. rugosa* Thunb., above-ground shoots and rhizomes of *Filipendula rubra* (Hill) Robinson and *F. vulgaris* Moench were sampled from the plants grown in the Botanical Garden of Lomonosov Moscow State University. Shoots and rhizomes of *F. ulmaria* (L.) Maxim. were collected in its habitat near Zvenigorod town (Moscow Region). All the samples were fixed with 70 % (v/v) ethanol. We used branch fragments of herbarium specimens of *Rosa abyssinica* R. Br. gathered by Dr. V. N. Pavlov, Lomonosov Moscow State University, in Bale Mountains National Park, Ethiopia. The fragments were softened with an ethanol—glycerol—water (1 : 1 : 1) mixture at 30 °C for a month. Dr. A. A. Butnik, Institute of Botany, Uzbek Academy of Sciences, Tashkent, kindly provided us with ethanol-fixed branches of *Hulthemia persica* (Michx.) Bornm.

Hand-razor slides were processed with either phloroglucinol and hydrochloric acid or 5 % alcoholic iodine. Thereafter the slides were embedded in glycerol and examined with

light microscope. Measurements were taken directly from the slides with calibrated ocular micrometer. Camera lucida drawings were made.

Results

Tribe *Roseae*

Rosa abyssinica, *R. acicularis*, *R. rugosa*

Erect deciduous (*R. acicularis*, *R. rugosa*) and semi-evergreen lianoid (*R. abyssinica*) shrubs with long-lived branches.

Annual stem is spiny. It is nearly glabrous in both *R. acicularis* (fig. 1, A) and *R. abyssinica* and pubescent with unicellular subulate trichomes in *R. rugosa* (fig. 1, E). The epidermis is one-layered, external walls of its cells are very thick in *R. abyssinica*. The cuticle (fig. 1, B) is thin in all the species.

There are spine pedestals of lignifying and unlignifying tight parenchyma in *R. abyssinica* and *R. acicularis*, respectively. The pedestals of hard sclerenchyma are in *R. rugosa* (fig. 1, E). The pedestal tissue spreads laterally from the spine base.

The angular-lamellar collenchyma (*R. acicularis*, *R. rugosa*) or lamellar collenchyma (*R. abyssinica*) is under the epidermis (fig. 1, A, B) and the pedestal tissue (fig. 1, E), respectively. It is 3- to 4-layered in *R. acicularis*, 4- to 5-layered in *R. rugosa*, and 5- to 6-layered in *R. abyssinica*.

Under the collenchyma there is 3—6-layered chlorenchyma (fig. 1, A, B) which intergrades inwards into 3—5-layered cortical parenchyma.

The innermost cortical layer is a starch-bearing endodermis (fig. 1, D). Idioblasts with calcium oxalate druse (fig. 1, B) are scattered through the cortex.

The first phellogen arises from the epidermis (fig. 1, C) between the spine pedestals and from the outmost collenchyma layer beneath the pedestals (fig. 1, E).

There is a parenchymal pericycle consisting of 1 to 2 cell layers in *R. abyssinica* and *R. acicularis* and of 2 to 3 layers in *R. rugosa*. It is discontinuous in *R. abyssinica*.

The stem is eustelic (fig. 1, A). The protophloem fibres (fig. 1, D) form massive «caps» of vascular bundles (fig. 1, A). There are no other hard phloem elements in the annual branch (fig. 1, A, F). The soft phloem is 0.03 to 0.05 mm (*R. acicularis*, *R. rugosa*), up to 0.07 mm (*R. abyssinica*) thick. All phloem is conducting. Its elements slightly obliterate next to the fibres in *R. acicularis* and *R. rugosa*. In *R. abyssinica*, zone of obliterated phloem widens to 1/2—1/3 exterior phloem.

The sieve tubes are 4 to 5 μ m in width in *R. acicularis*, 6 to 7 μ m in *R. rugosa*, and 7—10 μ m in *R. abyssinica*. Each sieve tube member associates with a single strand of companion cells (fig. 1, F). Sieve plates are simple, transverse or oblique. Axial parenchyma is rather homogeneous (fig. 1, F).

The primary rays are wide (fig. 1, A) and high; they are slightly dilated in *R. abyssinica*. The secondary rays are uniseriate and hardly discernible.

Perennial branch is protected with multilayered phellem in both *R. acicularis* (fig. 2, A) and *R. rugosa* and with scaly rhytidome 0.2—1.0 mm wide in *R. abyssinica*. The rhytidome scales consist of multilayered periderm and distorted cortical tissues. The phellem is homogeneous in *R. abyssinica* and *R. rugosa*. There are layers of tangentially compressed brown cells in the phellem of *R. acicularis* (fig. 2, B). The phelloderm is 1-layered in *R. acicularis* (fig. 2, B) and *R. rugosa* and 2- to 3-layered, starch-bearing in *R. abyssinica*.

The cortex changes hardly in *R. acicularis* and *R. rugosa* (fig. 2, A). There are packed collenchyma cells in *R. acicularis* produced by successive radial divisions of its cells. The boundary between the collenchyma and inner cortical tissue is indistinct. The chlorenchyma cannot be distinguished from the cortical parenchyma. The parenchyma cells are tangentially stretched in *R. abyssinica* and *R. acicularis*. In *R. rugosa*, the layers of tangentially stretched cells alternate with those of roundish ones.

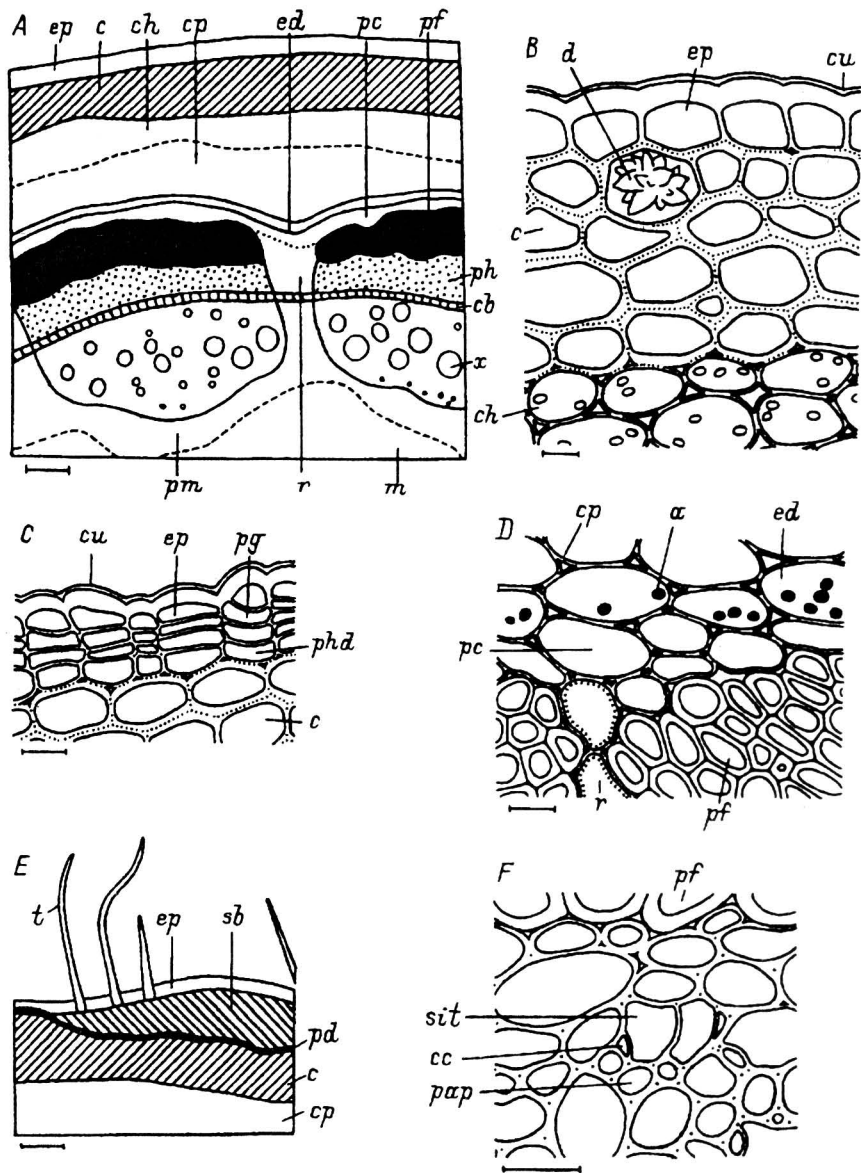


Fig. 1. Annual stems of *Rosa acicularis* (A—D, F) and *R. rugosa* (E), transverse sections.

A — scheme of the stem, B — outer cortex, C — origin of the first phellogen, D — inner cortex, E — scheme of the cortex, F — phloeem. *a* — amyloplast, *c* — collenchyma, *cb* — cambium, *cc* — companion cell, *ch* — chlorenchyma, *cp* — cortical parenchyma, *cu* — cuticle, *d* — calcium oxalate druse, *ed* — endodermis, *ep* — epidermis, *m* — medulla, *pap* — phloeem axial parenchyma, *pc* — pericycle, *pd* — periderm, *pf* — protofloeem fibres, *pg* — phellogen, *ph* — phloeem, *phd* — phellogen, *pm* — perimedulla, *r* — ray, *sb* — sclerenchymatous spine base (pedestal), *sit* — sieve tube, *t* — trichome, *x* — xylem. Bar: A, E — 0.1 mm; B—D, F — 0.01 mm.

The phloeem is about 1 mm thick in *R. acicularis* and *R. rugosa* and up to 1.3 mm thick in *R. abyssinica*; the conducting phloeem is by 0.1 mm and 0.2—0.3 mm, respectively. The conducting phloeem consists of soft elements (fig. 2, C). Few sieve tubes tend to be tangentially rowed. The sieve tube members are 10—12 × 100—110 μm in *R. acicularis*, 10—12 × 90—100 μm in *R. rugosa*, and 12—15 × 330—340 μm in *R. abyssinica*. Each member associates with a strand of companion cells (fig. 2, C). The sieve plates are simple, oblique (fig. 3, A, D). Axial parenchyma is homogeneous, though

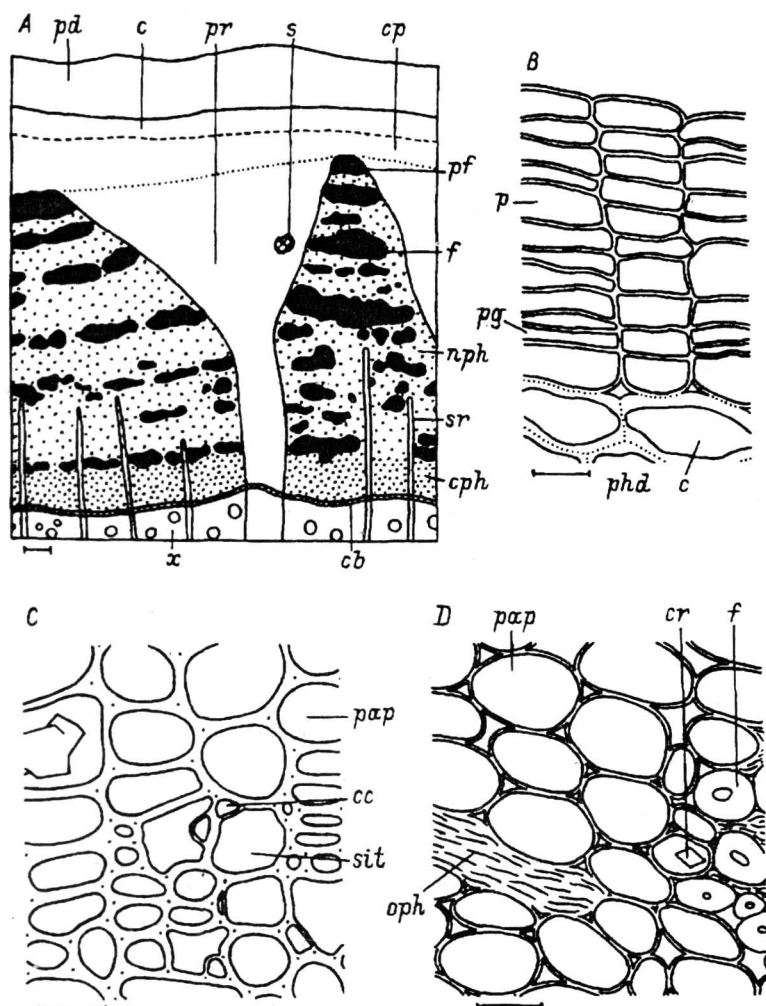


Fig. 2. Perennial branch of *Rosa acicularis*, transverse sections.

A — scheme of the branch, B — phellogen, C — conducting phloem, D — nonconducting phloem. cph — conducting phloem, cr — calcium oxalate crystal, f — secondary phloem fibres, npf — nonconducting phloem, oph — obliterated phloem, p — phellogen, pr — primary ray, s — sclereids, sr — secondary ray. Other signs are the same as in fig. 1. Bar: A — 0.1 mm; B—D — 0.01 mm.

some of its cells adjacent to the nonconducting zone contain a druse of calcium oxalate (fig. 2, C). In nonconducting phloem, the sieve tubes and companion cells die off to become strips of collapsed elements (fig. 2, D; 3, B) where the cells are indistinguishable.

The stereom appears in the nonconducting phloem (fig. 2, A). It consists of secondary phloem fibres in *R. acicularis* (fig. 2, D; 3, B) and *R. abyssinica* and of fibres to sclereids in *R. rugosa*. The hard elements are solitary or clustered. Lots of hard secondary phloem elements add to the protophloem fibre «caps» in *R. rugosa*.

Axial parenchyma slightly proliferates and differentiates into storage and crystaliferous parenchyma. The former outnumbers a lot the latter (fig. 2, D; 3, D). The storage parenchyma has smooth tangential cell walls and nodular radial ones (fig. 3, B—D). It stores starch.

Crystalliferous parenchyma is of two kinds. The first accompanies the stereom masses and contains one calcium oxalate prism or rhombohedron per cell (fig. 2, D). The second

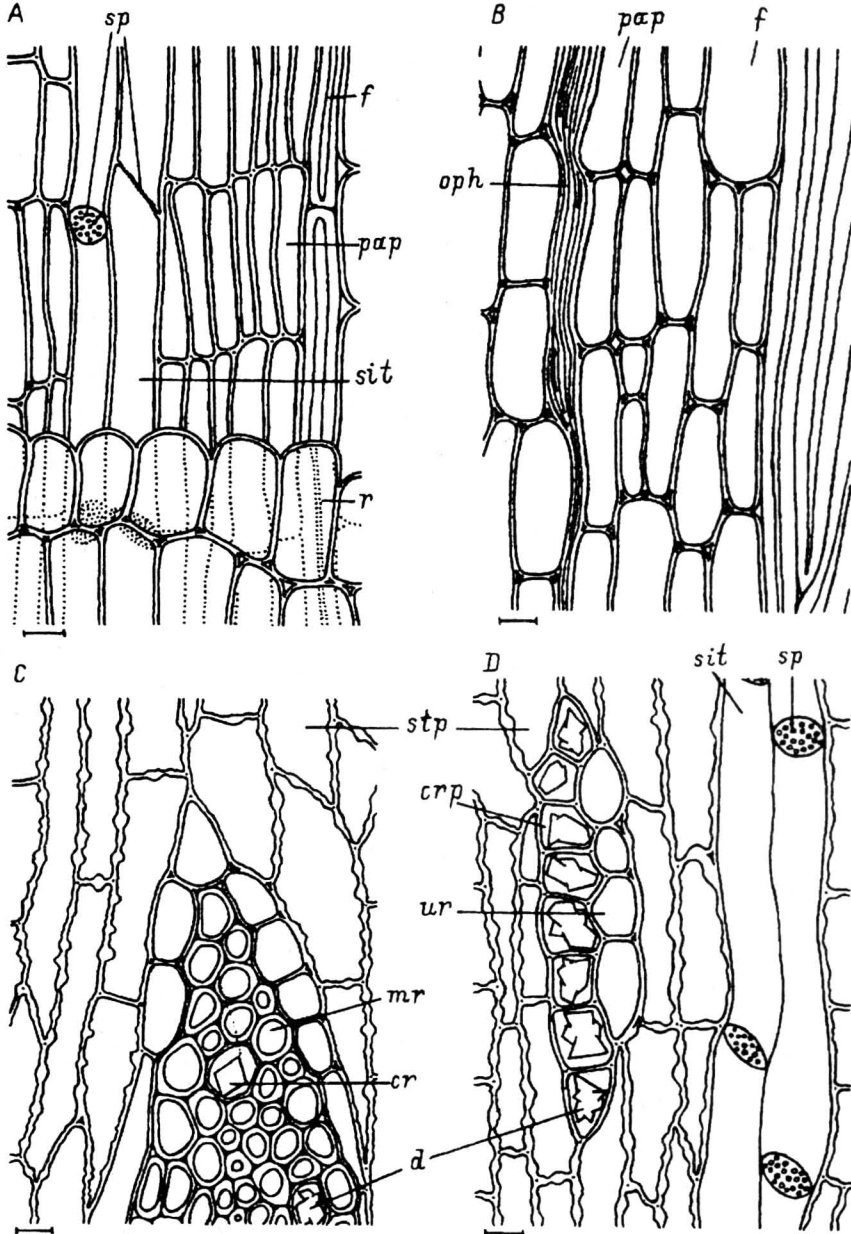


Fig. 3. Secondary phloem in *Rosa acicularis*.

A — conducting phloem, radial section; uB — nonconducting phloem, radial section; C — multiserial ray, tangential section; D — phloem, tangential section. crp — crystalliferous parenchyma, mr — multiserial ray, sp — sieve plate, stp — storage parenchyma, ur — uniserial ray. Other signs are the same as in figs 1, 2. Bar: 0.01 mm.

flanks the rays and contains one irregular crystal or druse of calcium oxalate per cell (fig. 3, D).

The rays are homogeneous in *R. acicularis* (fig. 3, A) and *R. rugosa* and nearly heterogeneous in *R. abyssinica*. The ray parenchyma stores starch.

The primary multiserial rays range from 0.05×0.50 to 0.15×3.00 mm in *R. acicularis*, 0.10×0.15 to 0.25×3.50 mm in *R. rugosa*, and 0.14×0.47 to 0.42×3.00 —

3.50 mm in *R. abyssinica*. They tend to aggregate in the latter species. The vast majority of the ray cells is thick-walled (fig. 3, C) and stores starch. Few ray cells are thin-walled and contain a calcium oxalate rhombohedron (*R. acicularis*) or irregular crystal (*R. abyssinica*, *R. rugosa*) or a druse (*R. rugosa*). A few sclereid clusters develop in proliferating ray parenchyma (fig. 2, A) in *R. acicularis*.

The secondary uniseriate rays are 2—7-celled in height. They cross the conducting zone and disappear in the nonconducting one.

Hulthemia persica

Erect deciduous shrub with somewhat arching long-lived branches.

Annual stem is spiny and densely pubescent with unicellular subulate trichomes (fig. 4, A). The epidermis is one-layered and covered with thin cuticle (fig. 4, B). There are spine pedestals of hard sclerenchyma (fig. 4, B) which nearly merge with each other under the epidermis (fig. 4, A).

The lamellar 3- to 4-layered collenchyma is under the epidermis (fig. 4, A) and the pedestal tissue (fig. 4, A, B), respectively. Under the collenchyma there is 3- to 4-layered cortical parenchyma (fig. 4, A, D) in which some cells contain a calcium oxalate druse or (more internal ones) rhombohedrons. Neither the endodermis nor the pericycle is distinctive (fig. 4, D).

The first phellogen arises from the epidermis between the spine pedestals and from the outermost collenchyma layer under the pedestals (fig. 4, B).

The protophloem fibres (fig. 4, D) compose «caps» of vascular bundles (fig. 4, A). There are no other hard phloem elements in the annual branch (fig. 4, A, E). The soft phloem is 0.04 to 0.05 mm thick. All phloem is conducting. Its elements have unevenly thickened walls (fig. 4, E). Some of them stretch tangentially. The sieve tubes are 4 to 5 μm in width. The strands of companion cells are hardly visible. Sieve plates are simple, transverse or oblique. Axial parenchyma is rather homogeneous (fig. 4, E). There are neither obliteration nor dilatation of the phloem.

The 2- to 3-seriate primary rays are slightly dilated (fig. 4, A). The uniseriate secondary rays are also occasionally dilated.

Perennial branch is protected with multilayered phellem (fig. 4, C) of thin-walled cells. The layers of brown cells alternate with those of transparent cells in the phellem.

The cortical tissues indistinctively differ as their cells are stretched a lot tangentially. The boundary between the cortex and the phloem gets lost because of phloem parenchyma proliferation and lateral shifting of the protophloem «caps».

The phloem is 0.32—0.34 mm thick, the conducting one is by 0.01 mm and consists of soft elements (fig. 5, C, D). Few sieve tubes tend to be tangentially rowed in the conducting zone (fig. 5, C). The sieve tube members are $10\text{--}12 \times 100\text{--}110 \mu\text{m}$, each associated with a strand of companion cells (fig. 5, B, C). The sieve plates are simple, oblique (fig. 5, B, D). Axial parenchyma is homogeneous.

In nonconducting phloem, the sieve tubes and companion cells die off to become strips of collapsed elements (fig. 5, A) where the cells are indistinguishable.

The stereom appears in the nonconducting phloem (fig. 4, C; 5, A, B, E). It consists of secondary phloem fibres and sclereids. The secondary phloem fibres tend to tangential clustering (fig. 4, C).

Axial parenchyma proliferates (fig. 4, C) and differentiates into storage and crystalliferous parenchyma. The storage parenchyma has nodular cell walls, especially the radial ones (fig. 5, B, D, E). It stores starch. The crystalliferous parenchyma accompanies the stereom masses and usually contains irregular calcium oxalate crystals per cell (fig. 5, B, E). Some cells in crystalliferous strand lacking the crystal change into sclereids (fig. 5, E).

The rays are homogeneous. The primary multiseriate rays are $0.08\text{--}0.10 \times \geq 2.5 \text{ mm}$. They moderately dilate in the nonconducting zone. Few ray cells contain a calcium oxalate prism. The secondary uniseriate rays are (2)5—9(17)-celled in height. They cross the conducting zone and disappear in the nonconducting one. The rays harden where they cross the stereom clusters.

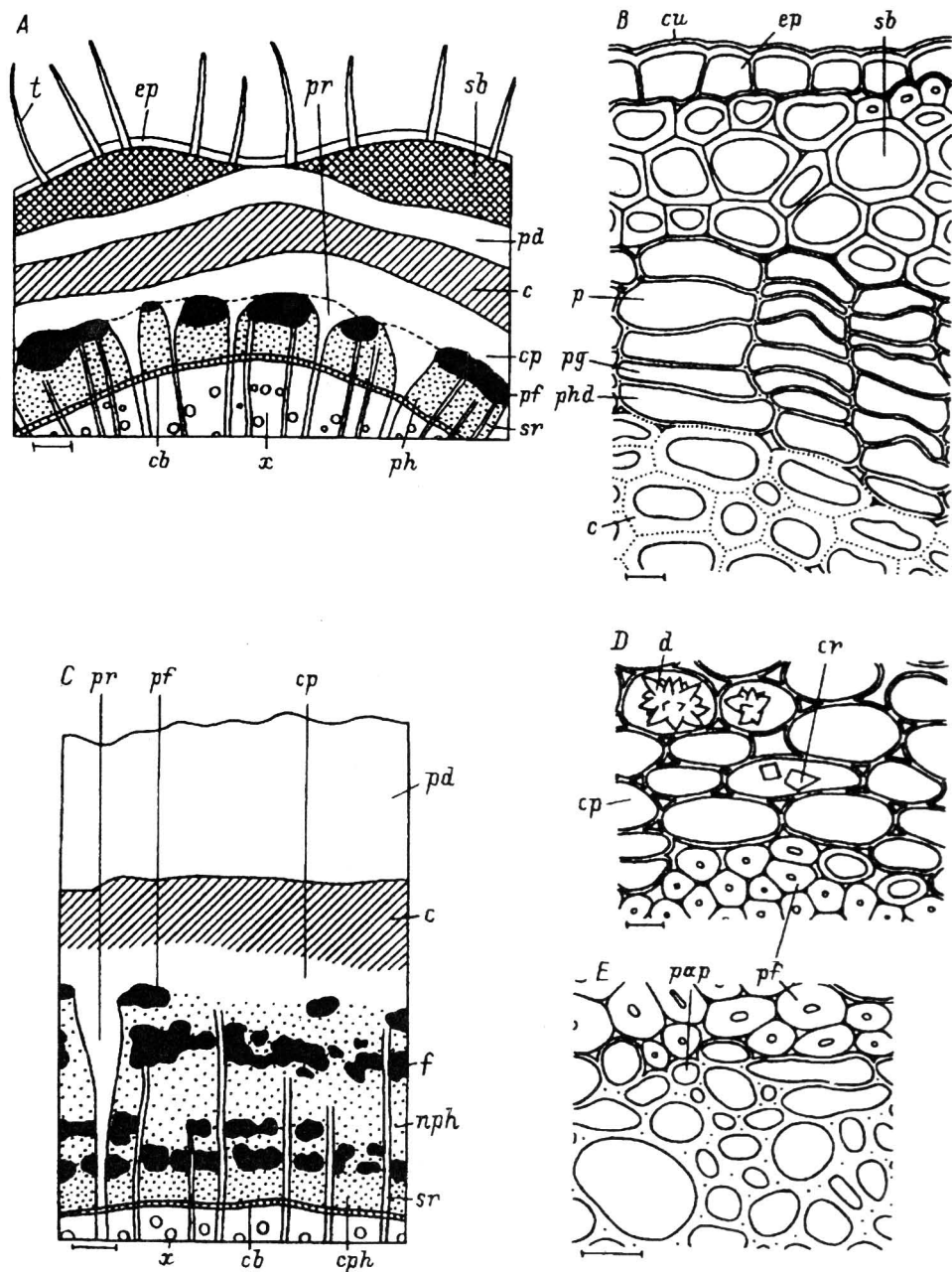


Fig. 4. Branches of *Hultemia persica*, transverse sections.

A — scheme of the annual stem, B — annual outer cortex, C — scheme of the perennial branch, D — annual inner cortex, E — annual phloem. Other signs are the same as in figs. 1—3. Bar: A, C — 0.1 mm; B, D, E — 0.01 mm.

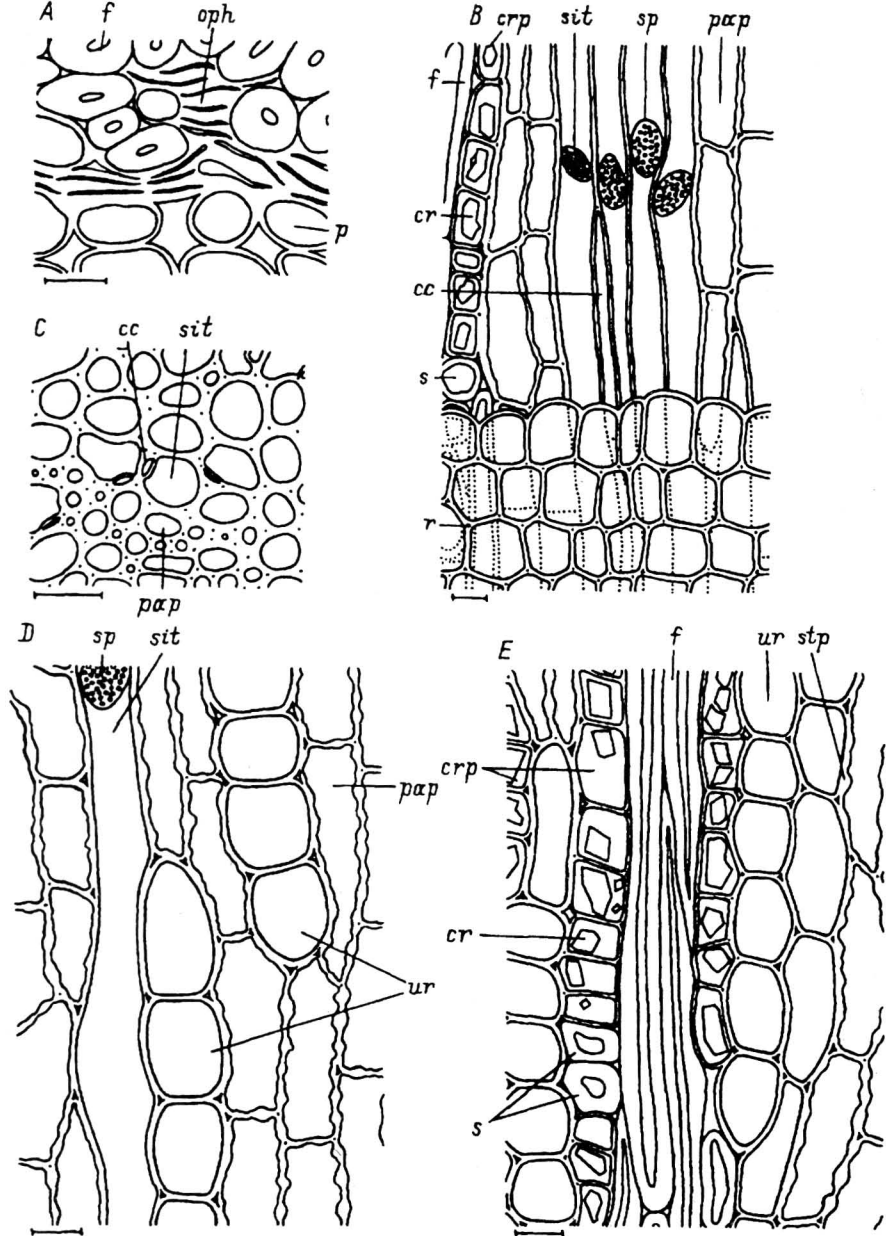


Fig. 5. Secondary phloem of *Hulthemia persica*.

A — nonconducting phloem, transverse section; B — radial section; C — conducting phloem, transverse section; D — conducting phloem, tangential section; E — nonconducting phloem, tangential section. Other signs are the same as in figs. 1—3.
Bar — 0.01 mm.

Filipendula rubra, *F. ulmaria*, *F. vulgaris*

Perennial rhizomatous herbs with erect shoots up to 1.0—1.5 m tall.

Aerial stem. The above-ground stem is loosely pubescent with unicellular subulate trichomes (fig. 6, A). Scarce stocked glands consist of short uniseriate stalk and unicellular brown head in *F. rubra*. The other investigated species lack glands. The 1-layered epidermis lignifies.

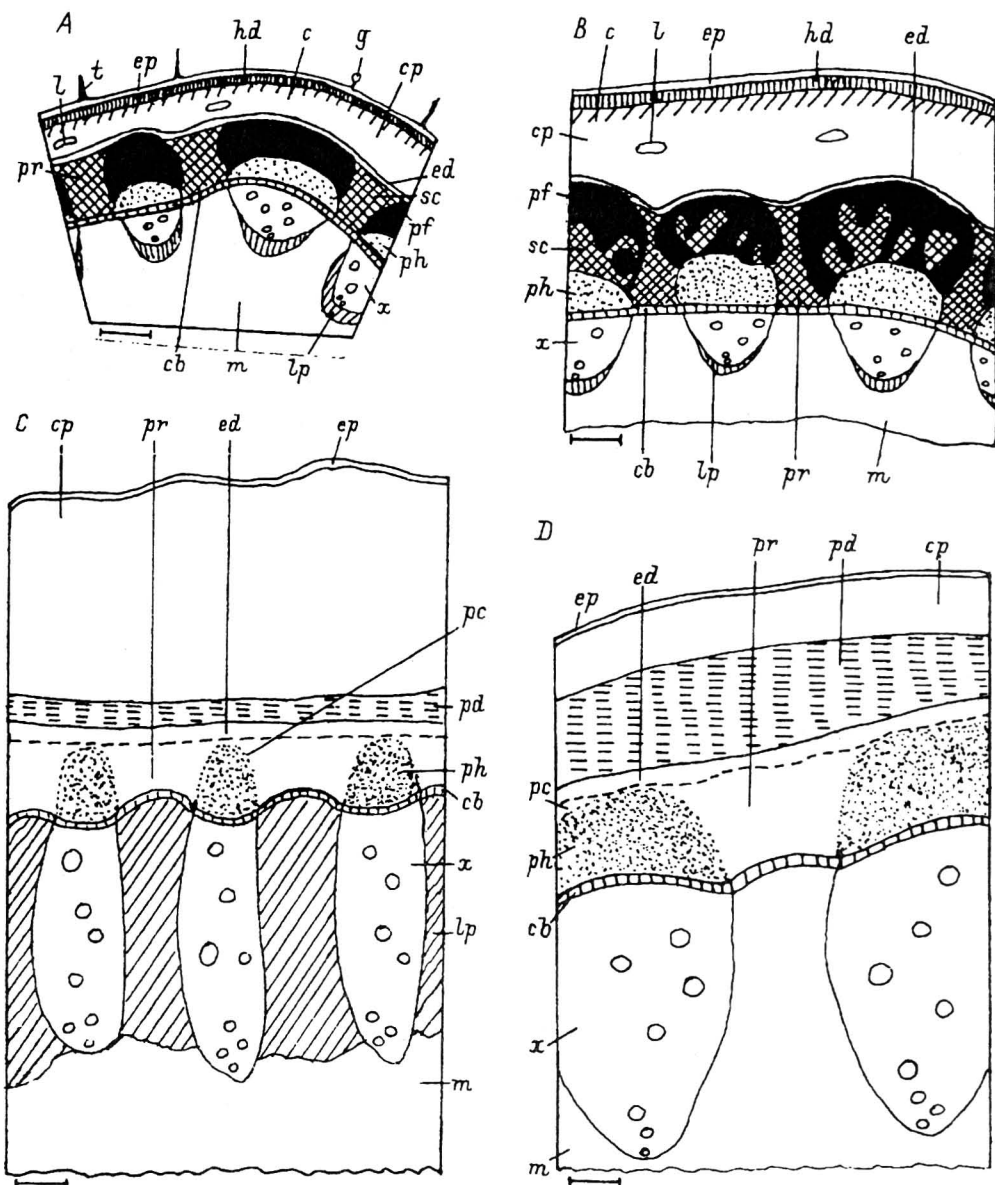


Fig. 6. Schemes of stem (A, B) and rhizome (C, D), transverse sections.

A—C — *Filipendula rubra*, D — *F. vulgaris*. g — gland, hd — hypodermis, l — lacuna, lp — lignifying parenchyma, sc — sclerenchyma. Other signs are the same as in figs. 1—3. Bar — 0.1 mm.

There is 1-layered (*F. vulgaris*), 2-layered (*F. rubra*; fig. 6, A, B) or 3- to 4-layered (*F. ulmaria*) lignifying hypodermis under the epidermis. In *F. rubra*, 2- to 3-layered angular collenchyma is under the hypodermis. Its cells produce secondary pitted walls in the middle and basal parts of the stem; then they lignify. Neither *F. ulmaria* nor *F. vulgaris* have collenchyma in their stems. Cortical parenchyma thickens downward the stem from 4—6 cell layers to about 15 ones (*F. rubra*); it contains small lacunae in *F. rubra* (fig. 6, A, B) and *F. vulgaris*. The parenchymal cells are bigger inwards. The outer cells lignify with time; the inner cells store starch. The innermost layer of the cortical cells might be considered an endodermis. The outer cortical parenchyma slightly lignifies by the end of the growing season in the above-ground basal part of aerial stem.

The stem is eustelic; collateral bundles are widely separated by primary rays (fig. 6, A, B) which is typical of dicotyledonous herbs (Dormer, 1946). Massive protophloem fibre «caps» develop in the bundles in distal part of the stem (fig. 6, A). Downwards, the protophloem fibres mix with clustered thin-walled lignifying parenchyma (fig. 6, B) produced by the procambium. There are no other hard phloem elements in *Filipendula* studied.

Soft phloem is about 0.1 mm thick; it consists of homogeneous axial parenchyma and sieve tube members 7—10 μm wide and 100—120 μm long (up to 200 μm in *F. ulmaria*). Each member associates with a strand of companion cells. The sieve plates are simple, slightly oblique.

Wide primary rays lignify (fig. 6, A, B). Secondary rays are indistinguishable.

Rhizome is glabrous and protected with the ordinary epidermis. There is thick (27—30 cell layers) cortical parenchyma under the epidermis (fig. 6, C), which cells increase in size inwards. The innermost cortical layer is an endodermis with typical Casparian bands in radial cell walls.

The periderm originates in the endodermis. 7- to 8-layered phellem of homogeneous, thin-walled, slightly compressed cells arises by the middle of the growing season. The phellem thickens with aging of the rhizome. The cortex loses its shape after the periderm has developed but still remains on the rhizomes (fig. 6, D) as like a case.

There is a 4- to 5-layered parenchymal pericycle between the endodermis and the bundles. Its cells slightly thicken their walls and lignify in the aged rhizome of *F. vulgaris*.

The rhizome is typically eustelic (fig. 6, C, D). Wide unlignifying primary rays separate phloem strands of vascular bundles. We failed to recognize the secondary rays. There is only soft phloem in the rhizome; even the protophloem fibres are absent (fig. 6, C, D). The sieve tube members with slightly oblique simple sieve plates are 10—12 μm wide and 120—200 μm long and associated each with a 4—5-celled strand of companion cells. Axial parenchyma is homogeneous.

Discussion

Both tribes share such characters as eustelic annual stems, clustered protophloem fibres constituting sclerenchymatous «caps» of the bundles, soft annual phloem, simple sieve plates. All the characters occur in a wide range of dicotyledonous plants, however. That is why they are unlikely to be of great taxonomical importance.

Distinctive features are much more numerous. These are: lignifying hypodermis (only in *Filipendula*), cortical chlorenchyma (only in *Roseae*), pericycle (only in *Roseae*), sclerenchymatous bundle «caps» of protophloem fibres (in *Roseae*) or of protophloem fibres and lignifying parenchyma (in *Filipendula*), hardening primary rays (only in *Filipendula*), strips of collapsing sieve tubes, crystalliferous axial parenchyma and fibres in secondary phloem (all in *Roseae*), origin of the first phellogen in the epidermis or outermost collenchyma (in *Roseae*) or in innermost cortical parenchyma (in *Filipendula*). So, we do not think two tribes to be closely related.

Rosa and *Hulthemia* are very similar in their cortex and phloem anatomy. The most conspicuous differences between the two are: much more massive sclerenchymatous pedestals of spines in *Hulthemia*, presence of the cortical chlorenchyma under the

collenchyma in *Rosa*, more narrow and weakly dilated primary rays in *Hulthemia*, presence of the sclereids in crystalliferous parenchyma strands in *Hulthemia*, and diffuse dilatation of the phloem in *Hulthemia*'s perennial branches. Nearly all the differences can be due to the xerophytic adaptations of *Hulthemia*. So, only the dilatation mode could be really considered their distinguishing character. Therefore, we would not prefer *Hulthemia* to be segregated from other *Rosa* species.

Filipendula resembles a bit herbaceous members of *Spiraeoideae* (compare Lotova, Timonin, 1998a, b), especially in deep origin of the first phellogen. That confirms Takhtajan's (1997) statement about the intermediate position of the genus between *Spiraeoideae* and *Rosoideae* subfamilies as well its inclusion into the *Spiraeoideae* (see Kalkman, 1988). However, the similarity of their cortex and phloem anatomies could be a result of the same growth habit rather than an evidence of their relationship. By the way, the rhizome phloem architectures are quite different in *Filipendula* and both spiraeoid's herbs, *Aruncus* (Lotova, Timonin, 1998a) and *Gillenia* (Lotova, Timonin, 1998b). Anyway further investigations are desired to enlighten the relations of *Ulmariaceae* to other rosaceous.

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РЕЗЮМЕ

Трибы *Roseae* и *Ulmariaceae* различаются многими признаками строения первичной коры и флоэмы, но пока неясно, связано ли это с их разными родственными связями или разными жизненными формами. Виды *Rosa* и *Hulthemia* настолько сходны по анатомии первичной коры и флоэмы, что их не следовало бы относить к разным родам. По ряду признаков первичной коры и флоэмы виды трибы *Ulmariaceae* оказались сходными с травянистыми представителями подсемейства *Spiraeoideae*.