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ANATOMY OF CORTEX AND SECONDARY PHLOEM IN ROSACEAE. 5. KERRIEAE AND CERCOCARPEAE (ROSOIDEAE)

Л. И. ЛОТОВА, А. К. ТИМОНИН. АНАТОМИЯ ПЕРВИЧНОЙ И ВТОРИЧНОЙ КОРЫ ROSACEAE.

5. KERRIEAE И CERCOCARPEAE (ROSOIDEAE)

Cortex and phloem anatomy are described in all the genera of Takhtajan's (1987) Kerrieae (Kerria, Neviusia, Rhodotypos) and in one (Cercocarpus) of the two genera of his Cercocarpeae. The Kerrieae genera share many characters of cortex and phloem. However, the specificity of Rhodotypos is likely to be enough for separating in from the Kerria—Neviusia assemblage. Rhodotypos remotely resembles Cercocarpus. Indeed, Cercocarpus markedly differs from both Kerria—Neviusia assemblage and Rhodotypos.

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

Taxonomy of both tribes (Kerrieae and Cercocarpeae) is contestable. W. Focko (1894) recognized Kerrieae of 3 genera (Rhodotypos, Kerria, Neviusia) and Cercocarpeae of 5 genera (Cercocarpus, Adenostoma, Coleogyne, Purshia, Chamaebatia). A. Takhtajan (1987) and G. Hegi (1995) adhered to Focko's version of the Kerrieae. However, C. Kalkman (1988) and Takhtajan (1997) considered Rhodotypos a member of the tribe of itself, the Rhodotypeae, and G. Schulze-Menz (1964) moved Coleogyne from the Cercocarpeae into the Kerrieae.

The Focko's Cercocarpeae was diversely restricted. Schulze-Menz (1964) abolished the tribe entirely placing Chamaebatia, Purshia, Cercocarpus in Dryadeae, Coleogyne in Kerrieae, and Adenostoma in Adenostomeae, respectively. Kalkman (1988) and Hegi (1995) restricted the tribe to 3 genera, Cercocarpus, Coleogyne, and Potaninia. Takhtajan recognized 2 genera (Cercocarpus and Coleogyne) (Takhtajan, 1987) or only one genus (Cercocarpus) (Takhtajan, 1997) to be members of the tribe Cercocarpeae.

Importantly, the bark anatomy is unlikely to have been used for testing the taxonomy of the tribes. It might have never been thoroughly investigated. That is why we examined anatomically the cortex and phloem in *Kerria japonica DC.*, *Rhodotypos kerrioides* Sieb. et Zucc., *R. scandens* (Thunb.) Makino, *Neviusia alabamensis* A. Gray, and *Cercocarpus parvifolius* Nutt. ex Hook. et Arnold which represent all the genera of Takhtajan's (1987) *Kerrieae* and his (Takhtajan, 1997) *Cercocarpeae*, respectively.

Material and methods

One- to two-year-old stems and bark of perennial branch and trunk were sampled from living shrubs grown in Main Botanical Garden of Russian Academy of Sciences, Moscow (Kerria, Rhodotypos kerrioides), in Arboretum «Белые ночи», Sochi, Russia (Kerria, Rhodotypos kerrioides), in Arboretum of Central Republic Botanical Garden of Ukraine, Kiev (Rhodotypos scandens, Neviusia, Cercocarpus). All the samples were fixed with 70 % (v/v) ethanol and sectioned with the hand razor. The sections were treated with either phloroglycinol and hydrochloric acid or 5 % alcoholic iodine. Thereafter, the sections were embedded in glycerol and examined with light microscope. Measurements were taken directly from the slides with calibrated ocular micrometer. Drawings were prepared using the camera lucida technique.

Results

Tribe Kerrieae

Kerria japonica

Deciduous shrub with biennial erect shoots up to 2.0—2.5 m tall (proto-hemicrypto-

phyte by Raunkiaer, 1907).

Annual stem is glabrous (fig. 1, A). One-layered epidermis has very thick outer cell walls. Subepidermal lamellar collenchyma (fig. 1, A) usually consists of 1 discontinuous cell layer. Under the collenchyma, there is 7—9-layered chlorenchyma (fig. 1, A) of thick-walled, roundish or angular cells. Few idioblasts with calcium oxalate druses are scattered among the chlorenchyma cells. Rather large intercellular spaces or even lacunal occur in the cortex.

One-layered endodermis consists of transparent or brown cells (fig. 1, A, D).

There is 1- to 2-layered discontinuous parenchymal pericycle under the endodermis (fig. 1, A, D). Some of its cells divide tangentially (fig. 1, D), but the phellogen does not

appear.

Thick-walled protophloem fibres (fig. 1, D) are in 1—3-layered tangential clusters. Their walls unlignify or hardly lignify. Diverse sclereids with thick lignifying pitted walls laterally adjoin the clusters (fig. 1, A). The protophloem fibres are the only hard elements of annual phloem (fig. 1, A). Sieve tube members are about 10 μ m in width, each associated with a strand of 1—3 companion cells. Sieve plates are simple or compound of 2—4 sieve areas. The axial parenchyma is crystalliferous and mixed.

All the rays are primary, 2-6-seriate.

Biennial branch is still protected with epidermis underlied by the 1-layered angular

collenchyma (fig. 1, C).

The structure of the parenchymal cortex is the same (fig. 1, C) but the cortex widens to 0.14—0.15 mm. One-layered endodermis of transparent or brown cells is clearly visible. The discontinuous parenchymal pericycle under the endodermis is 2- to 3(4)-layered.

There are no phellogen in the branch.

The protophloem fibres are clustered on the outer bundle edges (fig. 1, C). Groups of variable thick-walled lignifying sclereids adjoin the protophloem fibre clusters from

the inside (fig. 1, C).

All other phloem is soft. It is 0.10-0.18 mm thick, the conducting one is 0.04-0.05 mm. The sieve tube members (fig. 1, B) are $10-11\times200-400$ µm, accompanied with a strand of 1-3 companion cells. The sieve plates are simple (oblique or transverse) or compound of 2-4 sieve areas.

Axial parenchyma (fig. 1, B) consists of storage and crystalliferous cells. The former are 1.5—2 times as long as wide; the latter are nearly square in longitudinal section and contain a calcium oxalate druse. The crystalliferous cells are assembled in 5—10-celled

strands or combined as smaller groups with storage cells in a mixed strand.

The nonconducting phloem is similar but the sieve tubes are slightly deformed and

axial parenchyma is stretched.

All the rays are primary. They are straight, homogeneous, 2—6-seriate and extremely high (> 1.5 mm). Some of them rarely aggregate. The ray cells are mostly starch-storing but a few cells with a calcium oxalate rhombohedron, polyhedron or even a druse occur, too.

Rhodotypos kerrioides, R. scandens

Deciduous shrubs with erect long-living branches up to 3 m tall.

Annual stem. One-layered epidermis whose cells have evenly thickened walls is a protective tissue of a young stem (fig. 2, C). It bears very thick cuticle on its surface (fig. 2, C).

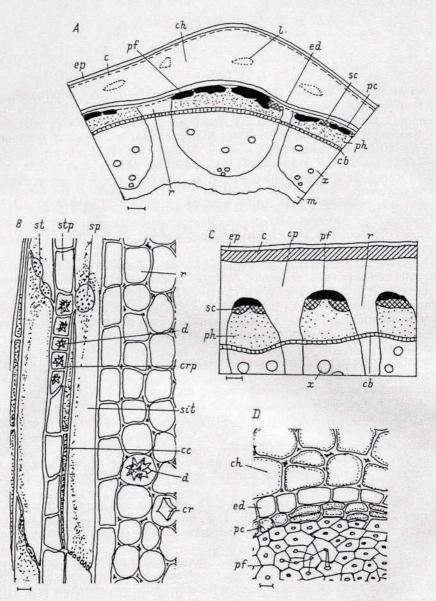


Fig. 1. Kerria japonica.

A— scheme of the annual stem, transverse section; B— secondary phloem, longitudinal section; C— scheme of the biennial stem, transverse section; D— inner cortex of annual stem, transverse section. c— collenchyma, cb— cambium, cc— companion cell, c0— chlorenchyma, c0— cortical parenchyma, c7— calcium oxalate crystal, c7— axial crystalliferous parenchyma, d— calcium oxalate druse, e4— endodermis, e9— epidermis, e1— lacuna, e7— medulla, e7— pericycle, e7— protophloem fibres, e8— phloem, e8— ray, e8— selve tube, e8— sieve tube, e8— axial storage parenchyma, e8— xylem. Bar: e8— e9— 0.01 mm; e8— 0.01 mm.

Subepidermal 2- to 3-layered collenchyma of angular type merges inwards into 4—6-layered cortical parenchyma (fig. 2, A, C). There are numerous idioblasts with 25—27 µm calcium oxalate druse in the cortical parenchyma in R. kerrioides. In R. scandens, the crystalliferous idioblasts are lacking.

The innermost cortical layer is a clearly visible endodermis (fig. 2, A) storing starch.

There are no pericycle in the stem.

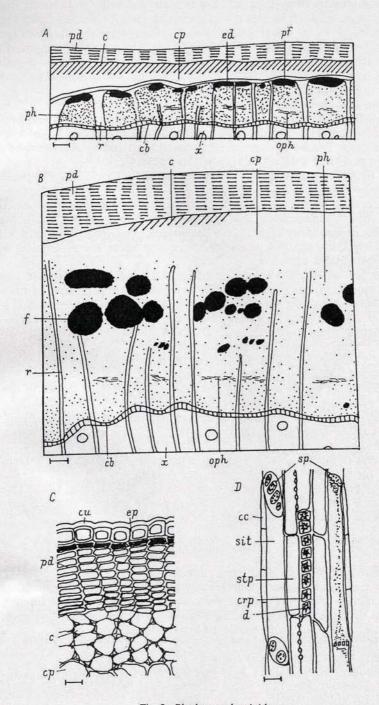


Fig. 2. Rhodotypos kerrioides.

A— scheme of the annual stem, transverse section; B— scheme of the perennial stem, transverse section; C— outer cortex and periderm, transverse section; D— secondary phloem, longitudinal section. cu— cuticle, f— secondary phloem fibres, oph— obliterated compressed phloem, pd— periderm; other signs see fig. 1. Bar: A, B— 0.1 mm; C, D— 0.01 mm.

2—4-layered clusters of protophloem fibres occur under the endodermis (fig. 2, A). The inner phloem is 0.25—0.30 mm thick. It consists only of soft elements (fig. 2, A). The sieve tube members are about 7 μ m wide; the sieve plates are simple or compound of 2 to 3 sieve areas. The simple sieve plates outnumber a lot the compound ones in R. scandens. Each sieve tube member associates with a strand of companion cells. Axial parenchyma is homogeneous. Tangential layers of obliterated phloem occur somewhere in the secondary phloem (fig. 2, A).

The rays are homogeneous, 1—3-seriate.

The first phellogen originates from subepidermal cells and produces periderm (fig. 2, A, C) by the end of the growing season. The brownish phelloderm consists of 3 to 4 layers of thick-walled cells. The 8—10-layered (in R. kerrioides) and 5—8-layered (in R. scandens) phellem consists of uniform thin-walled transparent cells.

Perennial branch is covered by multilayered periderm (fig. 2, B). The phellem cells

are uniform, thin-walled and slightly flattened.

The cortex remains and widens (fig. 2, B) due to proliferation of its tissues. There are rather small pieces of collenchyma under the periderm. Bulky parenchyma is a principal constituent of the cortex. Many cortical cells contain calcium oxalate druse in R. kerrioides.

The endodermis is indistinguishable. That is why there are no distinct boundary

between the cortex and the phloem.

The phloem is 0.40-0.50 mm thick. It differentiates into conducting and nonconducting zones whose interface is obscure. The inner conducting phloem is only 0.12-0.17 mm thick. It consists of soft elements (fig. 2, B). The sieve tube members are about 8 μ m wide and 100 μ m long; the sieve plates are simple or compound of 2-7 sieve areas, with narrow sieve pores (fig. 2, D) in R. kerrioides and mostly simple in R. scandens. Each sieve tube member associates with a 3- to 4-celled strand of the companion cells. There are tangential layers of obliterated sieve tubes between the conducting and nonconducting phloem (fig. 2, B).

Axial parenchyma consists of storage cell strands and of mixed strands of storage and crystalliferous cells. The storage cells are elongated; their walls are often nodular (fig. 2, D). The crystalliferous cells are nearly square in longitudinal section and contain 5 to 6 μ m calcium oxalate druse (fig. 2, D). In R. kerrioides, there are large clusters of brown

cells of the axial parenchyma.

There are lots of fibres in large clusters in the outer nonconducting phloem (fig. 2,

B). The fibres are scanty in the inner conducting phloem.

The rays are homogeneous or nearly homogeneous, 1—3-seriate, 14- to 15-celled in height. They do not dilate. The majority of the ray cells contains starch. Some of them contain 8—20 μ m calcium oxalate druse in *R. kerrioides*.

Neviusia alabamensis

Erect deciduous shrub with long-lived branches.

Annual stem is quadrangularly round in cross section and sparsely pubescent with 1-to 2-celled trichomes (fig. 3, A) whose thick non-lignifying walls are finely papillose through all but the base of a trichome. The epidermis is one-layered and covered with thick cuticle (fig. 3, B). The outer epidermal cell walls are thick.

The lamellar or angular 2-layered collenchyma is under the epidermis (fig. 3, A, B).

Both the epidermal and the collenchymal cells contain brown matter.

Under the collenchyma there is 3—8-layered cortical parenchyma (fig. 3, A, B) of rather large thick-walled cells. Their pitted walls lignify in the early summer. Some cortical cells contain a 10—14 µm calcium oxalate druse.

The innermost layer of the cortex is the endodermis of thin-walled cells (fig. 3, A, B)

with brown contents.

1—3-layered parenchymal pericycle is under the endodermis (fig. 3, A). It slightly proliferates and produces the first phellogen. The latter forms the 10—12-layered periderm by the middle of the growing season (fig. 3, B). The protophloem fibres are clustered like

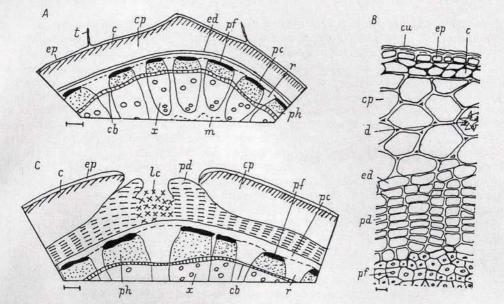


Fig. 3. Neviusia alabamensis.

A — scheme of the annual stem, B — cortex, C — scheme of the perennial stem (A—C — transverse sections). lc — lenticel, t — trichome; other signs see figs. 1, 2. Bar: A, C — 0.1 mm; B — 0.01 mm.

the «caps» over vascular bundles (fig. 3, A, B). There are no other hard phloem elements in the annual branch (fig. 3, A). The soft phloem is 0.06 to 0.10 mm thick. All phloem is conducting. The sieve tube members are $8-9 \times 70-80 \,\mu\text{m}$, associated with a strand of a few companion cells. Simple sieve plates outnumber the compound ones which consist of up to 5 sieve areas. Axial parenchyma is homogeneous, starch-storing. The dilation of the phloem is diffuse.

The primary rays are 4—9-seriate (fig. 3, A). A few secondary rays are uniseriate.

Perennial branch (3 year old). The anatomy of the perennial branch is very similar to that of the annual one. The epidermis and the cortex are mostly preserved (fig. 3, C) though the periderm thickens. The parenchymal pericycle slightly thickens, too.

The clustered protophloem fibres are still the only hard elements of the phloem (fig. 3, C). The soft phloem is 0.80—0.90 mm thick, the conducting phloem is hardly distinguishable from the nonconducting one. The sieve tube members are 8—9 × 70—80 μ m, each associated with a strand of a few companion cells. The sieve plates are usually simple, but compound ones of 2—5 sieve areas do occur. Axial parenchyma is homogeneous. It stores brown substance in the outer phloem.

The rays are homogeneous. The primary 4—9-seriate rays are > 1 mm in height. The

secondary uniseriate rays are 7-15-celled in height.

Cercocarpus parvifolius

Erect deciduous shrub with long-lived branches up to 8 m tall or shrubby tree.

Annual stem is densely pubescent with unicellular subulate lignifying trichomes (fig. 4, A). The epidermis is one-layered and covered with thin cuticle (fig. 4, B). The outer walls of the epidermal cells are extremely thick. There is 1- to 2-layered thin-walled hypodermis under the epidermis (fig. 4, A, B). The subhypodermal 5—7-layered collenchyma is angular at first (fig. 4, B). Then, it changes into the lamellar one. All the collenchymal cells contain chloroplasts. There are idioblasts with a calcium oxalate druse or a calcium oxalate crystal of other from (fig. 4, B) in the collenchyma.

Under the collenchyma there is 4- to 5-layered cortical parenchyma (fig. 4, A, D) which some cells contain a calcium oxalate druse. The starch-storing endodermis is

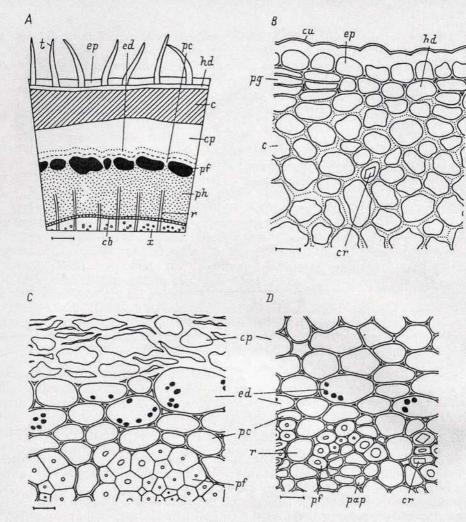


Fig. 4. Cercocarpus parvifolius annual stem, transverse sections.

A — scheme, B — outer cortex, C — inner cortex and outer stele in thickened stem, D — inner cortex and outer stele in thin stem. hd — hypodermis, pap — axial phloem parenchyma, pg — phellogen, other signs see figs. 1—3. Bar: A — 0.1 mm; B - D — 0.01 mm.

1-layered, discontinuous (fig. 4, A, D). The continuous parenchymal pericycle is 1(2)-layered (fig. 4, A, D). At first, both the endodermis and the pericycle are hardly distinguishable from the cortical parenchyma (fig. 4, D).

The first phellogen arises from the hypodermis and produces the phellem of uniform

transparent thin-walled cells.

Clusters of protophloem fibres constitute nearly continuous ring 6—8 fibres thick (fig. 4, A, D). Sparse pits are seen in the fibre walls. There are thin-walled lignifying parenchymal cells with a calcium oxalate crystal among the fibres (fig. 4, D). There are no other hard phloem elements in the annual branch (fig. 4, A). The soft phloem is 0.06 to 0.07 mm thick. The sieve tubes are 4—8 μ m in width. The sieve tube members associate with a strand of 1 to 2 companion cells. The sieve plates are simple, transverse or oblique. Axial parenchyma is fairly homogeneous. Varying pieces of obliterated phloem develop very early

The primary 1- to 2-seriate rays disappear in the outer half of the phloem zone (fig. 4, A). As the annual branch thickens, the periderm replaces the epidermis. Outer cell layers of the multilayered phellem gradually slough off.

The collenchyma becomes lamellar; solitary thin-walled lignifying fibres appear in the collenchyma. The cortical parenchyma obliterates up to 3 parenchymal cell layers adjoining the protophloem fibres (fig. 4, C). Those are the endodermis and pericycle combined, because by this time the two cannot be distinguished. Some starch occurs in some cells of each layer. The protophloem clusters depart slightly from one another due to parenchyma dilation. The phloem width increases to 0.19—0.23 mm; the conducting phloem is about 0.05 mm wide. It consists only of soft elements. The sieve tubes are 4—8 µm in width. The sieve tube members associate with a strand of 1 to 2 companion cells. The sieve plates are simple, transverse or oblique.

Axial parenchyma is homogeneous. The rays are uniseriate and 2- to 3-seriate, straight. Nearly continuous 2—4-layered ring of secondary phloem fibres marks the inner boundary of the nonconducting phloem. Very thin layer of obliterated soft phloem adjoins in from the inside. The ring of small dispersed clusters of the secondary phloem fibres is in the middle of the nonconducting phloem zone. There are numerous radial masses of obliterated phloem in between the fibre rings. The axial parenchyma is mostly storage though there are no starch there, yet. A few strands of crystalliferous cells with calcium oxalate prism and lignifying walls neighbour the fibre clusters.

The rays are quite visible; they undulate and slightly dilate.

The phloem in between the second ring of the secondary phloem fibres and the protophloem fibre clusters consists of bulky parenchyma dilating diffusely and scanty obliterated phloem. The rays are invisible.

Perennial branch is protected with multilayered, small-scaly phellem. The multilayered zones of brown cells alternate with those of transparent cells in the phellem. The

phelloderm is 1-layered.

The cells of the 6—8-layered lamellar colenchyma are very stretched tangentially. There are 5 to 6 layers of the cortical parenchyma under the collenchyma which proliferate and store starch. Neither the endodermis nor the pericycle can be recognized in the cortex.

The boundary between the cortex and the phloem disappears because of phloem parenchyma proliferation and lateral shifting of the protophloem clusters. The phloem is 0.32-0.39 mm thick, the conducting one is 0.03 mm. The sieve tube members are tangentially flattened, $10-11\times6-7$ μm in width. A strand of (1)2 companion cells accompanies each sieve tube member. The sieve plates are simple, oblique.

Axial parenchyma is homogeneous. The rays are straight, 2(3)-seriate.

In nonconducting phloem, the sieve tubes and companion cells die off to become a bulky obliterated phloem in between the more or less continuous rings of secondary phloem fibres. The parenchyma differentiates into storage and crystalliferous ones. The former proliferates, especially outside the outer secondary phloem fibres' ring. The latter adjoins the secondary phloem fibres' clusters; its cells contain a calcium oxalate prism.

The rays undulate and slightly dilate in the inner nonconducting phloem and dissapear

outside the outer ring of the secondary phloem fibres.

Trunk is covered with scaly rhytidome resulted from successive periderms that arise inwards the cortex and outer phloem. First the cortex, then the outer phloem gradually slough off with shedding of the outer rhytidome scales. So, the innermost trunk periderm adjoins the nonconducting phloem (fig. 5, A). The tissue in between periderms consists of brown dead parenchyma cells and dispersed secondary phloem fibres, lots of which are tangentially re-arranged. Strand(s) of crystalliferous cells acompany(ies) the fibres (fig. 5, B). Multilayered phellem consists of alternating zones of roundish and tangentially flattened cells; slightly lignifying phelloids are scattered there (fig. 5, C).

The total phloem is extremely wide, about 2.0—2.1 mm. The conducting phloem, however, does not exceed 0.03 mm in width. It consists only of soft elements (fig. 5, A, 6, A). The sieve tube members are tangentially flattened, $10-11 \times 6-7$ μ m wide and 97—105 μ m long. A strand of 2 to 3 companion cells associates with each sieve tube member (fig. 6, B, C). The sieve plates are simple, oblique (fig. 6, C, D). Axial

parenchyma is homogeneous (fig. 6, B).

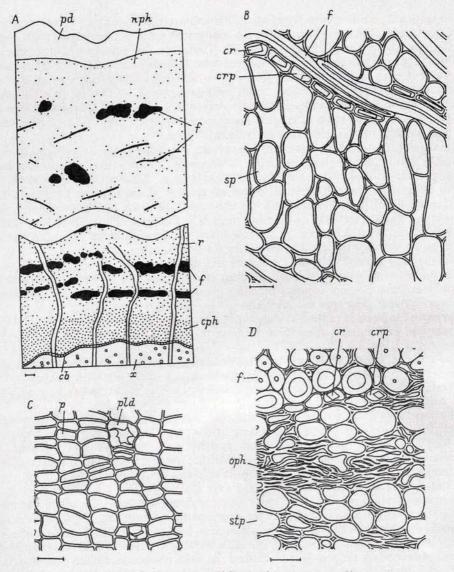


Fig. 5. Cercocarpus parvifolius trunk, transverse sections.

A— scheme, B— the outermost nonconducting phloem, C— phellem, D— inner nonconducting phloem, cph— conducting phloem, cph— nonconducting phloem, p— phellem, pld— phelloid; other signs see figs. 1—3. Bar: A— 0.1 mm; B—D— 0.01 mm.

The rays are nearly heterogeneous (fig. 6, C). 2-seriate rays considerably outnumber uniseriate ones; a few rays are partly 3-seriate (fig. 6, C). The 2-seriate rays are 14—35 cells in hight, with high uniseriate wedges; the uniseriate rays are 5—7(12) cells in height.

The inner $\sim 40\%$ of nonconducting phloem consist of more or less complete rings of secondary phloem fibres which alternate with the soft phloem (fig. 5, A). The sieve tubes and the companion cells die off (fig. 6, A) to form bulky mass of the fully compressed tissue (fig. 5, D) where no cells usually distinguishable. Axial parenchyma differentiates into storage and crystalliferous parenchyma. Rather scanty crystalliferous one acompanies the secondary phloem fibres' clusters (fig. 5, D). Its cells contain a calcium oxalate prism (fig. 5, D, 6, C, D). The storage parenchyma slightly proliferates and stores little starch (fig. 5, D, 6, C, D).

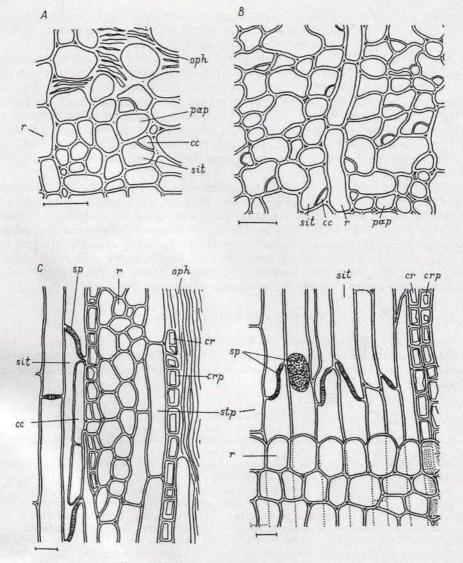


Fig. 6. Cercocarpus parvifolius trunk phloem.

A — outer conducting phloem, transverse section;
 B — conducting phloem, transverse section;
 C — outer conducting phloem, transverse section;
 D — outer conducting phloem, radial section.
 Signs see figs. 1, 2, 4. Bar — 0.01 mm.

Rays hardly undulate and a bit dilate (fig. 5, A). They harden where they cross the fibre clusters.

The outer nonconducting phloem mostly consists of bulky storage parenchyma which a lot proliferates (fig. 5, A, B). So, the dilation is diffuse. The rings of secondary phloem fibres dispart. Original longitudinal arrangement of some fibres changes to oblique or even tangential one (fig. 5, A, B). Single and clustered sclereids appear in the phloem. The rays are invisible in the outer nonconducting phloem (fig. 5, A).

Discussion

The tribes seem to be distantly related. Indeed, Cercocarpus differs from the Kerrieae members in simple sieve plates, nearly continuous rings of secondary phloem fibres in

the inner nonconducting phloem, conspicuous dilation of the storage parenchyma (causing re-orientation of some fibres), scaly rhytidome and calcium oxalate prisms. Besides, it

differs from Neviusia in hypodermal origin of the first phellogen.

The 3 genera of Focko's tribe Kerrieae share only both simple and compound sieve plates, calcium oxalate druses in the axial crystalliferous parenchyma, protophloem fibres' clusters and cortex structure. Kerria and Neviusia are much more similar while Rhodotypos differs from the both by the fine structure of the epidermis, absence of the pericycle, narrow primary rays, masses of compressed soft phloem in nonconducting zone, development of the secondary phloem fibres there. Besides, the first phellogen arises in the hypodermis in Rhodotypos and in the pericycle in Neviusia; there is no phellogen in Kerria though rare tangential divisions of some pericyclic cells could be a vestige of the phellogen origin.

The place where the first phellogen arises must be a character of importance for classifying Rosaceae (Focko, 1894; Lotova, Timonin, 1998, 1999). Then, we believe Rhodotypos to be worth separating from the Kerria—Neviusia assemblage in harmony with Kalkman (1988) and Takhtajan (1997). Rhodotypos could even be likened to Cercocarpus in that character. Nevertheless we do not really consider Rhodotypos and Cercocarpus to be closely related. However, these results do not seem to be enough for confirming segregation the Rhodotypos—Kerria—Neviusia complex from traditional

Rosoideae into specific subfamily Kerrioideae (Takhtajan, 1997).

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РЕЗЮМЕ

Описана анатомия кортекса и флоэмы у всех трех родов, включаемых А. Л. Тахтаджяном (1987) в трибу Kerrieae (Kerria, Neviusia, Rhodotypos), и одного (Cercocarpus) из двух родов, относимых им к трибе Cercocarpeae. Роды из трибы Kerrieae сходны по многим признакам кортекса и флоэмы, однако своеобразие рода Rhodotypos представляется достаточным для того, чтобы отделить его от комплекса Kerria—Neviusia. Этот род несколько напоминает Cercocarpus. В то же время род Cercocarpus весьма существенно отличается как от комплекса Kerria—Neviusia, так и от рода Rhodotypos.