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ANATOMY OF CORTEX AND SECONDARY PHLOEM IN ROSACEAE. 3. QUILLAJOIDEAE

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3. QUILLAJOIDEAE

Cortex and phloem anatomy is described in two (*Quillaja*, *Holodiscus*) of three genera of Takhtajan's (1987) *Quillajoideae* subfamily which represent both of its tribes. The two differ in cortex patterns, sites of the first phellogen initiation, protective structures of old branches, modes of secondary phloem dilatation, and contents of the axial crystalliferous parenchyma. Common characters are very few. Moreover, some of them are distinctive in details. Therefore, the congregating of both in one subfamily can be inappropriate.

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

A. L. Takhtajan (1987) has created new subfamily *Quillajoideae* to set apart three genera, *Quillaja*, *Kageneckia*, and *Holodiscus*, which are usually considered the members of *Spiraeoideae* subfamily (Focko, 1894; Lehmann, 1971; Hegi, 1995). These genera are subordinated to two tribes: *Quillajeae* (*Quillaja*, *Kageneckia*) and *Holodisceae* (*Holodiscus*).

Being of use for a long time the *Quillaja* bark is the most scrutinized anatomically now. Yet, J. Moeller (1882) already described it stressing such its attributes as saponin-bearing cells in cortex, tangential layers of phloem fibres, simple sieve plates, large calcium oxalate styloids, etc. The latter features used to be recognized elsewhere as a unique character among rosaceous (Focko, 1894; Metcalfe, Chalk, 1950; Lehmann, 1971). Data of *Holodiscus* bark is exhausted with the notion of deep origin of the phellogen (Focko, 1894). We have not found any information on the anatomy of *Kageneckia* bark.

Importantly, the barks of the three genera were, perhaps, never compared to test their affinity. We have examined anatomically the cortex and phloem in *Quillaja brasiliensis* Mart. and *Holodiscus discolor* Maxim. to fill this gap.

Material and methods

One- to two-year-old stems and bark of perennial branch and trunk in *Quillaja brasiliensis* were sampled from living tree grown in the greenhouse of Main Botanical Garden of Russian Academy of Sciences, Moscow. Samples of *Holodiscus discolor* bark were collected in Arboretum of Central Republic Botanical Garden of Ukraine, Kiev. All the samples were fixed with 70 % (v/v) ethanol and sectioned with the hand razor. The slides were processed with either phloroglycinol 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. Drawings were prepared using the camera lucida.

Quillaja brasiliensis

Underwoody ever-green tree.

Annual stem (Fig. 1). One-layered epidermis protects very young stem. Outer walls of its cells are rather vaulted (fig. 1, B). Subepidermal lamellar collenchyma (fig. 1, A, B) consists of 1 to 2(3) cell layers and is interrupted under the stomata.

Then, the outermost collenchyma cells give rise to phellogen which produces thin periderm (fig. 1, B). It extends circumferentially replacing the epidermis almost completely by the end of a year.

Under the collenchyma there is 6—8-layered chlorenchyma (fig. 1, A) which intergrades inwards into 5- to 6-layered cortical parenchyma. The border between the two is very obscure. Fairly large intercellular spaces occur in both tissues. Crystalliferous idioblasts are scattered within the cortex inside the collenchyma. They contain calcium oxalate druse or, more rarely, calcium oxalate styloid. Clustered cells with coagulated yellow-brown contents occur predominantly in the cortical chlorenchyma. These would correspond to the saponin-bearing cells in *Q. saponaria* mentioned by Moeller (1882).

There is no distinguishable endodermis in *Q. brasiliensis* cortex.

Clustered protophloem fibres are the only hard elements of annual phloem (fig. 1, A). Soft phloem elements slightly obliterate somewhere under the fibres' clusters. Sieve tube members are about 8 to 10 μ m in width, each associated with single strand of companion cells. Sieve plates are simple, transverse and bear wide sieve pores. The axial parenchyma is rather homogeneous though some giant cells do occur in outer phloem. Uniseriate rays predominate; bi(tri)-seriate rays are very scanty. Rays are heterogeneous. The ray parenchyma never hardens.

Initially, the whole phloem is fairly thin and conducting. It gradually widens and outer nonconducting phloem appears with aging of stem. The axial parenchyma becomes heterogeneous consisting of crystalliferous and potentially storage cell strands. The crystalliferous cells with calcium oxalate styloid differentiate quite quickly becoming visible adjacent to the cambium. Similar cells appear less frequently in rays as well.

Perennial branch. Multi-layered periderm protects the perennial branch. The phellem consists of uniform thick-walled cells. The cortex remains under the periderm. The

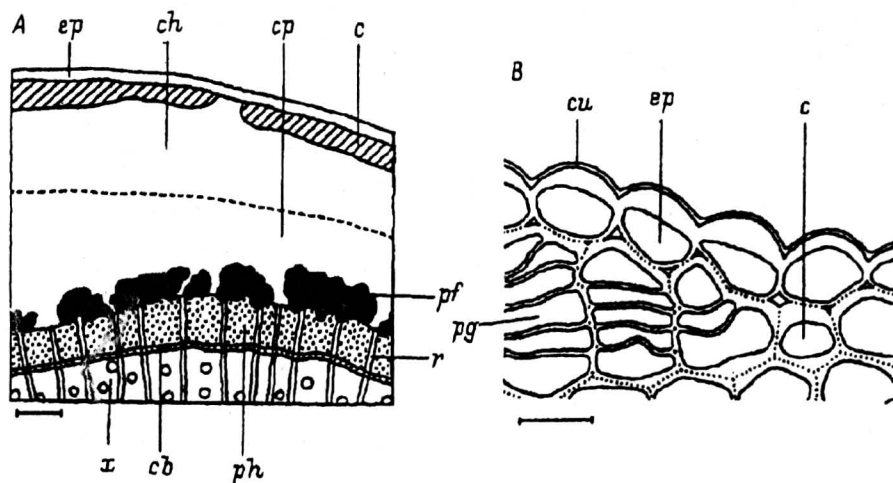


Fig. 1. *Quillaja brasiliensis* annual stem, transverse sections.

A — scheme of the stem, B — origin of the first phellogen. c — collenchyma, cb — cambium, ch — chlorenchyma, cp — cortical parenchyma, cu — cuticle, ep — epidermis, pf — protophloem fibres, pg — phellogen, ph — phloem, r — ray, x — xylem. Bar: A — 0.1 mm, B — 0.01 mm.

distinction between cortical tissues decreases with the proliferation and dilatation of their cells. So, the cortex of old branches seems homogeneous.

The border between the cortex and the stele is much less distinctive because the external phloem parenchyma exceedingly proliferates and widely moves aside the protophloem fibres' clusters that mark the border, while both cortical and ray parenchyma are very similar.

The phloem widens up to 1 to 1.2 mm; its conducting zone does not exceed a half of its total width. The conducting phloem consists of soft elements only. Sieve tubes are about twice as wide as those in annual stem. Sieve plates are simple. Styloid-bearing cells are numerous throughout the conducting phloem. Storage parenchyma does not contain starch.

In nonconducting phloem, the sieve tubes obliterate and axial parenchyma proliferates except the crystal-bearing cells. Single and clustered fibres develop in this zone. They tend to aggregate into small tangential rows.

Rays are heterogeneous. Uniseriate rays are as numerous as the 2(3)-seriate ones. All the rays cross the conducting phloem and disappear in nonconducting phloem.

Trunk (fig. 2, 3). The trunk is covered with scaly rhytidome (fig. 2, A) formed by periderms that arise successively inwards the cortex and outer phloem. Then, the cortex and outer phloem gradually slough off with shedding of the outer rhytidome scales. So, the innermost trunk periderm adjoins the nonconducting phloem. The latter constitutes the scale tissue in between the periderms. Phellem comprises about 30 layers of uniform thick-walled cells (fig. 2, B).

The total phloem is extremely wide, about 3 mm. The conducting phloem, however, does not exceed 0.3 mm in width. It consists of soft elements only (fig. 2, A, D). The sieve tube members are 22—28 μm wide and 100—135 μm long. Each member is associated with a 3—5-celled strand of companion cells. Sieve plates are simple, oblique, with giant sieve pores (fig. 3, C, D). Axial parenchyma (fig. 2, E; 3, C, D) consists of abundant styloid-bearing strands and prospective storage strands. The former are short, 4—6-celled. Each their cell usually contains single styloid of calcium oxalate (fig. 3, C, D) which is rarely accompanied by smaller one(s) (fig. 3, D) or contains single or clustered crystals (fig. 3, A). Storage parenchyma strands are longer, up to 8—10 cells in length. When in adjacent nonconducting phloem, they store starch.

The nonconducting phloem consists of two zones (fig. 2, A). The inner one dilates moderately. Its sieve tubes obliterate, axial storage parenchyma proliferates slightly (fig. 2, D). Abundant fibres, single or clustered, develop in the zone (fig. 2, A, D). They tend to aggregate in tangential rows. A few solitary and weakly clustered pitted sclereids as well as cells with clustered crystals arise in peripheral inner zone of nonconducting phloem (fig. 2, C).

Soft tissue of the outer nonconducting zone extremely dilates. Its cells extend tangentially causing tangential returning of some styloids (fig. 3, B). The hard elements moved aside by dilating soft tissue look nearly absent (fig. 2, A).

Heterogeneous 2- to 3-seriate rays (fig. 3, C, D) cross the conducting and inner nonconducting phloem and disappear in the outer nonconducting phloem (fig. 2, A). Rays range from 35 to 40 μm in width and from 140 to 180 μm in height.

Holodiscus discolor

Deciduous shrub with arching branches.

Annual stem (fig. 4). Ordinary one-layered epidermis is a protective tissue of young stem (fig. 4, A). It bears numerous unicellular, thick-walled, long, strait or hooked trichomes. Subepidermal collenchyma of angular type occurs only in stem ribs (fig. 4, A). It lignifies then. 3- to 4-layered cortical parenchyma consists of very large cells (fig. 4, C) which walls lignify by the end of growing season. The innermost cortical layer is a clearly discernible endodermis of large uniform thin-walled cells (fig. 4, C) with brown contents.

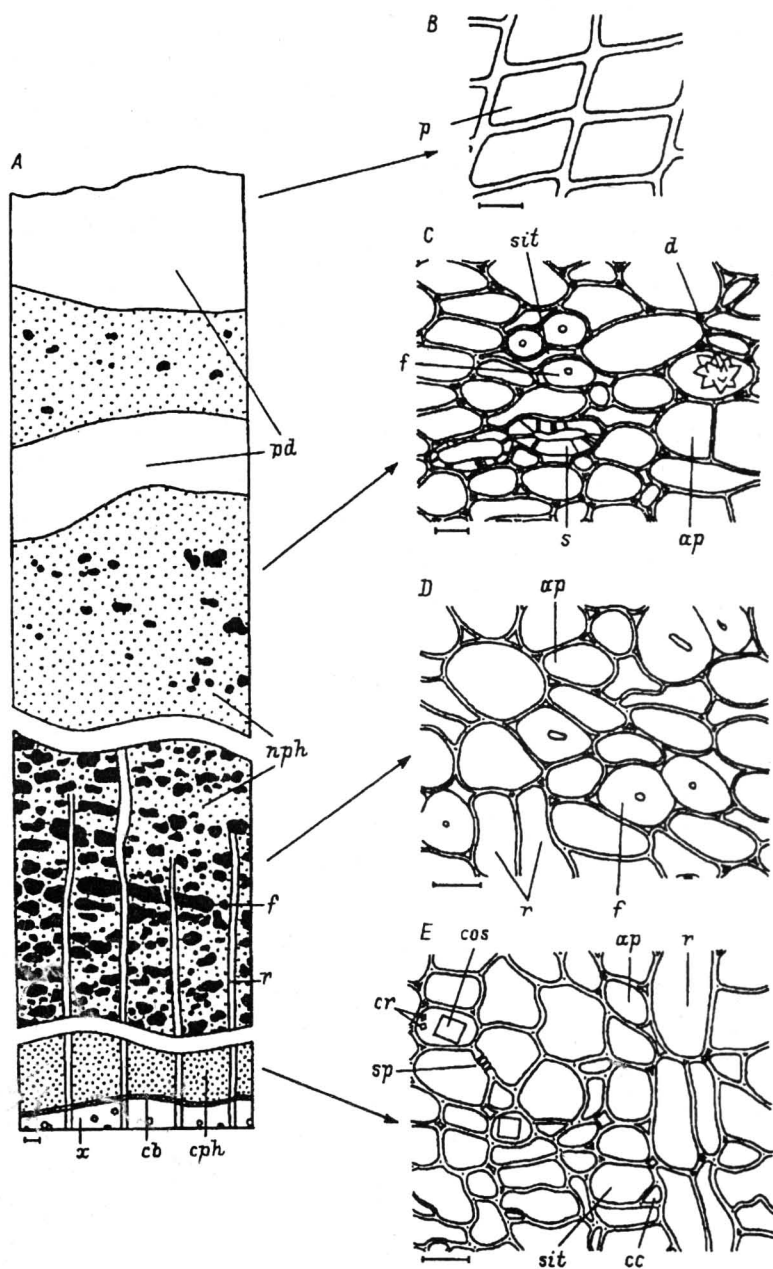


Fig. 2. *Quillaja brasiliensis* trunk bark, transverse sections.

A — scheme of the bark, B — phellem, C — outer nonconducting phloem, D — inner nonconducting phloem, E — conducting phloem. *ap* — axial parenchyma, *cc* — companion cell, *cph* — conducting phloem, *cos* — calcium oxalate styloid, *cr* — calcium oxalate crystal, *d* — calcium oxalate druse, *f* — secondary phloem fibres, *nph* — nonconducting phloem, *pd* — periderm, *p* — phellem, *s* — sclereid, *sp* — sieve plate, *sit* — sieve tube. Other signs are the same as in fig 1. Bar: A — 0.1 mm, B—E — 0.01 mm.

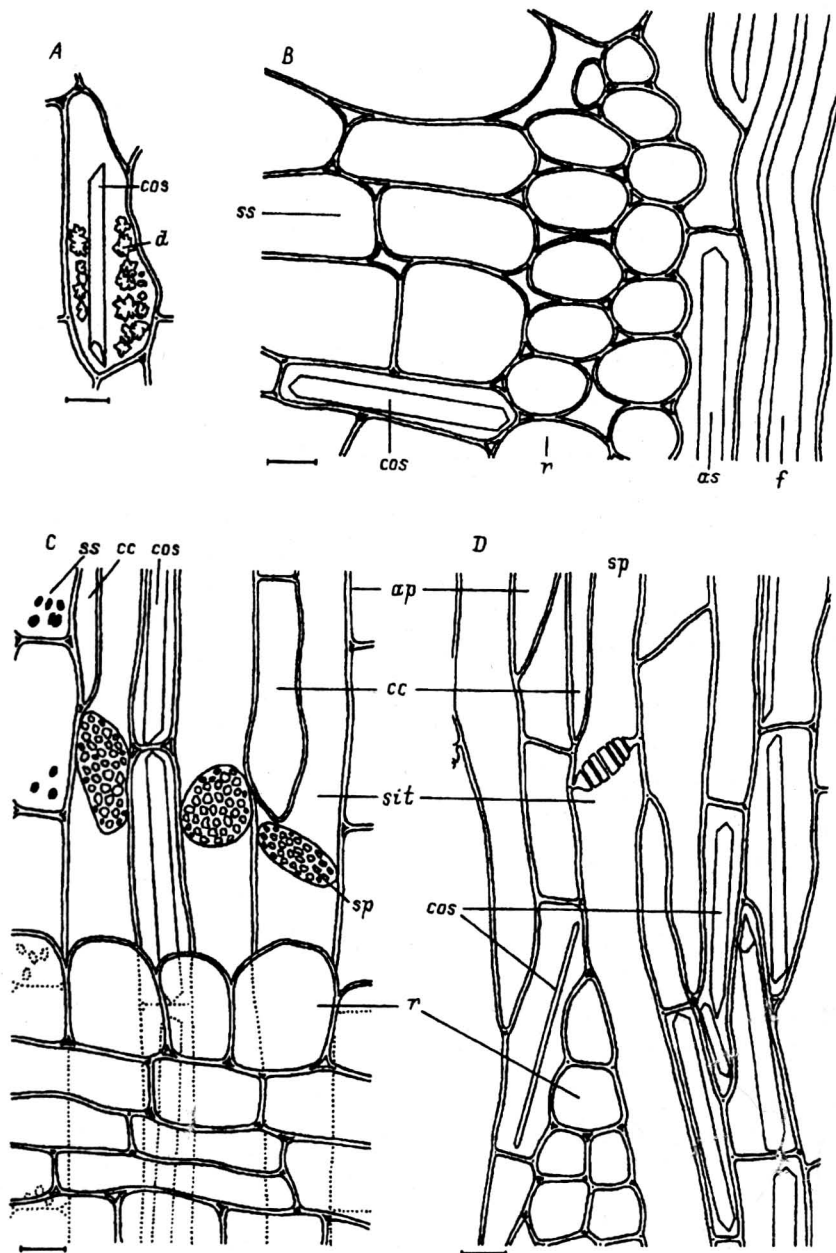


Fig. 3. *Quillaja brasiliensis* trunk phloem.

A — styloid-bearing cell of axial parenchyma, longitudinal section; B — outer nonconducting phloem, tangential section; C — outer conducting phloem, radial section; D — outer conducting phloem, tangential section. ss — starch-storing parenchyma. Other signs are the same as in figs. 1, 2. Bar — 0.01 mm.

Under the endodermis there is 4- to 5-layered small-celled parenchymal pericycle (fig. 4, A). Its external cells give rise to the phellogen which produces only 1—3 layers of thin-walled phellem cells during the first growing season (fig. 4, C).

Clustered protophloem fibres occur under the pericycle (fig. 4, A, C). Inner phloem consists only of soft elements (fig. 4, A). The sieve tube members are 10—12 μ m wide,

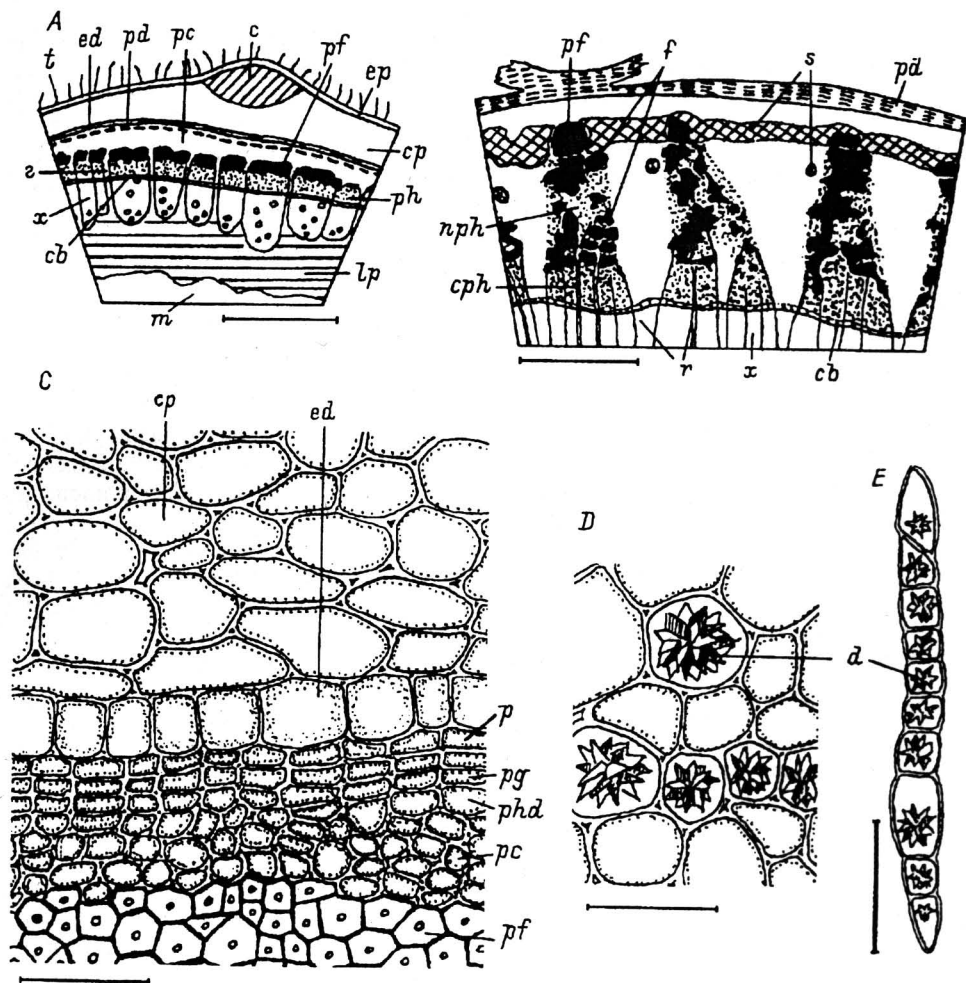


Fig. 4. *Holodiscus discolor*.

A — annual stem, transverse section; B — perennial branch, transverse section; C — developing first periderm, transverse section; D — ray crystaliferous cells, radial section; E — axial crystaliferous cells, longitudinal section. ed — endodermis, lp — lignified parenchyma, m — medulla, pc — pericycle, phd — phelloderm, t — trichome. Other signs are the same as in figs. 1—3. Bar: A, B — 0.1 mm; C—E — 0.01 mm.

with simple sieve plates and single strand of companion cells. Axial parenchyma is homogeneous. Neither obliterated nor dilated phloem elements are seen.

The rays are homogeneous, uni- and 2—4-seriate.

Perennial branch (fig. 4). Multi-layered periderm covers the perennial branch (fig. 4, B). Uniform flattened phellem cells with thick walls contain brown contents. Outer parts of the phellem slough off time to time. The phelloderm is 2- to 3-layered, parenchymal. 4- to 6-layered pericyclic parenchyma occurs under the phelloderm (fig. 4, B).

Continuous ring of sclerenchyma develops along the phloem periphery. It consists of clustered protophloem fibres and hardening outer ray parenchyma (fig. 4, B). The phloem differentiates into conducting and nonconducting zones which border is obscure.

The inner conducting phloem consists of soft elements (fig. 4, B). The sieve tube members are 12 to 13 μ m wide and 160—170 μ m long; sieve plates are simple, transverse or oblique, with narrow sieve pores. The companion cells are usually invisible. Axial parenchyma is homogeneous.

In nonconducting phloem, the sieve tubes obliterate. Axial parenchyma differentiates into crystalliferous and storage cell strands. The crystalliferous cells contain calcium oxalate druse (fig. 4, *E*). Axial parenchyma cells lose their shapes in the outermost nonconducting phloem. Fibres' clusters of different shapes and sizes develop in nonconducting phloem (fig. 4, *B*). Sometimes, scanty sclereids are seen among the fibres.

The rays are homogeneous. The primary ones are multiseriate. They extremely dilate outwards (fig. 4, *B*); almost all of their cells contain calcium oxalate druse (fig. 4, *D*). The secondary rays are either uniseriate or 2–4-seriate, 8–30-celled in height. Only some of them slightly dilate (fig. 4, *B*). Small clusters of hardened cells are scattered within the rays (fig. 4, *B*).

Discussion

There are only a few common characters in the two investigated genera. Both have clustered protophloem fibres, simple sieve plates, and similar architecture of secondary phloem. The similarity is caused by the diverse clustering of the secondary phloem fibres in small groups.

Distinctive features are, however, much more numerous. Indeed, *Quillaja* has a well-developed chlorenchyma and no endodermis in its cortex while *Holodiscus* sharply contrasts with conspicuous endodermis and no chlorenchyma. Subepidermal collenchyma constitutes almost complete ring in *Quillaja* and is restricted to the stem ribs in *Holodiscus*. The first phellogen arises in subepidermal cell layer in *Quillaja* and in the pericycle in *Holodiscus*. The first periderm remains for branch life in *Holodiscus*, but scaly rhytidome develops on *Quillaja*'s trunk and aging branches.

Secondary phloem diffusely dilates in *Quillaja*. On the contrary, extreme dilatation of the primary rays is inherent in *Holodiscus*, while its axial phloem elements dilate quite weakly. The crystalliferous phloem parenchyma bears calcium oxalate styloids in *Quillaja* and calcium oxalate druses in *Holodiscus*.

2- to 3-seriate rays cross the aged phloem in *Quillaja* but both uniseriate rays and exceedingly dilated multiseriate primary rays occur in *Holodiscus*. The rays are heterogeneous in *Quillaja* and homogeneous in *Holodiscus*.

Even the common features differ in detail in both genera. In *Quillaja*, the clusters of the secondary phloem fibres tend to be tangentially rowed. In *Holodiscus*, they are scattered rather irregularly. Sieve pores are quite narrow in *Holodiscus* and are extremely wide in *Quillaja*.

Above-mentioned prevalence of bark distinctions over the similarities between the two genera shows, perhaps, miscellaneous nature of Takhtajan's (1987) *Quillajoideae*. Then, separating *Quillaja* and *Holodiscus* is quite reasonable. Takhtajan (1997) re-placed *Holodiscus* into *Spiraeoideae* in his latest version of *Rosaceae* taxonomy. The genus shares deep origin of the first phellogen with the members of subfamily *Spiraeoideae*. However, anatomy of both cortex and secondary phloem is highly variable in *Spiraeoideae* and only deep origin of the first phellogen is a real taxonomic mark of the subfamily (Focke, 1894; Lotova, Timonin, 1998). Thus, the taxonomic position of *Holodiscus* is still disputable.

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РЕЗЮМЕ

Описана анатомия первичной и вторичной коры у двух (*Quillaja*, *Holodiscus*) из трех родов, относимых А. Л. Тахтаджяном (1987) к подсемейству *Quillajoideae*, которые представляют обе его трибы. Оба рода различаются по общей структуре первичной коры, месту заложения первого феллогена, характеру покровных структур многолетних ветвей, типу дилатации вторичной флоэмы и типу кристаллических включений флоэмной паренхимы. Общие признаки очень немногочисленны, а некоторые из них в деталях различны. Поэтому объединение обоих родов в одном подсемействе нецелесообразно.