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**ANATOMY OF CORTEX AND SECONDARY PHLOEM OF ROSACEAE.  
6. RUBEAE AND ADENOSTOMEAE (ROSOIDEAE)**

Л. И. ЛОТОВА, А. К. ТИМОНИН. АНАТОМИЯ ПЕРВИЧНОЙ КОРЫ И ВТОРИЧНОЙ ROSACEAE.  
6. RUBEAE И ADENOSTOMEAE (ROSOIDEAE)

Cortex and phloem anatomy of annual and perennial stems and rhizomes is described in 7 *Rubus* and 1 *Adenostoma* species. The structural patterns are rather variable in *Rubus* but they correlate neither with growth habits nor with taxonomy of the species. The separation of *Rubacer* from other *Rubus* members is not confirmed. The some similarities between the tribes *Rubeae* and *Potentilleae* are presented. The tribe *Adenostomeae* is established to be distantly related with the tribe *Cercocarpeae*.

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

The article is a continuation of serial researchs of rosaceous cortex and bark anatomy to have an insight into the subfamilial classification of the family. We adhere to A. Takhtajan's (1987) version of rosaceous classification here just as we did in our previous articles.

Takhtajan (1987) followed G. Schulze-Menz (1964) in considering the two tribes monotypic. The standpoint was later confirmed by C. Kalkman (1988) and G. Hegi (1995) as well. *Rubus* and *Adenostoma* were traditionally regarded (Focke, 1894) to belong to tribes *Potentilleae* (as a member of monotypic subtribe *Rubinae*) and *Cercocarpeae*, respectively. Takhtajan (1997) raised *Rubeae* up to subfamily *Rubioideae* and transferred *Adenostomeae* to the subfamily *Spiraeoideae* in his latest version of *Rosaceae* taxonomy.

*Rubus* species vary from erect tall shrubs with perennial branches through erect or creeping shrubs with biennial branches (proto-hemicryptophyte by Raunkiaer, 1907) to rhizomatous herbs with or without stolons. Few *Adenostoma* species are invariably perennially-branched shrubs. Both the cortex and the bark of the two genera have been anatomically scrutinized.

**Materials and methods**

Annual and perennial branches of shrubs and aerial shoots, stolons, and rhizomes of herbs were sampled for investigation. The samples were taken from living plants grown in the Botanical Garden of Lomonosov Moscow State University (*Rubus deliciosus* Torr., *R. odoratus* L., *R. turkestanicus* (Regel) Regel) or dwelling their natural habitats near 50 km west to Moscow (*R. idaeus* L., *R. saxatilis* L.). The living branches of *Adenostoma fasciculatum* Hook. et Arn. were provided by Dr. J. L. S. Keesing, Royal Botanic Gardens, Kew. We used branch fragments of herbarium specimens of *Rubus steudneri* Schweinf. gathered in Bale Mountains National Park, Ethiopia, by Dr. V. N. Pavlov, Lomonosov Moscow State University.

All material sampled from living plants was fixed with 70 % (v/v) ethanol. The voucher fragments were softened with an ethanol—glycerol—water (1 : 1 : 1) mixture at 30 °C for a month. The plants' fixed and softened pieces were sectioned with the hand razor. The transverse, tangential, and radial slides were processed with either phlorogly-

cinol and hydrochloric acid or with 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 technique.

## Results

### Tribe *Rubeae*

*Rubus deliciosus*, *R. idaeus*, *R. odoratus*, *R. saxatilis*,  
*R. steudneri*, *R. turkestanicus*

Stoloniferous rhizomatous herb (*R. saxatilis*), rather tall erect shrub with perennial branches (*R. steudneri*), creeping (*R. deliciosus*) or erect shrubs with biennial branches (others).

Annual stems are quadrangular (*R. odoratus*), 5-ridged (*R. steudneri*, fig. 2, A) or roundish (others).

Ordinary epidermis bears more or less numerous unicellular thick-walled subulate trichomes (fig. 1, B, F) some of which are hooked in *R. odoratus*. The trichomes are much longer in *R. steudneri*. There are glandular emergences among the trichomes (fig. 1, A, B; 2, A). The emergence consists of long multicellular multiseriate stock (fig. 1, B, D) and roundish multicellular glandular head (fig. 1, D).

2- to 5-layered collenchyma of angular or lamellar-angular types is subepidermal in all species (fig. 1, A, F; 2, E) except for *R. idaeus* which has 2-layered chlorenchyma between the epidermis and the chlorenchyma. Inner cortical tissue consists of 4 to 5 layers of parenchyma cells (fig. 1, A, C, F; 2, E), those adjoining the collenchyma are darker in *R. turkestanicus* and slightly deformed in *R. steudneri*. The cortical parenchyma contains numerous idioblasts with a druse of calcium oxalate in *R. steudneri* (fig. 2, B). The innermost cortical layer develops into starch-bearing endodermis (fig. 1, F; 2, B).

The stems are eustelic in all studied species (fig. 1, A, F; 2, A, B). Protophloem fibres differentiate in clusters which are nearly square (*R. steudneri*, thinner branches — fig. 2, A), radially elongated (*R. steudneri*, thicker branches — fig. 2, B), and tangentially elongated (other species — fig. 1, A, F) in transverse section. The fibres are thin-walled in *R. turkestanicus*. Only protophloem fibres are hard phloem elements in annual stem (fig. 1, A, F; 2, A, B). The soft phloem is as thick as the protophloem clusters in most species studied and only half as thick as the clusters in *R. steudneri*.

Sieve tube members (fig. 1, E) are  $10-18 \times 80-180 \mu\text{m}$  ( $20-30 \times 200-300 \mu\text{m}$  in *R. steudneri*), each member associates with single strand of 2 to 3 companion cells. The sieve plates are always simple, oblique or very oblique in *R. steudneri*. (The simple sieve plates strongly oppose the composed perforate plates in *R. turkestanicus*). The axial parenchyma consists of uniform elongated storing cells (fig. 2, D) in all species but *R. odoratus*. The latter has elongated-celled storing parenchyma as well as short-celled crystalliferous one (fig. 1, E). Each its cell contains a  $7.5 \times 12.5 \mu\text{m}$  druse of calcium oxalate.

2—6-seriate primary rays are heterogeneous in *R. steudneri*, *R. turkestanicus*, homogeneous procumbent-celled in *R. deliciosus*, *R. odoratus*, and homogeneous erect-celled in *R. idaeus*, *R. saxatilis*. The rays lignify between the protophloem clusters in *R. saxatilis* and thicker branches of *R. steudneri* (fig. 2, B). All the phloem primary rays lignify in *R. odoratus*. Some primary rays dilate in *R. deliciosus*. Uniseriate secondary rays develop in bi(per)ennial branches of shrubby species (fig. 1, A; 2, C). Clustered secondary phloem fibres develop in 2 or 3 years in *R. steudneri* (fig. 2, C).

Phellogen arises in annual branches just inside the collenchyma in *R. steudneri* (fig. 2, E) or in the endodermis in others (fig. 1, A, C). The phellem consists of 15—20 layers of thin-walled cells; the outermost layers gradually slough off. The phellem is quite

homogeneous in most species studied. It consists of alternating zones of light and red-brown cells. The phellem causes the cortex to slough off.

Very thick phellem of homogeneous thin-walled cells protects the rhizome in *R. saxatilis* (fig. 1, G). There is soft secondary phloem under the periderm. The hard elements are lacking. The rays are 2- to 3-seriate.

## Tribe *Adenostomeae*

### *Adenostoma fasciculatum*

Erect deciduous shrub with perennial branches.

**Annual stem** is pubescent with unicellular subulate thick-walled trichomes (fig. 3, A). The epidermis is one-layered, external walls of its cells are rather thick while the cuticle is thin (fig. 3, B).

The subepidermal collenchyma of angular-lamellar or angular type is discontinuous and varies from 1 to 3 cell layers in width (fig. 3, A, B). Under the collenchyma there is 3- to 4-layered cortical parenchyma. The innermost cortical layer is an endodermis of thin-walled brown cells (fig. 3, B).

The first phellogen arises from the endodermis (fig. 3, C). Therefore the cortex falls down with the periderm development.

The stem is eustelic (fig. 3, A). The protophloem fibres (fig. 3) compose vascular bundles' «caps» 1—3(4) cells in width. There are no other hard phloem elements in the annual branch (fig. 3, A, D).

The soft phloem is 0.018 to 0.023 mm thick. All phloem is conducting. Its elements are unevenly walled (fig. 3, D). The sieve tubes are about 2  $\mu$ m in width. Each sieve tube member associates with a single strand of companion cells. Sieve plates are simple, transverse or oblique. Axial parenchyma is rather homogeneous (fig. 3, D).

The primary rays are bi-seriate; the secondary rays are uniseriate (fig. 1, A).

**Biennial branch** is protected with ring rhytidome (fig. 4, A) which outermost rings gradually abscise. The 5—7-layered phellem consists of uniform thin-walled slightly flattened cells.

The phloem is 0.32—0.35 mm thick; the conducting phloem is 0.07—0.10 mm. The conducting phloem consists of soft elements (fig. 4, A, C). The sieve tube members are 3 to 4  $\mu$ m in diameter and by 80  $\mu$ m in length. Each member associates with a strand of 3 to 4 companion cells. The sieve plates are oblique and have (1)2 sieve areas (fig. 4, C). Axial parenchyma is homogeneous (fig. 4, B, D); the phloem cells usually have unevenly thickened walls (fig. 4, B).

In nonconducting phloem, the sieve tubes and companion cells die off to become strips of collapsed elements (fig. 4, B) where the cells are indistinguishable. The stereom appears in the nonconducting phloem (fig. 4, A—C). It consists of 5—8 cells thick rings of the secondary phloem fibres interrupted by the rays. Axial parenchyma remains homogeneous and slightly proliferates in the rhytidome rings.

The phellogen arises just outside each ring of the secondary phloem fibres (fig. 4, A—C).

The rays are homogeneous (fig. 4, C) or indistinctively heterogeneous. Very many rays are 2- to 3-seriate (fig. 4, D) and 0.35—1.00 mm high; a few uniseriate rays are 3—7 cells in height. The ray parenchyma slightly lignifies when the ray crosses the ring of the secondary phloem fibres.

## Discussion

Both the cortex and the phloem vary in studied *Rubus* species. Their patterns correlate though neither with growth habits nor with taxonomical positions of species. The variation range covers the cortex and phloem patterns of *R. odoratus* which is sometimes regarded

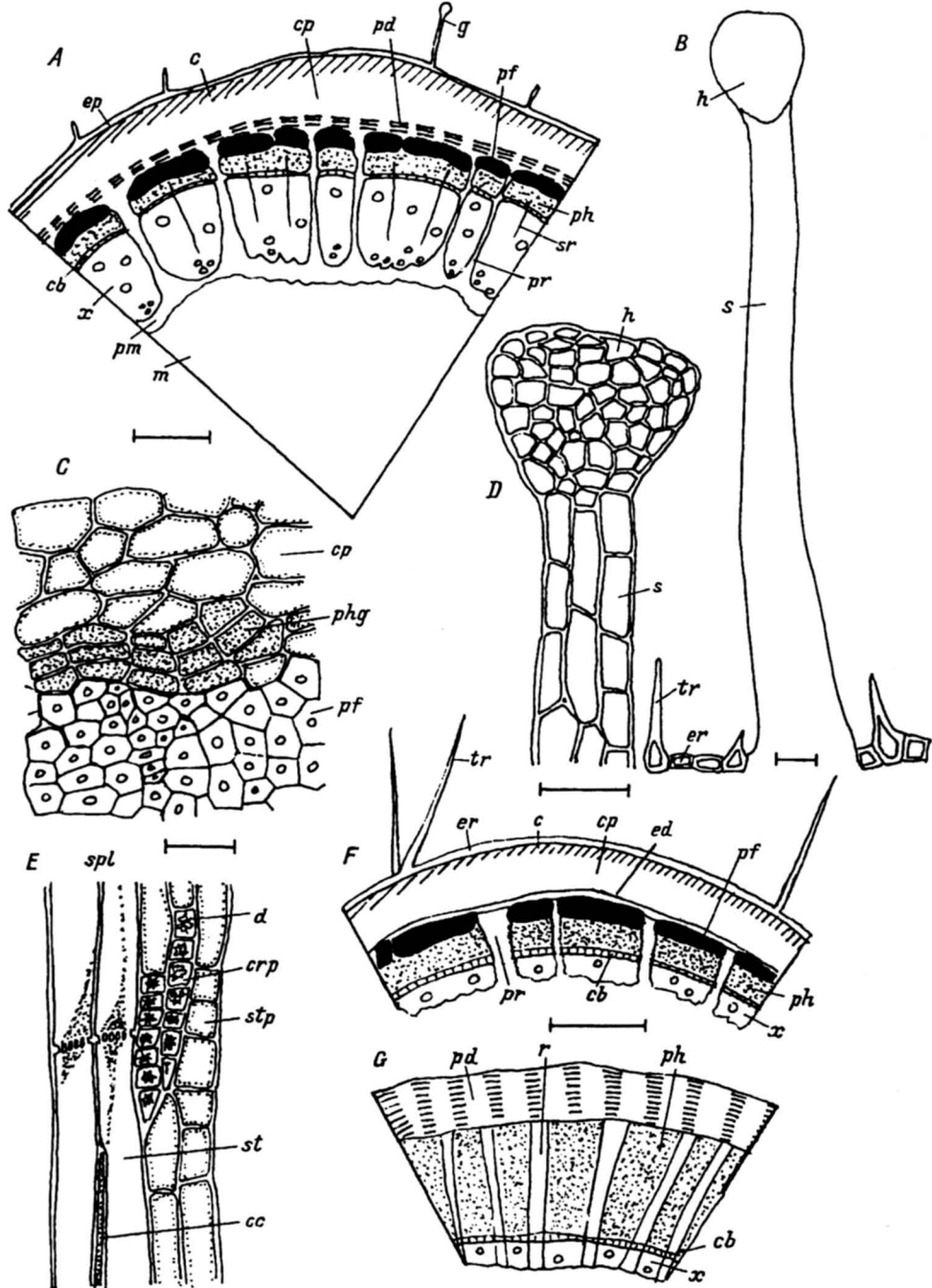


Fig. 1. Anatomy of axial organs of *Rubus odoratus* (A-E) and *R. saxatilis* (F-G).

A — scheme of the stem, transverse section; B — semischeme of the epidermis, transverse section; C — inner cortex and outer stele, origin of the first phellogen, transverse section; D — glandular emergence, transverse section; E — secondary phloem, longitudinal section; F — scheme of the aerial stem, transverse section; G — scheme of the rhizome, transverse section. c — collenchyma, cb — cambium, cc — companion cell, cp — cortical parenchyma, crp — crystalliferous parenchyma, d — calcium oxalate druse, ed — endodermis, ep — epidermis, g — glandular emergence, h — glandular head, m — medulla, pd — periderm, pf — protophloem fibres, ph — phloem, phg — phellogen, pm — perimedulla, pr — primary ray, r — ray, s — stock, sr — secondary ray, st — sieve tube, stp — storing parenchyma, tr — trichome, x — xylem. Bar: A, F, G — 0.1 mm; C-E — 0.01 mm.

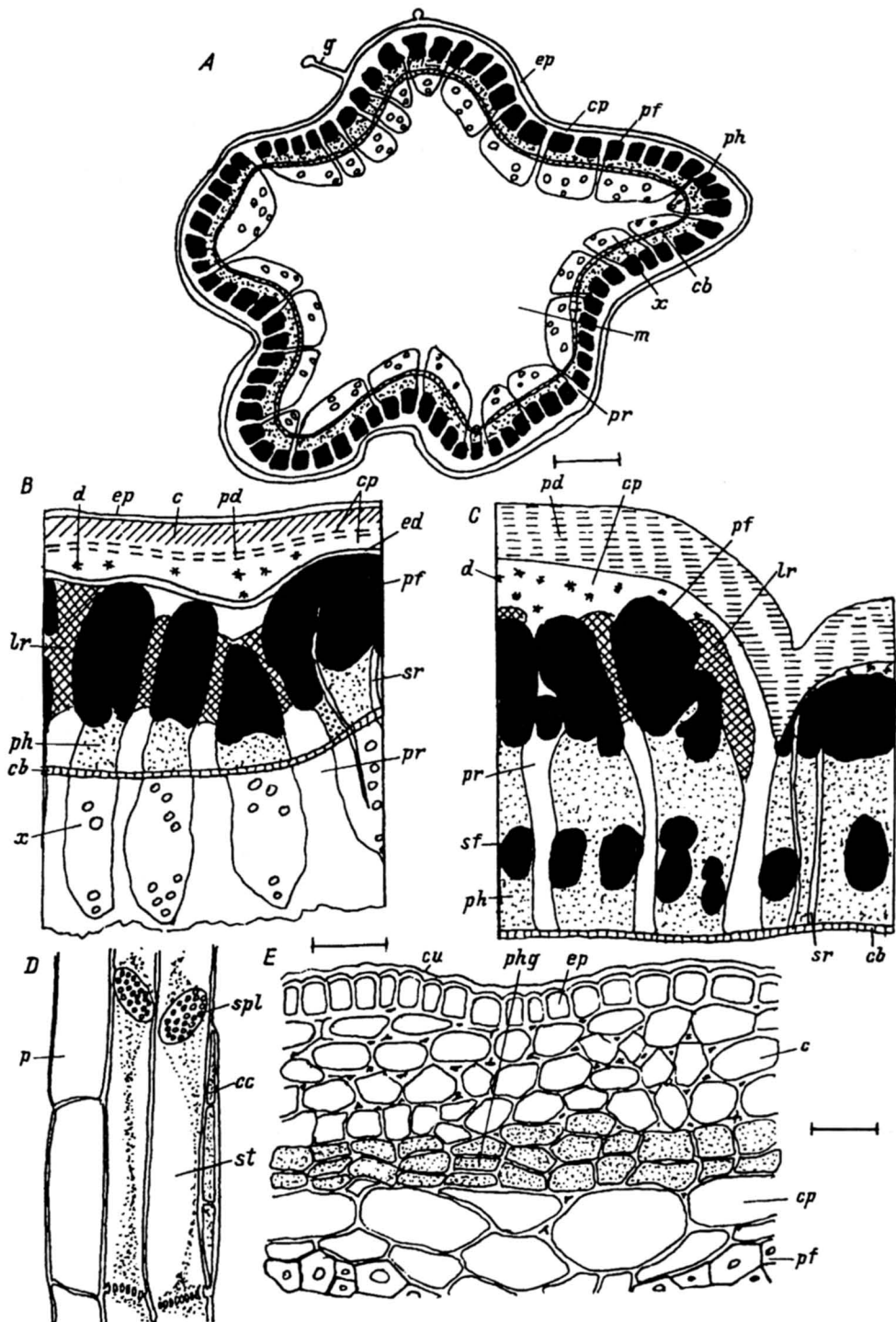


Fig. 2. Anatomy of the stem in *Rubus steudneri*.

A — scheme of thinner annual stem, transverse section; B — scheme of thicker annual stem, transverse section; C — scheme of perennial stem, transverse section; D — phloem in longitudinal section; E — cortex, transverse section. cu — cuticle, lr — lignifying ray, p — phloem axial parenchyma, sf — secondary phloem fibres, spl — sieve plate. Other signs see fig. 1. Bar: A — 1 mm, B—E — 0.05 mm.

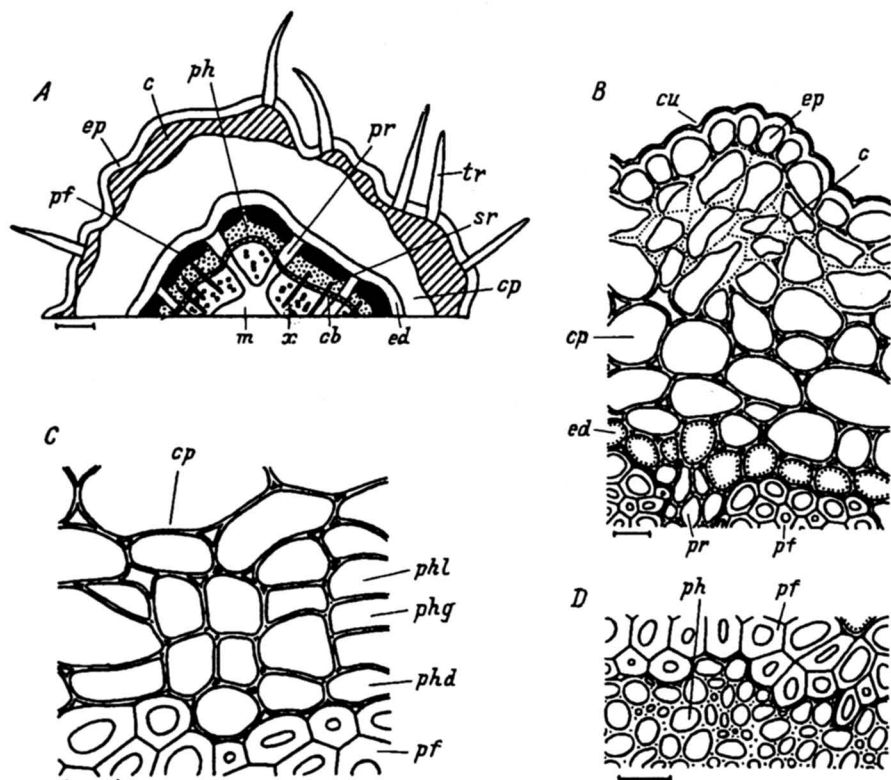


Fig. 3. Annual stem of *Adenostoma fasciculatum*, transverse sections.

A — scheme of the stem, B — cortex, C — young periderm, D — phloem. *phd* — phelloderm, *phl* — phellogen. Other signs see fig. 1, 2. Bar: A — 0.1 mm, B—D — 0.01 mm.

to be a member of the genus *Rubacer* (see Czerepanov, 1981 for more details). That is why we consider the latter unsubstantiated and confirm the habitual version of the tribe *Rubeae* of sole genus *Rubus*. The cortex and the phloem of *Rubus* species anatomically liken a lot their counterparts of *Potentilleae* members. Then, the closer relations between the two tribes than Takhtajan (1997) thought could be probable.

The *Adenostoma*'s cortex and phloem essentially differ from those of *Cercocarpus* (Lotova, Timonin, 1999) as the former genus has no hypodermis in its cortex nor the pericycle in its stele. Besides, the endodermal origin of the first phellogen in *Adenostoma* strongly opposes its hypodermal origin in *Cercocarpus*. The site where the first phellogen arises is proved to be of paramount taxonomical importance in rosaceous (Focko, 1894; Lotova, Timonin, 1999). The rhytidome is ringlike in *Adenostoma* and scally in *Cercocarpus*; the sieve plates are simple in *Cercocarpus* and mostly compound in *Adenostoma*; the axial parenchyma is homogeneous in *Adenostoma* and differentiates into storing and crystalliferous parenchymas in *Cercocarpus*. The common characters are much less numerous. So, our results undoubtedly confirm separation of *Adenostoma* from *Cercocarpeae*. It must be a member of special tribe as it has been considered since Schulze-Menz (1964).

*Adenostoma* is similar with *Sorbaria* of *Spiraeoideae* subfamily in originating of the first phellogen from the innermost cortical layer (Lotova, Timonin, 1998b). Secondary bark pattern of *Adenostoma* can be compared to that of *Physocarpus* of the subfamily (Lotova, Timonin, 1998b). Therefore, our results are in accordance with arranging *Adenostomeae* among tribes of *Spiraeoideae* (Takhtajan, 1997, sub *Adenostomeae*).

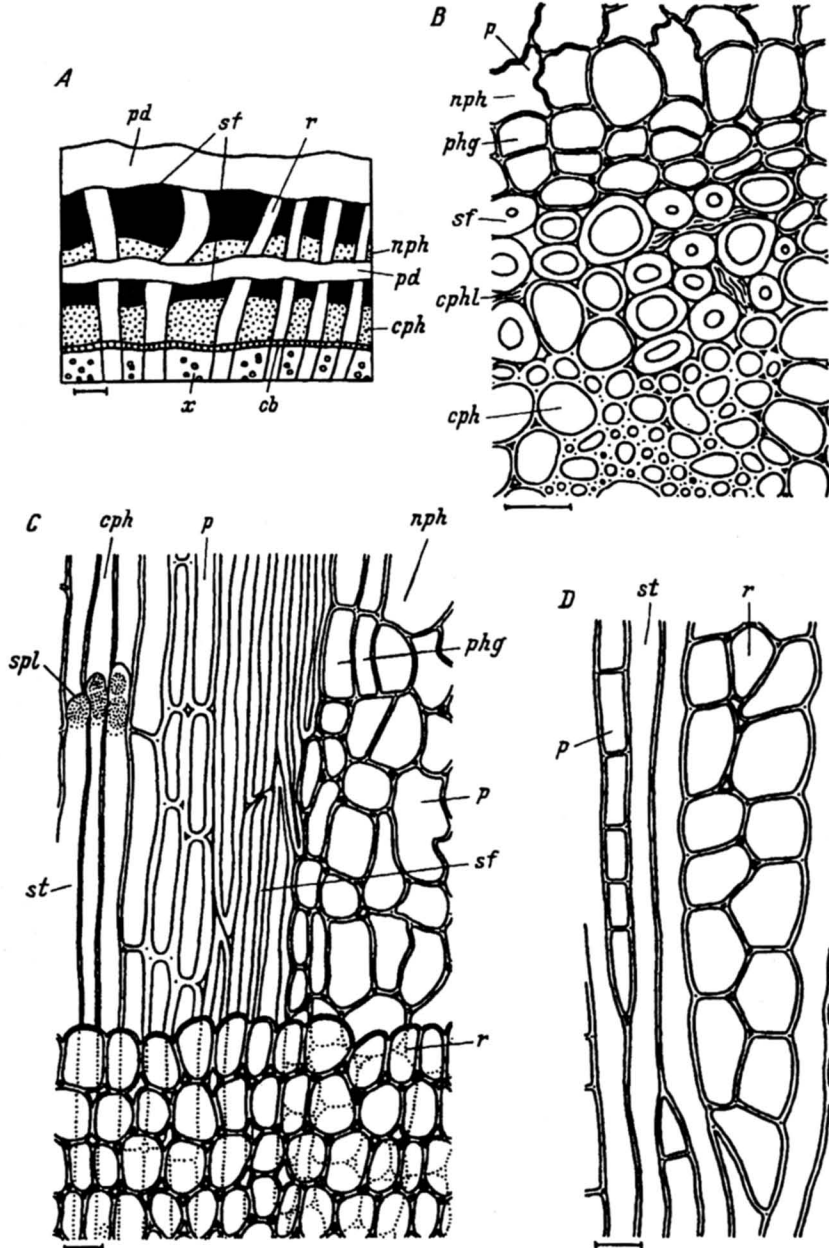


Fig. 4. Perennial stem and phloem in *Adenostoma fasciculatum*.

A — scheme of the stem, transverse section; B — phloem, transverse section; C — phloem, radial section; D — phloem, tangential section. *cph* — conducting phloem, *cphl* — compressed phloem, *nph* — nonconducting phloem. Other signs see fig. 1—3. Bar: A — 0.1 mm; B—D — 0.01 mm.

However, the latter subfamily is too variable in its cortex and secondary phloem anatomies (Lotova, Timonin, 1998a) to attach great taxonomic significance to the revealed similarities between *Adenostomeae* and different *Spiraeoideae* members.

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#### РЕЗЮМЕ

Анатомия кортекса и вторичной флоэмы однолетних и многолетних стеблей и корневищ описана у 7 видов рода *Rubus* и одного вида рода *Adenostoma*. Эти структуры оказались довольно вариabельными в роде *Rubus*, но строение не коррелирует ни с жизненными формами, ни с таксономическими связями видов. Полученные данные не подтверждают правомерность выделения из *Rubus* рода *Rubacer*. Между трибами *Rubeae* и *Potentilleae* имеется определенное сходство по строению кортекса и коры. Трибы *Adenostomeae* и *Cercocarpeae*, в которые ранее включали род *Adenostoma*, по-видимому, не имеют близких родственных связей.