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ANATOMY OF CORTEX AND SECONDARY PHLOEM OF *ROSACEAE*. 14. *COLEOGYNE* AND *KAGENECKIA*

Л. И. ЛОТОВА, А. К. ТИМОНИН. АНАТОМИЯ ПЕРВИЧНОЙ И ВТОРИЧНОЙ КОРЫ *ROSACEAE*. 14. *COLEOGYNE* И *KAGENECKIA*

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The bark anatomy of *Coleogyne ramosissima* shows its remote affinity to *Kerrieae*, though some common characters especially with bark of *Rhodotypos* are revealed. It does not confirm erecting subfamily *Coleogynoideae* because shared characters are numerous to arrange *Coleogyne* nearby *Cercocarpus*. *Kageneckia* sharply contrasts with *Quillaja* in its bark pattern and bears similarities to *Vauquelinia* species of tribe *Lindleyeae* from subfamily *Maloideae*. It differs, however, from all members of the subfamily in casual simple sieve plates. The difference interferes with its inclusion into anyone recognised maloid's tribe and makes the genus to be held as aberrant member of the subfamily.

Key words: bark, cortex, secondary phloem, anatomy, *Coleogyne*, *Kageneckia*, *Adenostomeae*, *Kerrieae*, *Cercocarpeae*, *Quillajeae*, *Maloideae*.

The genus *Coleogyne* used to be placed nearby the genus *Cercocarpus* (Focke, 1894; Takhtajan, 1987; Kalkman, 1988; Hegi, 1995) as members of the tribe *Cercocarpeae* of subfamily *Rosoideae* but Schulze-Menz (1964) transferred it to the tribe *Kerrieae* while Takhtajan (1997) arranged monotypic subfamily *Coleogynoideae* for the genus.

The genus *Kageneckia* was usually allied with genus *Quillaja* (Kalkman, 1988) both ranging from members of tribe *Quillajeae* of subfamily *Spiraeoideae* (Focke, 1894; Hegi, 1995) to members of separate subfamily *Quillajoideae* (Goldblatt, 1976; Challice, 1981; Thorne, 1983; Takhtajan, 1987). Takhtajan (1997) positioned it into separate tribe *Kageneckieae* which he considered a member of subfamily *Pyroideae* (=*Maloideae*) closer related to the tribe *Lindleyeae*, however.

Takhtajan's late taxonomical decisions are worth to being tested with data that have been ignored by taxonomists so far. Such data can be anatomies of the cortex and secondary phloem as evidenced by us elsewhere (Lotova, Timonin, 1999a, b; Lotova, Timonin, 2002).

Materials and methods

The barks of *Coleogyne ramosissima* Torr. and *Kageneckia* sp. were sampled from voucher specimens from Herbarium of Komarov Botanical Institute of Russian Academy of Science (LE) («Southern Utah, Northern Arizona, &c. No. 139 *Coleogyne ramosissima* Torr. Coll. Dr. E. Palmer. 1877») and Herbarium of Lomonosov Moscow State University (MW) («*Kageneckia* Chile, Provincia de Santiago, Quebrada de la Plata (Maipú) 1968 13/02. Oleg Zalensky»), respectively. The samples were softened with glycerol—alcohol—water (1 : 1 : 1) medium at 40 °C for a month before sectioning. Hand razor sections were successively treated with phloroglycinol and hydrochloric acid or stained with 5 %

alcoholic iodine and examined with light microscope. All the measurements were directly taken from the slides with calibrated ocular micrometer. The illustrations were drawn with camera lucida RA—6.

Results

Coleogyne ramosissima

Spiny evergreen divaricate shrub 0.5—5 m tall.

Biennial branch bears circular rhytidome (fig. 1, *A*). The thin-walled phellem cells range from outer colourless unflattened to inner brown tangentially flattened ones. Nearly continuous fibre ring adjoins the inner periderm and is separated from the outer periderm by highly destroyed soft tissue where cells are hardly distinguishable. Some parenchyma cells with calcium oxalate prism accompany externally the fibre ring. Zone of the inner phloem 0.007—0.013 mm thick is traversed by thin ring of underdeveloped fibres (fig. 1, *A*). The soft phloem constituents are very deformed due, perhaps, to desiccating of the voucher specimen at hand. The sieve tubes are about 4 to 5 μm in crosssections and have simple sieve plates. 2—4-seriate rays are indistinctively visible in the phloem.

Spine is protected with two periderms and deformed parenchyma in between (fig. 1, *B*). The phellems consist of uniform thin-walled colourless unflattened cells. Few-fibred clusters are in the body of the parenchyma nearer to the inner periderm (fig. 1, *B*). The inner phloem is completely compressed.

Perennial branch is covered with multilayered phellem (fig. 1, *C*) of alternate zones of colourless unflattened cells and brown tangentially flattened ones, respectively. A bulk of secondary phloem fibres intersected with sclerified rays adjoins the outer periderm. Thin zone of destroyed soft elements is between the bulk and the inner periderm (fig. 1, *C*). Inner phloem is approximately 0.06 mm thick. The sieve tube members about 4×80 μm have simple sieve plates (fig. 1, *E*). Crystalliferous phloem cells contain calcium oxalate prisms (fig. 1, *E*) and mostly neighbour the fibre masses. Numerous phloem parenchyma cells have neither crystals nor starch. Rays are heterogeneous (fig. 1, *D*) 2- to 3-seriate about 0.06 mm in width and 0.4 to more than 1.5 mm in heigh. Some ray cells contain calcium oxalate prisms.

Kageneckia sp.

Evergreen shrub up to 10 m tall.

Triennial branch is protected with periderm (fig. 2, *A*) covered by unidentified tissue remnants. The phellem tends to be stratified of 1-layered unflattened or radially elongate cells and 1- to 2-layered highly tangentially flattened ones. 1—3-layered discontinuous lamellar collenchyma underlays the periderm (fig. 2, *A*). Numerous cells with calcium oxalate polyhedron as well as 1- to 2-celled clusters of sclereids are scattered through deformed cortical parenchyma.

Distant clusters of the protophloem fibres alternate with ray parenchyma or fibre sclereids. The phloem is about 0.40 mm thick, its inner ~0.15—0.20 mm zone is conducting phloem (fig. 2, *A*). 1 to 2 discontinuous rings of secondary phloem fibres are developed in the outer nonconducting phloem. Small masses of completely compressed soft phloem neighbour the rings both internally and externally. Very many soft phloem constituents are tangentially flattened (fig. 2, *B*). This might be a result of specimen desiccating. The constituents tend to be in radial files.

The sieve tube members are near 7×20 μm in crosssections and 190—220 μm in lengths. The sieve plates are both simple and compound of 3—9 sieve areas (fig. 2, *E*); the two co-occur in some members. The phloem parenchyma cells with calcium oxalate prisms (fig. 2, *D*) are scant and usually associated with the fibres (fig. 2, *B*). Bulky

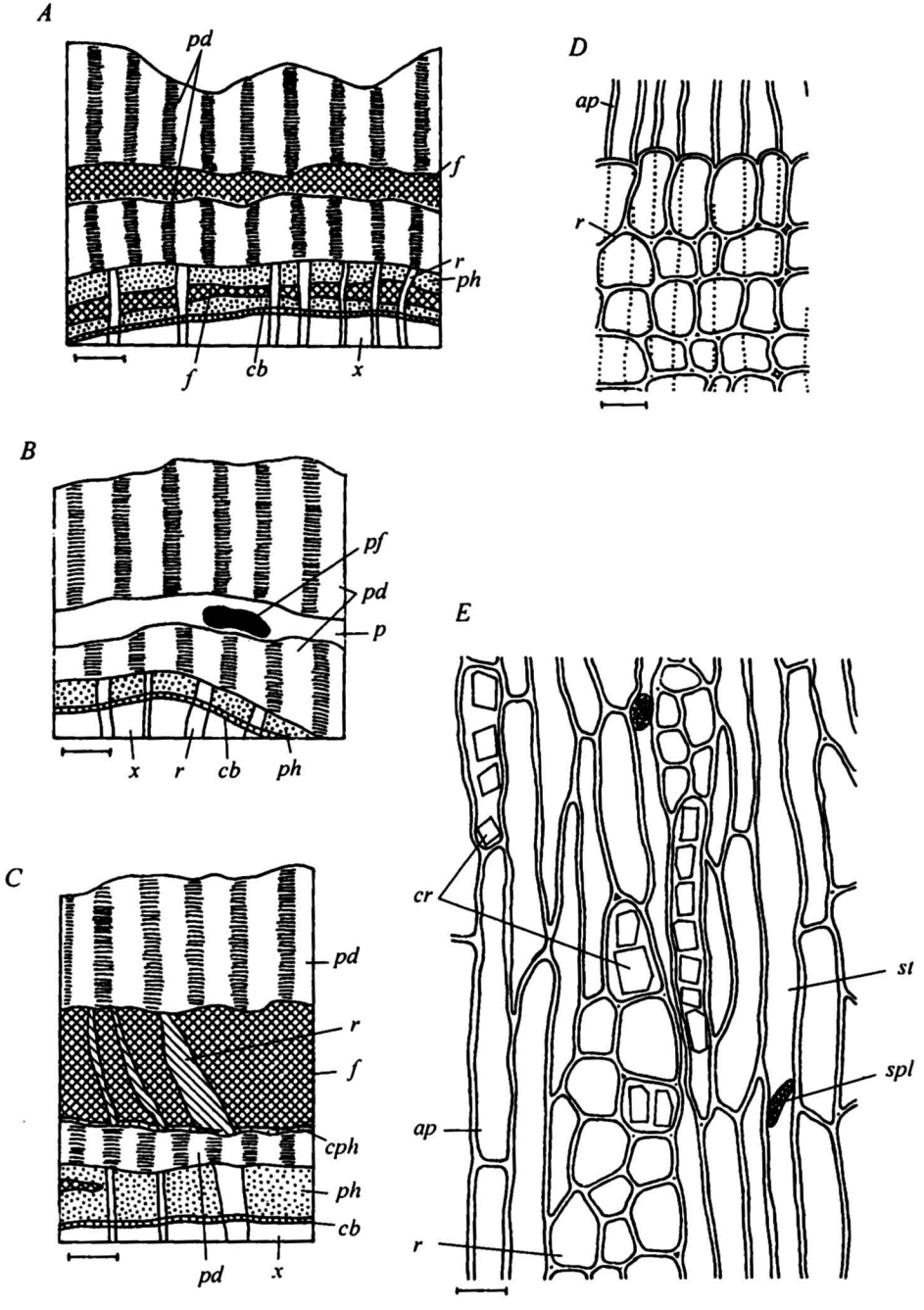

Fig. 1. *Coleogyne ramosissima* bark.

A — scheme of the bark in biennial branch, crosssection; *B* — scheme of the bark in spine, crosssection; *C* — scheme of the bark in perennial branch, crosssection; *D* — secondary phloem, radial section; *E* — secondary phloem, tangential section. *ap* — axial phloem parenchyma; *cb* — cambium; *cph* — compressed phloem; *cr* — calcium oxalate crystal; *f* — secondary phloem fibres; *p* — parenchyma; *pd* — periderm; *pf* — protophloem fibres; *ph* — soft phloem; *r* — ray; *spl* — sieve plate; *st* — sieve tube; *x* — xylem. Bar: *A*—*C* — 0.1 mm; *D*, *E* — 0.01 mm.

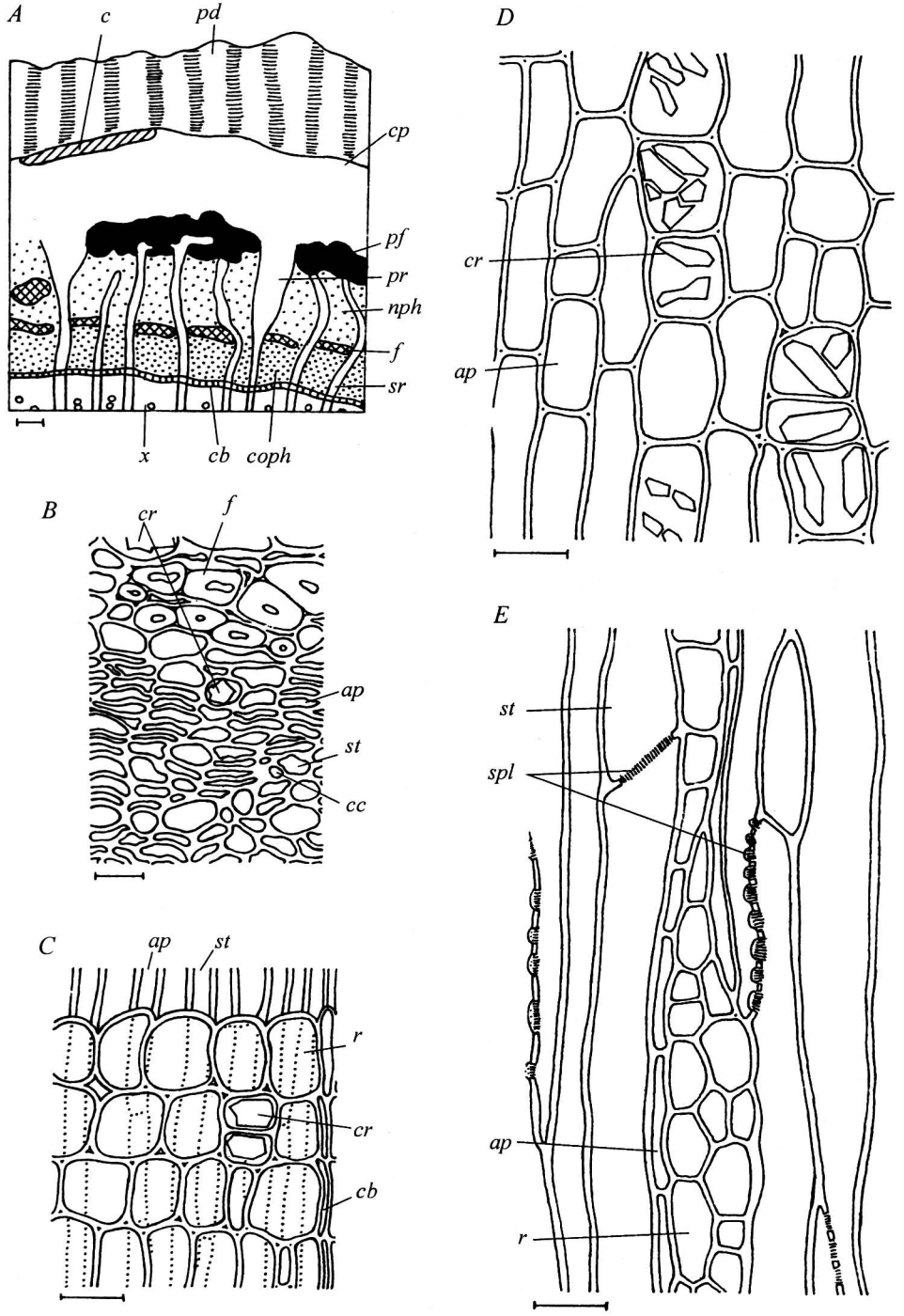

Fig. 2. *Kageneckia* sp. bark in triennial branch.

A — scheme of the bark, crosssection; *B* — conducting secondary phloem, crosssection; *C* — conducting secondary phloem, radial section; *D* — nonconducting secondary phloem, tangential section; *E* — conducting secondary phloem, tangential section. *c* — collenchyma; *cc* — companion cell; *coph* — conducting phloem; *cp* — cortical parenchyma; *nph* — nonconducting phloem; *pr* — primary ray; *sr* — secondary ray; see fig. 1 legend for other explanation. Bar: *A* — 0.1 mm; *B*—*E* — 0.01 mm.

parenchyma cells contain neither crystals nor storage starch (fig. 2, *B*, *D*, *E*). The rays are homogeneous (fig. 2, *C*), 2(3)-seriate (fig. 2, *E*), up to 25 cells in heigh; some ray cells contain calcium oxalate prisms (fig. 2, *C*). Primary rays are dilated (fig. 2, *A*).

Discussion

The state of material of *Coleogyne ramosissima* we had at our hands does not allow us to reveal with confidence some important characters of its bark. The site the first phellogen arises in the branch is a feature of paramount taxonomical importance in the family *Rosaceae* (Lotova, Timonin, 1998 etc.). The youngest branch we have investigated is too advanced to recognize the site of the first phellogen origin (fig. 1, *A*), however. Yet, the anatomy of the spine could throw light on the subject. The clusters of fibres which are scattered through the balky parenchyma between two periderms (fig. 1, *B*) must be a protophloem. If so, the first phellogen must has developed in the epidermis or somewhere in the outer cortex. Peripheral first phellogen contrasts with phellogen developing in the endodermis in *Neviusia alabamensis* A. Gray and arrested phellogen developing in the pericycle in *Kerria japonica* DC. (both from the tribe *Kerrieae*) but it is similar with the first phellogen of subepidermal origin inherent in both *Rhodotypos* sp. sp. (*Kerrieae*) and *Cercocarpus parvifolius* Nutt. (*Cercocarpeae*) (Lotova, Timonin, 1999b).

Coleogyne's bark differs from those of all *Kerrieae* members in formation of rhytidome, stereom architecture, exclusively simple sieve plates, calcium oxalate prisms in axial phloem parenchyma cells, and heterogeneous rays. It shares with the bark of *Cercocarpus* stratified phellem, rhytidome, masses of compresses soft phloem, simple sieve plates, calcium oxalate prisms in axial phloem parenchyma cells, and heterogeneous 2- to 3-seriate rays (Lotova, Timonin, 1999b). The differences between the two are plainly visible, however. Phelloids typical of *Cercocarpus*'s phellem are absent in the *Coleogyne*'s phellem. The rhytidome is circular in *Coleogyne* and scaly in *Cercocarpus*. Massive rings of the secondary phloem fibres preclude the phloem from dilating in the former genus while diffuse dilatation of the phloem is quite evident in the latter one due to highly discontinuous tangential layers of the secondary phloem fibres. Compressed soft phloem seems to be much more developed in *Cercocarpus* than in *Coleogyne*.

Therefore, *Coleogyne*'s bark completely concurs anatomically with neither *Cercocarpus*'s nor *Kerrieae*'s ones.

The bark of *Coleogyne* has a set of characters in common with that of *Adenostoma fasciculatum* Hook. et Arn. (Lotova, Timonin, 2000) which used to be placed into the tribe *Cercocarpeae* (Focke, 1894); it has been held as a member of tribe *Adenostomeae* since 1960s (Schulze-Menz, 1964; Takhtajan, 1987, 1997; Kalkman, 1988; Hegi, 1995). Architectures of the rhytidomes and secondary phloems are strikingly similar. Yet, the first phellogen develops in the endodermis and subsequent phellogens arise just externally to the rings of secondary phloem fibres in *Adenostomeae* but the first phellogen seems to differentiate in the outer cortex or epidermis and subsequent ones must appear just internally to the rings of secondary phloem fibres in *Coleogyne*. Besides, *Adenostoma* has both simple and compound sieve plates, fairly homogeneous rays, and no crystalliferous axial phloem parenchyma.

In sum, *Coleogyne* is evidenced by its bark anatomy to be closer related to *Cercocarpus* though placement of two genera into the same tribe is arbitrary. The rank of subfamily *Coleogynoideae* (Takhtajan, 1997) is likely to be exaggerated.

Kageneckia sp. shares periferal first phellogen with *Quillaja brasiliensis* Mart. (Lotova, Timonin, 1999a) but many characters of its bark are rather different from their counterparts in the latter species. Compound sieve plates, prismatic crystals of calcium oxalate, homogeneous rays inherent in *Kageneckia* are dissimilar with exclusively simple sieve plates, styloids of calcium oxalate, and heterogeneous rays typical of *Quillaja*. Even occasional simple sieve plates of *Kageneckia* basically differ from those of *Quillaja* as

the latter have unique to rosaceous giant sieve pores. Therefore, two genera are unlikely to be closely related.

Epidermal or subepidermal origin of the first phellogen, architectures of the cortex and secondary phloem, radial files of flattened elements of the secondary phloem, compound sieve plates with rather numerous sieve areas, calcium oxalate patterning, and homogeneous rays are all similar with those revealed in some *Vauquelinia* species (Lotova, Timonin, 2002). The simple sieve plates occurring in *Kageneckia* sharply contrasts, however, with compound plates with numerous sieve areas which must be characteristic of the tribe *Lindleyeae* and whole subfamily *Maloideae*. So, the genus could be held in separate tribe *Kageneckeae* nearby *Lindleyeae* (Takhtajan, 1997) as the deviating member of subfamily *Maloideae*.

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LITERATURE CITED

Challice J. S. Chemotaxonomic studies in the family *Rosaceae* and the evolutionary origins of the subfamily *Maloideae* // Preslia. 1981. Vol. 53. N 4. P. 259—289.

Focke W. O. Rosaceae // Engler A., Prantl K. A. Die natürlichen Pflanzenfamilien. Leipzig, 1894. Teil 3. Abt. 3. S. 1—61.

Goldblatt P. Cytotaxonomic studies in the tribe *Quillajeae* (*Rosaceae*) // Ann. Missouri Bot. Gard. 1976. Vol. 63. N 2. P. 200—206.

Hegi G. Illustrierte Flora von Mitteleuropa. Berlin a. o., 1995. Bd 4. Teil 2A. *Spermatophyta*: *Angiospermae*: *Dicotyledones* 2(2). X + 693 S.

Kalkman C. The phylogeny of the *Rosaceae* // Bot. J. Linn. Soc. 1988. Vol. 98. N 1. P. 37—59.

Lotova L. I., Timonin A. C. Anatomy of cortex and secondary phloem in *Rosaceae* 2. *Spiraeoideae* except *Spiraeeae* and *Lyonothamneae* // Bot. J. (St. Petersburg). 1998. Vol. 83. N 9. P. 14—27.

Lotova L. I., Timonin A. C. Anatomy of cortex and secondary phloem in *Rosaceae*. 3. *Quillajoideae* // Bot. J. (St. Petersburg). 1999a. Vol. 84. N 2. P. 34—41.

Lotova L. I., Timonin A. C. Anatomy of cortex and secondary phloem in *Rosaceae*. 5. *Kerrieae* and *Cercocarpeae* // Bot. J. (St. Petersburg). 1999b. Vol. 84. N 9. P. 10—20.

Lotova L. I., Timonin A. C. Anatomy of cortex and secondary phloem in *Rosaceae*. 6. *Rubeae* and *Adenostomeae* (*Rosoideae*) // Bot. J. (St. Petersburg). 2000. Vol. 85. N 11. P. 21—28.

Lotova L. I., Timonin A. C. Anatomy of cortex and secondary phloem in *Rosaceae*. 13. *Maloideae* // Bot. J. (St. Petersburg). 2002. Vol. 87. N 10. P. 31—53.

Schulze-Menz G. K. Rosaceae // Engler A. Syllabus der Pflanzenfamilien. 13. Aufl. Berlin, 1964. Bd 2. S. 209—218.

Takhtajan A. Systema magnoliophytorum. Leningrad, 1987. 439 p. (in Russ.).

Takhtajan A. Diversity and classification of flowering plants. New York, 1997. X + 643 p.

Thorne R. F. Proposed new realignments in the angiosperms // Nordic J. Bot. 1983. Vol. 3. N 1. P. 85—117.

РЕЗЮМЕ

Анатомия коры *Coleogyne ramosissima* свидетельствует об отсутствии близкого родства этого рода с представителями трибы *Kerrieae*, хотя у них имеются некоторые общие признаки, особенно с *Rhodotypos*. Выделение монотипного подсемейства *Coleogynoideae* не подтверждается из-за многочисленных сходств в анатомии коры между *Coleogyne* и *Cercocarpus*, что позволяет сближать эти два рода. По строению коры *Kageneckia* резко отличается от *Quillaja* и проявляет сходство с *Vauquelinia* (триба *Lindleyeae* из подсемейства *Maloideae*). Она, однако, отличается от всех представителей этого подсемейства наличием простых ситовидных пластинок, что не позволяет включить ее ни в одну из признаваемых триб яблоневых и заставляет считать уклоняющимся членом данного подсемейства.