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Fruit structure and some details of fruit morphogenesis in subfamily *Tripterygioideae* Loes. (Celastraceae R. Br.)

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Summary. Fruit structure and morphogenesis in subfamily *Tripterygioideae* Loes. (Celastraceae R. Br.) are presented. Fruits are either with 2, 3 or 5 lateral wings, nested along the fruit, or with one apical wing (on the fruit's sides and its apex). The wings are wide or narrow, membranous; the body of the fruit is shorter than its wings. The wings usually possess a net of vascular bundle derivatives. The topography of vascular bundles defines the way of pericarp expansion. For all examined fruits style on the apex always remains. Peculiarities of pericarp structure and development suggest morphogenetical type of the fruit in *Tripterygioideae* – pseudomonomerous unilocular one-seeded winged pyrenarium with a pyrene, which can be formed by 3 to 5 layers of tangential elongated macrosclereids (in many examined taxa). Fruit type of *Ptelidium* is uni- or bilocular and one(two)-seeded nut, because its pericarp is lignified entirely. Fruit of *Rzedowskia* has only one layer of radially elongated sclereids in endocarp. Seeds of all examined species are small, without aril. Two genera appeared to be more isolated – *Ptelidium* and *Rzedowskia*. All examined taxa have demonstrated one special evolutionary trend in common – the reduction of the number of seeds per fruit and the development of wings as an adaptation to the dispersal by wind. According to the latest molecular data, such fruit types have been formed in Celastraceae at least six times in the course of evolution.

Структура и некоторые черты морфогенеза плодов представителей подсемейства *Tripterygioideae* Loes. (Celastraceae R. Br.)

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Ключевые слова: крылатый пиренарий, крылатый орех, морфогенез, подсемейство *Tripterygioideae*, родственные связи, семейство Celastraceae, структура плодов, структура семян, *Platypterocarpus*, *Plenckia*, *Ptelidium*, *Rzedowskia*, *Tripterygium*, *Wimmeria*, *Zinowiewia*.

Аннотация. Представлены результаты сравнительного изучения структуры плодов и некоторые черты их морфогенеза у представителей подсемейства *Tripterygioideae* Loes. (Celastraceae R. Br.). Плоды изученных видов несут 2, 3 или 5 боковых крыловидных выростов вдоль тела плода, либо только 1 апикальное крыло. Крылья широкие или узкие, пленчатые, тело самого плода короче его крыла. Крылья обычно содержат сеть дериватов проводящих пучков. Топография пучков демонстрирует путь (направление) разрастания перикарпия в процессе развития. Плоды всех изученных видов содержат остатки столбика на верхушке. Особенности структуры и развития перикарпия подтверждают, что морфогенетический тип плода у видов *Tripterygioideae* – псевдомономерный одногнездный односеменной крылатый пиренарий с косточкой, которая образована 3–5 слоями тангентально расположенных макросклерейд (во многих изученных видах). Тип плода у видов *Ptelidi-*

um – одно- или двухгнездный и одно(двух-)семенной орех, поскольку его перикарпий полностью лигнифицирован. Плод у *Rzedowskia* имеет только один слой радиально вытянутых склереид в эндокарпии. Семена всех изученных видов очень мелкие, без ариллуса. По результатам исследования два рода оказались более изолированными – *Ptelidium* и *Rzedowskia*. Все изученные представители демонстрируют одну специфическую эволюционную тенденцию – редукцию числа семян в плоде и развитие крыльев как адаптацию к распространению их ветром. Согласно последним молекулярным данным, такие типы плодов формировались в ходе эволюции семейства Celastraceae как минимум шесть раз.

Introduction

Just like many other families of angiosperms, Celastraceae has changed greatly in their circumscription following recent molecular phylogenetic studies (APG III, 2009). Additional detailed and comprehensive study of different aspects of plant morphology will be required in order to obtain a reasonable, accurate picture of intra-familial relationships. In particular, there is interest to fruit and seed structure and development in the subfamily *Tripterygioideae* Loes., which is characterized by indehiscent winged fruits (Savinov, Solomonova, original data). In literature, the description of fruit morphology and anatomy for the specific taxon in detail is missing to date, except for some general information. So, some interesting materials on the morphology of wings with details of their venation for fin-winged fruits in some Celastraceae (*Platypterotheca*, *Stackhousia*, *Tripterococcus*, *Tripterygium*, *Wimmeria*) are presented by S. Manchester and E. O’Leary (2010). In fundamental book on the fruit morphogenesis in Magnoliophyta (Bobrov et al., 2009) interpretation of fruits in *Tripterygioideae* is given as the pseudomonomerous upper one-seeded syncarpous winged pyrenariums with pyrene of unknown nature, and fruit of the *Rzedowskia* is included to upper nuts.

According to Th. Loesener (1942) with supplements by Dunkley et Brenan (1948, cit.: Robson et al., 1994) and by F. Gonzalez-Medrano (1981), there are 7 woody genera attributable to *Tripterygioideae* subfamily. These genera consist of 40 species, distributed in Central and South America, Tropical East Africa, Madagascar and eastern Asia (Simmons, 2004). However, Theodor Loesener’s subfamilies and tribes of Celastraceae s. str. are generally not supported by cladistic morphological analysis (Simmons, Hedin, 1999), as well as by molecular phylogenetic data (Simmons et al., 2001a–b, 2008, 2012a–b; Coughenour et al., 2010, 2011). Finally, M. P. Simmons with colleagues came to the conclusion that the *Tripterygioideae* was an artificial subfamily. So, the actual problem is a search for new morphological characters and

their comparison with available data on molecular phylogenetics.

Materials and methods

Fruits for the present study (developing and mature) were collected in botanical gardens (see App. A) or received by authors from carpological collections and herbaria (K, LE, MHA, P) and fixed in 70 % ethanol. When possible, several samples of fruits and seeds of each species were studied. Specimens of fruits and seeds were used for light microscopy. Cross sections of fruits and seeds in the middle part were taken according to classical anatomical methods (Barykina et al., 2000). Commonly accepted terminology was used in the descriptions of fruits and seeds (Melikjan, Devjatov, 2001). Fruits and seeds of 6 genera and 12 species were examined; all of them traditionally belong to the *Tripterygioideae* subfamily: *Plenckia* Reissek (1 species), *Ptelidium* Thouars (2 species), *Rzedowskia* Medrano (1 species), *Tripterygium* Hook. f. (3 species), *Wimmeria* Schldl. et Cham. (4 species), *Zinowiewia* Turcz. (1 species). Specimens studied are presented in Appendix A. In comparative aspect, the structure of fruits and seeds for 39 genera and 102 species of other Celastraceae was previously studied (Savinov, 2012).

Results

Plenckia populnea Reiss.

Fruit – one-seeded one-winged, greenish brown in color, up to 35 mm long and 7 mm wide (Fig. 1a, i). Groups of vascular bundles are found to pass through the center of the wing. The pericarp consists of 10–12 cell layers (Fig. 2a). The exocarp is made of a single layer presented on rectangular cross-section, tangentially elongated cells with thickened outer and (to a lesser extent) side walls. The mesocarp is a few-layered, formed by three to four layers of phlobaphene-containing, tangential elongated parenchyma cells. In mesocarp, the derivatives of vascular bundles are separate. The endocarp is differentiated in two topographic zones. The outer area consists of five to six layers of tangentially elongated macrosclereids, and the

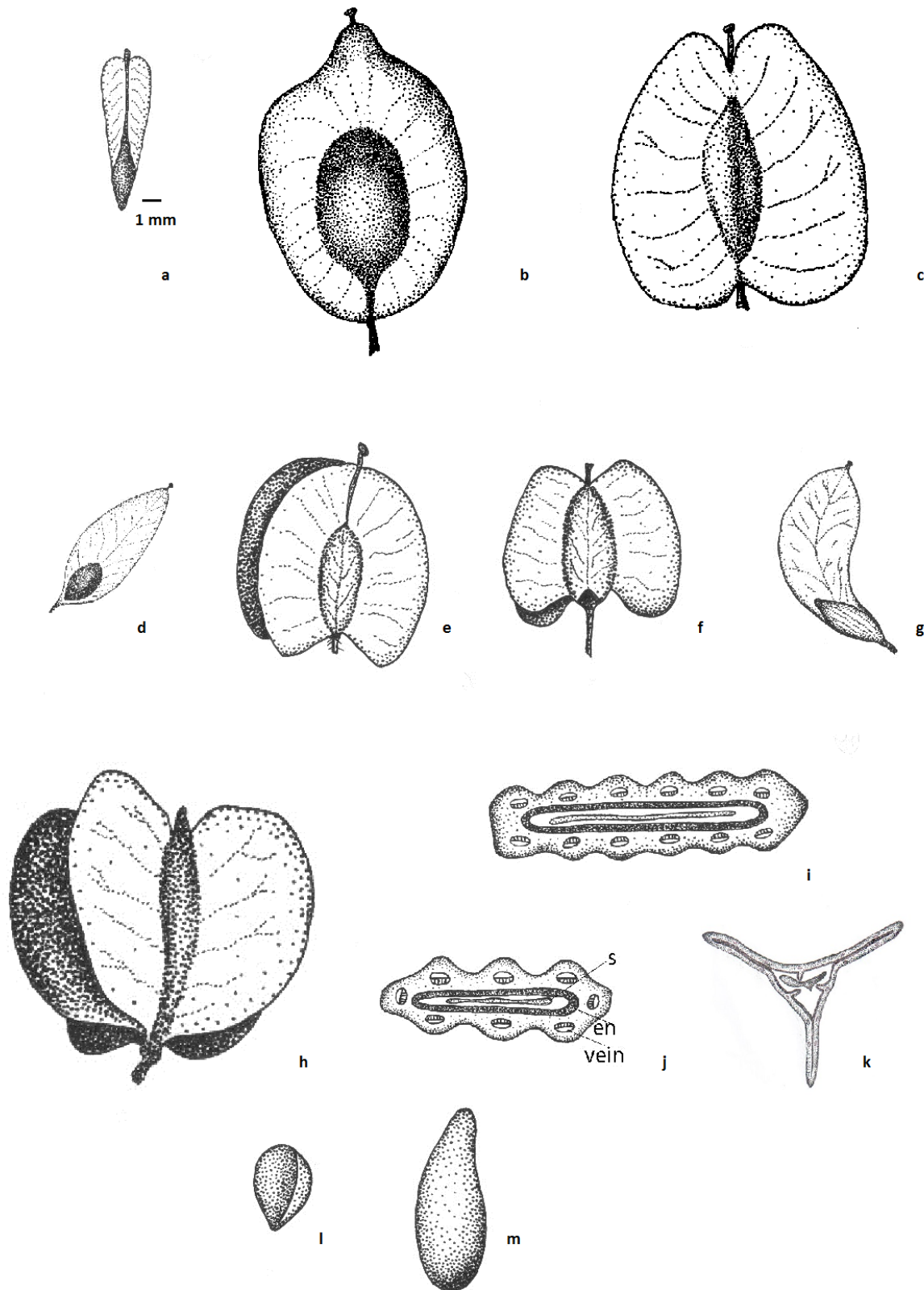


Fig. 1. Fruit and seed morphology of *Tripterygioideae*. Fruits: a – *Plenckia populnea* Reiss.; b – *Ptelidium ovatum* Poir.; c – *P. samberanensis* R. Capoen.; d – *Rzedowskia tolantonguensis* Medrano; e – *Tripterygium regelii* Sprague et Takeda; f – *Wimmeria persicifolia* Radlk.; g – *Zinowiewia integerrima* Turcz.; h – *Platypterocarpus tanganyikensis* Dunkley et Brenan (according to Robson et al., 1994); transverse section of fruit: i – *Plenckia populnea*; j – *Zinowiewia integerrima*; k – *Tripterygium regelii*; seeds: l – *Tripterygium regelii*; m – *Wimmeria persicifolia*. Scale bar = 1 mm; s – seed, vein – vascular bundles, en – endocarp.

internal one – of one layer of discolored cells with evenly thickened walls.

Seed is oval, elongated, brownish, up to 15 mm long and 3 mm wide. The seedcoat consists of 10–12 layers (Fig. 3a). The exotesta is composed of a single layer, represented by phlobaphene-containing, rectangular in cross section, cells with markedly thickened outer walls. The cuticle is thin. The mesotesta is formed by four to five layers of tangentially elongated, phlobaphene-containing parenchyma cells. The endotesta is presented by a single layer of small cells, slightly elongated tangentially. The exotegmen is a single layer, which consists of small tabular cells with uniformly thickened walls. Meso- and endotegmen presented by 3(4) layers are made of slightly compressed, phlobaphene-containing parenchymatous cells.

***Ptelidium samberanensis* R. Capeen.**

Fruit – one-seeded two-winged, app. 60 mm long, sometimes with underdeveloped third wing (Fig. 1c). The pericarp consists of 8–9 layers (Fig. 2b). Exocarp is presented by one layer of very small cells with uniformly thickened walls. Mesocarp consists of 3 layers of cells with evenly thickened (poorly lignified) walls. Endocarp is formed by 4 layers of macrosclereids. Macrosclereids are elongated in tangential direction forming a single supporting cord.

Only small seed is located in the locule of the fruit. Unfortunately, it was not possible to obtain acceptable sections for anatomical study from a single specimen.

***Rzedowskia tolantonguensis* Medrano**

Fruit – one-seeded, with vascularized wing, extended from the apex of the fruit (“samara”), 12 mm long, 6 mm wide in the middle part (Fig. 1d). The pericarp is not very thick, only 6–7 layers of cells (Fig. 2c). Exocarp consists of a single layer of cells almost square in cross section, with thickened outer walls. The mesocarp is not differentiated and formed by 4 layers of small parenchymatous cells. Endocarp forms a supporting tissue strand, which consists of a single layer of large sclereids, elongated in the radial direction. The inner zone of the endocarp (1 layer) consists of markedly compressed cells.

Seed is very small. Spermoderm consists of 4(5) layers of cells (Fig. 3b). Exotesta is formed by a single layer of very large cells with thickened outer walls. They contain phlobaphene and occupy almost ½ of spermoderm. Mesotesta forms 2 layers of parenchyma cells, slightly elongated in tangential

direction. Exotegmen consists of a single layer of fibrous cells. The other layers of tegmen are not preserved in mature spermoderm. Endosperm cells are quite large.

***Tripterygium regelii* Sprague et Takeda**

Fruit – one-seeded, three-winged, with remains of a long style at the top (Fig. 1e, k). Wings of the fruit are broad, longitudinal. The body of the fruit is almost equal to its entire length. The pericarp consists of 12–13 layers (Fig. 2d). Exocarp is represented by a single epidermal layer of small cells, the surface of which has a homogeneous, smooth cuticle layer. Mesocarp is formed by 7 layers of small parenchymatous cells containing phlobaphene. Endocarp is not differentiated and consists of 4–5 layers of medium-sized macrosclereids, elongated in tangential direction, located very tightly, forming a solid strand. It stretches through the whole wing of the fruit.

Seed is small (Fig. 1l). Spermoderm consists of 7 layers (Fig. 3c). Exotesta is formed by a single layer, presented by several cells elongated in tangential direction, with thickened walls. Layers of cuticle and epicuticular wax are pronounced. Mesotesta is formed by 3 layers of parenchymous cells containing phlobaphene. Endotesta is not expressed. Exotegmen consists of a single layer of small sclereids. The other two layers of the tegmen are represented by small, compressed parenchymous cells.

***Wimmeria persicifolia* Radlk.**

Fruit is one-seeded, with three longitudinal wing-like appendages, about 10–12 mm long (Fig. 1f). Pericarp consists of 8 to 9 layers (Fig. 2e). Exocarp is one-layered, presented by small cells rectangular in cross section. The cuticle layer is uniform. Mesocarp is formed by 5 layers of large-celled parenchyma. Endocarp consists of 2 to 3 layers of macrosclereids elongated in tangential direction.

Seed is oblong, about 7–8 mm long, dark red (Fig. 1m). Spermoderm is of few layers (6 to 7), slightly differentiated (Fig. 3d). Exotesta is formed by a single layer of small cells, rectangular in cross section. Mesotesta is presented by 4 layers of small-celled parenchyma, the cells of which are slightly compressed. Exotegmen is a single layer of small sclereids.

***Zinowiewia integerrima* Turcz.**

Fruit is one-seeded, with one wing, pale yellow in color (body of the fruit is brownish), 20–23 mm long and 5 mm wide (Fig. 1g, j). The body of the

fruit is about 10 mm long and 2–3 mm wide. Wing possesses a network of vascular bundles. Main bundle has a cusp at the apex of the fruit. Pericarp consists of 16–17 layers (Fig. 2f). Exocarp is single-layered, presented by small tabular cells with U-shaped wall thickenings (external and internal). Cuticle on their surface is deposited as a thin uniform layer. Mesocarp consists of 9 to 10 layers of medium-sized, almost isodiametric parenchymal cells. In the mesocarp, very large vascular bundles derivatives apparently performing the supporting function, are seen. Endocarp is differentiated in two topographic zones. The outer zone is formed by 4–5 layers of short macrosclereids, which form a continuous supporting strand (they are profusely penetrated by pore canals); and the inner zone is of

one layer, consisting of colorless cells of the inner epidermis with markedly thickened walls.

Seed is medium-sized, oval, about 7 mm long and 1.5–2 mm wide. Spermoderm is formed by 8 to 10 cell layers (Fig. 3e). Exotesta is of a single layer, presented by small papillate cells, with walls abundantly impregnated by phlobaphene. External sides of their walls are thickened. Cuticle is presented by a thin layer. Mesotesta is formed by large, tangentially elongated parenchymal cells. They are abundantly filled with phlobaphenes. Endotesta is obsolete. Exotegmen is represented by a single layer, of tabular cells with uniformly thickened walls. The remaining 2 layers of parenchymal cells of tegmen are slightly compressed. Endosperm is fairly abundant. Embryo is small but well differentiated.

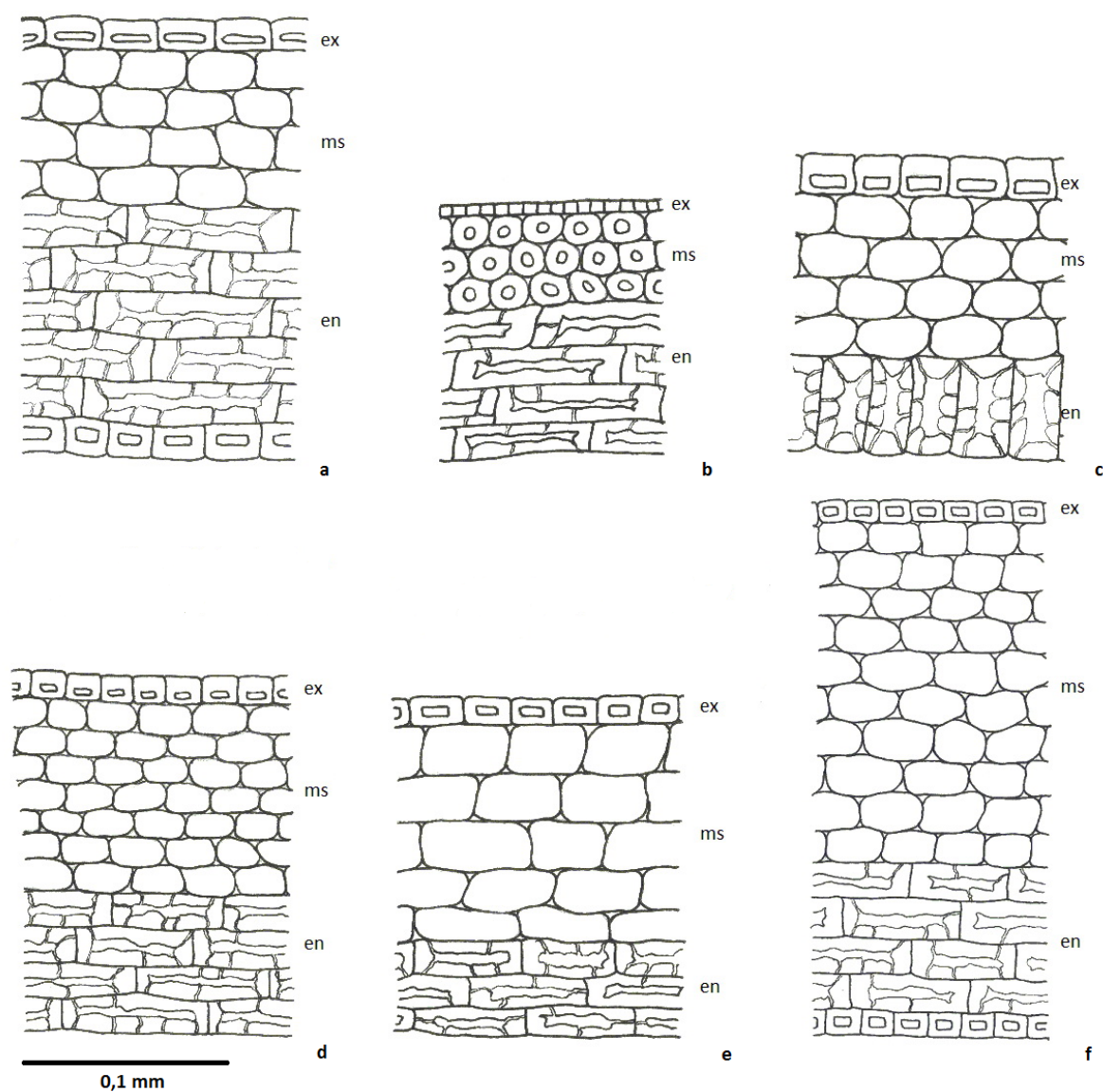


Fig. 2. Fruit anatomy of *Tripterygioidae* (cross sections): a – *Plenckia populnea*; b – *Ptetidium samberanensis*; c – *Rzedowskia tolantonguensis*; d – *Tripterygium regelii*; e – *Wimmeria persicifolia*; f – *Zinowiewia integerrima*. Scale bar = 0.1 mm; ex – exocarp, ms – mesocarp, en – endocarp.

Discussion

General fruit morphology. All seven genera are characterized by indehiscent unilocular (rarely bilocular – *Ptelidium*) winged fruits (“samara”). Fruit size: the length of the wing ranging from 12 mm in *Rzedowskia* to 55 mm in *Platypterocarpus*; the width of the wing ranging from 5–6 mm in *Rzedowskia* to 36 mm in *Platypterocarpus*. The shape of the fruit may be: 1) discoid (*Ptelidium*); 2) “sailing” one-winged samara (*Plenckia*, *Zinowiewia*); 3) fruits with 3–5 lateral wings (*Platypterocarpus*, *Tripterygium*, *Wimmeria*) (Fig. 1a–g). Fruits are either with 2, 3 or 5 lateral wings, nested along the fruit, or with one apical wing (on the fruit’s sides and its apex). The wings are wide or narrow, membranous; the body of the fruit is shorter than its wings. The wings usually possess a net of vascular bundle derivates. The topography of vascular bundles defines the way of pericarp expansion. Such a fruit type may be considered as an adaptation to anemochorous dispersal.

Pericarp structure. Pericarp is differentiated into outer one-layered exocarp, middle parenchymous mesocarp and inner fibrous endocarp. The only exception is the pericarp of *Ptelidium* which is lignified entirely. Fruits contain a pyrene, which can be formed by 3 to 5 layers of tangential elongated macrosclereids (in many examined taxa) or only

layer of radially elongated sclereids (*Rzedowskia*). Obviously, the pyrene is formed by the endocarp. Such pericarp structure is unknown for other groups of Celastraceae (Savinov, Solomonova, original data), what allows us to assume that this character is unique for the family (Fig. 2a–f).

Seed structure. Seeds are very small, with a well-developed embryo and copious endosperm, without arils. The thin seedcoat (spermoderm) is derived from both ovular integuments. It is differentiated into the multi-layered testa and the few-layered tegmen. The few-layered spermoderm is correlated with a pronounced, well-developed pericarp with inner zone of sclereids, forming the pyrene (Fig. 3a–e).

Some details of fruit morphogenesis. Apparently, the morphogenetical type of the fruit in *Tripterygioideae* is a pseudomonomerous one-seeded winged pyrenarium with remains of style (except in the genus *Ptelidium*). Wings of the fruit are formed due to radial expansion of the pericarp in the area of the carpels’ back side along the fruit longitudinal axis. Such fruits are known to develop from an oligomerous gynoecium (of 2 to 3 or 4 to 5 carpels) with 2(4–8) ovules in each locule. Underdevelopment of locules often takes place. As a result, only one locule is often pronounced and incomplete partitions are preserved in mature fruits

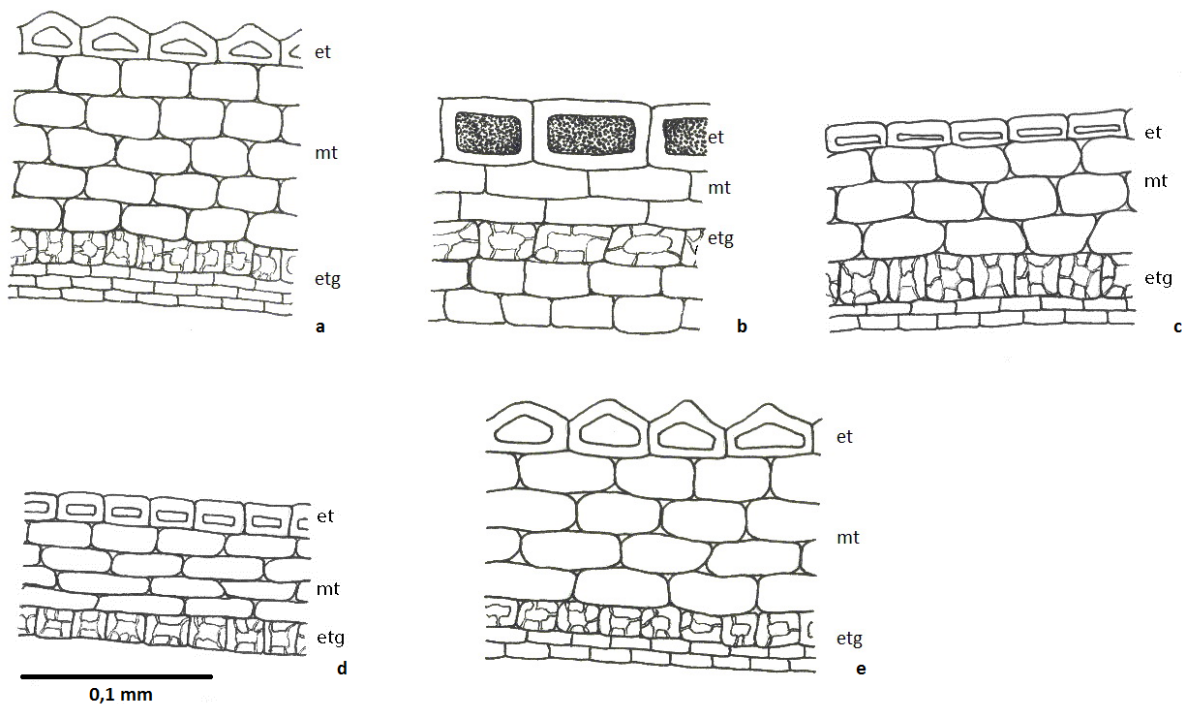


Fig. 3. Seed anatomy of *Tripterygioideae* (cross sections): a – *Plenckia populnea*; b – *Rzedowskia tolangouensis*; c – *Tripterygium regelii*; d – *Wimmeria persicifolia*; e – *Zinowiewia integerrima*. Scale bar = 0.1 mm; et – exotesta, mt – mesotesta, etg – exotegmen.

(Fig. 1i–k). The number of wings in the fruit usually corresponds to the number of carpels that form the gynoeceium.

So, morphogenetical type of the fruit in *Tripterygioideae* is pseudomonomerous unilocular one-seeded winged pyrenarium with a pyrene. Fruit type of *Ptelidium* is uni- or bilocular and one(two)-seeded nut, because its pericarp is lignified entirely.

We compared our findings with the results of molecular phylogenetic studies of the subfamilies *Cassinoideae* and *Tripterygioideae* (Simmons et al., 2012a). Here, *Tripterygioideae* subfamily is splitted into 6 clades, and they are related to different representatives of *Cassinoideae* and even *Celastroideae*.

As previously demonstrated in our research (Savinov et al., 2015), winged fruits of the family Celastraceae can be divided into four types based on the nature of wing-like outgrowths, and these types are characterized appropriate clades very well. Type I is more heterogeneous, and we were able to distinguish two subtypes: anemochorous (Type IA) and non-anemochorous (Type IB). They differ quite well in the pericarp structure and morphogenetic type of fruit – pyrenarium or capsule respectively. The genus *Ptelidium* is more isolated in comparison with others, because its pericarp is lignified entirely and its fruit type is a winged nut. Based on molecular data (Simmons et al., 2012a), we came to conclusion that winged fruits of *Tripterygioideae* were formed on

Table

Summary of fruit types in *Tripterygioideae* in comparison with main clades of Celastraceae

Family or sub-family	Genus	The number of species examined / Total species	Distribution	Habit	Pericarp structure	Fruit type
<i>Tripterygioideae</i>	<i>Plenckia</i>	1 / 4	Southern America	Trees or shrubs	Few-layered; tangential elongated macrosclereids	Winged pirenarium
	<i>Ptelidium</i>	2 / 2	Madagascar	Scandent or erect shrubs	Few-layered; lignified entirely	Winged nut
	<i>Rzedowskia</i>	1 / 1	Mexico	Shrubs	Few-layered; only layer of radially elongated sclereids	Winged pirenarium
	<i>Tripterygium</i>	3 / 3***	Japan, China, Korea, Taiwan, Northern Myanmar	Scandent shrubs (Lianas)	Few-layered; tangential elongated macrosclereids	Winged pirenarium
	<i>Wimmeria</i>	4 / 12	Central America	Trees or shrubs	Few-layered; tangential elongated macrosclereids	Winged pirenarium
	<i>Zinowiewia</i>	1 / 17	Central and Southern America	Trees or shrubs	Few-layered; tangential elongated macrosclereids	Winged pirenarium
Other Celastraceae*	91 genera (from them 39 examined)	102 / 1170	Widely	Trees, shrubs, lianas	Multi- or few-layered; with different structure (sclereids in meso- or/and endocarps)	Capsules, pirenaria**, nuts**, berries

* Mainly according to: Savinov, 2012.

** never winged

*** according to original studies

the basis of a monomerous dry pyrenarium in various representatives of the subfamily *Cassinoideae*. For the genera *Plenckia*, *Tripterygium*, *Wimmeria*, and *Zinowiewia*, a similar structure of the pericarp and spermoderm was shown; more isolated in terms of these characters – for *Rzedowskia*, *Ptelidium*. Winged fruits of *Stackhousioideae* are divided and non-homologous to fruits of *Tripterygioideae* (Savinov et al., 2015).

Conclusion

The common characters of all studied representatives of the *Tripterygioideae* can be summarized. 1) Oligomerous gynoecium (2–3,

rarely 4–5), usually with 2 ovules per locule. 2) Unilocular one-seeded winged fruits – pyrenaria with remains of style on the apex. 3) Small seeds lacking arils. Two genera appeared to be more isolated – *Ptelidium* and *Rzedowskia*, because they have specific characters of pericarp structure (Table). All examined taxa have demonstrated one special evolutionary trend in common – the reduction of the number of seeds per fruit and the development of wings as an adaptation to the dispersal by wind.

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Appendix A:

List of vouchers for examined specimens

<i>Plenckia populnea</i> Reiss. (LE, Botanical museum of RAS, St. Petersburg)	<i>T. wilfordii</i> Hook. f. (MHA)
<i>Ptelidium ovatum</i> Poir. (P)	<i>Wimmeria acuminata</i> L. Wins. (LE)
<i>P. samberanensis</i> R. Capoen. (P)	<i>W. bartlettii</i> Lundell. (MHA)
<i>Rzedowskia tolantonguensis</i> Medrano (K)	<i>W. confusa</i> Hemsl. (LE)
<i>Tripterygium hypoglaucum</i> (Levl.) Hutch. (MHA)	<i>W. persicifolia</i> Radlk. (LE)
<i>T. regelii</i> Sprague et Takeda (Arboretum of Main Botanical Garden of RAS, Moscow)	<i>Zinowiewia integerrima</i> Turcz. (Botanical museum of RAS, St. Petersburg)

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