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Evolution of the arils of *Euonymus* in comparison with some other genera of Celastraceae

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Keywords: arils, degree of seed covering, development, morphological origin, morphology-anatomical structure, trends of evolution.

Summary. The family Celastraceae R. Br. is characterized by the difference between the genera according to the types of fruits and the presence of arils in fruits of representatives of some genera. Attempts to reconstruct the evolution of arils in the Celastraceae were made earlier, while trying to trace the relationship of arils with the mucilagenous pulp and wings on the seed. In particular, earlier attempts were made to reconstruct the evolution of *Euonymus* arils. But, at present, significant changes in the phylogeny of the genus *Euonymus* and the family Celastraceae as a whole, as well as new accumulated material require another revision of the evolution of arils of *Euonymus*. We have studied the morphology-anatomical structure of mature arils of 28 species of *Euonymus*, as well as (additionally) the development of arils in 8 species of the genus. It is assumed that the aril of ancestral taxa of *Euonymus* had a funicular-exostomal origin, partially covered the seed, was colored orange, and composed of a single-layered epidermis and undifferentiated multi-layered parenchyma. In the cells of aril there were rounded chromoplasts, and large oil drops were absent. In the process of evolution of the aril of *Euonymus*, funicular arils appeared, while the funicular-exostomal ones were preserved. The degree of seed covering by aril in some modern species has increased and decreased again, arils have appeared with a small "window", partially (by 1/2–2/3) covering the seed and small fleshy structures in the basal part of the seed near funicule. The color of arils has been preserved in orange hues, but arils of some species have become red in color. The anatomical structure of the arils has changed. At present, along with multi-layer arils with a multi-layer undifferentiated or weakly differentiated parenchyma, there are arils with a strongly differentiated parenchyma and, conversely, with a parenchyma that is reduced in the process of development. In the process of evolution, fibrous and crystalline chromoplasts and large oil drops of different sizes appear in the cells of the arils.

Эволюция ариллусов *Euonymus* в сравнении с некоторыми другими родами Celastraceae

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Ключевые слова: ариллусы, морфологическая природа, морфолого-анатомическая структура, направления эволюции, развитие, степень прикрывания семени.

Аннотация. Для семейства Celastraceae R. Br. характерно различие между родами по типам плодов, а также наличие у семян представителей некоторых родов ариллусов. Попытки реконструкции эволюции ариллусов в семействе Celastraceae предпринимались ранее, при этом пытались проследить связь ариллуса с сочной частью семенной кожуры и крыловидными выростами на семени. В том числе, ранее были предприняты попытки реконструкции эволюции ариллусов у *Euonymus*. Но в настоящее время значительные изменения в филогении рода *Euonymus* и семейства Celastraceae в целом, а также новый накопленный материал требуют

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очередного пересмотра эволюции ариллусов у *Euonymus*. Нами было изучено строение зрелых ариллусов 28 видов *Euonymus*, а также (дополнительно) развитие ариллусов у 8 видов рода. Предполагается, что ариллус у предковых таксонов *Euonymus* имел фуникулярно-экзостомную природу, частично прикрывал семя, был окрашен в оранжевый цвет, состоял из однослойной эпидермы и недифференцированной многослойной паренхимы. В его клетках имелись округлые хромопласты, а крупные жировые включения отсутствовали. В процессе эволюции ариллуса *Euonymus* появились фуникулярные ариллусы, при этом фуникулярно-экзостомные сохранились. Степень прикрывания ариллусом семени у некоторых современных видов увеличилась и снова сократилась, появились ариллусы, имеющие небольшое «окошечко», частично (на 1/2–2/3) прикрывающие семя и небольшие мясистые образования в базальной части семени у фуникулуса. Окраска ариллусов сохранилась в оранжевых оттенках, но у некоторых видов ариллусы стали иметь красную окраску. Анатомическая структура ариллусов видоизменилась. В настоящее время наряду с многослойными ариллусами, имеющими многослойную практически недифференцированную или слабо дифференцированную паренхиму, есть ариллусы с сильно дифференцированной паренхимой и, наоборот, с редуцирующейся в процессе развития паренхимой. В процессе эволюции в клетках ариллусов появляются волокнистые и кристаллические хромопласты и крупные жировые включения разных размеров.

Introduction

Family Celastraceae R. Br. includes about 100 genera of plants. The family is characterized by the difference between the genera according to the types of fruits and the presence of arils in fruits of representatives of some genera. According to Simmons et al. (2001a), the presence of fleshy arils is a derived character state that arose twice in the family (once in *Canotia* Torr., and once in the most recent common ancestor of *Catha edulis* (Vahl) Forssk. ex Scop., *Euonymus* L., and *Polycardia* Juss.) and has been independently lost in six different lineages. According to modern data, representatives of the numerous genus *Euonymus* have 2 types of arils with different morphological origin: funicular arils and funicular-exostomal arils.

According to Zhang et al. (2011) and the results of original studies, a fleshy small hump around the micropyle also appears during the formation of funicular aril of *Euonymus europaeus* L. but in comparison with the massive outgrowth in the funicular-exostomal arils of *Euonymus*, such a slight thickening, does not give reason to associate these structures and interpret alike them morphological origin. Arils of *Euonymus* are different in morphology characters: cover the seeds surround, or a small "window" remains uncovered, or cover the seed by 1/2–2/3, or they are a small hump in the basal part of the seed. Arils of *Euonymus* are orange or red, smooth or folded.

Arils are multi-layered, consisting of the epidermis and the parenchyma underlying it. The parenchyma is lysing during the formation of the structure in some species. The surface of the arils can be smooth or folded. Arils of representatives of the closely related genus *Celastrus* L. are funicular-exostomal and completely cover the seed, consist of epidermis and multi-layered parenchyma; orange, folded (Trusov, Sozonova, 2011). Arils of other genera of Celastraceae have been studied in less detail.

Sarawakodendron filamentosum Ding Hou is characterized by a double aril. One part of the aril is a multi-layered (epidermis and multi-layered parenchyma) formation (appendage), developing from the exostome and funicule near the base of the seed, and the other part is filamentous structures (between two layers of elongated epidermal cells there is 1 layer of similar cells) arising at the base of the funicule (Hou, 1967; Corner, 1976). The color of the aril is not described. There is an assumption, that the filamentous part of the aril of *Sarawakodendron filamentosum* is homologous to the spiral filaments in the mucilagenous pulp of *Salacioideae* (*Sarawakodendron* L. as sister to *Salacioideae*) (Coughenour et al., 2010).

Helictonema velutinum (Afzel.) R. Wilczek has a small (< 0.5 × < 2 mm), white, spongy aril that is located at the base of the seed wing. Other *Hippocrateoideae* did not have aril. It has been suggested (Halle, 1983), that the presence of the aril in *Helictonema* Pierre is rudimentary, while the loss of the aril in *Hippocrateoideae* is a morphological synapomorphy.

According to more contemporary data, due to the fact, that *Helictonema* is sister to all representatives of the *Hippocrateoideae* and not a member of it, it was assumed that the arils of *Helictonema* and *Sarawakodendron* are inferred to be derived from the more typical fleshy arils of Celastraceae that are present in genera such as *Celastrus*, *Euonymus*, *Gymnosporia* (Wight et Arn.) Hook. f., *Maytenus* Molina, and *Salaciopsis* Baker f. (Coughenour et al., 2011).

Probable, those fleshy arils were present in the most recent common ancestor of *Hippocrateoideae*

+ *Sarawakodendron* + *Salacioideae* and were subsequently lost within the *Hippocrateoideae* (Coughenour et al., 2010). It should be noted here that the arils in modern representatives of *Sarawakodendron* have a funicular-exostomal morphological origin and do not completely cover the seed. The representatives of *Salacioideae*, although their seeds have a mucilagenous pulp, are recognized as more advanced representatives of the family, basing amongst other things on fruit type a berry, not a capsule (Simmons et al., 2001b; Bobrov et al., 2009).

Arils of *Paxistima* Raf. are yellow or white, lacerate or fringed, surrounding base and one side of seed (Navaro, Blackwell, 1990). Most representatives of the genus *Maytenus* from the Old World have thick basal arils, which are presumably a primitive character. In a smaller number of species, some of which are currently assigned to the genus *Gymnosporia*, the arils partially or completely cover the seeds and are therefore considered specialized (Sebsebe, 1985).

Representatives of the genus *Maytenus* from the New World with fruits-capsules that open with 2–3 valves have red arils (there is a report about yellowish arils (Lourteig, O'Donell, 1955)), completely or partially covered the seeds. Representatives with fruits-capsules that open with 2 curved valves, have white arils, completely covered the seeds (Biral et al., 2017). Seeds of *Monimopetalum chinense* Rehder have basal arils of undetermined color (Ma, Funston, 2008; Savinov et al., 2015).

Seeds of *Putterlickia pyracantha* (L.) Szyszyl. and *Denhamia obscura* (A. Rich.) Meisn. ex Walp. have multi-layer slightly folded arils, protruding and covering the seeds on one side (Savinov, 2006). There is a report that, in at least one representative of *Putterlickia* Endl., the aril is orange, wrinkled, completely covering the seed (Wyk, Mostert, 1987; Savinov, 2006). Arils of *Gymnosporia* are basal, shallowly cupola-shared, basal to partially enveloping seed, or nearly covering seed, white, yellowish or red (Quanru, Funston, 2008).

Arils of *Pterocelastrus* Meisn. cover the seed almost entirely (Savinov et al., 2015). Arils *Polycardia* Juss. are basal (Savinov, 2001). At the same time, a lacerated aril was described in *Polycardia* of Madagascar, presumably similar to the filamentous part of the aril of *Sarawakodendron filamentosum* (Hou, 1967). As a statement of fact, without descriptions, there are data on the presence of arils in *Psammomoya* Diels et Loes., *Dicarpellum* (Loes.) A. C. Sm., *Salaciopsis*, *Moya* Griseb., and *Platypterocarpus* Dunkley et Brenan (Melikian, Savinov, 2000; Simmons et al., 2001).

For representatives of *Lophopyxis* Hook., there is a report of the presence of an arillate structure on the seeds. Previously, this genus belonged to the Celastraceae, and now is better placed in the Euphorbiaceae Juss. (Simmons, Hedin, 1999). Zhang et al. (2011) suggest that arils in Celastraceae should be called *caruncula*. This based on the fact that in the system of APG III (2009) Celastrales Link is the only sister group of the orders Malpighiales Juss. ex Bercht. et J. Presl and Oxalidales Bercht. et J. Presl, and assuming that the relationship between the Celastraceae and Euphobiaceae is closer than generally suggested, as well as on their own research.

Also, the genus *Bhesa* Buch.-Ham. ex Arn., currently belonging to the Centroplacaceae Doweld et Reveal (Malpigiales) (Angiosperm Phylogeny Group, 2009, 2016), was previously considered as part of the Celastraceae family. Seeds of representatives of the genus have crimson or orange multilayer arils of a funicular-exostomal morphological origin (Corner, 1976).

Attempts to reconstruct the evolution of arils in the Celastraceae were made earlier while trying to trace the relationship of arils with the ucilaginous pulp and wings on the seed. Simmons and Hedin (1999) suggested that the typical fleshy arils of the common ancestor of *Catha edulis*, *Euonymus*, and *Polycardia*, which completely covers the seed, have advanced modification, resulting appeared four forms: the aril completely covering the seed, the aril partially covering the seed, the wings on the seeds, the mucilagenous pulp. At the same time, the arils completely covering the seed appeared three times, partially covering the seed twice. It also follows from this assumption that the aril, which does not completely cover the seed and has filamentous outgrowths, and the mucilagenous pulp arose in advanced taxa, while they had a closer ancestor.

Savinov (2011) had a different opinion, guided by the well-known van der Pijl scheme for the evolution of arils (Pijl, 1955), he recognized sarcotesta as an ancestral sign. Savinov (2011) derived the funicular aril, fleshy saccular exostomal aril and wing of seed from the sarcotesta; membranous exostomal aril, "partial" (?) exostomal aril, and funicular-exostomal aril from fleshy sac-like exostomal aril. Funicular-exostomal aril is also derived from funicular aril. Other transformations of the form and structure of the arils of Celastraceae are also assumed: 1) symmetrical, bilateral → asymmetric, unilateral → basal; 2) multi-layered, histological differentiated → few-layered, with compressed parenchymal cells; 3) with large schizogenic space in the parenchyma

→ with small schizogenic space or large intercellular spaces in the parenchyma; 4) smooth → wrinkled; 5) whole → dissected.

Before, in another paper, Savinov (2001) thought that the funicular arils in Celastraceae, which originated from sarcotesta, are basal, and did not mention about "partial" (?) exostomal aril. At the same time, in this paper, the classification of Celastraceae arils according to the degree of seed framing is mentioned: whole, hair-like-separate, collared (partial). The latter, in turn, depending on the degree of seed covering and position relative to the seed axis, are subdivided into roller-shaped or basal (no more than 1/8 of the seed length), comb-shaped (lateral location in relation to the seed axis), cup-shaped (1/2 of the seed length) and dome-shaped (2/3 or more of the length of the seed). Cup-shaped arils include aril of *Gymnosporia*, while *Paxistima myrsinites* (Pursh) Raf. belongs to domed arils, which contradicts the data of Quanru and Funston (2008), and Navaro and Blackwell (1990), and points to the insufficient study of arils of representatives of these genus.

Earlier attempts were made to reconstruct the evolution of arils of *Euonymus* (Trusov, Sozonova, 2008; Trusov, 2011, 2019). But, at present, significant changes in the phylogeny of the genus *Euonymus* and the family Celastraceae as a whole (Simmons et al., 2012), as well as new accumulated material require another revision of the evolution of arils of *Euonymus*.

Materials and methods

We have studied the morphology-anatomical structure of mature arils of 28 species of *Euonymus*, as well as (additionally) the development of arils in 8 species of the genus (table 1).

The genus *Euonymus* is accepted according to Plants of the World Online (POWO, 2023), with the assumption that *E. bungeanus* Maxim., *E. maximowiczianus* Prokh., *E. nicoensis* Nakai, *E. pauciflorus* Maxim., *E. semiexsertus* Koehne, *E. sieboldianus* Blume and *E. yedoensis* Koehne exist as accepted species according to T. G. Leonova (1974). The division into sections is according to Li et al. (2013). Synonyms of sections accepted according to T. G. Leonova (1974).

The fruits were collected in the arboretum of the Tsitsin Main Botanical Garden RAS, Botanical Garden of Moscow State University, Subtropical Botanical Garden of Kuban and in nature: Moscow Region, Primorsky Krai.

Fresh and fixed (in 70 % ethanol) material was reviewed. The binocular magnifiers MBS-1 and MBS-10 and the SIGMA EX 150mm 1: 2.8 APO Macro DG HSM; microscopes MBR-1A, Biolam LOMO C1, and Biomed S-2 were used. The longitudinal and transverse sections of arils were performed manually using a Gillet razor blade. The water and glycerin preparations made from them were studied. The lipid nature of the inclusions was determined with Sudan III. Photos were taken a Canon EOS 650D.

Results

Currently, representatives of *Euonymus* have the following morphological modifications of arils.

Modification 1 (Fig. 4D). Aril is funicular-exostomal, covering the seed around. It is typical for *E. japonicus* Thunb. (section *Ilicifolia*), *E. americanus* L., and *E. obovatus* Nutt. (section *Echinococcus*), *E. oxyphyllus* Miq. and *E. sashalinensis* (Fr. Schmidt) Maxim. (section *Kalonymus*), as well as for representatives of *Celastrus* (Fig. 1E–G, 2J–L).

Modification 2 (Fig. 4C). Aril is funicular-exostomal, covering the seed partially; the small "window" incovered. It is typical for *E. latifolius* (L.) Mill., *E. macropterus* Rupr., and *E. maximowiczianus* (section *Kalonymus*) (Fig. 1, 2E).

Modification 3 (Fig. 4B). Aril is funicular, covering the seed partially; the small «window» uncovered. Seed has a small hump near the exostome. It is typical for *E. semiexsertus*, *E. sieboldianus*, *E. velutinus* Fisch. et Mey., and *E. yedoensis* (section *Euonymus*).

Modification 4 (Fig. 4F). Aril is funicular, covering the seed around. Seed has a small hump near the exostome. Parenchyma is differentiated, reducing (see below), which seems to be a slightly more advanced modification. It is typical for some species of section *Euonymus* (*E. bungeanus*, *E. europaeus*, *E. hamiltonianus* Wall., *E. maackii* Rupr., and *E. nicoensis* Nakai) (Fig. 2F).

Modification 5 (Fig. 4I). Aril is funicular, covering the seed around, with the extreme case of parenchymal reduction. Seed without hump near the exostome. It is typical for *E. myrianthus* Hemsl. (section *Euonymus* (= *Myrianthus*)), *E. phellomanus* Loes. (section *Euonymus*) and the evolutionarily advanced section *Melanocarya* (*E. alatus* (Thunb.) Siebold) and appears to be the following modification derived from previous one (see below) (Fig. 1B–C, 2G–H).

Table 1

Morphology-anatomical structure of arils of some species of *Euonymus* and *Celastrus* sp.

Characters / Species	Morphological origin	Degree of covering	Color	Number of cell layers	Differentiation of parenchyma	Oil drops	Chromoplasts
Section *Ilicifolia*							
E. japonicus Thunb.	funicular-exostomal	around	orange	multi-layered	weakly differentiation	rare large and small oil drops	rounded
Section *Echinococcus*							
E. americanus L.	funicular-exostomal	around	orange	multi-layered	weakly differentiation	rare large and small oil drops	rounded
E. obovatus Nutt.	funicular-exostomal	around	orange	multi-layered	weakly differentiation	rare large and small oil drops	rounded
Section *Euonymus* (= *Multiovulatus*)							
E. carnosus Hemsl.	funicular	small part (marginal)	orange	multi-layered	strongly differentiation	large and small oil drops (epidermis)	rounded, fibrous
E. grandiflorus Wall.	funicular	small part (marginal)	orange	multi-layered	strongly differentiation	large and small oil drops (epidermis)	rounded, fibrous
Section *Euonymus* (= *Myrianthus*)							
E. myrianthus Hemsl.	funicular	around	orange	low-layer	reduction	large and small oil drops	rounded, fibrous
Section *Euonymus* (= *Vyenomus*)							
E. pendulus Wall.	funicular	half	orange	multi-layered	weakly differentiation	large and small oil drops	rounded
Section *Euonymus* (= *Pseudovyenomus*)							
E. nanus M. Bieb.	funicular	half	orange	multi-layered	weakly differentiation	large and small oil drops	rounded, fibrous, crystalline
E. nitidus Benth.	funicular	half	orange	multi-layered	weakly differentiation	large and small oil drops	rounded, fibrous
E. pauciflorus Maxim.	funicular	half	orange	multi-layered	weakly differentiation	large and small oil drops	rounded, fibrous
E. verrucosus Scop.	funicular	half	orange	multi-layered	weakly differentiation	small oil drops	rounded, fibrous
Section *Euonymus* (= *Humphrya*)							
E. atropurpureus Jacq.	funicular	small «window» uncovered	orange	multi-layered	weakly differentiation	large and small oil drops	rounded, fibrous
Section *Euonymus*							
E. bungeanus Maxim.	funicular	around	orange	low-layer	reduction	large and small oil drops	rounded, crystalline
E. europaeus L.	funicular	around	orange	low-layer	reduction	large and small oil drops	rounded, crystalline
E. hamiltonianus Wall.	funicular	around	orange	low-layer	reduction	large and small oil drops	rounded, crystalline
E. maackii Rupr.	funicular	around	orange	low-layer	reduction	large and small oil drops	rounded, crystalline

Table 1 (continued)

Characters / Species	Morphological origin	Degree of covering	Color	Number of cell layers	Differentiation of parenchyma	Oil drops	Chromoplasts
E. nicoensis Nakai	funicular	around	orange	low-layer	reduction	large and small oil drops	rounded, crystalline
E. phellomanus Loes.	funicular	small “window” uncovered	red	2-layer	reduction	large and small oil drops	rounded, fibrous
E. semiexsertus Koehne	funicular	small “window” uncovered	orange	low-layer	reduction	large and small oil drops	rounded, crystalline
E. sieboldianus Blume	funicular	small «window» uncovered	orange	low-layer	reduction	large and small oil drops	rounded, crystalline
E. velutinus Fisch. et Mey.	funicular	small “window” uncovered	orange	low-layer	reduction	large and small oil drops	rounded, crystalline
E. yedoensis Koehne	funicular	small “window” uncovered	orange	low-layer	reduction	large and small oil drops	rounded, crystalline
Section *Melanocarya*							
E. alatus (Thunb.) Siebold	funicular	around	orange	low-layer	reduction	large and small oil drops	rounded, fibrous, crystalline
Section *Kalonymus*							
E. latifolius (L.) Mill.	funicular-exostomal	small “window” uncovered	orange	multi-layered	weakly differentiation	large and small oil drops	rounded, fibrous
E. macropterus Rupr.	funicular-exostomal	small “window” uncovered	orange	multi-layered	weakly differentiation	large and small oil drops	rounded, fibrous, crystalline
E. maximowiczianus Prokh.	funicular-exostomal	small “window” uncovered	orange	multi-layered	weakly differentiation	large and small oil drops	rounded, fibrous, crystalline
E. oxyphyllus Miq.	funicular-exostomal	around	orange	multi-layered	weakly differentiation	large and small oil drops	rounded, crystalline
E. sashalinensis (Fr. Schmidt) Maxim.	funicular-exostomal	around	orange	multi-layered	weakly differentiation	large and small oil drops	rounded, crystalline
Celastrus sp.							
Celastrus sp.	funicular-exostomal	small “window” uncovered	orange	multi-layered	weakly differentiation	small oil drops	rounded, fibrous

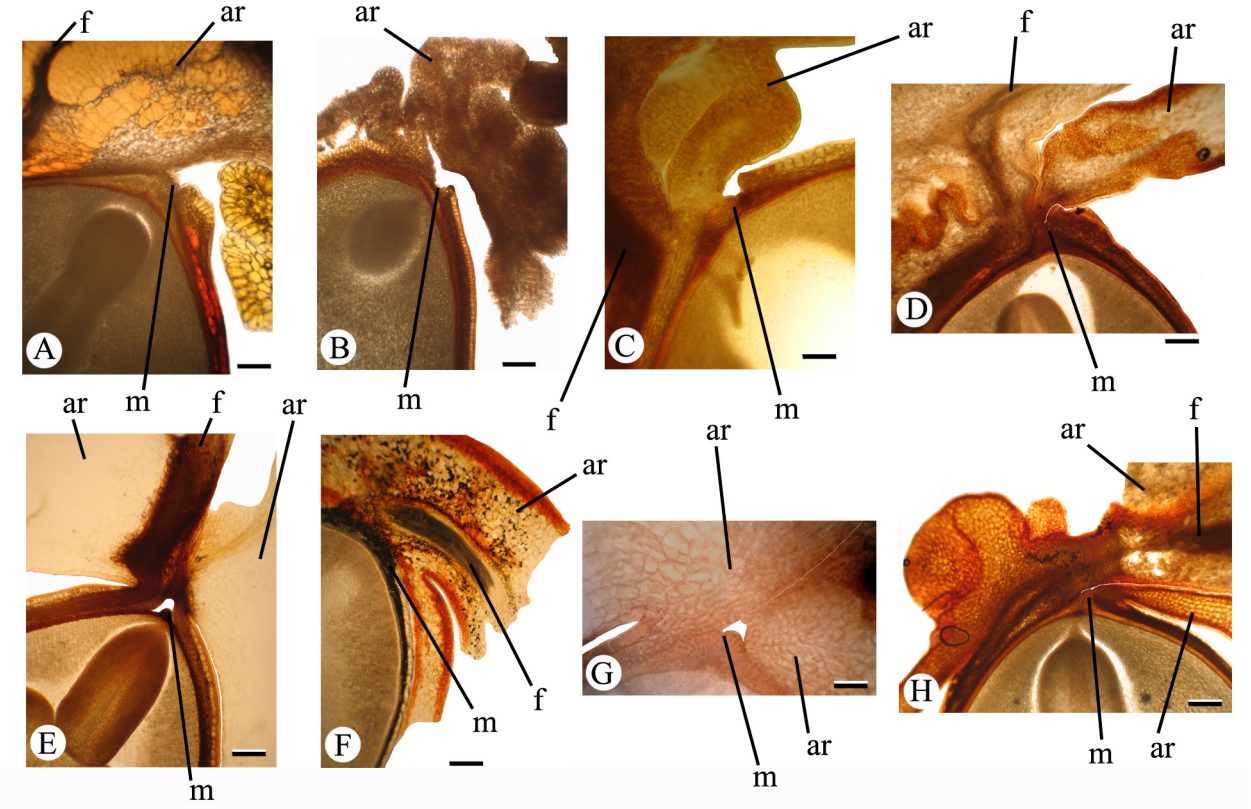

Fig. 1. Morphological origin of arils of various species of *Euonymus* and *Celastrus rugosus*: A – *E. grandiflorus*; B – *E. phellomanus*; C – *E. alatus*; D – *E. pauciflorus*; E – *C. rugosus*; F – *E. japonicus*; G – *E. americanus*; H – *E. macropterus*. ar – aril; m – micropyle; f – funicle. Scale bar – 0.1 mm.

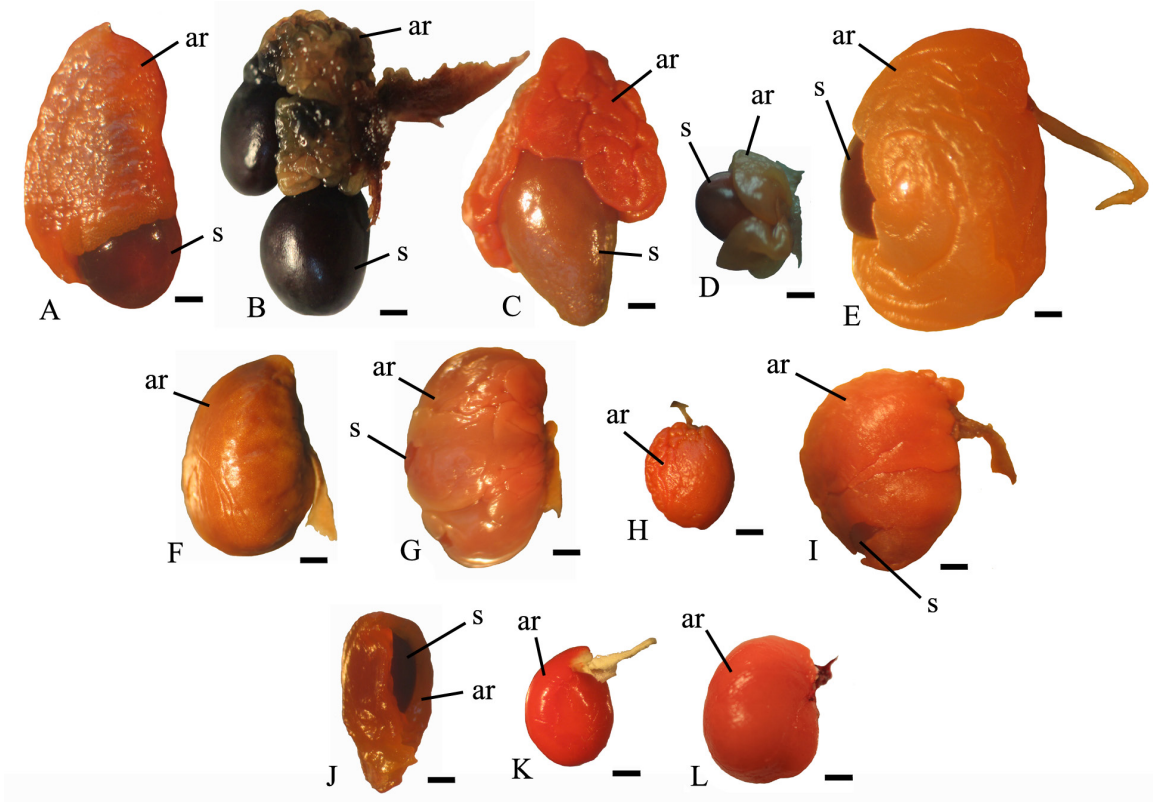

Fig. 2. Seeds with arils of various species of *Euonymus* and *Celastrus rugosus*: A – *E. grandiflorus*, B – *E. carnosus*; C – *E. pauciflorus*; D – *E. nanus*; E – *E. verrucosus*; F – *E. europaeus*; G – *E. phellomanus*; H – *E. alatus*; I – *E. macropterus*; J – *C. rugosus*; K – *E. japonicas*; L – *E. americanus*. ar – aril; s – seed. Scale bar – 1 mm.

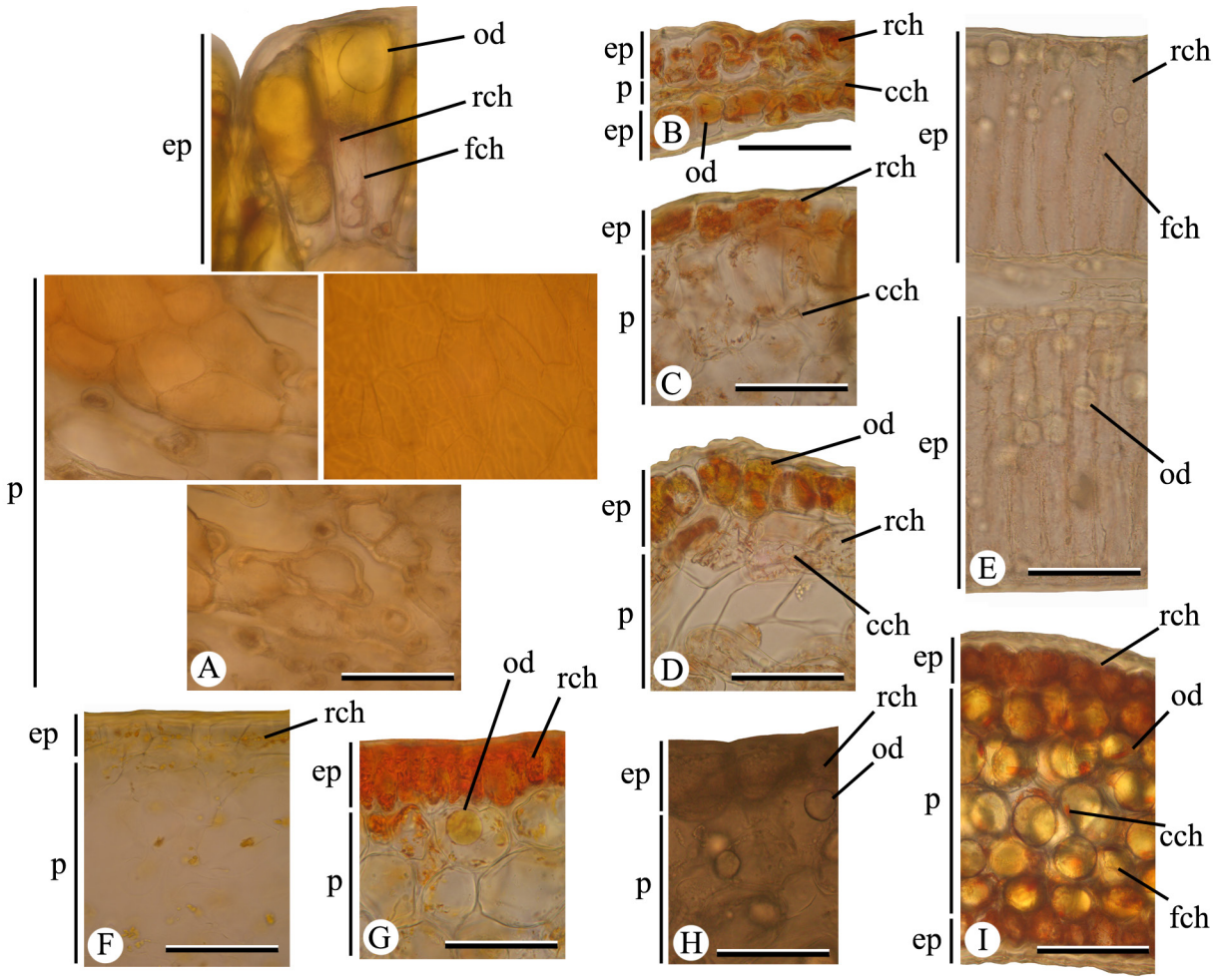

Fig. 3. Anatomical structure of arils of various species of *Euonymus* and *Celastrus orbiculatus*.
A – *E. grandiflorus*, B – *E. alatus*; C – *E. verrucosus*; D – *E. pauciflorus*; E – *E. phellomanus*; F – *C. orbiculatus*; G – *E. japonicus*; H – *E. americanus*; I – *E. macropterus*. cch – crystalline chromoplast; ep – epidermis; fch – fibrous chromoplast; od – oil drop; p – parenchyma; rch – rounded chromoplast. Scale bar – 0.01 mm.

Modification 6 (Fig. 4E). Aril is funicular, partially covering the seed. Seed without hump near the exostome. It is typical for *E. atropurpureus* Jacq. (section *Euonymus* (= *Humphrya*)).

Modification 7 (Fig. 4H). Aril is funicular, covering the seed by 1/2–2/3 and having a weakly differentiated parenchyma. It is typical for species of the section *Euonymus*: *E. pendulus* Wall. (formerly the section *Vyenomus*) and *E. nanus* M. Bieb., *E. nitidus* Benth., *E. pauciflorus*, and *E. verrucosus* Scop. (formerly the section *Pseudovyenomus*) (Fig. 1E, 2C–E).

Modification 8 (Fig. 4G). Aril is funicular, small appendage on the funicule. It is typical for *E. carnosus* Hemsl. and *E. grandiflorus* Wall. (section *Euonymus* (= *Multiovulatus*)) (Fig. 1A, 2A–B). These species are considered to be evolutionarily advanced and related to *Melanocarya* (Li et al., 2013).

Currently, representatives of *Euonymus* have the following anatomical modifications of arils:

Modification 1 (Fig. 5B). Aril with small oil drops and rounded chromoplasts in the cells of the epidermis and multi-layered undifferentiated parenchyma, and with rare larger oil drops in the cell parenchyma. It is typical for sections *Ilicifolia* and *Echinococcus* (Fig. 3G–H). For arils of *Celastrus* typical small oil drops and rounded and fibrous chromoplasts in the cells of the epidermis and multi-layered undifferentiated parenchyma (Fig. 3F).

Modification 2 (Fig. 5C). Aril with multi-layer undifferentiated parenchyma with a few large and small oil drops in its cells and more numerous in epidermal cells, with rounded and fibrous, sometimes crystalline chromoplasts (section *Euonymus* (= *Pseudovyenomus*)) (Fig. 3D).

Modification 3 (Fig. 5G). Aril with multi-layer undifferentiated parenchyma and more numerous large and small oil drops in the parenchyma cells and few in the epidermal cells, and rounded chromoplasts (*E. pendulus*, section *Euonymus* (= *Vyenomus*)).

Modification 4 (Fig. 5H). Aril with multi-layer undifferentiated parenchyma and with numerous large and small oil drops in all cells of the aril, with rounded and crystalline, sometimes fibrous chromoplasts (section *Kalonymus*) (Fig. 3I).

Modification 5 (Fig. 5F). Aril with multi-layer undifferentiated parenchyma, without large oil drops in its cells and parenchyma cells, with rounded and fibrous chromoplasts (*E. verrucosus*, section *Euonymus* (= *Pseudovyenomus*)) (Fig. 3C).

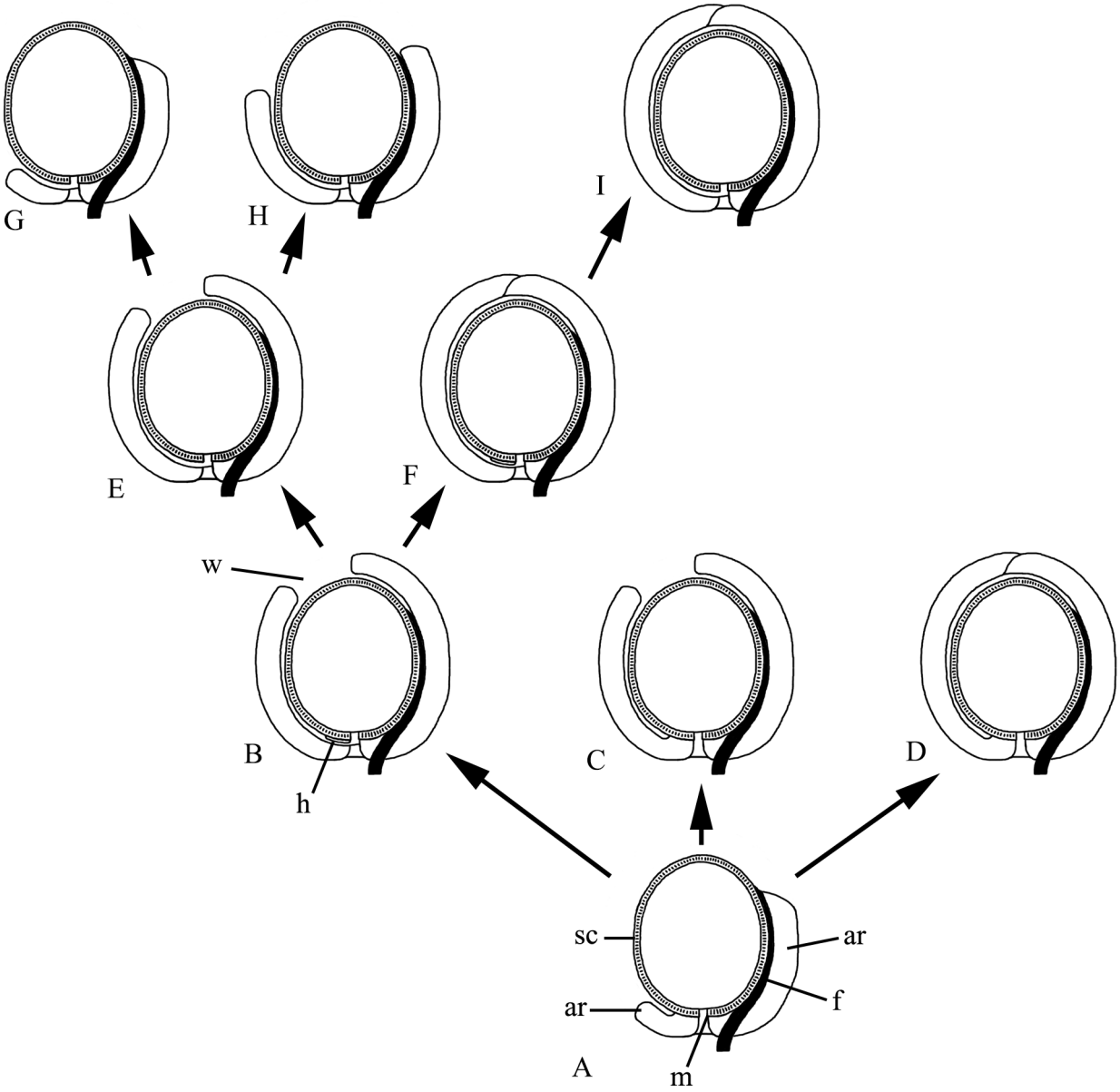

Fig. 4. Modifications and evolutionary trends of the morphological structure and morphological origin of the arils of *Euonymus*: A – aril is funicular-exostomal, covering the seed partially (aril of ancestral taxa of *Euonymus*); B – aril is funicular, covering the seed partially, the small "window" uncovered; seed have a small hump near the exostome (modification 3); C – aril is funicular-exostomal, covering the seed partially, the small "window" uncovered (modification 2); D – aril is funicular-exostomal, covering the seed around (modification 1); E – aril is funicular, partially covering the seed (modification 6); F – aril is funicular, covering the seed around; seed have a small hump near the exostome; parenchyma is differentiated, reducing (modification 4); G – aril is funicular, small appendage on the funicule (modification 8); H – aril is funicular, covering the seed by 1/2-2/3 and having a weakly differentiated parenchyma (modification 7); I – aril is funicular, covering the seed around, with the extreme case of parenchymal reduction (modification 5). ar – aril; f – funicle; h – hump; m – micropyle; sc – seed coat; w – "window".

Modification 6 (Fig. 5D). Aril with differentiated, partially reduced parenchyma, with more numerous large and small oil drops in epidermal cells and rounded and crystalline (section *Euonymus*) (Fig. 3E).

Modification 7 (Fig. 5I). Aril only from epidermal cells (the parenchyma is completely reduced), with numerous large and small oil drops in the cells and rounded, fibrous and crystalline chromoplasts (section *Melanocarya*) (Fig. 3B).

Modification 8 (Fig. 5E). Aril with strongly differentiated parenchyma and large and small oil drops, as well as rounded and fibrous chromoplasts exclusively in epidermal cells (section *Euonymus* (= *Multiovulatus*)) (Fig. 3A).

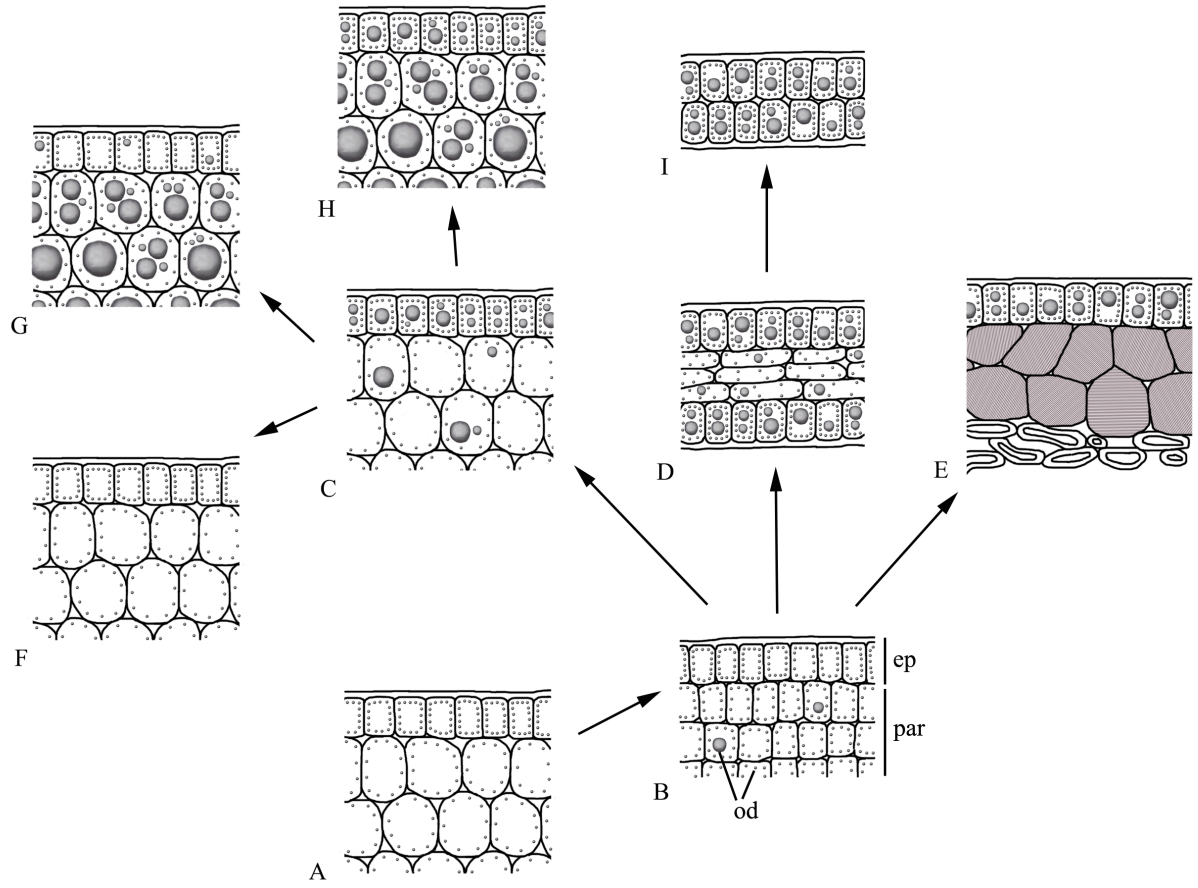

Fig. 5. Modifications and evolutionary trends of the anatomical structure of the arils of *Euonymus*: A – aril with small oil drops in the cells of the epidermis and multi-layered undifferentiated parenchyma (aril of ancestral taxa of *Euonymus*); B – aril with small oil drops in the cells of the epidermis and multi-layered undifferentiated parenchyma, and with rare larger oil drops in the cells parenchyma (modification 1); C – aril with multi-layer undifferentiated parenchyma with a few large and small oil drops in its cells and more numerous in epidermal cells (modification 2); D – aril with differentiated, partially reduced parenchyma, with more numerous large and small oil drops in epidermal cells (modification 6); E – aril with strongly differentiated parenchyma and large and small oil drops (modification 8); F – aril with multi-layer undifferentiated parenchyma, without large oil drops in its cells and parenchyma cells (modification 5); G – aril with multi-layer undifferentiated parenchyma and more numerous large and small oil drops in the parenchyma cells and few in the epidermal cells (modification 3); H – aril with multi-layer undifferentiated parenchyma and with numerous large and small oil drops in all cells (modification 4); I – aril only from epidermal cells (the parenchyma is completely reduced), with numerous large and small oil drops in the cells (modification 7). ep – epidermis; od – oil drop; p – parenchyma.

Discussion

Based on the fact that the fleshy part of the seed coat (mucilagenous pulp) is characteristic of advanced taxa of Celastraceae (*Salacioideae*), and most of the modern representatives of Celastraceae (*Celastrus*, *Sarawakodendron*, some of *Euonymus*) are characterized by funicular-exostomal arils, which is also described in representatives of the *Lophopyxis* and *Bhesa*, previously included in the Celastraceae, and the fact that the order Celastrales is the only sister group to the order Malpighiales,

whose members of the family, Euphorbiaceae, also have arils of a funicular-exostomal morphological nature, it can be assumed that the ancestral aril in *Euonymus* also has a funicular-exostomal morphological origin (Simmons, Hedin, 1999; Simmons et al., 2001; Angiosperm Phylogeny Group, 2016). This assumption is consistent with van der Pijl's (1955) assumptions on the evolution of arils, in which he allowed for the independent appear of different types of arils in plants.

The author's working hypothesis about the origin of arils in plants in general is the assumption that the growth of funicule and/or seed coat tissues and, as a result, the formation of arils, can occur only with an excessive influx of nutrients into these tissues and the inability of the developing seed to fully use these nutrients for your needs (Trusov, 2016). Despite the fact that arils in Celastraceae appeared several times, based on modern data that the mechanism for the emergence of fleshy seed appendages is quite ancient, a number of MADS-box genes are responsible for the development of fleshy structures in Angiosperm fruits, which are also involved in the growth of fleshy structures of the seeds of *Taxus baccata* L. (Lovisetto et al., 2012), it can be supposed that related taxa of Celastraceae (*Celastreae*, *Euonymeae*) still had one type of ancestral aril, and this was the funicular-exostomal aril. Thus, this type of aril is most likely ancestral to all *Euonymus*, especially since it is characteristic of modern representatives of the sect. *Kalonymus* and *Echinococcus*, while *Euonymus europaeus* (sect. *Euonymus*) has a small fleshy hump around the micropyle during the formation of funicular aril (Fig. 1). In representatives of the closely related genus *Celastrus*, arils also have a funicular-exostomal morphological origin. The degree to which the ancestral aril covered the seed of the *Euonymus* remains an open question. As an ancestral, we offer aril covering the seed by 1/2–2/3 (Fig. 4A). In the majority of representatives of the genus, in species close to ancestral forms, in species having an aril of a funicular-exostomal morphological origin, as well as in representatives of *Celastrus*, their arils completely cover the seeds, or a small area remains uncovered (Fig. 2). Arils covering only a very small part of the seed are characteristic of advanced representatives of the genus (of those studied, these are *E. grandiflorus* and *E. carnosus*) and have a differentiated anatomical structure. This does not contradict the assumption that the small aril in plants is in most cases an adaptation to myrmecochory. And in the case of the ornitochory seed dispersal of *Euonymus*, the aril should cover all or most of the seed, but the diaspore should remain attractive to birds. As a result, it can be assumed that having formed as a completely covering structure, the aril could then decrease until the balance was maintained: the diaspores remained attractive to the disseminators and the formation of the structure would not be unnecessarily energy-intensive. It should also be noted here that the mucilagenous pulp is characteristic of advanced members of the Celastraceae, which indicates that the ancestral structure of the sarcotesta type, which was reduced to a ridge-like growth near the funicule and/or exostome and then again covered the seed, only already as an aril, could hardly exist. We assume that 3 types of morphological modifications of the aril in *Euonymus* and representatives of related genera originated from the ancestral aril, which has a funicular-exostomal origin, covers the seed by 1/2–2/3, and is multi-layered, with a weakly differentiation of the parenchyma. From one of these modifications, there were 5 more modifications later.

The arils of ancestral taxa of *Euonymus* were most likely multi-layered but weakly differentiated, consisting of epidermis and multi-layered parenchyma from cells comparable in size to each other and to epidermal cells (Fig. 5A). In more advanced representatives of the genus, parenchymal cells differentiate (Fig. 3). It is possible to identify 3 trends of differentiation (3 anatomical modifications): 1 – enlargement of the cells of the central layers of the parenchyma (weakly differentiation); 2 – stretching of the parenchymal cells in the tangential direction during the formation of the aril's structure and their obliteration by the time of maturation (reduction), until the complete absence of the parenchyma, as *E. phellonanus* Loes.; 3 – differentiation into 2 zones: adjacent to the seed from small thick-walled cells elongated in various directions, and adjacent to the free part of the funicule from large thin-walled densely spaced cells with colored contents of a non-lipid nature (strongly differentiation). Arils in representatives of *Celastrus* have weakly cell differentiation. Later, arils which differed in the deposition of large oil drops in the cells of the epidermis and parenchyma occurred from the first modification. Arils with a completely reducing parenchyma occurred from second modification.

Large oil drops of different sizes are found in the cells of the arils of many species of *Euonymus*. In parenchymal cells of species close to ancestral (for example, *E. japonicus*), large oil drops are few. In arils with weakly differentiated multi-layered parenchyma, its cells contain numerous large oil drops of

different sizes (an exception is *E. verrucosus*, which does not have large oil drops). In arils with a reducing parenchyma, rare large oil drops appear in the cells of the parenchyma, but they are not very large and few. At the same time, large oil drops are present in the cells of the epidermis. In arils with a strong differentiated parenchyma, large oil drops in the parenchymal cells are absent, but they are very numerous in the epidermal cells. It can be assumed that initially the arils of *Euonymus* did not accumulate a many of oil and did not have large oil drops in the cells. Then, the oil began to accumulate in the cells of the parenchyma, and with its reduction or differentiation, the function of oil deposition passed to the cells of the epidermis. Indirect evidence of the ancestral non-oily aril of *Euonymus* can also be the fact that the arils of representatives of the closely related genus *Celastrus* without large oil drops in the cells, and the parenchyma cells are weakly differentiated. The absence of large oil drops in the cells of *E. verrucosus*, a relatively advanced species of *Euonymus*, can be considered as a hypomorphosis.

Three forms of chromoplasts were found in the cells of mature arils *Euonymus*: rounded, fibrous, and crystalline (chromoplast forms according to Marano et al., 1993). Rounded chromoplasts are present in aril's cells of all studied species of *Euonymus*. In species like to primitive (*E. japonicus* and *E. obovatus*), only rounded chromoplasts were found in aril's cells. More advanced species also have crystalline and/or fibrous chromoplasts. It is believed that crystalline chromoplasts are more ontogenetic advanced than round ones (Matiyenko, 1967; Lobov, Petrov, 1987). Crystalline chromoplasts were found in aril's cells in most of the studied species. Fibrous chromoplasts are characteristic of only a few species of *Euonymus*. They are present in the cells of the arils of representatives of most of the studied species of the early isolated sect. *Kalonymus* and in some representatives of the sections *Euonymus*. On the contrary, representatives of *Celastrus*, are characterized by the presence of rounded and fibrous chromoplasts in the cells of the epidermis and parenchyma of the arils, very rarely large prismatic crystalline chromoplasts are found in the cells of the parenchyma (Trusov, Sozonova, 2011).

Color of arils is due to the presence of pigments in them, including chromoplasts. Most arils of *Euonymus*, as in *Celastrus*, are orange in color. Of the studied representatives of *Euonymus*, the red color of aril is typical only for *E. phellomanus*, contained in the epidermal cells (parenchyma is absent) is rounded and fibrous chromoplasts. It is possible that the red color of the aril compensates for its few-layering while remaining attractive to seed disseminators.

Conclusion

Thus, it can be assumed that the ancestral aril of *Euonymus* and representatives of related genera had a funicular-exostomal origin, partially covered the seed, was colored orange, and composed of a single-layered epidermis and undifferentiated multilayered parenchyma. In the cells of aril there were rounded chromoplasts, and large oil drops were absent. In the process of evolution of the aril of *Euonymus*, funicular arils appeared, while the funicular-exostomal ones were preserved (Fig. 4). The degree of seed covering by aril in some modern species has increased and decreased again, arils have appeared with a small "window", partially (by 1/2–2/3) covering the seed and small fleshy structures in the basal part of the seed near funicule.

The color of arils has been preserved in orange hues, but arils of some species have become red in color. The anatomical structure of the arils has changed (Fig. 5). At present, along with multi-layer arils with a multi-layer undifferentiated or weakly differentiated parenchyma, there are arils with a strongly differentiated parenchyma and, conversely, with a parenchyma that is reduced in the process of development. In the process of evolution, fibrous and crystalline chromoplasts and large oil drops of different sizes appear in the cells of the arils.

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