Botanica Pacifica. A journal of plant science and conservation. 2026.
DOI: 10.17581/bp.2026.15203

RESEARCH PAPER

Structure and development of fruit of *Asarum* (Aristolochiaceae)

Nikolay A. Trusov

Nikolay A. Trusov *
e-mail: n-trusov@mail.ru

Tsytsin Main Botanical Garden RAS, Moscow, Russia

* corresponding author

Manuscript received: 01.12.2025
Review completed: 12.07.2026
Accepted for publication: 18.07.2026
Published online: 24.07.2026

ABSTRACT

Mature fruit structure and development of *Asarum europaeum* were studied. The fruit is a leathery, pubescent capsule comprising 6 carpels. The pericarp is multilayered: exocarp is single-layered with cuticle; mesocarp is multilayered, differentiated into two zones of densely and loosely located parenchymatous cells; endocarp is single-layered, composed of tangentially elongated, thin-walled or slightly thickened cells. The yellowish, fleshy aril grows along raphe, is multilayered, with a thin epidermis and enlarged upper parenchyma cells. Seed is ovoid, brown; seed coat has 5 layers: flattened exotesta with cuticle, endotesta with crystals and thickened walls, exotegmen of longitudinal sclerenchymatous fibers, and endotegmen comprising transverse fibers and thin-walled tangentially elongated cells. Endosperm is copious, embryo small (heart-shaped or linear), both with oil droplets. Development spans 7 weeks (4 growth, 3 maturation). Fruit, aril, and seed grow synchronously via a sigmoid curve. Cell specialization in the pericarp and the seed coat occurs after rapid fruit growth, earlier in the aril. Fatty oil accumulates in the endosperm after seed isolation, in the embryo before fruit maturation, but not in the aril. The aril functions are to attract dispersers and possibly protect seeds early.

Keywords: *Asarum*, fruit, aril, seed, pericarp, seed coat, morphological and anatomical structure, development, functions

РЕЗЮМЕ

Трусов Н.А. Строение и развитие плодов *Asarum* (Aristolochiaceae). Исследовано строение зрелого плода и развитие плодов *Asarum europaeum*. Плод представляет собой кожистую опушённую коробочку, состоящую из 6 плодолистиков. Околоплодник многослойный: экзокарпий однослойный, покрыт кутикулой; мезокарпий многослойный, дифференцирован на две зоны из плотно и рыхло расположенных паренхимных клеток; эндокарпий однослойный, образован тангенциально вытянутыми тонкостенными или слегка утолщёнными клетками. Желтоватый мясистый ариллус развивается вдоль рафе, многослойный, с тонкой эпидермой и увеличенными верхними паренхимными клетками. Семя яйцевидное, бурое; семенная кожура состоит из 5 слоёв: уплощённая экзотеста с кутикулой, эндотеста с кристаллами и утолщёнными стенками, экзотегмен из продольных склеренхимных волокон, а также эндотегмен, включающий поперечные волокна и тонкостенные тангенциально вытянутые клетки. Эндосперм обильный, зародыш мелкий (сердцевидный или линейный), оба содержат масляные капли. Развитие длится 7 недель (4 недели – фаза роста, 3 недели – фаза созревания). Рост плода, ариллуса и семени происходит синхронно по сигмоидной кривой. Специализация клеток в околоплоднике и семенной кожуре происходит после быстрого роста плода, а в ариллусе – раньше. Жирное масло накапливается в эндосперме после обособления семени, в зародыше – перед созреванием плода, тогда как в ариллусе оно не накапливается. Функциями ариллуса являются привлечение распространителей семян и, возможно, защита семян на ранних этапах развития.

Ключевые слова: копытень, плод, ариллус, семя, перикарпий, семенная кожура, морфолого-анатомическое строение, развитие, функции

In some representatives of Angiospermae succulent appendes, called "aril", develop near the seeds (Baillon 1876–1878, Pfeiffer 1891, Goebel 1923, Maheshwari 1950, Corner 1953, Corner 1954, Pijl 1955, Eames 1961, Komar 1965, Kozlowski 1972, Artyushenko 1990, Shamrov 2008, Trusov 2016, 2021). In Aristolochiaceae Juss. aril are present in representatives of the *Asarum* L. and *Aristolochia* L. They are considered to be an appendes of the funicle in the raphe region and are sometimes called "strophiole" (Vovk & Komar 1988, Trusov 2012, 2014). The structure of the *Asarum* strophiole is described as follows: in the lower part, it is formed by small-celled tissue, and in the upper part it consists of large thin-walled cells, arranged fan-shaped and containing lipids. It is indicated that the *Asarum* strophiole

attracts ants – seed dispersers. Mature fruits and seeds of *Asarum* are also described in the literature. The fruits are multi-seeded capsules that dehisce irregularly. The seeds are elongated-ovate. The seed coat of representatives of Asaroideae develops from two integuments. The cells of the outer layer of the testa are thin-walled, tangentially flattened. Cells of the inner layer of the testa have a thickened inner cell wall parallel to the surface and contain single crystals. The tegmen consists of three cell layers. The cells of the outer and middle layers are fibers oriented along and across the seed axis, respectively. The cells of the inner layer are short, parenchymal, thin-walled, with brown contents. The seeds retain remnants of the nucellus, in the form of a single layer of obliterated cells. The endosperm is copious. The embryo is linear and small. It is known that *Asarum* seeds disperse myrmecochory (Planchon 1845, Vovk & Komar 1988, Gubanov et al. 2003, Englický & Šera 2018). Vovk & Komar (1988) believe that ants are attracted by lipids contained in the aril cells. Emphasizing this, the authors even call the aril – "elaiosome". According to more recent data, ants are attracted by oleic and linoleic acids contained in the aril (Pfeiffer et al. 2010).

However, data on the structure of fruits, arils, and seeds of *Asarum* are very fragmentary. There are isolated illustrations of the structure of integuments in the early stages of development, mature fruits, and seeds with arils. However, a comprehensive study of fruit of *Asarum* development has not been conducted.

The aim of this research is to identify patterns of fruit of *Asarum* formation in the pericarp-aril-seed system and to establish the relationships between the processes occurring in these fruit parts.

The following objectives were set:
- to study mature fruits and fruits during development;
- to identify morphological and anatomical features of pericarp, aril and seed formation;
- to establish relationships in the development of pericarp, arils and seeds.

This study is part of a comprehensive study of fruits whose seeds have arils (Trusov 2013a).

MATERIAL AND METHODS

The study material consisted of mature fruits of *Asarum canadense* L. and *A. caudatum* Lindl., collected in the Botanical Garden of the Moscow Palace of Pioneers. Fruits of *A. europaeum* L. were studied during development. They were collected at the Tsitsin Main Botanical Garden RAS at weekly intervals, from the third ten-day period of April to the first ten-day period of June.

The plant material was fixed in 70 % ethanol. Fruit morphological characteristics were examined using MBS-1 and MBS-10 microscopes, and anatomical characteristics were examined using MBR-1A and Biomed S-2 microscopes. Temporary water and glycerol slides were prepared for light microscopy, and sections of various orientations were made freehand with a razor blade (Barykina et al. 2000). Photographs were taken with a Canon video camera. To describe the fruits, we used the terminology from the dictionary "Basic Carpological Terms" (Melikyan & Devyatov 2001). The classification of aril was give according to Bailon (1876–1878), with changes by Trusov (2016).

RESULTS

Structure of the mature fruits of *Asarum*

A description of the structure of mature fruits of *Asarum* is presented below.

Asarum canadense

The **fruit** is a 6-locular, spherical or slightly cylindrical, 6-sided greenish-brown capsule, 1.3–1.5 cm long and 1.1–1.4 cm wide, pubescent with white hairs (Fig. 1A). The sepals are retained on the capsule. The sepals are accreted into a tube 1.1–1.3 cm long, lilac-brown with three elongated triangular limbs 1.2–1.3 cm long. The carpels are fused in such a way that a thickening is formed in the middle of the central zone. In the central zone of fusion of carpels in the middle of the fruit, a narrow cavity is formed (Fig. 1G). The seeds are numerous, attached to each carpel in two longitudinal rows in the middle part (Fig. 1B, C). Most of the seeds are oriented in such a way that the dorsal side of the seed is adjacent to the septum, and the ventral side of the seed is oriented towards the inside of the carpel, so that the seeds are adjacent to each other with their arils.

The **pericarp** is 1.3–1.8 mm thick, consisting of 16–18 cell layers (Fig. 1F). The exocarp is single-layered. The epidermal cells are tabular or rounded in cross section, 0.03–0.04 × 0.03–0.04 mm, with larger ones located near the multicellular hairs. The cell walls are with a cuticle on the outside. The mesocarp consists of 14–16 layers of parenchymal cells. The cells of the peripheral layers, about up to the middle of the pericarp, are ellipsoidal, 0.015–0.03 × 0.02–0.03 mm, loosely arranged, with large intercellular spaces. The cells of the underlying layers, down to the endocarp, are elongated, thin, 0.02–0.03 mm thick. In the fruit's ribs, in the mesocarp area adjacent to the endocarp, vascular bundles extend, occupying up to half the mesocarp (Fig. 1H). The endocarp consists of a single layer of tangentially elongated, densely plasma-rich cells, 0.05–0.08 mm thick. In the rib areas of the fruit, beneath the vascular bundle, the endocarp cells extend along the fruit.

The **aril** is yellowish, fleshy, located on one side of the seed, and grows along the raphe (Fig. 1D, E). The aril is multilayered (Fig. 2). It consists of the epidermis and parenchyma. The epidermis is single-layered, consisting of radially flattened cells, about 0.015 mm thick. The main part of the aril is formed by single-layer parenchyma. Parenchyma cells are cubic or slightly elongated radially, 0.2–0.3 × 0.15–0.2 mm. On the side of the funicle, multilayered parenchyma is adjacent to the seed; it is surrounded by the epidermis that is common with the seed coat and aril. Parenchyma cells are polygonal or short-ellipsoidal, 0.02–0.03 × 0.02–0.04 mm (Fig. 3A). Around the part of the funicle that has grown to the seed, there are small parenchymal cells (about 0.015 × 0.015 mm): 5 layers towards the aril, 6 towards the seed. Essentially, the thickness of the aril is formed by the overgrown cells of the upper layer of the parenchyma near to the vascular bundle of the funicle.

The **seeds** are ovoid, 4.0–4.5 × 2.5–3.0 mm, fulvous-brown, and shining (Fig. 1D, E). The seed coat consists of 5 layers of cells (Fig. 3B–E). The exotesta is single-layered, consisting of radially flattened cells, about 0.005 × 0.01–0.015 mm. They have a cuticle on the outside. The endotesta consists of a single layer of slightly radially flattened cells, 0.01–0.015 × 0.01–0.015 mm. The cells have thickenings of the cell walls adjacent to the exotegmen, extending onto the radial walls to the middle of the cells. Single large crystals in the shape of parallelepipeds are located inside the endotesta

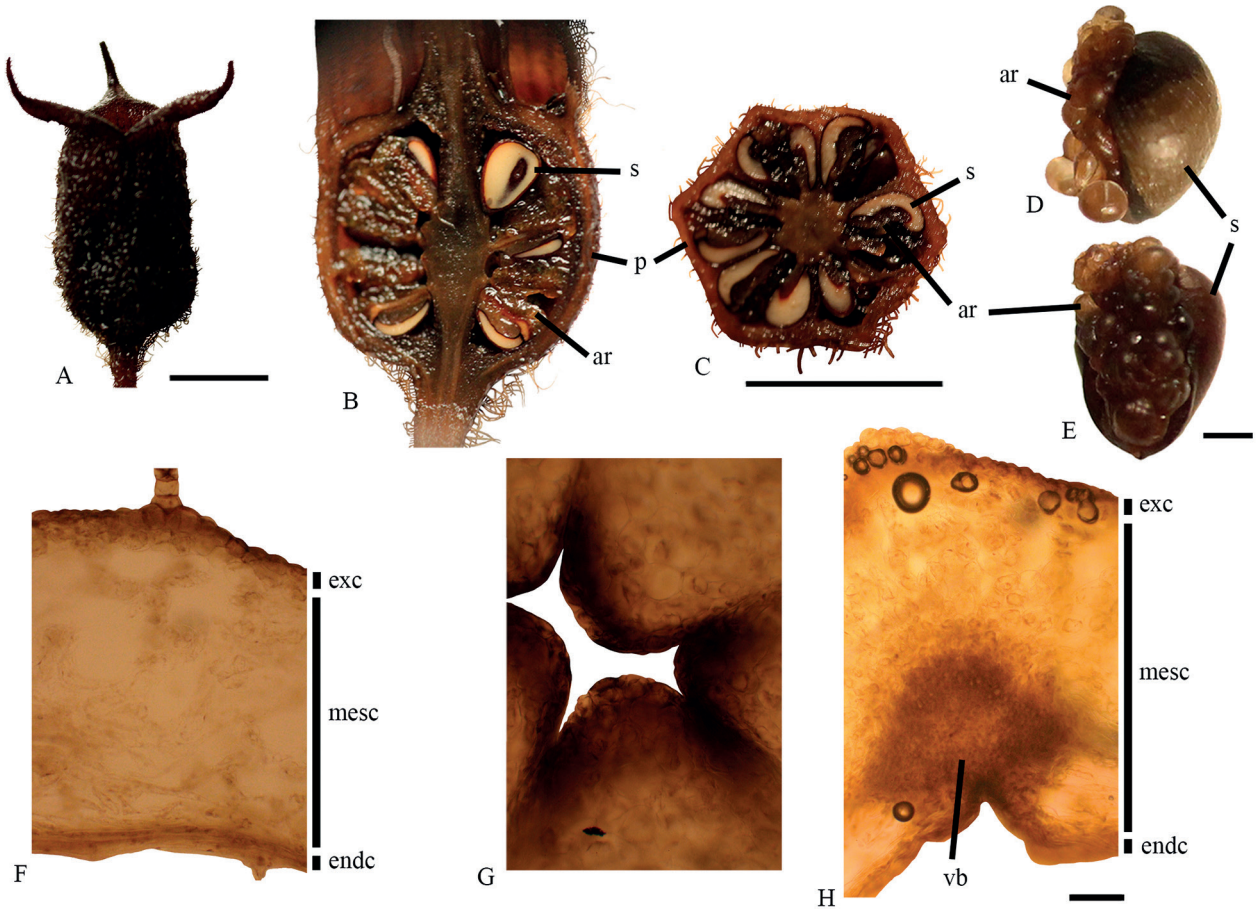

Figure 1 Structure of the mature fruit, seed, and pericarp of *Asarum canadense*. A – lateral view of the fruit; B – longitudinal section of the fruit; C – transverse section of the fruit; D – lateral view of the seed; E – seed from the rafeal side; F – transverse section of the pericarp; G – transverse section of the central zone of the pericarp; H – transverse section of the pericarp near the rib. Abbreviations: ar – aril; endc – endocarp; exc – exocarp; mesc – mesocarp; p – pericarp; s – seed; vb – vascular bundle. Scale bar: A-C – 1 cm; D, E – 1 mm, F–H – 0.1 mm

cells. The exotegmen consists of a single layer of sclerified fibers extending longitudinally along the seed, slightly radially elongated or rounded in cross section, 0.005–0.006 × about 0.05 mm. The mesotegmen is single-layered. Its cells are similar to those of the exotegmen but extend transversely across the seed. The endotegmen consists of thin-walled, larger cells, 0.012–0.015 × 0.008–0.010 mm, extending longitudinally. In cross section, the cells are tabular, with a convex, thickened cell wall toward the center of the seed. A single-layer nucellus of thin-walled, slightly radially elongated cells, 0.02–0.025 × 0.008–0.010 mm, is preserved within the seed. The endosperm is copious; the cells are polygonal, 0.015–0.025 × 0.025–0.035 mm, densely arranged, and filled with oil droplets (Fig. 3G). The embryo is yellowish, heart-shaped, and occupies a small part of the seed (Fig. 3F). The cells are polygonal, about 0.010 × 0.010 mm, and contain numerous oil droplets. There are no intercellular spaces (Fig. 3H).

Asarum caudatum

The **fruit** is a 6-locular, spherical, 6-sided, dark yellowish, pubescent capsule, 1.3–1.5 cm long and 1.5–1.8 cm wide (Fig. 4A). The capsule retains elongated, triangular, dark reddish sepals with a strongly drawn-out apex. They do not accrete into a tube. Inside the fruit, the carpels are fused in such a way that a thickening is formed in the middle of the central zone. In the central zone of carpel fusion, a narrow cavity is formed in the middle of the fruit (Fig. 4G). The seeds are numerous, attached to each carpel in two longitudinal rows in the middle part (Fig. 4B, C). Most of the seeds are oriented such that the dorsal side of the seed is adjacent to the septum, and the ventral side of the seed is oriented inside the carpel, so that the seeds adjoin each other with arils.

The **pericarp** is 1.3–2.3 mm thick, consisting of 13–23 cell layers (Fig. 4F). The exocarp is single-layered. The epidermal cells are tabular or rounded in cross section, 0.04–0.06 × 0.04–0.06 mm, with larger ones located near the multicellular hairs. The cell walls are with a thick cuticle on the outside. The mesocarp consists of 11–21 layers of parenchymal cells. The cells of the peripheral layers, about up to the middle of the pericarp, are ellipsoidal, 0.04–0.07 × 0.04–0.12 mm, loosely arranged, with large intercellular spaces. The cells of the underlying layers, down to the endocarp, are elongated, thin, 0.025–0.035 mm thick. In the mesocarp zone adjacent to the endocarp, vascular bundles extend through the ribs of the fruit, occupying up to half of the mesocarp (Fig. 4H). The endocarp consists of a single layer of tangentially elongated cylindrical cells, 0.06–0.09 × 0.15–0.20 mm, with numerous small pores in the cell walls. In the rib areas of the fruit, beneath the vascular bundle, the endocarp cells are elongated along the fruit and slightly flattened tangentially.

The **aril** is yellowish, fleshy, located on one side of the seed, and grows along the raphe (Fig. 4D, E). The aril is multilayered (Fig. 5). It consists of the epidermis and parenchyma. The epidermis is single-layered, consisting of radially flattened cells, about 0.015 mm thick. The main part of the aril is formed by single-layer parenchyma. Parenchyma cells are cubic or slightly elongated radially, 0.2–0.4 × 0.25–0.3 mm. On the side of the funicle, multilayered parenchyma is adjacent to the seed; it is surrounded by the epidermis that is

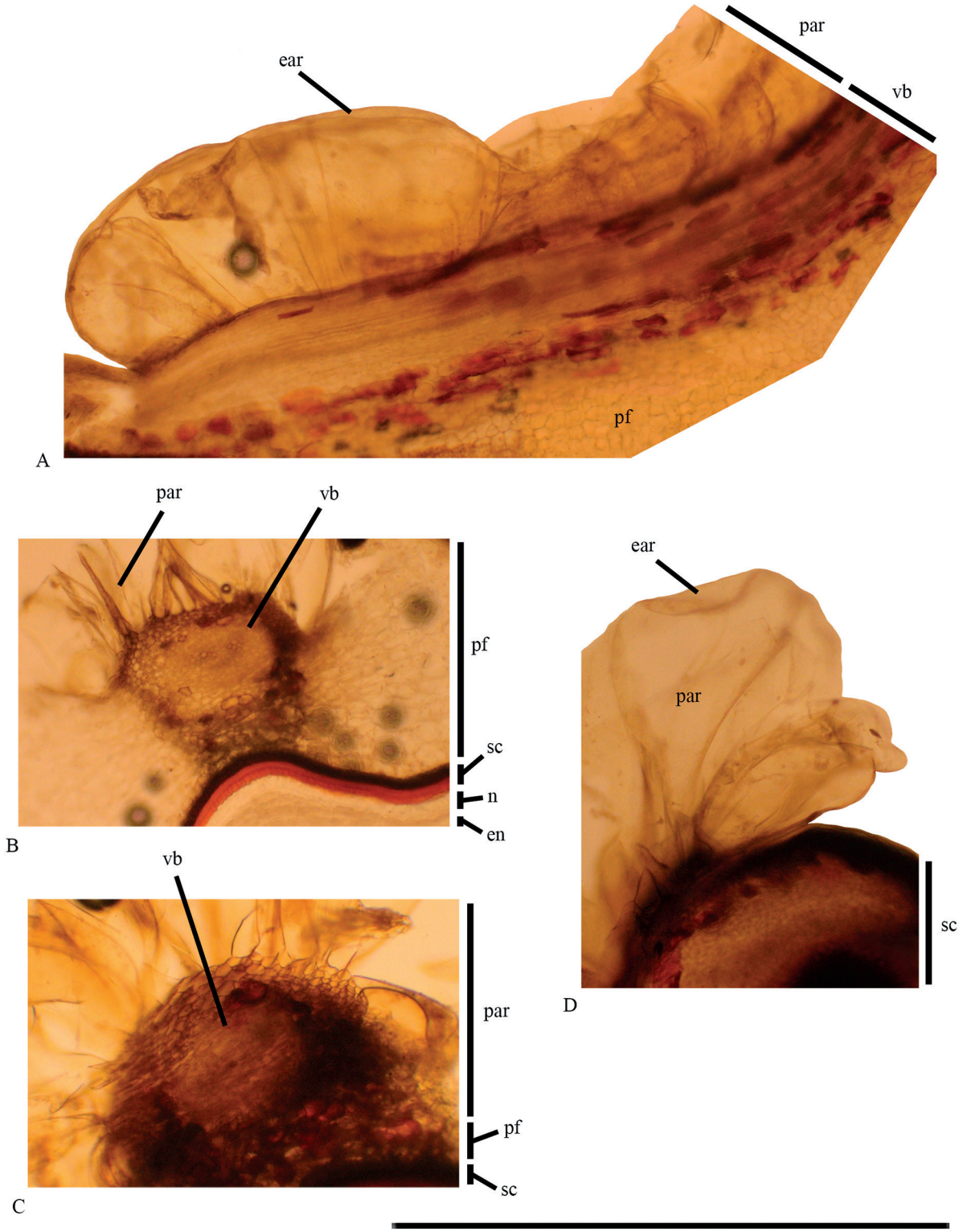

Figure 2 Details of the structure of the aril of *Asarum canadense*. A – longitudinal section; B-D – transverse sections. Abbreviations: ear – epidermis of aril; en – endosperm; n – nucellus; par – parenchyma of aril; pf – parenchyma of funicle; sc – seed coat; vb – vascular bundle. Scale bar – 1 mm

common with the seed coat and aril. Parenchyma cells are polygonal or short-ellipsoidal, 0.015–0.02 × 0.01–0.02 mm (Fig. 6A). Around the part of the funicle that has grown to the seed, there are small parenchymal cells (0.015–0.02 × 0.015–0.02 mm): 4 layers towards the aril, 5 towards the seed. Essentially, the thickness of the aril is formed by the overgrown cells of the upper layer of the parenchyma near to the vascular bundle of the funicle.

The **seeds** are ovoid, 3.5–4.0 × 2.0–2.5 mm, fulvous-brown, shining (Fig. 4D, E). The seed coat consists of 5 layers of cells (Fig. 6B–E). The exotesta is single-layered, consisting of radially flattened cells, 0.008–0.010 × 0.016–0.022 mm. They have a cuticle on the outside. The endotesta consists of a single layer of slightly radially flattened cells, 0.012–0.015 × 0.017–0.025 mm. The cells have thickenings of the cell walls adjacent to the exotegmen, extending onto the radial walls to the middle of the cells. Single large crystals in

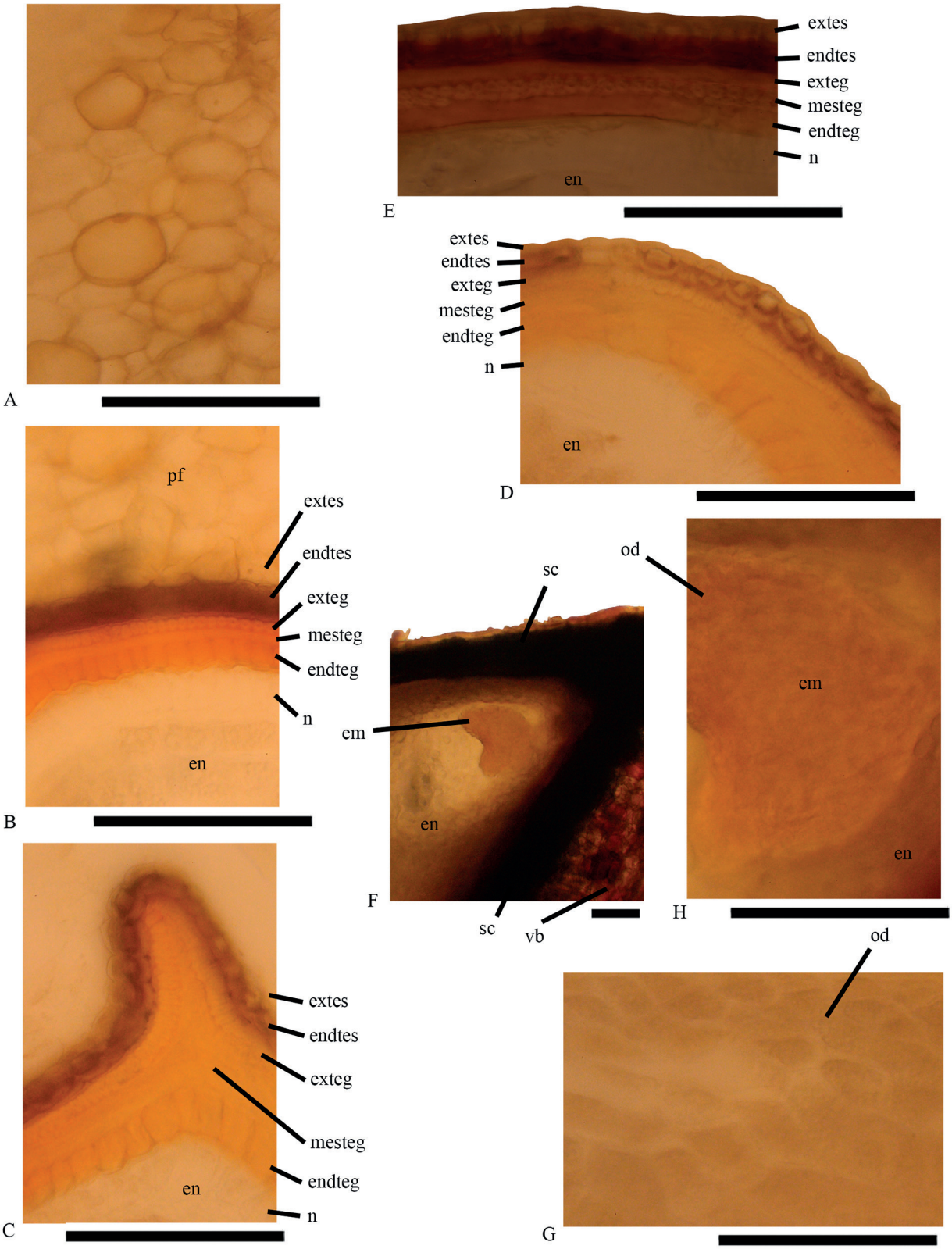

Figure 3 Details of the structure of the seed of *Asarum canadense*. A – parenchyma of funicle; B, C – cross-sections of the seed from the rafeal side; D – cross-section of the seed; E, F – longitudinal section of the seed; G – cells of endosperm; H – cells of embryo. Abbreviations: en – endosperm; endteg – endotegmen; endtes – endotesta; em – embryo; exteg – exotegmen; extes – exotesta; mesteg – mesotegmen; n – nucellus; od – oil drops; vb – vascular bundle. Scale bar – 0.1 mm

the shape of parallelepipeds are located inside the endotesta cells. The exotegmen consists of a single layer of sclerified fibers extending longitudinally along the seed, slightly elongated radially or rounded in cross section, 0.005–0.006 × about 0.005 mm. The mesotegmen is single-layered. Its cells are similar to those of the exotegmen but extend transversely across the seed. The endotegmen consists of thin-walled, radially flattened cells, about 0.004 × 0.008–0.010 mm, extending longitudinally along the seed. The seed retains a single-layered nucellus of thin-walled, tabular cells, 0.015–

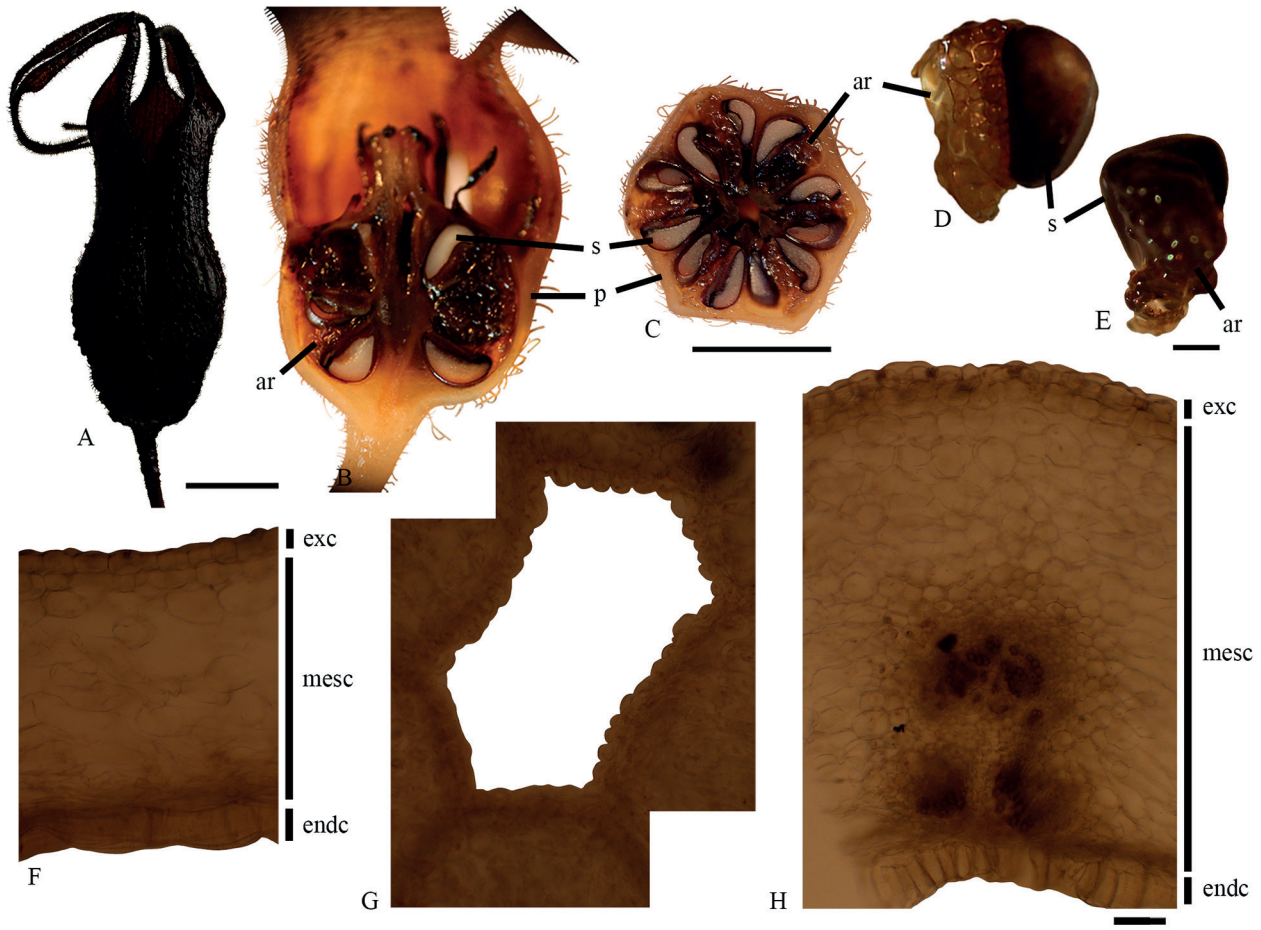

Figure 4 Structure of the mature fruit, seed, and pericarp of *Asarum caudatum*. A – lateral view of the fruit; B – longitudinal section of the fruit; C – transverse section of the fruit; D – side view of the seed; E – rafeal side of the seed; F – transverse section of the pericarp; G – transverse section of the central zone of the pericarp; H – transverse section of the pericarp near the rib. Abbreviations: ar – aril; endc – endocarp; exc – exocarp; mesc – mesocarp; p – pericarp; s – seed; vb – vascular bundle. Scale bar: A-C – 1 cm; D, E – 1 mm, F-H – 0.1 mm.

0.020 × 0.010–0.015 mm, with sinuous radial cell walls. The endosperm is copious; the cells are polygonal, 0.030–0.045 × 0.025–0.035 mm, densely packed, and filled with oil droplets (Fig. 6G). The embryo is yellowish, heart-shaped, and occupies a small portion of the seed (Fig. 6F). The cells are polygonal, about 0.007 × 0.007 mm, and contain numerous oil droplets. There are no intercellular spaces (Fig. 6H).

Asarum europaeum

The **fruit** is a 6-locular, spherical, slightly flattened, 6-sided, dark yellowish, pubescent capsule, 0.7-0.8 cm long and 0.9–1.1 cm wide (Fig. 7G). The capsule retains elongated, triangular, dark reddish sepals with a tapering apex. They do not accrete into a tube. Inside the fruit, the carpels fuse in such a way that a thickening forms in the middle of the central zone. In the central zone of carpel fusion, a narrow cavity forms in the middle of the fruit (Fig. 8G1). The seeds are numerous, attached to each carpel in two longitudinal rows in the middle part (Fig. 7G1-G2). Most of the seeds are oriented in such a way that the dorsal side of the seed is adjacent to the septum, and the ventral side of the seed is oriented towards the inside of the carpel, so that the seeds are adjacent to each other with their arils.

The **pericarp** is 1.9–2.2 mm thick, consisting of 22–25 cell layers (Fig. 8G). The exocarp is single-layered. The epidermal cells are tabular or rounded in cross section, 0.04–0.06 × 0.04–0.06 mm, with larger ones located near the multicellular hairs. The cell walls are with a thick cuticle on the outside. The mesocarp consists of 20–23 layers of parenchymal cells. The cells of the peripheral layers, about up to the middle of the pericarp, are ellipsoidal, 0.06–0.12 × 0.05–0.12 mm, loosely arranged, with large intercellular spaces. The cells of the underlying layers, down to the endocarp, are elongated, thin, 0.04–0.09 mm thick. In the mesocarp zone adjacent to the endocarp, vascular bundles extend through the ribs of the fruit, occupying up to half of the mesocarp (Fig. 8G2). The endocarp consists of a single layer of tangentially elongated cylindrical cells, 0.06–0.10 × 0.18–0.24 mm, with numerous small pores in the cell walls. In the rib areas of the fruit, beneath the vascular bundle, the endocarp cells are elongated along the fruit and slightly flattened tangentially.

The **aril** is yellowish, fleshy, located on one side of the seed, and grows along the raphe (Fig. 9G–G2). The aril is multilayered (Fig. 9G3–G7). It consists of the epidermis and parenchyma. The epidermis is single-layered, consisting of radially flattened cells, about 0.01–0.015 mm thick. The main part of the aril is formed by single-layer parenchyma. Parenchyma cells are cubic or slightly elongated radially, 0.3–0.6 × 0.2–0.3 mm. On the side of the funicle, multilayer parenchyma is adjacent to the seed; it is surrounded by the epidermis that is common with the seed coat and aril. Parenchyma cells are polygonal or short-ellipsoidal, 0.04–0.06 × 0.03–0.05 mm (Fig. 9G2, G3, G8). Around the part of the funicle that has grown to the seed, there are small parenchymal cells (about 0.01 × 0.01–0.02 mm): 4 layers towards the aril, 5 towards the seed. In essence, the thickness of the aril is formed by the overgrown cells of the upper layer of the parenchyma near to the vascular bundle of the funicle.

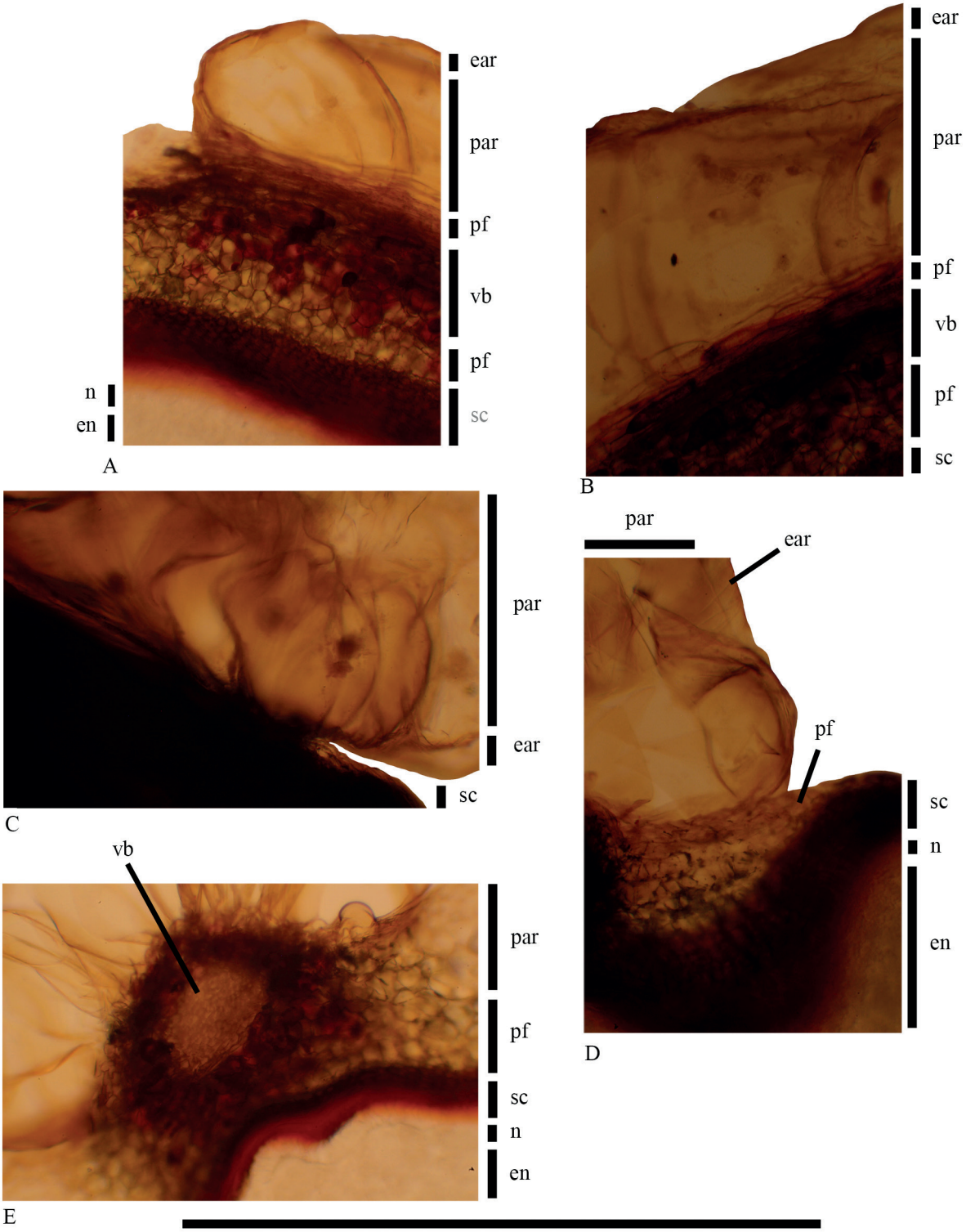

Figure 5 Details of the structure of the aril of *Asarum caudatum*. A-B – longitudinal sections; C-E – cross sections. Abbreviations: ear – epidermis of aril; en – endosperm; n – nucellus; par – parenchyma of aril; pf – parenchyma of funicle; sc – seed coat; vb – vascular bundle. Scale bar – 1 mm

The **seeds** are ovoid, 3.0–3.5 × 1.4–2.1 mm, fulvous-brown, and shiny (Fig. 9G). The seed coat consists of 5 layers of cells (Fig. 9G9–G10). The exotesta is single-layered, consisting of radially flattened cells, 0.008–0.01 × 0.04–0.05 mm. They have a cuticle on the outside. The endotesta consists of a single layer of slightly radially flattened cells, 0.015–0.02 × 0.02–0.025 mm. The cells have thickenings of the cell walls adjacent to the exotegmen, extending onto the radial walls to the middle of the cells. Single large crystals in the shape of parallelepipeds are located inside the endotesta cells. The exotegmen consists of a single layer of sclerified fibers extending longitudinally along the seed, slightly elongated radially or rounded in cross section, 0.008–0.01 × about 0.008 mm. The mesotegmen is single-layered. Its cells are similar to those of the exotegmen but extend transversely across the seed. The endotegmen consists of thin-walled, radially flattened cells, about 0.012 × 0.012 mm, extending longitudinally along the seed. The seed retains

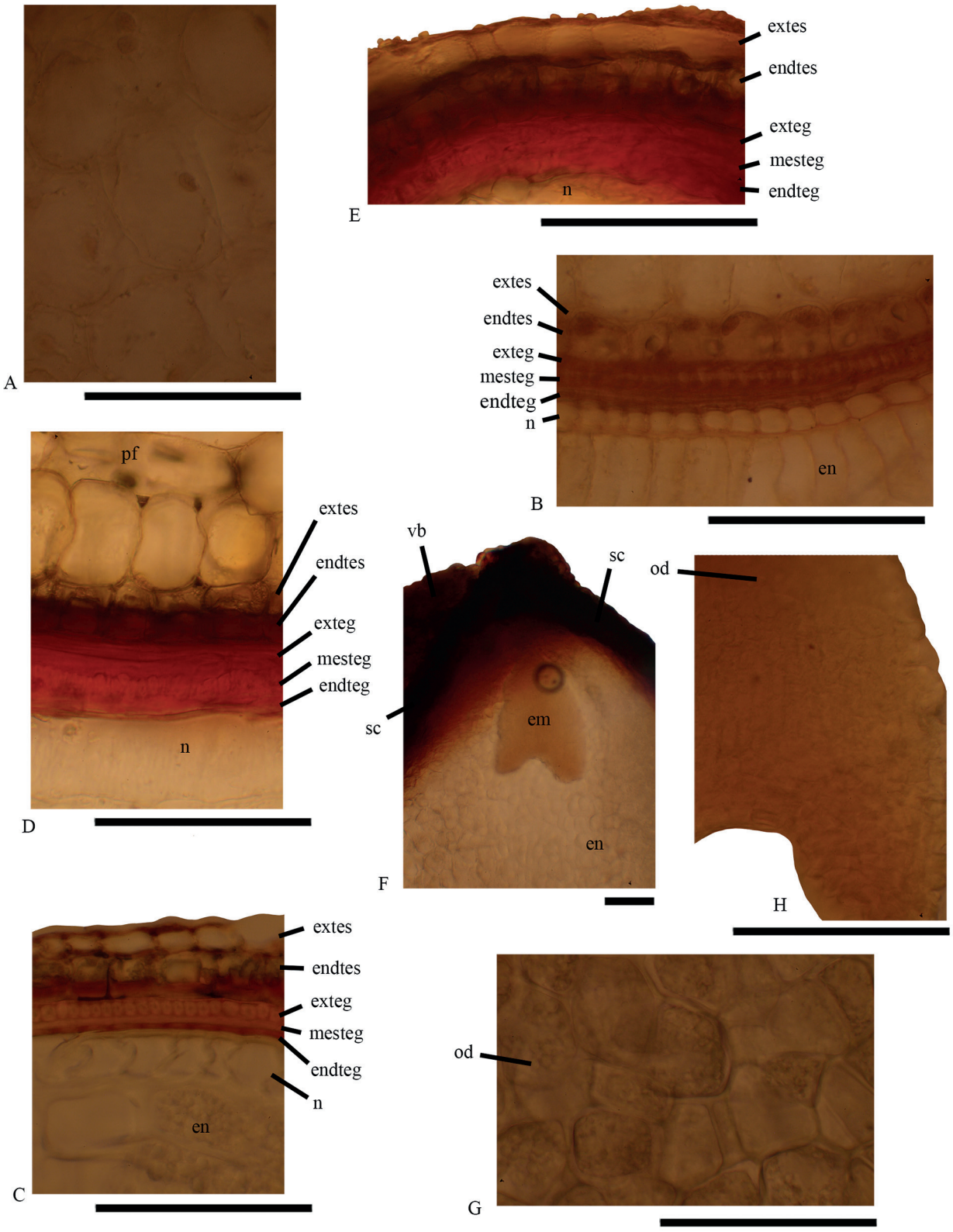

Figure 6 Details of the structure of the seed of *Asarum caudatum*. A – parenchyma of funicle; B – cross section of the seed from the rafeal side; C – cross section of the seed; D – longitudinal section of the seed from the rafeal side; E, F – longitudinal sections of the seed; G – cells of endosperm; H – cells of embryo. Abbreviations: en – endosperm; endteg – endotegmen; endtes – endotesta; em – embryo; exteg – exotegmen; extes – exotesta; mesteg – mesotegmen; n – nucellus; od – oil drops; vb – vascular bundle. Scale bar – 0.1 mm

a single-layered nucellus of thin-walled, tabular cells, 0.02–0.025 × 0.02–0.025 mm, with sinuous radial cell walls. The endosperm is copious, the cells are polygonal, 0.04–0.06 × 0.03–0.05 mm, densely arranged, filled with oil droplets (Fig. 9G11). The embryo is yellowish, linear, occupies a small part of the seed (Fig. 9G1). The cells are polygonal, about 0.02 × 0.02 mm, with oil droplets. There are no intercellular spaces (Fig. 9G12).

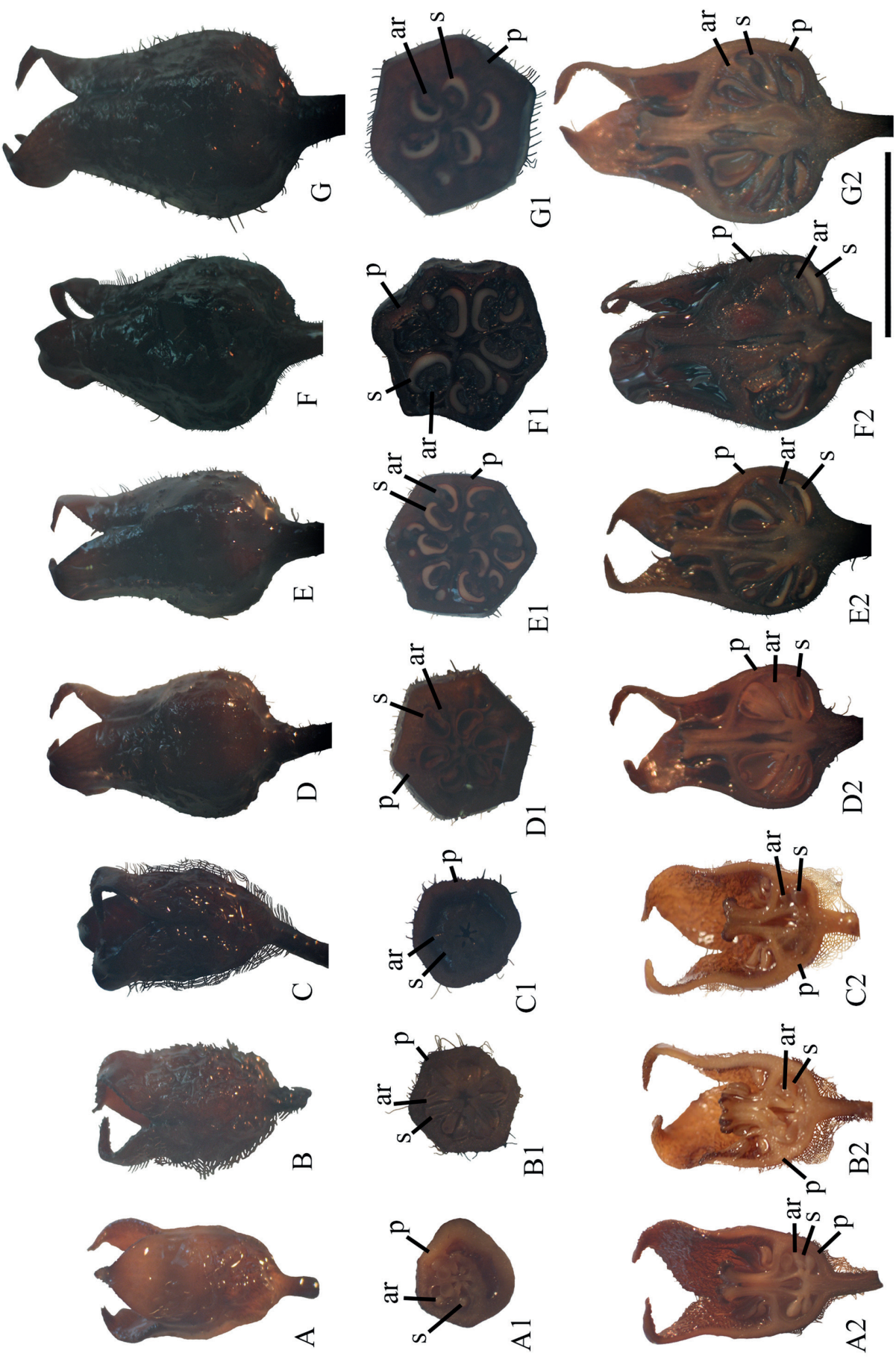

Figure 7 Development of the fruit of *Asarum europaeum*. A-G – lateral view of fruit; A1-G1 – cross-section of fruit; A2-G2 – longitudinal section of fruit. A-A2 – third decade of April; B-B2 – end of April; C-C2 – first decade of May; D-D2 – second decade of May; E-E2 – third decade of May; F-F2 – beginning of June; G-G2 – first decade of June. Abbreviations: ar – aril; p – pericarp; s – seed. Scale bar – 1 cm.

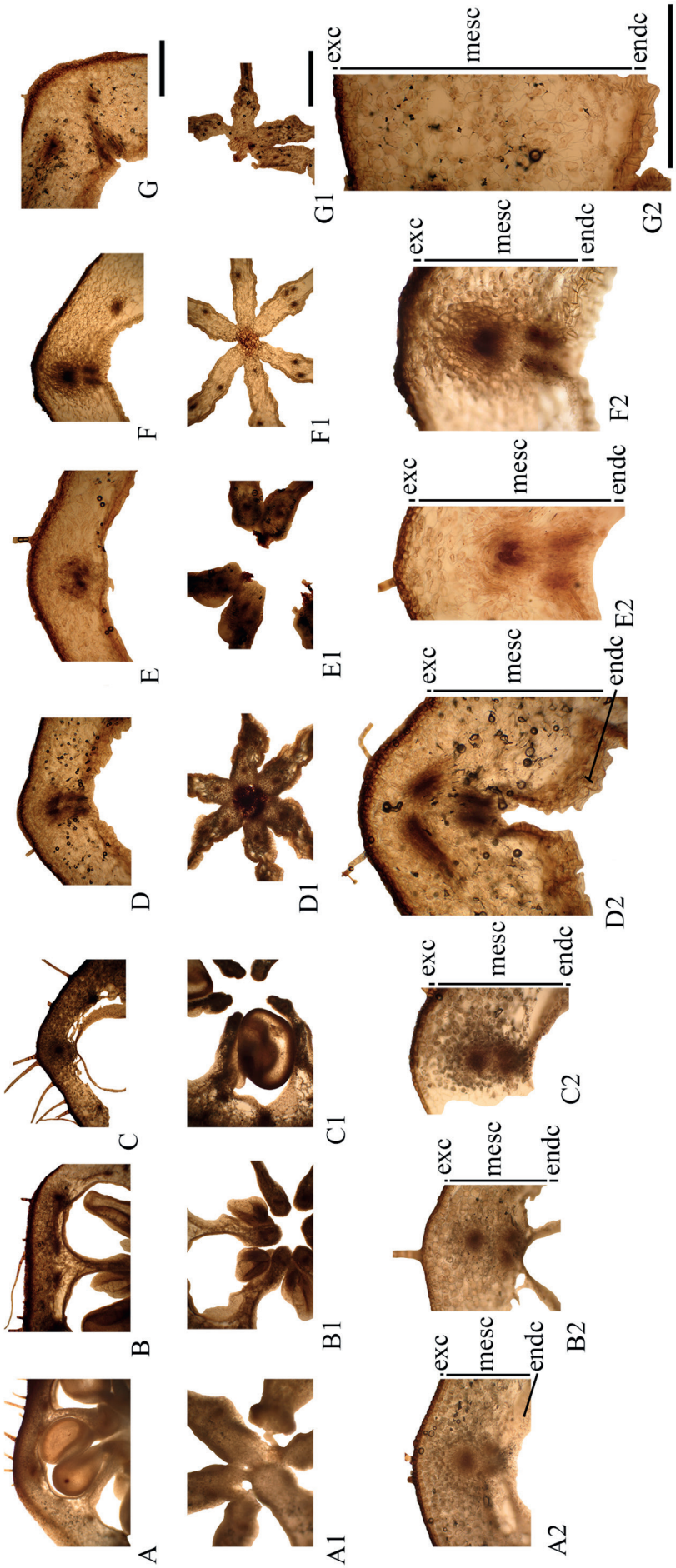

Figure 8 Development of the pericarp of *Asarum europaeum*. A-G – cross-section of pericarp; A1-G1 – cross-section of the central zone of the pericarp; A2-G2 – cross-section of the pericarp in the rib area. A-A2 – third decade of April; B-B2 – end of April; C-C2 – first decade of May; D-D2 – second decade of May; E-F2 – third decade of May; F-F2 – beginning of June; G-G2 – first decade of June. Abbreviations: endc – endocarp; exc – exocarp; mesc – mesocarp. Scale bar – 1 mm.

Development of fruit of the model species – *Asarum europaeum*

Term I – third decade of April

The fruit is ellipsoidal, flattened at the apex, measuring about 0.3 × 0.5 cm (the body of the fruit), with sepals about 0.8 cm long (Fig. 7A–A2). The seeds are numerous, ovoid, about 1.00 × 0.65 × 0.50 mm in size. The aril appears as a small hump on one side of the seed (Fig. 9A).

Pericarp 0.45–0.60 mm thick (Fig. 8A). Exocarp single-layered. Epidermal cells 0.025–0.045 × 0.025–0.04 mm, square or slightly elongated radially in cross section, with cuticle on the outside. Mesocarp cells 0.03–0.07 × 0.035–0.06 mm, thin-walled. Cells of the layers located closer to the exocarp (about 1/3 of the mesocarp) are polygonal, sometimes almost round. Cells of the middle layers (about 1/3 of the mesocarp) are larger, ellipsoidal. Cells of the layers located closer to the endocarp (about 1/3 of the mesocarp) are elongated in various directions, 0.015–0.025 mm thick, with large intercellular spaces. The cells of the mesocarp, excluding the layer adjacent to the exocarp, contain numerous small inclusions of an unknown nature. The endocarp consists of a single layer of thin-walled, slightly elongated tangentially cells, about 0.02 × 0.04 mm. In the ribs of the fruit, the endocarp is represented by thin-walled cells elongated along the fruit. In the septum, closer to the central zone, there are amphicribral vascular bundles, two per septum, not fused (ventral vascular bundles of the carpels) (Fig. 8A1). In the ribs of the fruit (in the middle part), in the mesocarp closer to the endocarp, there are 3 vascular bundles (dorsal vascular bundles of the carpel). Closer to the periphery of the pericarp is a large amphicribral vascular bundle, and closer to the endocarp there are 2 vascular bundles, with the phloem facing the periphery of the pericarp (Fig. 8A2).

The aril is inconspicuous, about 0.05 mm thick, and multilayered (Fig. 9A–A4). The epidermis consists of tabular cells, about 0.01 × 0.01 mm. The cuticle is not pronounced. The parenchymal cells of the aril and funicle are undifferentiated, polygonal, about 0.01 × 0.01 mm, and densely arranged.

The seed coat is about 0.45 mm thick, consisting of 5 cell layers

Figure 9 Development of the aril and seed of *Asarum europaeum*. A-G – development of seed by terms, rafeal and lateral views; A1-G1 – development of seed, longitudinal section; C2-G2 – development of seed, cross-section; A2-B2, A3-B3, C5-F5, D6-G6, G7 – details of the aril structure by terms (longitudinal sections); C3-G3, C4-G4, G5 – aril structure details by terms (cross-sections); A4-B4, C6, D7-F7, G8 – development of funicle's parenchyma; A5-B5, C7, D8-F8, G9 – development of seed coat, longitudinal sections; F9, G10 – development of seed coat, transverse sections; A3-G3 – development of endosperm; E10, F11, G12 – development of embryo, longitudinal sections. Abbreviations: ar – aril; ear – epidermis of aril; en – endosperm; n – nucellus; nen – nucellus and endosperm; par – parenchyma of aril; pf – parenchyma of funicle; sc – seed coat; vb – vascular bundle. Scale bar: A-G, A1-G1, C2-G2 – 1 mm, A2-G2, A3-G3, A4-G4, A5-G5, A6-G6, C7-G7, C8-G8, D9-G9, E10-G10, F11-G11, G12 – 0.1 mm

(Fig. 9A5). The exotesta is single-layered, consisting of flattened paradermal cells, 0.01–0.015 × 0.03–0.04 mm. They have a cuticle on the outside. The endotesta consists of a single layer of tabular cells, 0.008–0.012 × 0.008–0.01 mm. The exotegmen consists of a single layer of thin-walled cells, elongated longitudinally, about 0.006 × 0.006 mm. The mesotegmen is single-layered. Its cells are similar to those of the exotegmen but are elongated transversely. The endotegmen consists of thin-walled cells, elongated longitudinally, about 0.006 × 0.006 mm. The seed retains a single-layer nucellus of thin-walled tabular cells, 0.006–0.008 × 0.006–0.008 mm. The endosperm is at the nuclear stage, with a large vacuole and parietal cytoplasm. The forming cells are polygonal, 0.02–0.025 × 0.02–0.025 mm, and are densely arranged (Fig. 9A6). The embryo is not visible.

Term II – End of April

The fruit is ellipsoidal, flattened at the apex, measuring about 0.3 × 0.6 cm (the body of the fruit), with sepals about 0.8 cm long (Fig. 7B–B2). The seeds are numerous, ovoid, about 1.30 × 0.90 × 0.80 mm. The aril appears as a small hump along one side of the seed; the aril is more extensive at the top (Fig. 9B).

Pericarp 0.65–0.80 mm thick (Fig. 8B). Exocarp single-layered. Epidermal cells 0.025–0.045 × 0.025–0.04 mm, square or slightly elongated radially in cross section, with cuticle on the outside. Mesocarp cells 0.045–0.07 × 0.035–0.06 mm, thin-walled. Cells of the layers located closer to the exocarp (about 1/3 of the mesocarp) are polygonal, sometimes almost round. Cells of the middle layers (about 1/3 of the mesocarp) are larger, ellipsoidal. The cells of the layers located closer to the endocarp (about 1/3 of the mesocarp) are elongated in various directions, 0.025–0.035 mm thick, with large intercellular spaces. In the cells of the mesocarp, around the dorsal vascular bundles, there are numerous small inclusions of unknown nature. The endocarp consists of a single layer of thin-walled, slightly elongated tangentially cells, about 0.025 × 0.045 mm. In the ribs of the fruit, the endocarp is represented by thin-walled cells elongated along the fruit. In the septum, closer to the central zone, there are amphicribral vascular bundles, 2 per septum, not fused (ventral vascular bundles of the carpels) (Fig. 8B1). In the ribs of the fruit (in the middle part), in the mesocarp closer to the endocarp, there are 3 vascular bundles (dorsal vascular bundles of the carpels). Closer to the periphery of the pericarp there is a large amphicribral vascular bundle, and closer to the endocarp there are 2 vascular bundles with the phloem facing the periphery of the pericarp (Fig. 8B2).

The aril is multilayered, becomes visible (Fig. 9B–B4). The epidermis is composed of tabular cells, about 0.01 × 0.01 mm. The cuticle is not pronounced. The parenchymal cells of the funicle differentiate. The cells of the peripheral parenchyma layer above the funicle noticeably increase in size, 0.05–0.08 × 0.05–0.08 mm. The cells of the remaining parenchyma layers above and below the funicle are polygonal, about 0.01 × 0.01 mm, and densely arranged. The remaining parenchymal cells of the funicle are ellipsoidal. They increase in size to 0.01–0.015 × 0.01–0.015 mm (Fig. 9B2-B4).

The seed coat is about 0.45 mm thick, consisting of 5 cell layers (Fig. 9B5). The exotesta is single-layered, composed of flattened paradermal cells, 0.012–0.015 × 0.04–0.05 mm. They have a cuticle on the outside. The endotesta consists of a single layer of tabular or slightly radially elongated cells, 0.01–0.012 × 0.01–0.012 mm. The exotegmen consists of a single layer of thin-walled cells elongated along the seed, about 0.006 × 0.006 mm. The mesotegmen is single-layered. Its cells are similar to those of the exotegmen but are elongated transversely to the seed. The endotegmen consists of thin-walled cells elongated along the seed, about 0.008 × 0.008 mm. The seed retains a single-layered nucellus of thin-walled, tabular cells, 0.006–0.008 × 0.006–0.008 mm. The endosperm is at the end of nuclear stage with a large vacuole and parietal cytoplasm. The forming cells are polygonal, 0.02–0.025 × 0.02–0.025 mm, and densely packed (Fig. 9B6). The embryo is not visible.

Term III – First decade of May

The fruit is ellipsoidal, flattened at the apex, measuring about 0.3 × 0.6 cm (the body of the fruit), with sepals about 0.8 cm long (Fig. 7C–C2). The seeds are numerous, ovoid, about 1.60 × 1.30 × 0.90 mm. The aril appears as a small ridge along one side of the seed; at the apex, the aril is more expanded, extending above the apex (Fig. 9C).

The pericarp is 0.65–0.80 mm thick (Fig. 8C). The exocarp is single-layered. The epidermal cells are 0.025–0.045 × 0.025–0.04 mm, square in cross section, or slightly elongated radially, with a cuticle on the outside. The mesocarp cells are 0.045–0.07 × 0.035–0.07 mm, thin-walled. The cells of the layer underlying the exocarp are polygonal and densely packed. The cells of the layers located closer to the exocarp (about 2/3 of the mesocarp) are larger, ellipsoidal, sometimes almost round, with noticeable intercellular spaces. The cells of the layers located closer to the endocarp (about 1/3 of the mesocarp) are elongated in various directions, 0.025–0.035 mm thick, with large intercellular spaces. In the cells of the mesocarp, around the dorsal vascular bundles, there are numerous small inclusions of unknown nature. The endocarp consists of a single layer of thin-walled, slightly elongated tangentially cells, about 0.025 × 0.045 mm. In the ribs of the fruit, the endocarp is represented by thin-walled cells elongated along the fruit. In the septum, closer to the central zone, there are amphicribral vascular bundles, 2 per septum, not fused (ventral vascular bundles of the carpels) (Fig. 8C1). In the ribs of the fruit (in the middle part), in the mesocarp closer to the endocarp, there are 3 vascular bundles (dorsal vascular bundles of the carpels). Closer to the periphery of the pericarp there is a large amphicribral vascular bundle, and closer to the endocarp there are 2 vascular bundles with the phloem facing the periphery of the pericarp (Fig. 8C2).

The aril is multilayered, visible (Fig. 9C1–C6). The epidermis consists of slightly tangentially elongated cells, about 0.01–0.012 × 0.01–0.015 mm. The cuticle is thin. The cells of the peripheral parenchyma layer above the funicle increase in size to 0.16–0.18 × 0.04–0.06 mm. The cells of the remaining parenchyma layers above and below the funicle are polygonal, about 0.01 × 0.01–0.015 mm, and densely arranged. The remaining parenchymal cells of the funicle are ellipsoidal, increasing in size to 0.015–0.02 × 0.015–0.02 mm (Fig. 9C2, C3, C5, C6).

The seed coat is about 0.55 mm thick, consisting of 5 cell layers (Fig. 9C7). The exotesta is single-layered, composed of flattened paradermal cells, 0.015–0.018 × 0.04–0.05 mm. They have a cuticle on the outside. The endotesta consists of a single layer of tabular or slightly radially elongated cells, 0.01–0.012 × 0.01–0.012 mm. The exotegmen consists of a single layer of thin-walled cells elongated along the seed, about 0.006 × 0.006 mm. The mesotegmen is single-layered. Its cells are similar to those of the exotegmen but are elongated transversely to the seed. The endotegmen consists of thin-walled cells elongated along the seed, about 0.008 × 0.008 mm. The seed retains a single-layered nucellus of thin-walled, tabular cells, 0.008–0.01 × 0.008–0.01 mm. The endosperm is at the end of nuclear stage with a large vacuole and parietal cytoplasm. The forming cells are polygonal, 0.02–0.025 × 0.02–0.0025 mm, and densely packed (Fig. 9C8). The embryo is not visible.

Term IV – the second decade of May

The fruit is ellipsoidal, flattened at the apex, measuring about 0.55 × 0.75 cm (the body of the fruit), with sepals about 0.8 cm long (Fig. 7D-D2). The seeds are numerous, ovoid, about 3.30 × 2.30 × 1.60 mm. The aril appears as a ridge along one side of the seed; from the apex of the seed to about 1/3, the aril is more expanded, extending above the apex of the seed (Fig. 9D).

The pericarp is 1.20–1.50 mm thick (Fig. 8D). The exocarp is single-layered. The epidermal cells are 0.025–0.045 × 0.025–0.04 mm, square in cross section, or slightly elongated radially, with a cuticle on the outside. The mesocarp cells are 0.045–0.085 × 0.035–0.09 mm, thin-walled. The cells of the layer underlying the exocarp are polygonal, densely arranged. The cells of the layers located closer to the exocarp (about 2/3 of the mesocarp) are larger, ellipsoidal, sometimes almost round, with large intercellular spaces. The cells of the layers located closer to the endocarp (about 1/3 of the mesocarp) are elongated in various directions, 0.035–0.045 mm thick, with larger intercellular spaces. Inclusions were not found in the cells of the mesocarp, around the dorsal vascular bundles. The endocarp consists of a single layer of slightly tangentially elongated cells, about 0.065 × 0.1 mm. The cell walls of the endocarp cells are slightly thickened. In the ribs of the fruit, the endocarp is represented by thin-walled cells elongated along the fruit. In the septum, closer to the central zone, amphicribral vascular bundles are located, 2 per septum, not fused (ventral vascular bundles of carpels) (Fig. 8D1). In the ribs of the fruit (in the middle part), in the mesocarp closer to the endocarp, there are three vascular bundles (dorsal vascular bundles of the carpel). Closer to the periphery of the pericarp there is a large amphicribral vascular bundle, and closer to the endocarp there are 2 vascular bundles with the phloem facing the periphery of the pericarp (Fig. 8D2).

The aril is multilayered, expands in width (Fig. 9D1–D6). The epidermis is composed of slightly tangentially elongated cells, about 0.01 mm thick. The cuticle is thin. The cells of the peripheral parenchyma layer increase in size to 0.2–0.5 × 0.1–0.15 mm. The cells of the remaining parenchyma layers above and below the funicle are polygonal, about 0.01 × 0.01–0.02 mm and densely arranged. The remaining parenchymal cells of the funicle are ellipsoidal, increasing in size to 0.02–0.025 × 0.02–0.025 mm (Fig. 9D7).

The seed coat is about 0.65 mm thick, consisting of 5 cell layers (Fig. 9D8). The exotesta cells are strongly flattened tangentially, 0.01–0.015 × 0.04–0.05 mm. On the outside, they have a cuticular layer. The endotesta cells are increasing in size to 0.015–0.02 × 0.015–0.02 mm; single crystals are found within the cells. The cell wall adjacent to the exotegmen begins to thicken. The exotegmen consists of a single layer of cells elongated along the seed, about 0.008 × 0.008 mm. The mesotegmen is single-layered. Its cells are similar to those of the exotegmen but extend across the seed. The cell walls of the exotegmen and mesotegmen begin to thicken. The endotegmen consists of thin-walled cells elongated along the seed, about 0.012 × 0.012 mm. The seed retains a single-layer nucellus of thin-walled, tabular cells, 0.01–0.015 × 0.01–0.015 mm. The endosperm is perceivable. The cells are polygonal, 0.025–0.03 × 0.025–0.03 mm, and densely packed (Fig. 9D9). The embryo is not visible.

Term V – Third decade of May

The fruit is ellipsoidal, flattened at the apex, measuring about 0.7 × 0.8 cm (the body of the fruit), with sepals about 0.8 cm long (Fig. 7E–E2). The seeds are numerous, ovoid, about 3.30 × 2.30 × 1.60 mm. The aril appears as a ridge along one side of the seed; from the apex of the seed to about 1/3, the aril is more expanded, extending above the apex of the seed (Fig. 9E).

The pericarp is 1.30–1.50 mm thick (Fig. 8E). The exocarp is single-layered. The epidermal cells are 0.045–0.060 × 0.05–0.07 mm, slightly elongated tangentially in cross section, with a cuticle on the outside. The mesocarp cells are 0.060–0.12 × 0.05–0.12 mm, thin-walled. The cells of the layer underlying the exocarp are polygonal, slightly elongated tangentially, and densely arranged. The cells of the layers located closer to the exocarp (about 2/3 of the mesocarp) are larger, ellipsoidal, sometimes almost round, with large intercellular spaces. The cells of the layers located closer to the endocarp (about 1/3 of the mesocarp) are elongated in various directions, 0.040–0.090 mm thick, with larger intercellular spaces. The endocarp consists of a single layer of slightly tangentially elongated cells, about 0.1 × 0.15 mm. The cell walls of the endocarp cells are slightly thickened. In the ribs of the fruit, the endocarp is represented by thin-walled cells elongated along the fruit. In the septum, closer to the central zone, amphicribral vascular bundles are located, 2 per septum, not fused (ventral vascular bundles of carpels) (Fig. 8E1). In the ribs of the fruit (in the middle part), in the mesocarp closer to the endocarp, there are three vascular bundles (dorsal vascular bundles of the carpel). Closer to the periphery of the pericarp there is a large amphicribral vascular bundle, and closer to the endocarp there are 2 vascular bundles with the phloem facing the periphery of the pericarp (Fig. 8E2).

The aril is multilayered, enlarged (Fig. 9E–E6). The epidermis consists of slightly tangentially elongated cells, about 0.01 mm thick. The cuticle is thin. The cells of the peripheral parenchyma layer increase in size, measuring 0.25–0.6 × 0.15–0.25 mm. The cells of the remaining parenchyma layers above and below the funicle are polygonal, about 0.01 × 0.01–0.02 mm, and densely arranged. The remaining parenchymal cells of the funicle are ellipsoidal. They greatly increase in size to 0.04–0.05 × 0.03–0.04 mm (Fig. 9E7).

The seed coat is about 0.7 mm thick, consisting of 5 cell layers (Fig. 9E8). The exotesta cells are strongly flattened tangentially, measuring 0.01–0.015 × 0.04–0.05 mm. On the outside, they have a cuticle. The endotesta cells are increasing in size to 0.02–0.025 × 0.025–0.03 mm, with large, single crystals inside the cells. The cell wall adjacent to the exotegmen begins to thicken. The exotegmen consists of a single layer of fibers extending along the seed, 0.008–0.01 × about 0.008 mm. The mesotegmen is single-layered. Its cells are similar to those of the exotegmen but extend across the seed. The endotegmen consists of thin-walled cells extending along the seed, about 0.012 × 0.012 mm. The seed retains a single-layer nucellus of thin-walled, tabular cells, 0.018–0.02 × 0.015–0.02 mm. The endosperm is perceivable. The cells are polygonal, 0.04–0.06 × 0.03–0.04 mm, and densely packed (Fig. 9E9). Numerous small oil droplets appear within the cells. The embryo becomes visible in the micropylar region of the seed. In the middle of the embryo is a region with darker-stained cells. In longitudinal section, it is slightly elongated along the seed. The cells are spherical, about 0.007 × 0.007 mm, and densely packed (Fig. 9E10).

Term VI – Beginning of June

The fruit is ellipsoidal, slightly flattened at the apex, almost spherical, measuring about 0.75 × 0.85 cm (the body of the fruit), with sepals about 0.8 cm long (Fig. 7F–F2). The seeds are numerous, ovoid, about 3.30 × 2.30 × 1.60 mm. The aril appears as a ridge along one side of the seed; from the apex of the seed to about 1/3, the aril is more expanded, extending above the apex of the seed (Fig. 9F).

The pericarp is 1.3–1.5 mm thick (Fig. 8F). The exocarp is single-layered. The epidermal cells are 0.045–0.06 × 0.05–0.07 mm, slightly elongated tangentially in cross section, with a cuticle on the outside. The mesocarp cells are 0.06-

0.12 × 0.05-0.12 mm, thin-walled. The cells of the layer underlying the exocarp are polygonal, slightly elongated tangentially, and densely arranged. The cells of the layers located closer to the exocarp (about 2/3 of the mesocarp) are larger, ellipsoidal, sometimes almost round, with large intercellular spaces. The cells of the layers located closer to the endocarp (about 1/3 of the mesocarp) are elongated in various directions, 0.04–0.09 mm thick, with larger intercellular spaces. The endocarp consists of a single layer of slightly tangentially elongated cells, about 0.1 × 0.15 mm. Numerous pores are visible in the cell walls of the endocarp cells. In the ribs of the fruit, the endocarp is represented by thin-walled cells elongated along the fruit. In the septum, closer to the central zone, amphicribral vascular bundles are located, 2 per septum, not fused (ventral vascular bundles of carpels) (Fig. 8F1). In the ribs of the fruit (in the middle part), in the mesocarp closer to the endocarp, there are three vascular bundles (dorsal vascular bundles of the carpel). Closer to the periphery of the pericarp there is a large amphicribral vascular bundle, and closer to the endocarp there are 2 vascular bundles with the phloem facing the periphery of the pericarp (Fig. 8F2).

The aril is multilayered, enlarged (Fig. 9F–F6). The epidermis consists of slightly tangentially elongated cells, about 0.01 mm thick. The cuticle is thin. The cells of the peripheral parenchyma layer are enlarged, 0.3–0.6 × 0.2–0.3 mm. The cells of the remaining parenchyma layers above and below the funicle are polygonal, about 0.01 × 0.01–0.02 mm, and densely arranged. The remaining parenchymal cells of the funicle are ellipsoidal, 0.04–0.06 × 0.03–0.05 mm (Fig. 9F7).

The seed coat is about 0.65 mm thick, consisting of 5 cell layers (Fig. 9F8–F9). The exotesta cells are strongly flattened tangentially, abouit 0.01 × 0.04–0.05 mm. They have a cuticle on the outside. The endotesta cells are slightly radially flattened, 0.015–0.02 × 0.025–0.03 mm, with large, solitary crystals within them. The cell wall adjacent to the exotegmen is thickened. The exotegmen consists of a single layer of sclerified fibers extending longitudinally along the seed, 0.008–0.01 × about 0.008 mm. The mesotegmen is single-layered. Its cells are similar to those of the exotegmen but extend transversely across the seed. The endotegmen consists of thin-walled cells extending longitudinally along the seed, about 0.012 × 0.012 mm. The seed retains a single-layer nucellus of thin-walled, tabular cells, 0.02–0.025 × 0.02–0.25 mm. The endosperm is perceivable. The cells are polygonal, 0.04–0.06 × 0.03–0.05 mm, and densely packed (Fig. 9F10). The cells contain numerous small oil droplets. The embryo about doubles in size. In longitudinal section, it is slightly elongated along the seed. The area with darker-colored cells, located in the middle of the embryo, expands slightly. The cells are spherical, about 0.012 × 0.012 mm, and are densely packed (Fig. 9F11).

Term VII – First decade of June

The fruit is ellipsoidal, slightly flattened at the apex, almost spherical, measuring about 0.75 × 0.85 cm (the body of the fruit), with sepals about 0.8 cm long (Fig. 7G–G2). The seeds are numerous, ovoid, about 3.30 × 2.30 × 1.60 mm. The aril appears as a ridge along one side of the seed; from the apex of the seed to about 1/3, the aril is more expanded, extending above the apex of the seed (Fig. 9G).

The pericarp is 1.9–2.2 mm thick (Fig. 8G). The exocarp is single-layered. The epidermal cells are 0.04–0.06 × 0.04–0.06 mm, tabular or nearly round in cross section, with a cuticle on the outside. The mesocarp cells are 0.06–0.12 × 0.05–0.12 mm, thin-walled. The cells of the layer beneath the exocarp are polygonal, slightly elongated tangentially, and densely arranged. The cells of the layers located closer to the exocarp (about 2/3 of the mesocarp) are larger, ellipsoidal, sometimes nearly round, with large intercellular spaces. The cells of the layers located closer to the endocarp (about 1/3 of the mesocarp) are elongated in various directions, 0.04–0.09 mm thick, with larger intercellular spaces. The endocarp consists of a single layer of slightly tangentially elongated cells, about 0.1 × 0.2 mm. The cell walls are slightly thickened, with numerous pores. In the ribs of the fruit, the endocarp is represented by thin-walled cells elongated along the fruit. In the septum, closer to the central zone, amphicribral vascular bundles are located, 2 per septum, not fused (ventral vascular bundles of carpels) (Fig. 8G1). In the ribs of the fruit (in the middle part), in the mesocarp closer to the endocarp, there are three vascular bundles (dorsal vascular bundles of the carpel). Closer to the periphery of the pericarp there is a large amphicribral vascular bundle, and closer to the endocarp there are 2 vascular bundles with the phloem facing the periphery of the pericarp (Fig. 8G2).

The aril is multilayered, enlarged (Fig. 9G–G7). The epidermis consists of slightly tangentially elongated cells, about 0.01 mm thick. The cuticle is thin. The cells of the peripheral parenchyma layer are enlarged, 0.3–0.6 × 0.2–0.3 mm. The cells of the remaining parenchyma layers above and below the funicle are polygonal, about 0.01 × 0.01–0.02 mm, and densely arranged. The remaining parenchymal cells of the funicle are ellipsoidal, 0.04–0.06 × 0.03–0.05 mm (Fig. 9G8).

The seed coat is about 0.65 mm thick, consisting of 5 cell layers (Fig. 9G9–G10). The exotesta cells are strongly flattened tangentially, about 0.01 × 0.04–0.05 mm. They have a cuticle on the outside. The endotesta cells are slightly radially flattened, 0.015–0.02 × 0.025–0.03 mm, with large, solitary crystals within them. The cell wall adjacent to the exotegmen is thickened. The exotegmen consists of a single layer of sclerified fibers extending longitudinally along the seed, 0.008–0.01 × about 0.008 mm. The mesotegmen is single-layered. Its cells are similar to those of the exotegmen but extend transversely across the seed. The endotegmen consists of thin-walled cells extending longitudinally along the seed, about 0.012 × 0.012 mm. The seed retains a single-layer nucellus of thin-walled, tabular cells, 0.02–0.025 × 0.02–0.25 mm. The endosperm is perceivable. The cells are polygonal, 0.04–0.06 × 0.03–0.05 mm, and densely packed (Fig. 9G11). The cells contain numerous small oil droplets. The embryo increases in size about twofold. In longitudinal section, it is linear. The area with darker-stained cells, located in the middle of the embryo, expands slightly. The embryo's cells are polygonal, about 0.02 × 0.02 mm, and are densely packed. The cells contain small oil droplets (Fig. 9G12).

DISCUSSION

The mature fruits of the studied representatives of *Asarum* have a common structural plan. The fruits are capsules consisting of six carpels, spherical or flattened at the apex, with six longitudinal ribs, and pubescent. The fruits retain triangular sepals, which are free or partially fused into a tube. The pericarp is leathery and consists of an exocarp, a multilayered mesocarp that makes up the bulk of the pericarp, and a single-layered endocarp. The exocarp cells are tabular or rounded in cross section and covered with a cuticle. The mesocarp cells are parenchymatous and differentiated. In the part of the mesocarp closest to the exocarp, the cells are ellipsoidal or rounded, with small intercellular spaces. The mesocarp layer beneath the exocarp may be composed of smaller, tabular, densely packed cells. The portion of the mesocarp adjacent to the endocarp consists of thin cells, elongated tangentially or in various directions. In this portion of the mesocarp, in the ribs, run the dorsal vascular

bundles of the carpels, three of which are clearly separated from each other or closely spaced. The endocarp consists of tangentially elongated cells, thin-walled or with slightly thickened cell walls and numerous small pores. In the ribs of the fruit, the endocarp is composed of thin-walled cells elongated along the fruit. The septa are thin, composed of a small number of layers of parenchymatous cells, bounded by the endocarp. In the septa, closer to the central zone, are amphicribral vascular bundles, two per septa, which do not fuse (the ventral vascular bundles of the carpels). The absence of sclerified cells in the pericarp is likely due to the fact that fruits of *Asarum* are mostly gnaw through by ants before they open.

The aril is yellowish, fleshy, and located on one side of the seed along the raphe, slightly extending to the apex. The aril is multilayered, consisting of epidermis and parenchyma. The epidermis consists of a single layer of tangentially flattened cells with a cuticle. The parenchyma is differentiated. The main thickness of the aril is formed by a single layer of highly expanded cells. Closer to the vascular bundle of the funicle are 4-5 layers of small parenchymatous cells. Inclusions in the cells of aril were not detected. To the sides of the vascular bundle of the funicle, along the entire adjacent side of the seed, is the multilayered parenchyma of the funicle, consisting of ellipsoidal, polygonal, or spherical cells. It is surrounded by the same epidermis as the seed coat and aril.

The seeds are ovoid, brownish, and numerous, attached to each carpel in two longitudinal rows in the middle. Most seeds are oriented such that the dorsal side of the seed is adjacent to the septum, and the ventral side of the seed is oriented toward the inside of the carpel, so that the seeds adjoin each other at the aril. The seed coat consists of 5 cell layers. The exotesta cells are thin-walled, flattened radially or tangentially, with a cuticle. The endotesta cells are cubic, slightly flattened radially. The cells have thickenings of the cell walls adjacent to the exotegmen, extending onto the radial walls to the middle of the cells. Single large crystals in the shape of parallelepipeds are located within the endotesta cells. The exotegmen is represented by a single layer of sclerified fibers elongated along the seed, slightly elongated radially or rounded in cross section. The mesotegmen also consists of a single layer of sclerified fibers similar to the cells of the exotegmen but extending transversely across the seed. The endotegmen consists of thin-walled, larger cells extending longitudinally. The seed retains a single-layer nucellus of thin-walled cells extending longitudinally. The endosperm is copious. The endosperm cells are polygonal, densely arranged, and filled with numerous small oil droplets. The embryo is yellowish, cordate or linear, and occupies a small portion of the seed in the micropylar region. The embryo cells are polygonal, densely arranged, and contain small oil droplets.

The fruit and its parts of *A. europaeum* develop as follows. At the first term (the third decade of April), the fruit body is about 0.3 × 0.5 cm in length and width, and the seeds are about 1.00 × 0.65 × 0.50 mm. Pericarp differentiation is already observed at this stage. The exocarp, two mesocarp zones, and the endocarp are distinguished. The seed coat contains the exotesta, endotesta, exotegmen, mesotegmen, and endotegmen. The cells of the seed coat layers are distinct from each other but unspecialized. A single-layer nucellus is retained in the seeds. The endosperm is parietal. The aril appears as a small hump on one side of the seed. Its anatomical structure is undifferentiated. The parenchyma cells of the funicle are identical at this time. By the end of April, the aril becomes more noticeable and looks like a small ridge, more expanded in the upper part of the seed, slightly overlapping it. At the same time, the cells of the upper layer of the funicle parenchyma, located above the vascular bundle, noticeably grow. Almost a month later, at term IV (the second decade of May), the fruit grows noticeably. Its dimensions are about 0.55 × 0.75 cm. The seeds also noticeably increase in size and almost reach their final dimensions, about 3.30 × 2.30 × 1.60 mm. Specialization of the cells of the seed coat begins: the cells of the exotesta strongly flattened tangentially; the cell walls of the endotesta cells adjacent to the exotegmen thicken, and single crystals appear in the cells; the exotegmen and mesotegmen become sclerified; the cells of the endotegmen slightly increase in size. The cells of the nucellus and endosperm increase in size. At this time, the aril grows in thickness and width and appears as a distinct ridge along one side of the seed. From the apex of the seed to about 1/3, the aril is more expanded, extending above the apex of the seed. The parenchyma cells of the funicle, located on either side of the vascular bundle, along the seed, begin to noticeably increase in size. In the third decade of May (term V), differentiation of the cells of the seed coat continues; the endosperm occupies almost the entire of the seed, its cells reach their final size and contain numerous small oil droplets; the parenchyma cells of the funicle on either side of the vascular bundle also reach their final size. At this time, the embryo becomes visible and begins its active growth. It is slightly elongated, occupying a small part of the seed near the micropyle. By beginning of June (term VI), the fruit has almost reached its final size – about 0.75 × 0.85 cm. At this time, differentiation of the seed coat cells is complete. At this term, the embryo increases in size. In the first decade of June, the fruit is fully ripened. This can be judged by the ants gnawing through the pericarp to extract the seeds with aril. By this time, no visible changes in the structure of the pericarp, aril, seed coat, or endosperm are detectable. Only the embryo becomes larger and acquires a linear shape; small oil droplets appear in the embryonic cells.

Formation of fruit of *A. europaeum* takes about 7 weeks, from the third decade of April to the first decade of June. Fruit growth follows a sigmoid curve. From the third decade of April (term 1) to the first decade of May (term 3), the fruit grows slowly for 2 weeks. Then, rapid growth is observed. Within a week, its diameter increases by half, and its length by 2 times. Then, for 2 weeks, the fruit grows slowly again. By the beginning of June, the fruit reaches its final size. The fruit growth phase lasts 4 weeks, and the ripening phase lasts 3 weeks. The onset of the ripening phase coincides with the emergence of the embryo. Seeds grow synchronously with the fruit. Their rapid growth also occurs from the first to the second

decade of May. In this period, seed size increases about 3 times. During this period, maximum growth of the aril is observed, namely the differentiated parenchyma cells of the funicle that form the aril. Following rapid growth of all fruit parts, the beginning of specialization of endocarp and seed coat cells is observed in the second decade of May. Differentiation continues for two weeks, until beginning of June. The formation of crystals in endotesta cells is likely related to protection of the embryo from ant damage. Fatty oil accumulates in the endosperm and embryo cells. The appearance of oil droplets in endosperm cells occurs a week after the beginning of seed isolation, at the same time as the embryo becomes visible and begins its active growth. In the embryo cells, oil droplets appear even later, just before ripening. Fatty oil does not accumulate in the aril cells.

The following patterns can be identified in the development of fruit of *Asarum*. Fruit and seed growth occur simultaneously according to a sigmoid curve, with the arils growing slightly earlier but most actively during this same period. Following rapid growth, specialization of endocarp cells and all layers of the seed coat occurs. Active oil accumulation in endosperm cells occurs after seed isolation, concurrent with active embryo growth. In the embryonic cells, oil accumulates immediately before maturation. Nutrients are not stored in the arils.

Since the aril of *Asarum* does not accumulate nutrients, it has no storage function. The expansion of the parenchyma of funicle that forms the aril, prior to active growth and, especially, seed isolation, and even to the specialization of seed coat cells, indicates that the aril in this case does not receive nutrition on a residual basis. The small size of the aril, combined with the presence of multilayered parenchyma of funicle growing along one side of the seed and the relatively loose structure of the pericarp, indirectly indicate that creating a microclimate in the developing fruit is unlikely to be one of the functions of the aril. However, the parenchyma of funicle that grows along the seed in the early stages suggests just such a function for developing seeds. However, the presence of noticeable arils before active fruit and seed growth suggests that, in the early stages of fruit development, arils may act as shock absorbers in the fruit cavity during active growth. The primary function of the arils is to facilitate dissemination, thanks to their succulent structure and the attractants they contain. However, it cannot be generally assumed that the arils in Aristolichiaceae are formed solely as a specialized structure for dissemination. Representatives of *Aristolochia*, another genus in the Aristolochiaceae family, also develop arils. They are adjacent to the seed on one side, follow its shape and sometimes exceeding it in size. They are mostly composed of uniform parenchymatous cells. In representatives of the Aristolochiaceae family, ovules are generally anatropous, but there may be exceptions. Among other things, *Aristolochia* is reported to have apotropaic rather than anatropaic ovules, in which the funicle remains free (Vovk & Komar 1988). In *Aristolochia steupii* Woronow, the ovule is apotropaic and the aril does not adhere to the seed coat, but extends only from the free funicle, with the aril located on the dorsal side of the seed (Trusov 2015, 2021). In *Aristolochia arborescens* L., the ovule is anatropaic and the aril adheres to the seed coat in the raphe region, but it is formed by the entire parenchyma of the funicle, and is not an outgrowth of only one layer, like the aril in *Asarum* (Trusov 2013b). The relatively large size of the arils of *Aristolochia*, their position in the fruit between the seeds, completely covering one side, the uniformity and undifferentiation of their anatomical structure despite their varied morphological nature, and the lack of nutrient accumulation within them, as well as the presence of a similar parenchyma of funicle fused to the seed in *Asarum*, may indicate a protective and buffering function of the arils for developing seeds. In *Asarum*, these functions of protecting developing seeds and attracting dispersal agents are shared between the parenchyma of funicle fused to the seed and the arils themselves.

CONCLUSION

The fruits of *Asarum* have a common structural plan. They are leathery, spherical-hexagonal capsules with a single-layer exocarp, differentiated mesocarp, and a single-layer endocarp of slightly thickened cells. The seeds are numerous and ovoid. The seed coat consists of 5 cell layers: exotesta – thin-walled, tangentially flattened; endotesta – tabular with thickened lower walls and single large crystals; exo- and mesotegmen – fibers oriented respectively along and across the seed; endotegmen – tabular, thin-walled. Endosperm is copious. The embryo is small. The cells of the endosperm and embryo contain numerous oil droplets. On one side, the funicle grows to the seed, its parenchyma covers the ventral side of the seed. The aril is rapheal, multilayered. The aril epidermis consists of highly tangentially flattened cells; the parenchyma is differentiated: an upper layer of large cells and 4-5 layers of small cells. The fruit develops over three weeks: 4 weeks of growth and 3 weeks of maturation. The growth of the fruit parts occurs synchronously. Specialization of the endocarp and seed coat cells begins after active fruit growth, simultaneously with the embryo becoming visible and beginning to grow rapidly. The aril begins to develop before active fruit and seed growth. Its main function is to participate in dissemination.

ACKNOWLEDGEMENTS

The work was carried out within the framework of the state assignment of the Tsitsin Main Botanical Garden of Russian Academy of Science of the program: "Biological diversity, resource potential and conservation of natural and cultural flora in the context of climate and anthropogenic changes", No. 126020916823-0.

LITERATURE CITED

Artyushenko, Z.T. 1990. *Atlas on descriptive morphology of higher plants: seeds*. Nauka, Leningrad, 392 pp. (in Russian). [Артюшенко З.Т. 1990. Атлас по описательной морфологии высших растений: семена. Ленинград: Наука. 392 с.].

Baillon, M.H. 1876–1978. *Dictionnare de Botanique*. Librairie Hachette et C., Paris, 788 pp.

Barykina, R.P., T.D. Veselova, A.G. Devyatov, Kh.Kh. Dzhalilova, G.M. Il'ina & N.V. Chubatova 2000. *Fundamentals of microtechnical research in botany. Reference manual.* Izdatel'stvo kafrdry vysshikh rastenii biologicheskogo fakul'tetata

Moskovskogo gosudarstvennogo universiteta, Moscow, 127 pp. (in Russian). [Барыкина Р.П., Веселова Т.Д., Девятов А.Г., Джалилова Х.Х., Ильина Г.М., Чубатова Н.В. 2000. Основы микротехнических исследований в ботанике. Справочное руководство. Москва: Изд-во каф. высших растений биол. ф-та Моск. гос. ун-та. 127 с.].

Corner, E.J.H. 1953. The durian theory extended – I. *Phytomorphology* 3(4):465–476.

Corner, E.J.H. 1954. The durian theory extended – II. The arillate fruit and the compound leaf. *Phytomorphology* 4(1–2):152–165.

Eames, A.J. 1961. *Morphology of the Angiosperms*. McGraw-Hill, New York, 518 pp.

Englický, T. & B. Šera. 2018. The preference of some myrmecochorous plants of forest stands by red wood ant (*Formica rufa* L.) – Experiment on seeds with elaiosomes. *Russian Journal of Ecology* 49(6):577–583.

Goebel, K. 1923. *Organographie der Pflanzen Insbesondere der Archegoniaten und Samenpflanzen. Vol. 3*. Gustav Fischer, Jena, 634 pp.

Gubanov, I.A., K.V. Kiseleva, V.S. Novikov & V.N. Tikhomirov 2003. *Illustrated guide for identification of plants in Central Russia, vol. 2: Angiosperms (Dicotyledons: Choripetalae)*. KMK, Moscow, 668 pp. (in Russian). [Губанов И.А., Киселева К.В., Новиков В.С., Тихомиров В.Н. 2003. Иллюстрированный определитель растений Средней Полосы России. Том. 2. Покрытосеменные (двудольные: раздельнолепестные). Москва: КМК. 668 с.].

Komar, G.A. 1965. Arils, their nature, structure and function. *Botanicheskii Zhurnal* 50(5):715–724 (in Russian). [Комар Г.А. 1965. Ариллусы, их природа, строение и функции // Ботанический журнал. Т. 50, № 5. С. 715–724.].

Kozlowski, T.T. 1972. *Seed Biology. Volume I. Importance, Development and Germination*. Academic Press, New York, London, 416 pp.

Maheshwari, P. 1950. *An introduction to the embryology of Angiosperms*. McGraw-Hill, New York, 472 pp.

Melikyan A.P. & A.G. Devyatov. 2001. *Basic carpological terms. Handbook*. Tovarishchestvo nauchnykh izdaniy KMK, Moscow, 47 pp. (in Russian). [Меликян А.П., Девятов А.Г. 2001. Основные карпологические термины. Справочник. Москва: Товарищество научных изданий КМК. 47 с].

Pfeiffer, A. 1891. Die Arillargebilde der Pflanzensamen. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 13:482–540.

Pfeiffer, M., H. Huttenlocher & M. Ayasse. 2010. Myrmecochorous plants use chemical mimicry to cheat seed-dispersing ants. *Functional Ecology* 24:545–555.

Planchon, J.E. 1845. Développements et caractères des vrais et des faux arilles. *Annales des Sciences Naturelles* 3:275–312.

Shamrov, I.I. 2008. *Ovule of flowering plants: structure, function, origin*. Tovarishchestvo nauchnykh izdaniy KMK, Moscow, 350 pp. (in Russian). [Шамров И.И. 2008. Семязачаток цветковых растений: строение, функции, происхождение. Москва: Товарищество научных изданий КМК. 350 с.].

Trusov, N.A. 2012. Morphological and anatomical structure strophiolum *Asarum europaeum* (Aristolochiaceae). In: *Abstracts II (X) of the International Botanical Conference of young scientists in St. Petersburg, 11-16 November 2012*, p. 54, Izd-vo SPbGETU "LETI", Saint-Petersburg (in Russian). [Трусов Н.А. 2012. Морфолого-анатомическое строение строфиоли *Asarum europaeum* (Aristolochiaceae) // Тезисы докладов II (X) Международной Ботанической Конференции молодых ученых в Санкт-Петербурге 11–16 ноября 2012 года. Санкт-Петербург: Изд-во СПбГЭТУ «ЛЭТИ». С. 54].

Trusov, N.A. 2013a. Complex approach in arils studies. In: *Modern Phytomorphology: 2nd International Scientific Conference on Plant Morphology (14–16 May 2013, Lviv, Ukraine), vol. 4* (L.O. Tasenkevich, ed.), pp. 177–179, Lviv (in Russian). [Трусов Н.А. 2013а. Комплексный подход в изучении ариллусов // Сучасна Фітоморфологія: Матеріали 2-ї міжнародної наукової конференції з морфології рослин (Львів, 14–16 травня 2013 р.), Т. 4 / за ред. Л.О. Тасенкевича. Львів. С. 177–179].

Trusov, N.A. 2013b. Seed and aril structure of *Aristolochia arborescens* L. (Aristolochiaceae). In: *Current problems of botany and ecology. Materials of the international conference of young scientists (Shchelkino, June 18-22, 2013)*, pp. 121–122, Phytosociotsentr, Kyiv.

Trusov, N.A. 2014. Morphological characters of fruits and dissemination characteristics of *Asarum europaeum* L. (Aristolochiaceae). In: *Proceedings of the All-Russian Scientific Conference with International Participation "Fundamental and Applied Biomorphology in Botanical and Ecological Research"*, pp. 125–128, Raduga-Press, Kirov (in Russian). [Трусов Н.А. 2014. Морфологические признаки плодов и особенности диссеминации *Asarum europaeum* L. (Aristolochiaceae) // Материалы Всероссийской научной конференции с международным участием «Фундаментальная и прикладная биоморфология в ботанических и экологических исследованиях». Киров: Радуга-Пресс. С. 125–128].

Trusov, N.A. 2015. Morphological and anatomical structure of seed coat and aril *Aristolochia steupii* (Aristolochiaceae) In: *Abstracts III (XI) of the International Botanical Conference of young scientists in St. Petersburg, 4-9 October 2015*, p. 95, BIN RAN, Saint-Petersburg. (in Russian). [Трусов Н.А. 2015. Морфолого-анатомическое строение семенной кожуры и ариллуса *Aristolochia steupii* (Aristolochiaceae) // Тезисы докладов III (XI) Международной Ботанической Конференции молодых ученых в Санкт-Петербурге 4-9 октября 2015 года. Санкт-Петербург: БИН РАН. С. 95].

Trusov, N.A. 2016. Aril morphological nature and its function in some *Aristolochia*, *Asarum*, *Celastrus*, *Euonymus*, *Euphorbia*, *Viola*, and *Taxus*. *Turczaninowia* 19(3):106–114. (in Russian with English summary) [Трусов Н.А. 2016. Морфологическая природа и функции ариллусов некоторых представителей родов *Aristolochia*, *Asarum*, *Celastrus*, *Euonymus*, *Euphorbia*, *Viola* и *Taxus* // Turczaninowia. Вып. 19, № 3. С. 106–114].

Trusov, N.A. 2021. Arils of dried fruits and their relationship with dissemination. *Contemporary Problems of Ecology* 14(6):690–700.

Pijl, van der L. 1955. Sarcotesta, aril, pulpa and the evolution of the angiosperm fruit. II. *Verhandelingen der koninklijke nederlandsche akademie van wetenschappen; afdeeling natuurkunde; tweede sectie* 58:307–312.

Vovk, A.G. & G.A. Komar. 1988. Family Aristolochiaceae. In *Comparative Anatomy of Seeds. Vol. 2* (A.L. Takhtadzhyan, ed.), pp. 105–111, Nauka, Leningrad (in Russian). [Вовк А.Г., Комар Г.А. 1988. Семейство Aristolochiaceae // Сравнительная анатомия семян. Т. 2. / под ред. А.Л. Тахтаджана. Ленинград: Наука. С. 105–111].