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RESEARCH ARTICLE

Micromorphology and anatomy of fruit in *Iris pseudacorus* L.

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Abstract

Based on the suggestion that flower and fruit are integrally evolving structures, we aimed to reveal the floral traits persisting in the fruit structure in *Iris pseudacorus*, a widely distributed riparian species in Ukraine. We intended to compare the results with the other *Iris* species studied previously and reveal the constancy of micromorphological features of fruit interior structure. We revealed exomorphological and micromorphological peculiarities of the fruiting ovary using the model of vertical zonality of the gynoecium, vascular anatomy, and general anatomy of the fruit wall. In the fruiting ovary of *I. pseudacorus*, we revealed the presence of three vertical zones: short synascidiate zone, long symplicate zone bearing uniseriate seeds, and hemisymplicate zone located in the fruit beak. The vascular system of the ovary is composed of dorsal, septal, and ventral veins. Each of three dorsal veins divides radially into the outer tepal trace, stamen trace, and dorsal carpellary bundle, while each septal vein divides tangentially into three bundles of the inner tepal trace. Paired ventral veins enter the ovary from its bottom and supply ovules and seeds. The exocarp is composed of polygonal cells with thickened cellulose walls. The endocarp is uniseriate, unlignified, and composed of live prosenchymal cells, which are elongated tangentially. In the parenchymatous mesocarp, a great number of secretory canals with tannin-like content occur. The dehiscence of fruit on three valves proceeded by both dorsal and ventral slits. Dorsal slits are formed along dorsal grooves and provided by small-celled tissue surrounding the dorsal veins. The presence of ventral sutures of carpels in the symplicate zone of the ovary provides ventral dehiscence of fruit. Hence, the structure of the fruiting ovary in *I. pseudacorus* is comparable to that of other *Iris* species. Our investigation confirmed that the vertical zonality, placentation, and vascular system of the gynoecium in *Iris* can be appropriately estimated in the fruiting stage because the structural components of the ovary, which developed at the pre-anthetic phase, persist in the fruit.

Keywords: *Iris*, vascular anatomy, symplicate zone, fruit wall, fruiting ovary

Authors' contributions: Both authors sampled plant material, conducted microscopic studies, described the results, and wrote the text of the article. Anastasiya Odintsova made general supervision of the article, adopted the methodology, and wrote the original draft of the manuscript. Yaroslav Khomei provided microtechnique procedures, sectioned the material, made microphotographs, and designed the text of the article.

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Competing Interests: The authors declare that they have no conflict of interest.

Introduction

Iris L. is the most species-rich genus in the family Iridaceae, being treated morphologically for taxonomic purposes, mainly from the flower and vegetative morphology (Fomin & Bordzilovskyi, 1950; Goldblatt et al., 1998; Wilson, 2006; Sennikov et al., 2023). However, fruit structure in this genus, especially with the application of anatomical techniques, was poorly studied (Rodionenko, 1961; Gritsenko, 2020; Skrypec & Odintsova, 2020). For the whole Iridaceae family, the fruit was defined as a syncarpous inferior trilocular multi-seeded capsule with loculicidal dehiscence (Goldblatt et al., 1998). Two distinct dehiscence types were described for different *Iris* species (Rodionenko, 1961). The first type of fruit dehiscence is realized through the separation of the fruit into three declined valves formed by dorsal slits going through the whole fruit or only through its upper part. In some species, a column persists in the center of the fruit after valves are declined. The second type of fruit dehiscence proceeds by three dorsal slits without forming valves, so the fruit does not disintegrate. Since we suggest flower and fruit as a united evolving structure (Odintsova, 2022), we aimed to reveal the floral traits persisting in the fruit structure in *Iris* species that have large fleshy fruits suitable for anatomical research.

Being experienced in the study of flower and fruit morphology and anatomy in *Iris sibirica* L. (Skrypec & Odintsova, 2014, 2015, 2020), we intended to compare previous results with data on the *I. pseudacorus* L., a species belonging to the same section *Limniris* of the subgenus *Limniris*. The objectives of the present study were to reveal the constancy of micromorphological features of fruit interior structure, including those of the gynoecium (vertical zonality, placentation, vascular anatomy). The anatomy of the fruit wall was also investigated as having a substantial role in fruit dehiscence.

Iris pseudacorus is an Eurasian riparian species, growing in Ukraine throughout the entire country except wormwood steppe and Crimea (Zhygalova, 2014). It belongs to the series *Laevigatae* of the section *Limniris* (Rodionenko, 1961; Wilson, 2009). The habitats of *I. pseudacorus* are limited to the river banks, swamps, and ponds. It is highly tolerant to submersion, water pH, and soil properties, and is well reproduced by rhizome and water-dispersed seeds. The species has LC conservation status (IUCN, 2022) and is invasive in North America, where it escapes from cultivation spots (Gerwing et al., 2021; Stoneburner et al., 2021). Currently, *I. pseudacorus* is cultivated as an ornamental plant, while previously, its rhizome, being rich in tannins, was used to obtain a black color after adding ferrum salts, and flowers treated with acetic acid were used to get a yellow color for skin staining (Fomin & Bordzilovskyi, 1950). Tannins are abundant in the vegetative structures and flowers of some *Iris* species (Rodionenko, 1961). In *I. pseudacorus*, the phenolic compounds extracted from the rhizome were approved for antibacterial activity (Michalak et al., 2021).

Material and methods

The unripe green fruits of *Iris pseudacorus* L. were collected near Ivano-Frankove village, Yavoriv district, Lviv oblast (Ukraine), in the pond and channels (22 June 2015; 24 and 30 June 2023). Sampled materials were sectioned by hand in fresh condition and after fixation in 70 % ethanol. Obtained sections were treated with safranin solution or phloroglucinol reaction with chloride acid for lignin (Gaertner & Schweingruber, 2013; Pradhan Mitra & Loqué, 2014). Twenty fruits were examined in total. Images were captured by digital camera Sigeta M3CMOS 10000 applied to the light microscope XS-2610 (China).

For the micromorphological treatment, we used Leinfellner's (1950) model of vertical zonality of the gynoecium. For vascular anatomy, we followed Esau (1977) principles. The anatomy of the fruit wall was surveyed according to Roth (1977). As fruits of Iris are arranged in monochasial cyme inflorescence, they were at different stages of development at the sampling time. Due to this reason, we withheld quantitative data and statistical evaluation of the studied features.

Results

Fruit morphology and micromorphology

Fruits of *I. pseudacorus* at the studied stages were 5–8 cm long, banana-like, with a short apical beak (spout), obtuse-triangular in a

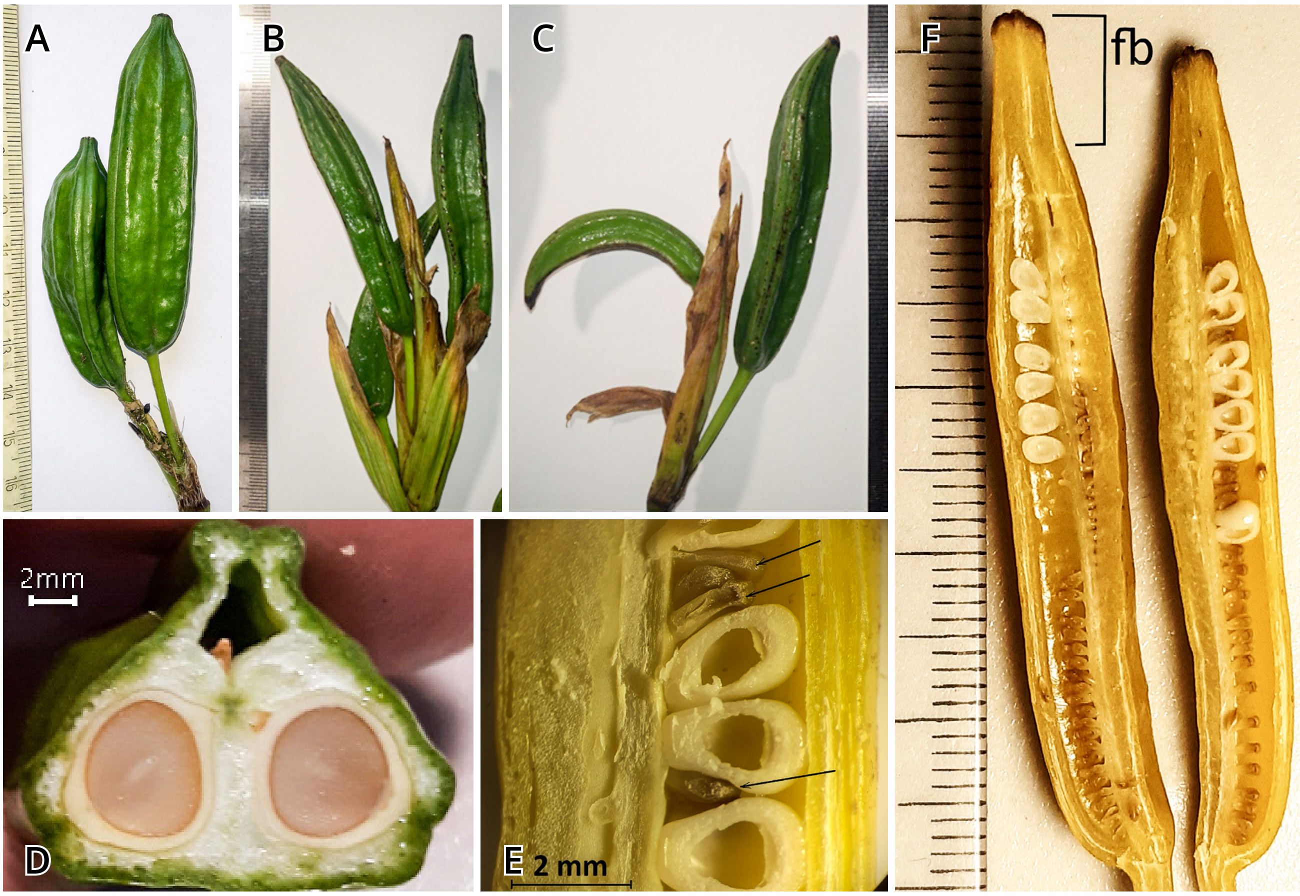

Figure 1. Exomorphology and interior structure of *Iris pseudacorus* fruit: **A–C** – unripe fruits of different shapes; **D** – transversely sectioned fruit with one sterile and two fertile locules with uniseriate seed arrangement; **E** – fragment of the longitudinally sectioned fruit with developing seeds and depressed ovules (**arrows**); **F** – longitudinal section of the whole fruit (**fb** – fruit beak). **A–D** – fresh material; **E, F** – fixed material.

transversal section, green and fleshy. Dorsal grooves were well defined (Fig. 1 A). In our materials, fruits had various sizes and shapes; sometimes, they were deformed and narrowed, depending on the abundance of seeds inside (Fig. 1 A–C). On the transverse section of the fruit, uniseriate pleurotropous seed arrangement in the locule was evident (Fig. 1 D). Many seeds in the fruit were underdeveloped (Fig. 1 E), and sometimes one locule was sterile (Fig. 1 D). Seeds were located along the whole locule height, from the very bottom to its top; in the fruit with low seed numbers, they occupy mostly the upper part of the locule (Fig. 1 F). On the radial section, it was visible that the fruit beak is solid (locules do not extend in it), and the abscission zone of the floral tube lies beneath the style base (Fig. 1 F), which means that the separation layer is formed in the beak tissues where floral tube and style are still fused.

On the transverse sections treated with safranin, a short zone with congenitally closed locules (without ventral sutures) was visible (Fig. 2 A). In this zone, locules were narrow, and seeds missing. Above it, ventral slits of carpels appeared from the center and the locule side, so a trilocular zone with a triradiate slit in the center was formed. This slit connected locules by the secretory epidermis (transmitting tract to the ovules in the anthetic ovary) (Fig. 2 B–E). Sometimes, at the base of this zone, septas did not touch each other, and a small gap was formed (Fig. 2 E). Seeds were born alternately at one of each carpel's margins. At the upper portion of the ovary, locules were diminished, and style channels formed from their proximal parts, covered with secretory epidermis (Fig. 2 F). In the fruit beak, initially triradiate style channel became labyrinthine, and then, the carpelar margins became free, so another three slits arose between style channels, and the central slit became hexaradiate (Fig. 3 A–D).

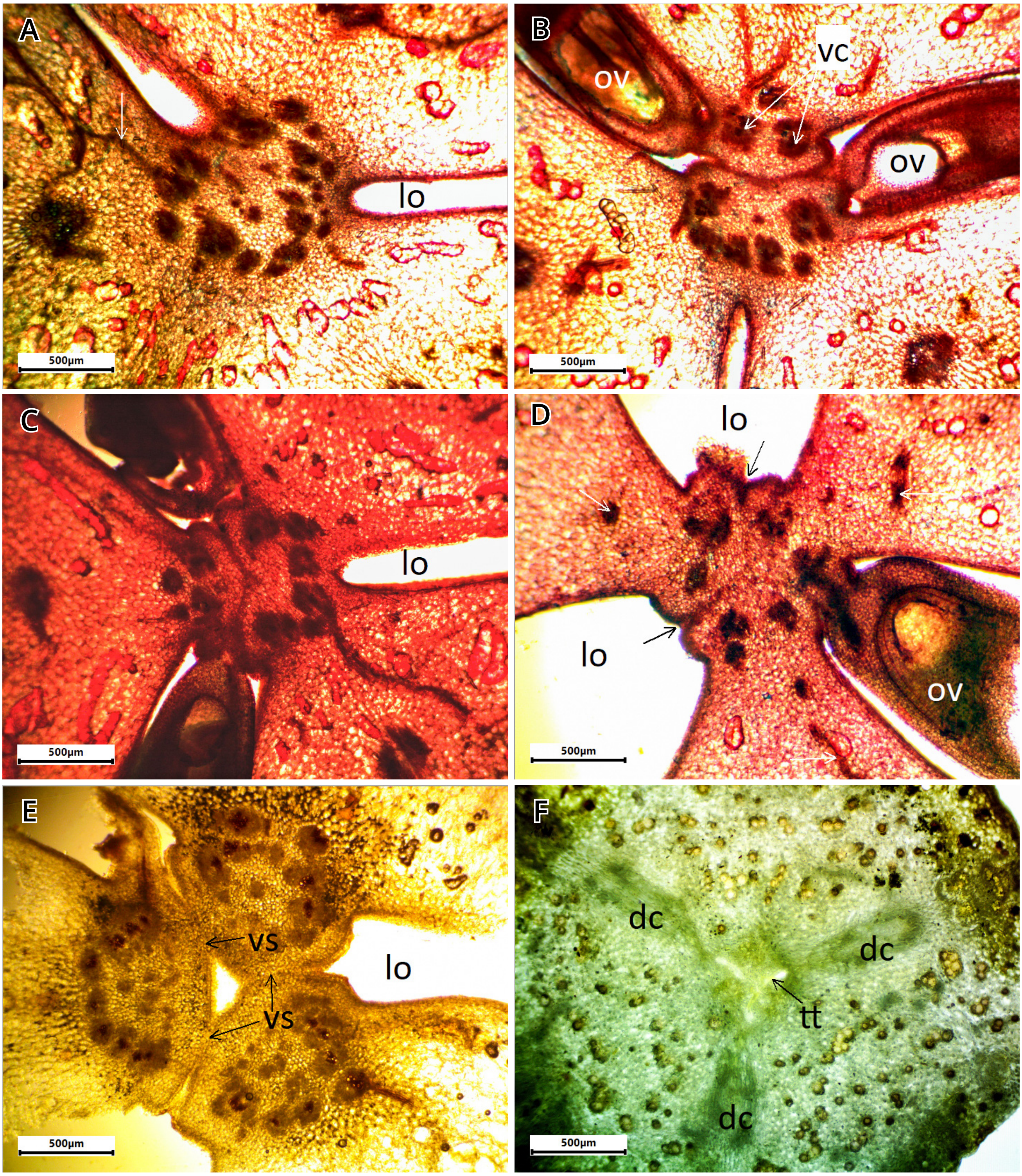

Figure 2. Micromorphology and anatomy of *Iris pseudacorus* fruit body on transversal sections: **A** – synascidiate zone of the fruiting gynoecium; **B–D** – transitions from synascidiate to symplicate zone, ventral suture marked in D with **black arrows**; **E** – symplicate zone with a gap in the center between incomplete septas; **F** – roof of the inferior ovary. **dc** – dorsal carpellary bundle; **lo** – locule; **ov** – ovule/seed; **tt** – transmitting tissue; **vc** – ventral carpellary veins; **vs** – ventral suture, small vascular bundles are marked with **white arrows**. **A–D** – safranin staining.

Therefore, in the fruiting ovary of *I. pseudacorus*, we revealed the presence of three vertical zones (Fig. 4): short and sterile synascidiate zone, long symplicate zone bearing placentas on the incomplete septas, and hemisymplicate zone in the fruit beak. The last zone continued into the style.

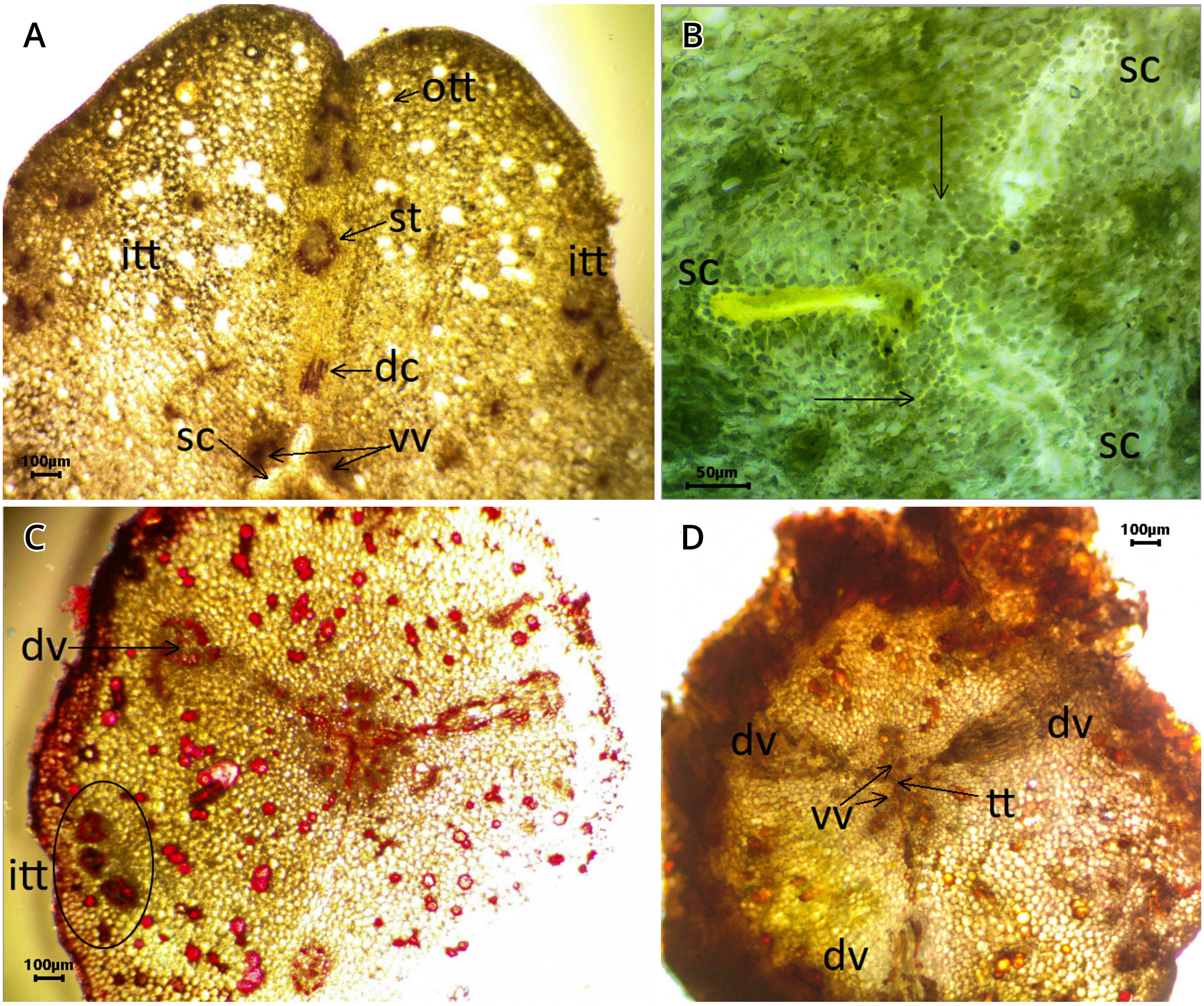

Figure 3. Micromorphology and anatomy of *Iris pseudacorus* fruit beak on ascending transversal sections (A→D): **dc** – dorsal carpellary bundle; **dv** – dorsal vein; **itt** – inner tepal trace; **ott** – outer tepal trace; **sc** – style canals; **st** – stamen trace; **tt** – transmitting tissue; **vv** – ventral veins; **arrows** in B mark transmitting tissue in hemisymplicate zone. **A, C, D** – safranin staining.

Vascular anatomy

On the series of transversal sections through the fruit, we can trace the arrangement of vascular bundles in the ovary. In the upper portion of *I. pseudacorus* peduncle, a dicyclic atactostele occurred, with an external ring composed of numerous closely spaced vascular bundles of various sizes and the inner ring composed of six bundles located on the tepal radii (Fig. 5 A). Above it, the inner bundles entered the external ring, the last divided into six trunk bundles entering the fruit wall, and the rest of the vascular bundles in the center of the ovary (Fig. 5 B, C). Three trunk bundles on the outer tepal's radii (on the carpel median plane) were doubled (Fig. 5 B), – we entitled them dorsal veins of carpels. The other three trunk bundles located on the septas radii were entitled septal veins. The remnants of the vascular tissue formed a plexus of small bundles, which develop paired ventral carpellary bundles in the ends of septas. These bundles gave rise to ovule traces (Fig. 2 A–C). Small anastomoses were formed between septal veins and ventral bundles, especially in the lower portion of the fruit (Figs. 2 B–D; 5 D, E). Dorsal veins gave tiny branches to the ovary wall (Fig. 5 F).

In the fruiting ovary, dorsal and septal veins were unitary (Fig. 5 E, F), while in the fruit beak, each dorsal vein branched radially onto three bundles: outer tepal trace, stamen

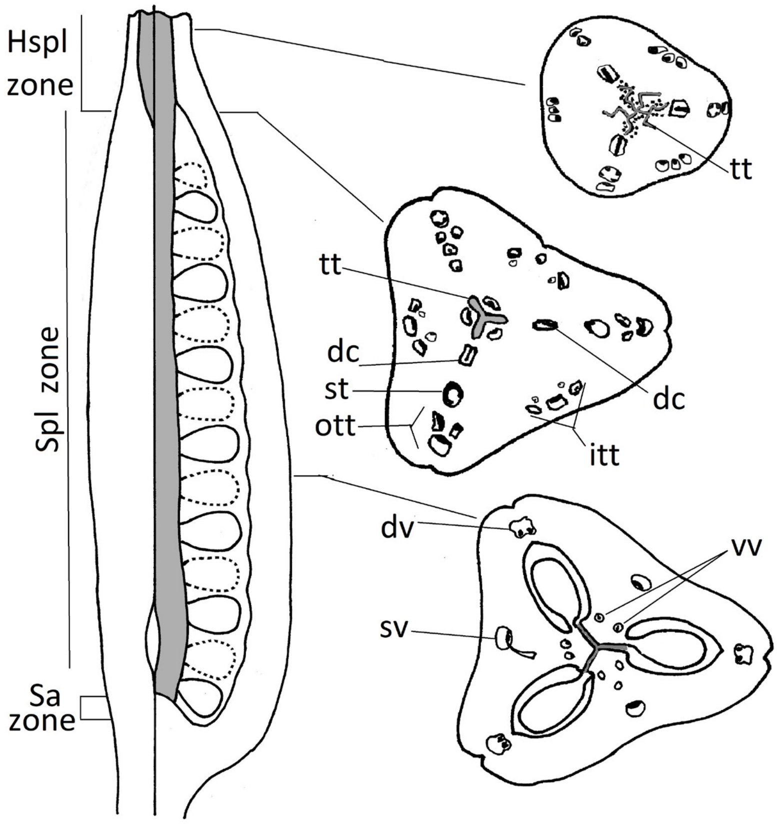

Figure 4. Schematic drawing of the fruit zonality and vascularization: **Hspl zone** – hemisymplicate zone; **Sa zone** – synascidiate zone; **Spl zone** – symplicate zone. Postgenitally fused epidermises of ventral sutures and carpel margins are colored in **grey**. **dc** – dorsal carpellary bundle; **dv** – dorsal vein; **itt** – inner tepal trace; **ott** – outer tepal trace; **st** – staminal trace; **sv** – septal vein; **tt** – transmitting tissue; **vv** – ventral veins.

trace, and dorsal carpellary bundle, which declined to the center and entered the style (Fig. 3 A). Stamen trace was basally concentric with xylem outwards (Fig. 3 A). The septal vein in the fruit beak divided into three bundles tangentially: two lateral bundles were larger than the central one and made tiny branches to the center (Fig. 3 A, C). Ventral bundles in the beak fused in each septa ending (Figs. 3 C; 4).

Therefore, the vascular system of *I. pseudacorus* ovary can be appropriately estimated during the fruiting stage because vascular bundles, which mainly developed at the pre-anthetic phase, persist in the fruit. The vascular system of the epigynous flower of *I. pseudacorus* is integrated: dorsal carpellary bundles are condensed with tepal and stamen traces, while septal veins are anastomosed with ventral carpellary bundles. Six trunk bundles supply the fruit wall, while ovules/seeds are supplied from ventral bundles entering the ovary from its bottom. In the beak, which is the narrowest part of the fruit, trunk bundles branch out. Small bundles between all main veins are visible. The occurrence of many small bundles in the fruit wall and septas is a regular characteristic of large fleshy fruits (Roth, 1977).

Anatomy of the fruit wall

The fruit wall of *I. pseudacorus* at the stage of green fruit was parenchymatous and fleshy. The exocarp was uniseriate, composed of polygonal isodiametric cells with thickened cellulose walls and a thick cuticle on the outer wall (Fig. 3 C). Stomata in the exocarp were surrounded by 4–7 cells, not sunken (Fig. 6 A, C). Endocarp at the investigated stage of fruit development was uniseriate, unlignified, and composed of prosenchyma cells, elongated tangentially, 200–400 mkm long, with oblique ends (Fig. 6 B, D). Endocarpial cells had evenly thickened walls and remained alive.

The mesocarp was at least 1.7 mm thick and composed of 27–38 cell layers (in the

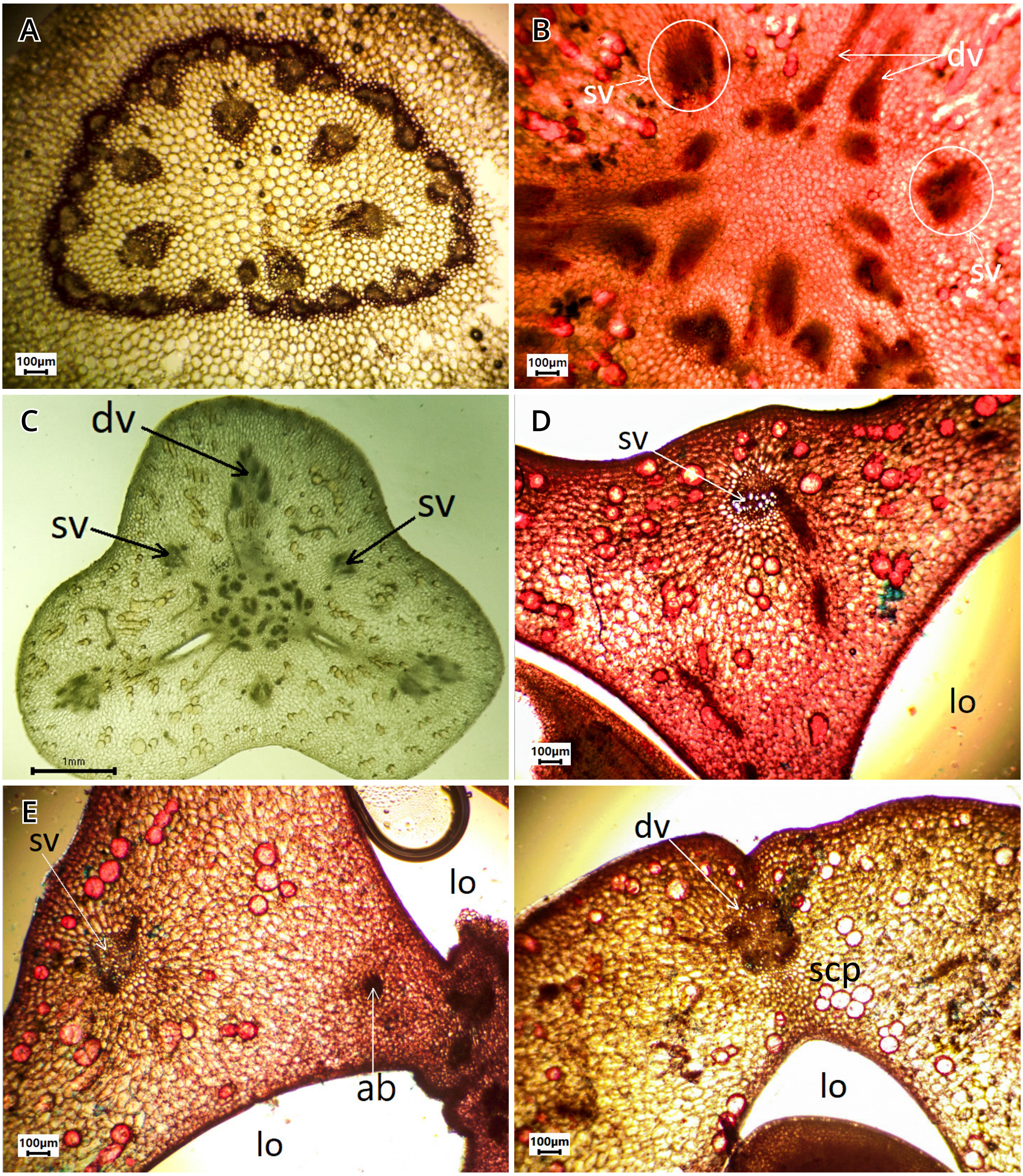

Figure 5. The vascular system of *Iris pseudacorus* fruit on transversal sections: **A** – the base of the fruiting ovary; **B** – formation of dorsal veins in receptacle; **C** – formation of septal and ventral veins at the locule base; **D, E** – septal vein at the middle height of the fruiting ovary, anastomosing to ventral veins; **F** – dorsal vein. **ab** – anastomosing bundle; **dv** – dorsal vein; **lo** – locule; **scp** – small-celled parenchyma; **sv** – septal vein. **A** – phloroglucinol-HCl staining; **B, D–F** – safranin staining.

median plane of the carpel near the dorsal vein). Mesocarp cells had almost equal sizes, but external chlorenchyma cells were slightly smaller. Chlorenchyma appeared in the external zone of the mesocarp as a continual layer; the inner zone of the fruit wall was colorless (Fig. 1 D). In the mesocarp of *I. pseudacorus*, the sporadic appearance of crystallin styloids, up to about 155 mkm long, was noticed (Fig. 7 A, B). Many secretory

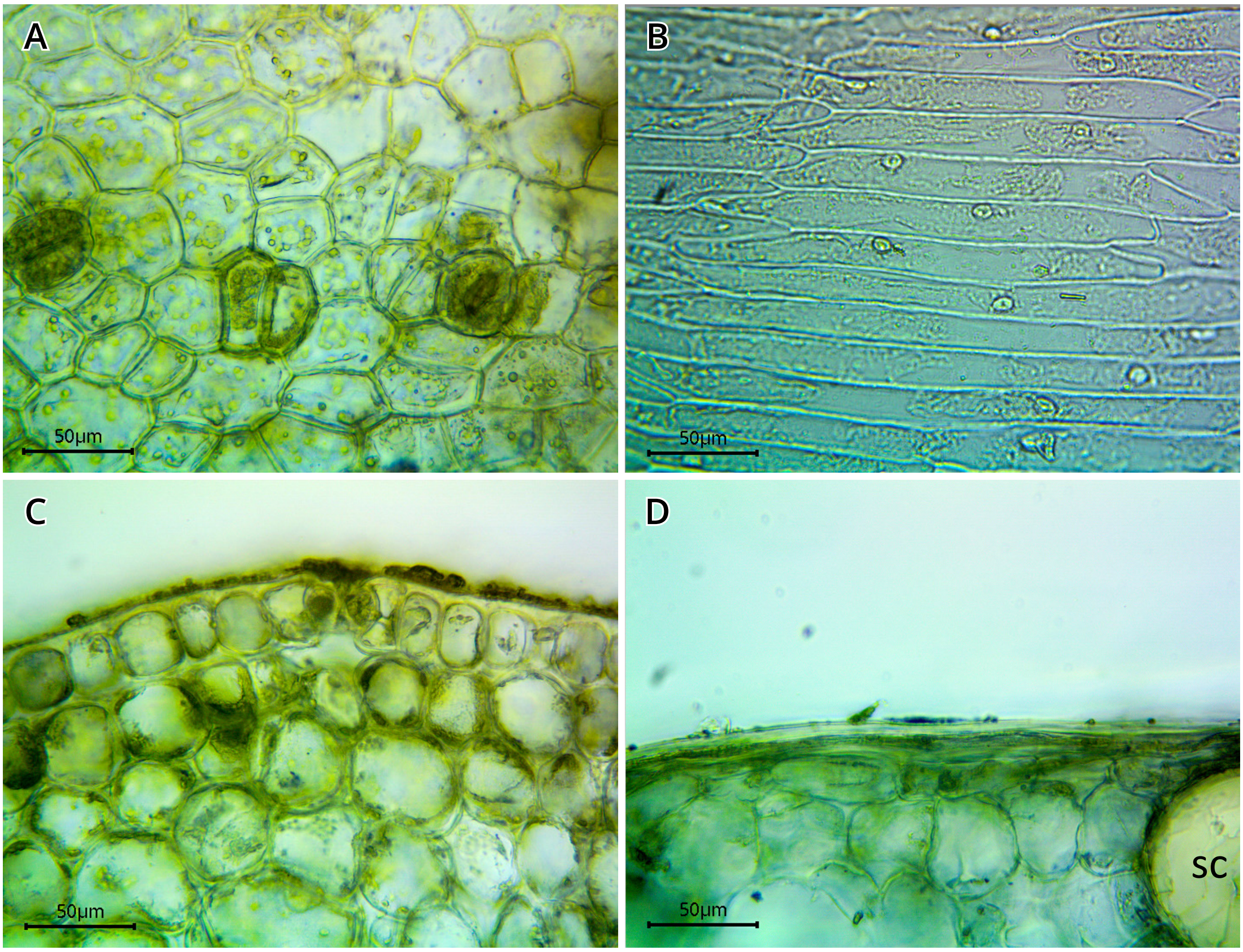

Figure 6. Epidermises of the fruit of *Iris pseudacorus*: **A, C** – exocarpium with stomata; **B, D** – endocarpium; **A, B** – paradermal sections; **C, D** – transversal sections of the fruit. **sc** – secretory canal.

canals occured in mesocarp, arranged solitary or grouped (Fig. 7 C, D). The secretory canals were 0.4–2.8 mm long (Fig. 7 C). They appeared in the external and inner zones of the mesocarp, in septas, in the fruit base, and a beak (Figs. 2; 3; 5; 7D). On fresh untreated sections of the fruit, they looked like round cavities, larger than parenchyma cells, while after safranin treatment, they showed a red outline or filling as tannins do. In the fixed material, the canals had yellow content (Fig. 7 C, D).

A significant element of the fruit dehiscence is the arrangement of the mechanical tissues enabling slit development. Morphologically, dorsal slits are predicted by grooves on the external face of the fruit. Anatomically, on the median plane of the carpel, proximally to the dorsal vein, small uncolored live cells appear in the mesocarp (Fig. 5 F; 7 D). Such small cells are precursors of dorsal slits of the fruit in many capsular fruits (Roth, 1977). The dehiscence of the capsule in *I. pseudacorus* was designated by Rodionenko (1961) as valvate. Three declined valves of fruit were evident in the photos of fruit made by Kovalchuk (2009); the dehiscing fruits on the images have a greenish color, and they are not dry and brown when dehisce. The disintegration of fruit on the valves proceeded by dorsal and ventral slits through the whole fruit. The presence of ventral sutures along the fruiting ovary supports ventral dehiscence in this species.

Discussion

Our research revealed the fruit characteristics common for *I. pseudacorus* and *I. sibirica*. In both species, the size of the fruit depends on the number of seeds inside; seeds are located horizontally from the very base to the top of

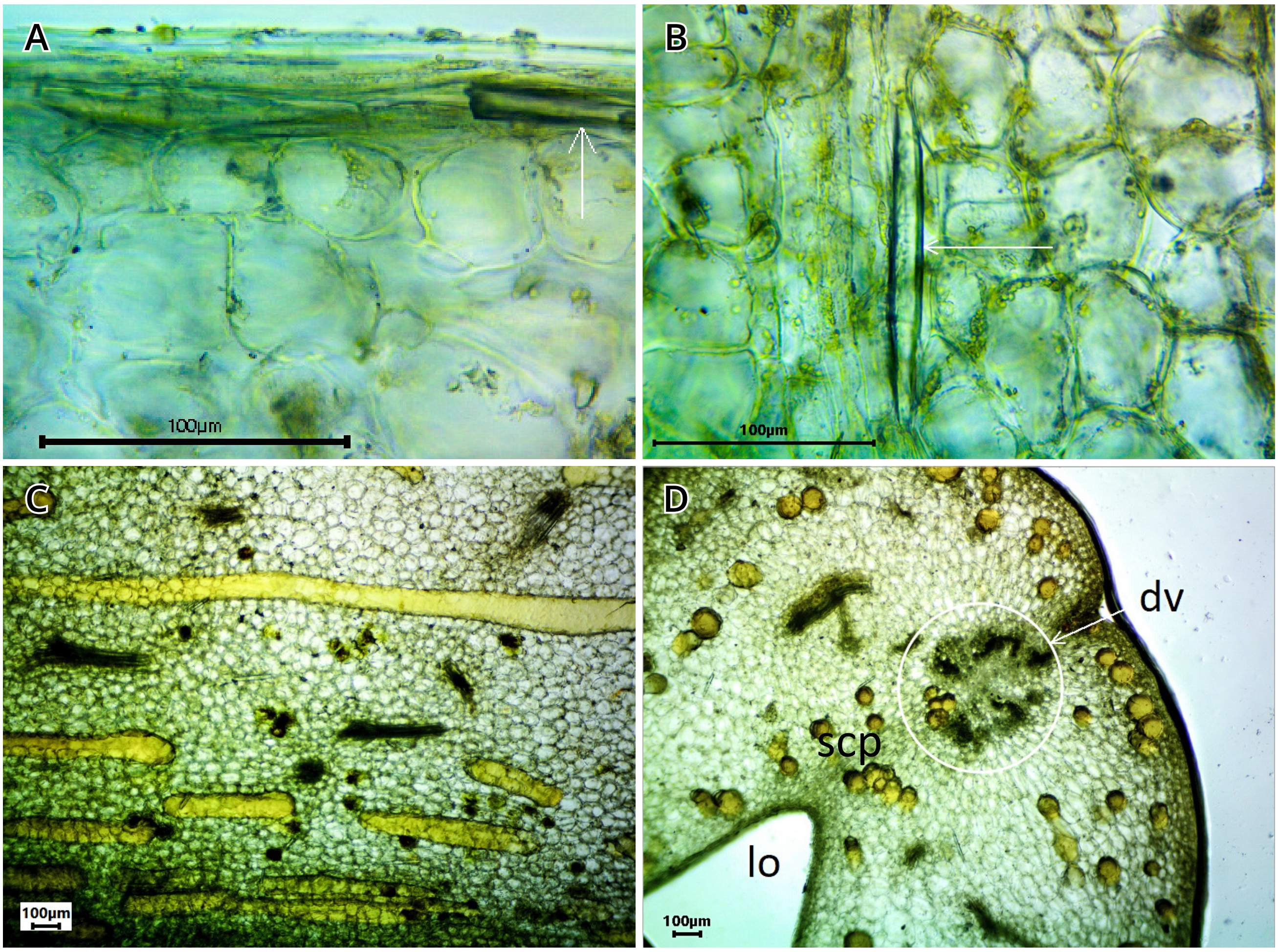

Figure 7. Anatomy of fruit wall in *Iris pseudacorus*: A, B – cristallic inclusion-styloid (**arrow**) in mesocarp; **C** – secretory canals on the tangential section and **D** – on the transverse section in the dorsal portion of the carpel. Dorsal vein (**dv**) and small-celled parenchyma (**scp**) are visible along the upcoming dorsal slit toward the locule (**lo**).

the locule (Skrypec & Odintsova, 2015). After anthesis, the floral tube falls out with an accrescent style in both species (Skrypec & Odintsova, 2020). However, in *I. pseudacorus* seeds arrangement is uniseriate, contrary to the biseriate arrangement in *I. sibirica* and many other *Iris* species (Rodionenko, 1961); dorsal grooves are visible in the green fruit, and slits are complete (arise from the top to base of fruit) contrary to *I. sibirica*, where grooves are not detectable and slits are mostly short (Skrypec & Odintsova, 2014).

The interior structure of the fruiting ovary in *I. pseudacorus* is characterized by the appearance of three zones. However, the synascidiate zone is short and sterile, contrary to *I. sibirica* (Skrypec & Odintsova, 2020). The appearance of synascidiate and symplicate zones in the ovary (but without entitling these zones) was clearly illustrated by Van Tieghem (1871) for *I. lutescens* Lam. (mentioned as *I. chamaeiris* Bertol in the original work). The sterile hemisymplicate zone at the upper part of the ovary and style is represented by Rodionenko (1961) for *I. pseudacorus*, *I. orientalis* Mill. (mentioned as *I. monnieri* DC. in the original work), and *I. korolkowii* Regel in fig. 26, while synascidiate and symplicate zones in some *Iris* species – in figs. 45–48. Those data suggested defining the gynoecium in *Iris* species and Iridaceae in general as eusyncarpous gynoecium according to Leinfellner's (1950) classification. The gynoecium having synascidiate, symplicate, and hemisymplicate zones is a widely distributed type of the gynoecium among monocots (Novikoff & Odintsova, 2008); however, the length and ratio of zones vary in a wide range. For instance, hemisymplicate zone can occupy a large portion of the ovary when it contains septal nectaries, which are missing in *Iris*.

The vascular system of the ovary in *I. pseudacorus* is very similar to the vascular system of other species of Iridaceae studied previously (Van Tieghem, 1871; Rodionenko, 1961; Skrypec & Odintsova, 2020). The main feature of the vascularization of the ovary is the occurrence of three types of veins: dorsal, septal, and ventral. The common pattern of the vascular system is a radial divide of the dorsal vein into three traces (outer tepal trace, stamen trace, and dorsal carpellary bundle), and tangential divide of the septal vein into three bundles, too. The exact structure of the vascular system is usual for epigynous flowers of lilioid monocots: i.e., *Iris lutescens*, *I. florentina* L., *Crocus vernus* (L.) Hill., *Gladiolus ×gandavensis* Van Houtte, *Narcissus pseudonarcissus* L. (Van Tieghem, 1871) as well *Iris sibirica* and *Gladiolus imbricatus* L. (Skrypec & Odintsova, 2020).

The most peculiar feature of the fruit of *I. pseudacorus* is the abundance of canals with tannin-like content, which usually occur in fruits (Roth, 1977). Considering the abundance of the secretory canals in *I. pseudacorus* fruits, we suggest using its fruits as medicinal raw resources.

Many capsular fruits of lilioid monocots have lignified endocarp, V-shaped xylem in the dorsal vein, and U-shaped cell wall thickening in the endocarp (Rasmussen et al., 2006). Instead, some fleshy capsules or berry-like fruits reveal delayed dehiscence and lacking lignification in the fruit wall. They arise in conditions of high humidity or in cases when the capsule lies on the ground when ripe and does not dehisce. Iridaceae was not mentioned as a family with berry-like fruits (Rasmussen et al., 2006; Thadeo et al., 2015), but we can denote the capsule is a long-time fleshy, lately desiccates and has delayed lignification of the endocarp. This can be caused by the hydrophilous habitats of the species.

Conclusions

The structure of the fruiting ovary in *Iris pseudacorus* is comparable to the ovary of other *Iris* species. Our investigation confirmed that the vertical zonality, placentation, and vascular system of the gynoecium in *Iris* could be estimated correctly in the fruiting stage because the structural components of the ovary, which developed at the pre-anthetic phase, persist in the fruit.

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Мікроморфологія та анатомія плоду *Iris pseudacorus* L.

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Ґрунтуючись на уявленнях про те, що квітка і плід є цілісною еволюціонуючою структурою, ми спробували з’ясувати особливості будови квітки, які проявляються у структурі плоду на прикладі *Iris pseudacorus*, широко поширеного в Україні прибережного виду. Ми мали намір порівняти результати з іншими видами *Iris*, дослідженими раніше, і виявити стабільність мікроморфологічних ознак внутрішньої будови плоду. Для цього дослідження ми вивчали екзоморфологічні та мікроморфологічні особливості зав’язі плоду, використовуючи модель вертикальної зональності гінецею, васкулярну анатомію та анатомію оплодня. У зав'язі *I. pseudacorus* на стадії плоду ми виявили три вертикальні зони: коротку синасцидіатну, довгу симплікатну зону з насінинами, розміщеними однорядно, та гемісимплікатну зону у носику плоду. Провідна система зав'язі складається з дорзальних, септальних і вентральних жилок. Кожна з трьох дорзальних жилок поділяється радіально на слід зовнішнього листочка оцвітини, слід тичинки і дорзальний пучок плодолистка. Кожна септальна жилка поділяється тангентально на три пучки сліду внутрішнього листочка оцвітини. Парні вентральні жилки входять у зав'язь знизу і живлять насінні зачатки і насінини. Екзокарпій складається з багатокутних клітин з потовщеними целюлозними стінками. Ендокарпій однорядний, нездерев'янілий, складається з прозенхімних клітин, витягнутих горизонтально. В паренхімному мезокарпії виявлено велику кількість секреторних канальців з танінoподібним вмістом. Розкривання плоду на три стулки здійснюється завдяки дорзальним та вентральним щілинам. Дорзальні щілини формуються вздовж дорзальних борозенок і з'являються завдяки дрібно-клітинній тканині навколо дорзальної жилки. Наявність вентральних швів плодолистків у симплікатній зоні зав'язі забезпечує вентральне розкривання плоду. Структура плоду *I. pseudacorus* подібна на структуру плодів інших видів роду *Iris*. Наше дослідження підтверджує, що вертикальну зональність гінецею, плацентацію та провідну систему гінецею в роді *Iris* можна належним чином проаналізувати на стадії плодоношення, оскільки компоненти будови зав'язі, які формуються на пре-антетичній стадії, зберігаються у плоді.

Ключові слова: *Iris*, васкулярна анатомія, симплікатна зона, оплодень, зав'язь плоду