

Regulatory Mechanisms in Biosystems

ISSN 2519-8521 (Print)
ISSN 2520-2588 (Online)
Regul. Mech. Biosyst.,
2021, 12(2), 192–198
doi: 10.15421/022127

Micromorphology and anatomy of the flower of *Zephyranthes candida* (Amaryllidaceae)

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Article info

Received 27.03.2021

Received in revised form
01.05.2021

Accepted 02.05.2021

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Fishchuk, O. S. (2021). Micromorphology and anatomy of the flower of *Zephyranthes candida* (Amaryllidaceae). *Regulatory Mechanisms in Biosystems*, 12(2), 192–198. doi:10.15421/022127

The use of morphological features of flowers in the taxonomy of plants is becoming increasingly important. The structure of the *Zephyranthes candida* (Lindl.) Herb. flowers on permanent cross-sectional and longitudinal sections was studied using a light microscope. The genus *Zephyranthes* belongs to the subtribe Hippeastrinae Walp. tribe Hippeastreae Sweet., family Amaryllidaceae s.l. Microscopic studies of the flower are considered as a tool to identify hitherto unknown structural adaptations of plants to specialized pollination methods and to elucidate the first stages of fruit morphogenesis, as many features of the fruit appear at the flower stage. The morphometric parameters, morphology, anatomy, and vascular anatomy of the ovary were described by using the flower's transverse sections. Ten flowers of *Z. candida* were sectioned using standard methods of Paraplast embedding and serial sectioning at 20 µm thickness. Sections were stained with Safranin and Astra Blau and mounted in Eukitt. It was found that in the studied species the tepals have multi-bundle traces of 10–12 leading bundles. We consider the gynoecium of the studied species to be eusincarpous. The vascular system of the inferior ovary consists of three dorsal and three septal bundles, paired ventral bundles of carpels, which form ovule traces. For the first time, the presence of the following gynoecium zones was detected: a synascidiate structural zone with a height of about 360 µm and a fertile symplicate structural zone with a height of about 1560 µm and a hemisymplicate zone of 480 µm. Septal nectaries appear in the hemisymplicate zone and open with nectary split at the base of the style, the total height of the septal nectary is 760 µm. The ovary roof is 280 µm. Bifurcated dorsal and septal bundles of carpels have been identified, which can be considered as adaptations of the early stages of fruit morphogenesis to opening. Anatomical features of the ovary of *Z. candida* are numerous vascular bundles in the pericarpium, non-lignified endocarp at the flower stage, we consider as adaptations to the formation of juicy fruit. New data on the anatomical structure of the flower are a significant addition to the information on antecological and post-anthetic features of the studied species. Also, these data can be used in the construction of parsimony branches of the family Amaryllidaceae.

Keywords: flower anatomy; septal nectary; ovary; gynoecium; vascular bundle; vertical zonality; flower morphology.

Introduction

Molecular taxonomy of monocotyledonous plants is based solely on molecular data, occasionally morphological features of a flower are used to construct taxonomic systems. And such important features as the presence and height of the vertical ovary zones, the number of ovules in the locule, the features of vascular anatomy of the flower and the structure of septal nectaries should be included in the construction of phylogenetic trees. The integration of molecular phylogenetics data and evolutionary comparative morphology of a flower is a promising direction for the construction of a modern evolutionary system of orders, families, subfamilies and genera. The study of micromorphology and vascular anatomy of monocotyledonous flowers is a modern direction in the study of evolutionary morphology (Nuraliev & Sokoloff, 2014; Odintsova & Fishchuk, 2017). Molecular-phylogenetic reconstructions of the family Amaryllidaceae J. St.-Hil. has been carried out by many scientists Meerow et al. (2006), Chase et al. (2009), García et al. (2019).

The objects of our study were selected *Zephyranthes candida*, which is widely grown as an ornamental flowering plant. Genus *Zephyranthes* Herb. belongs to the subtribe Hippeastrinae Walp. tribes Hippeastreae Sweet., subfamily Amaryllidoideae s. s., family Amaryllidaceae (Chase et al., 2009; Takhtajan, 2009; Chase et al., 2016). Data from the molecular taxonomy of the studied genera confirm the monophilia of the tribe (Lledó et al., 2004). The genus *Zephyranthes* includes about 70 herbaceous species of small-bulb perennials that are common in the subtropical and tropi-

cal regions of America, the mountains of Mexico, the sandy plateaus of Chile, and Southern Africa (Takhtajan, 2009). Characteristic features of the genus are hollow scape, terete, rarely retained entirely inside the bulb, single-flowered, spathe bracts fused and tubular below the middle (Meerow & Snijman, 1998).

The study of alkaloids in members of the genus *Zephyranthes* is relevant (Centeno-Betanzos et al., 2021; Kohelová et al., 2021), in particular in *Z. candida* (Zhan et al., 2016; Zhan et al., 2017; Murphy et al., 2020), flavans with potential anti-inflammatory activities from *Z. candida* (Zhan et al., 2016; Nguyen et al., 2020), chlorotic ringspot virus infecting *Z. candida* in China (Wu & Liu, 2017), the endosperm development and the variations of structures of embryo sacs (Chengqi, 2019).

It is proved that the embryo sac development in *Z. candida* follows the *Polygonum* type. The structure of the mature embryo sac in *Z. candida* is described and the behaviours of the synergids, the central cell and the antipodal cells are discussed (Ao et al., 20020). Mass propagation through direct and indirect organogenesis in three species of genus *Zephyranthes* and ploidy assessment of regenerants through flow cytometry were studied (Syed et al., 2021). Effects of leaf area index and degree of canopy cover of green turf and ground cover plants on rainwater interception in *Z. candida* was examined by Zhang et al. (2018). New geophytes for Tunisian and North African alien flora and among them *Z. candida* have been studied by Mokni et al. (2020). Karyological investigation on three *Zephyranthes* species and its taxonomic significance was described by Bangladesh researchers (Dash et al., 2020). Taxonomy and reproductive

biology of the genus *Zephyranthes* in Bangladesh were studied (Afroz et al., 2018). Phytochemistry and pharmacology of genus *Zephyranthes* were investigated by Katoch & Singh (2015) and pharmacological properties by Francisco et al. (2017). A new species of *Zephyranthes* (Amaryllidaceae) from Mexico has been described by American and Mexican scientists (Spurrier et al., 2015). Taxonomic novelties in Southern Brazilian Amaryllidaceae were studied (Büncker & Bastian, 2018). Genetic structure of *Zephyranthes fosteri* was described by Torres-Morán et al. (2019). Thus, the issues of reproductive biology, taxonomy and pharmacology of *Z. candida* attract considerable attention from modern researchers, but the anatomy and morphology of the flower, which are important for the analysis of pollination methods and post-anthesis morphogenesis (formation and fruit opening) remain unexplored.

The aim of our study was to elucidate the features of flower morphology and internal structure of the gynoecium, the structure of septal nectaries and to identify the vertical zonality of the gynoecium in members of the family Amaryllidaceae.

Material and methods

Plant material was collected in the A. V. Fomin Botanical Garden of the Taras Shevchenko National University of Kyiv and fixed in 70% alcohol. Ten *Z. candida* flower buds were dehydrated in t-butanol series (20%, 30%, 50%, 70 %, 100% – 2 h each, the last one 24 h) and stored in 100% t-butanol and Paraplast in the ratio 1:1. Infiltration was performed in Paraplast (Merck®) according to manufacturer's instructions (Barykina et al., 2004). Transverse and longitudinal sections of 20 µm thickness were obtained with manual rotary microtome (MPS-2 (USSR)) and stained in Safranin (Sigma-Aldrich®) and Astra Blau (Merck®). Slides were mounted in 'Eukitt®' (Sigma-Aldrich®) and images were obtained with an AMSCOPE 10MP digital camera attached to an AMSCOPE T490B-10M (USA) microscope.

For the morphological analysis, measurements were made on at least 15 fresh flowers. We used the concept of vertical zonality of the gynoecium by Leinfellner (1950) to analyze the gynoecium's internal structure, which considers only the congenital fusion of the carpels. According to this concept, with the carpels' growth, the congenital multilocular synascidiate, unilocular symplicate, transitional hemisymplicate, and asympicate (apocarpous) zones could be formed in the syncarpous gynoecium. In the conditions of incomplete fusion of carpels, a hemisymplicate gynoecium with hemisymplicate, hemisymplicate, and asympicate zones form only in their outer part; later, the method was elaborated for monocots (Odintsova, 2013). The height of the zones of the gynoecium was measured according to the number of cross-sections.

Results

The flower of *Z. candida* is up to 6.6–7.0 cm long, slightly zygomorphic, white. The scape is 24–27 cm long and 0.4 cm in diameter, flowers are solitary. The bracts are two conical fused into one, forming a two-keel structure about 2.5 cm long, 1.2 cm wide and 0.8 cm at the base, leathery, brown. The pedicel is up to 0.8 cm long, about 0.3 cm in diameter (Fig. 1a). The perigonium is simple, linear. The flower tube is funnel-shaped, about 0.3 cm long, 0.5 cm in diameter (Fig. 1f). The inner tepals are shorter than the outer (Fig. 5a). The outer tepals are 3.5, 3.6, 3.7 cm long and 1.0–1.1 cm wide, and the inner tepals are 3.2, 3.4, 3.4 cm long and 1.0 cm width (Fig. 1h).

The androecium in *Z. candida* consists of 6 stamens that have grown into a flower tube. The length of the inner stamens is 1.1 cm, and the length of the outer stamens is 3.0 cm. The filaments of the outer circle are 0.7–0.9 cm long, and the filaments of the inner circle are 1.0–1.1 cm and 0.05 cm in diameter (Fig. 1h). The anthers are bent at the apex, intrinsic, dorsifixed (Fig. 5b). The anthers of the outer stamens are 0.6 cm long and inner stamens 0.8 cm long, 0.1 cm in diameter. But the filaments attach to the anther in the outer and inner stamens below the middle (Fig. 1g).

The gynoecium of *Z. candida* is represented by three fused carpels. The ovary is ovoid, bright green 0.5 cm high and 0.4 cm in diameter (Fig. 1c, d), which turns into a slightly zygomorphic, green at the base, and above the white, s-shaped style 1.6 and 0.1 cm in diameter. The stigma is

massive, bright green with lobes 0.2 cm long and 0.2 cm in diameter (Fig. 5b). The fruit is a berry-like capsule with flattened black seeds.

In *Z. candida* in the upper part of the peduncle, at the base of the flower tube, in the filaments and in the ovary wall there are idioblasts with cellular inclusions – raphids (Fig. 3). They are absent in the tops of the free tepals, the connective and the style. The stomata are presented on the surface of the inferior ovary wall (Fig. 3). The protoplast of epidermal cells contains chloroplasts. Epidermal cells are elongated, prosenchymal, often straight-walled. The upper membrane of the ovary, in contact with the environment is thickened and cutinized. The outer layers of cutin form a very stable protective water-repellent lamina – the cuticle. Its thickness depends on lighting and water supply. Uneven layering of cutin forms a species-specific pattern – a bumpy cuticle in *Z. candida*. The studied species is characterized by the presence of anomocytic morphological type of stomata complexes. This means that the cells around the closing cells do not differ from the basal ones. A stoma in *Z. candida* is a hole in the epidermis, which is the main component of the stomata system and includes: closing cells, slit-like intercellular space – stomatal slit, as well as adjacent epidermal cells or specialized by-cells (Fig. 3a). Closing cells are paired bean-shaped, oriented parallel to the airway; contain photosynthetic chloroplasts with starch grains and numerous mitochondria. The membranes are unevenly thickened: dorsal, adjacent to the side cells, thin, easily stretched; abdominal, facing the slit, thickened, often their outer and inner parts form the characteristic cuticular spurs or beaks that cover the cavities – the outer (front) and inner (rear) courtyards of the respiratory slit (Fig. 3b). Depending on the state of the organism and external factors, the closing cells are stretched or contracted in the tangential direction and control the size of the airway. The lateral cells of the stomata are functionally and morphologically different from the basal ones (Fig. 3c). The wall of the inferior ovary is formed of about 20 layers of cells. The inner tepals consist of 15 layers of cells, the outer tepals consist of 17 layers of cells.

In the gynoecium of *Z. candida* we distinguish the following structural zones: the synascidiate structural zone, about 360 µm high (Fig. 1c) and the fertile symplicate structural zone (Fig. 1d), which is about 1560 µm high, and the hemisymplicate zone 480 µm (Fig. 1e). The roof of the ovary is 280 µm (Fig. 4b). Septal nectaries appear in the hemisymplicate zone (Fig. 2d) and open with nectary slits at the base of the style (Fig. 1f), the total height of the septal nectary is 760 µm. In the transversal sections, the septal nectary looks like three slits ("lilioid" septal nectary). The nectary epidermis is glandular on the whole of the nectary surface. In its lower portion (in hemisymplicate zone), it has a common epidermis, three nectary cavities are united with the non-secretory epidermis in the center of the ovary (Fig. 2d). The septal nectary comprises two structures: the septal nectary body and the nectary split where nectar can be released outside. The septal nectary body reaches half of the ovarian radius; in the ovary roof the septal body becomes slightly undulate. Narrow septal grooves on the ovary surface are connected with the nectary splits at the base of the style (Fig. 4b).

The septal nectaries in *Z. candida* are relatively small (Fig. 2d), consisting of isodiametrical cells that are slightly elongated in parallel to the surface of the nectary and very short cells of lobe-like shape, perpendicular to it, with protruding outer walls. Vascular bundles pass in the middle or in the immediate vicinity of the nectary, they direct the lateral branches directly into the nectary parenchyma, where they end blindly. It should be noted that these vascular bundles are mostly found only in the most developed central part of the nectary, but are absent at its edges. We consider this is specialization, the vascular bundles of septal nectaries that supplied the nectary cells. The vascular bundle ends in the nectary parenchyma, containing the xylem located outside.

The peduncle in *Z. candida* at the base contains 12 vascular bundles (Fig. 1a), which are reorganized above into a vascular cylinder, at the level of the receptacle from which depart septal vascular bundles and dorsal vascular bundles and above it divided on tepal traces (Fig. 1b). Dorsal and septal vascular bundles are two-bundle. In the center there are 12 vascular bundles – roots of a ventral complex (Fig. 1c). Higher, these vascular bundles are reorganized in pairs and supplied the ovules – the ventral bundles of carpels (Fig. 1d). There are many ovules in each locule (Fig. 4a). On a cross-section in each locule are two ovules, the trace of ovule is one-bundle.

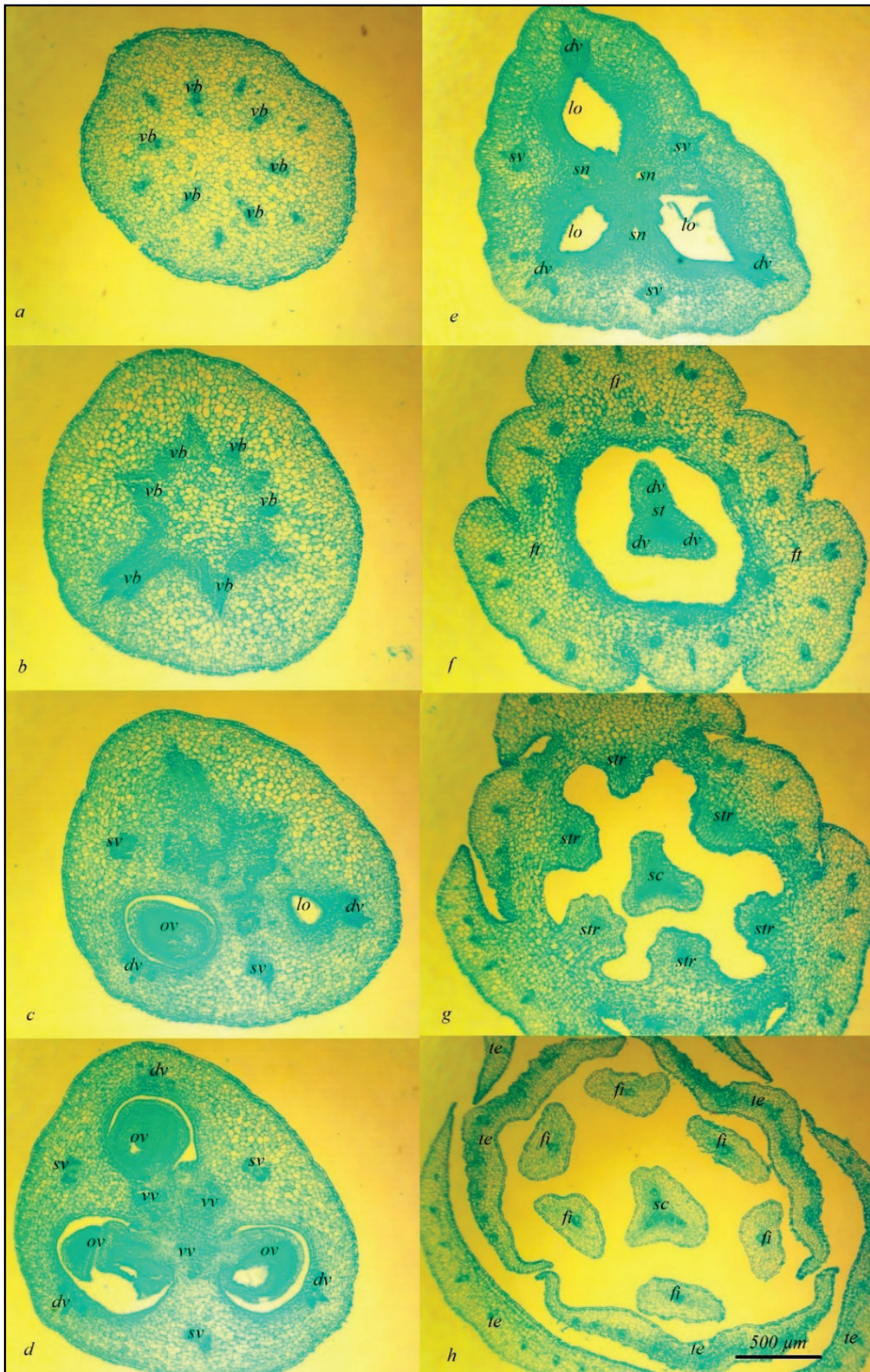


Fig. 1. Ascending series of transverse sections of the flower *Zephyranthes candida*: *a-b* – pedicel; *c-e* – inferior ovary; *c* – synasciadiate zone, *d* – symplicate zone; *e* – hemisymphic zone; *f* – flower tube and style; *g* – flower tube ending; *h* – free tepals, filaments and style; *dv* – dorsal vein; *fi* – filament; *lo* – ovary locule; *ov* – ovule; *str* – stamen trace; *sc* – style channel; *sv* – septal vein; *st* – style; *te* – tepal; *vb* – vascular bundle; *wv* – ventral vein

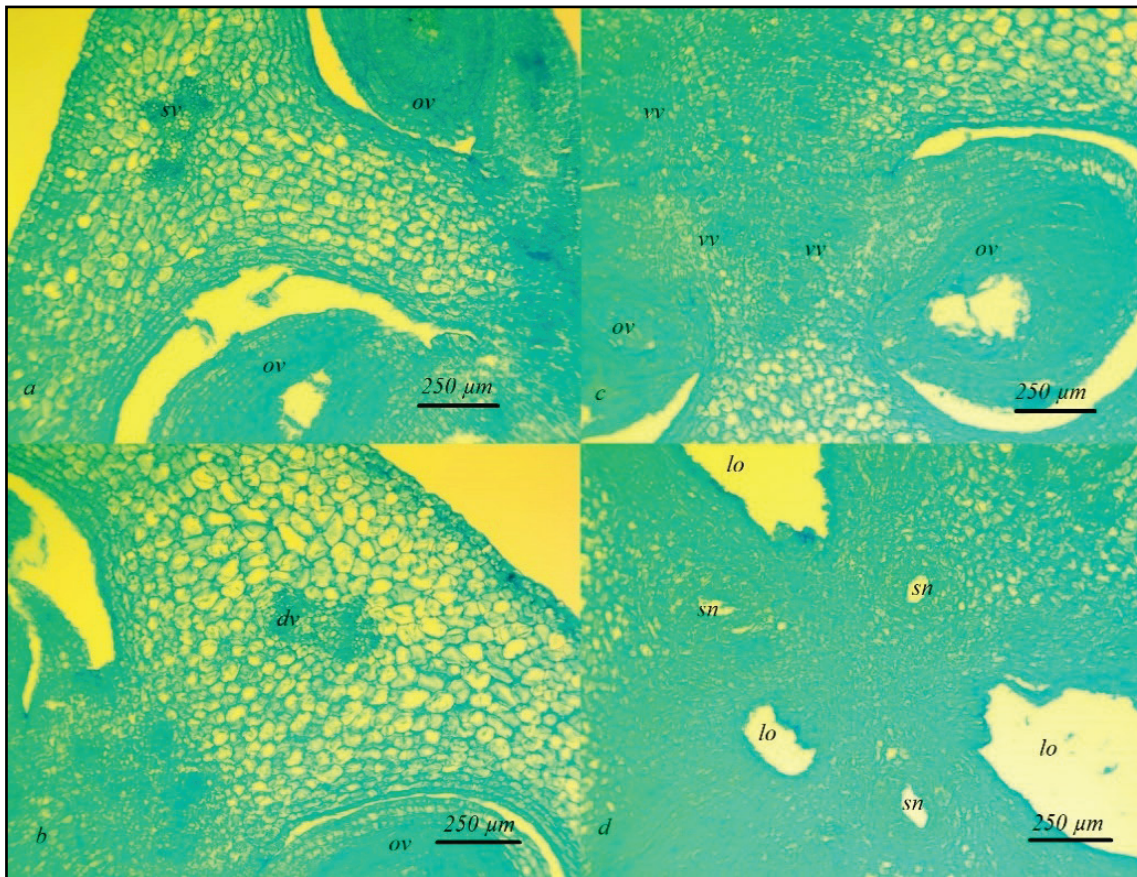


Fig. 2. Floral parts of *Zephyranthes candida*: *a* – ovary wall with septa attached, septal vascular bundle and additional bundles in wall aerial parenchyma; *b* – ovary wall in the median part of the carpel, dorsal vein composed of two bundles and additional veins are visible; *c* – central part of the ovary, ventral vascular bundles are visible; *d* – central part of the ovary with septal nectaries; *dv* – dorsal vein; *ov* – ovule; *lo* – locule; *sv* – septal vein; *vv* – ventral vein

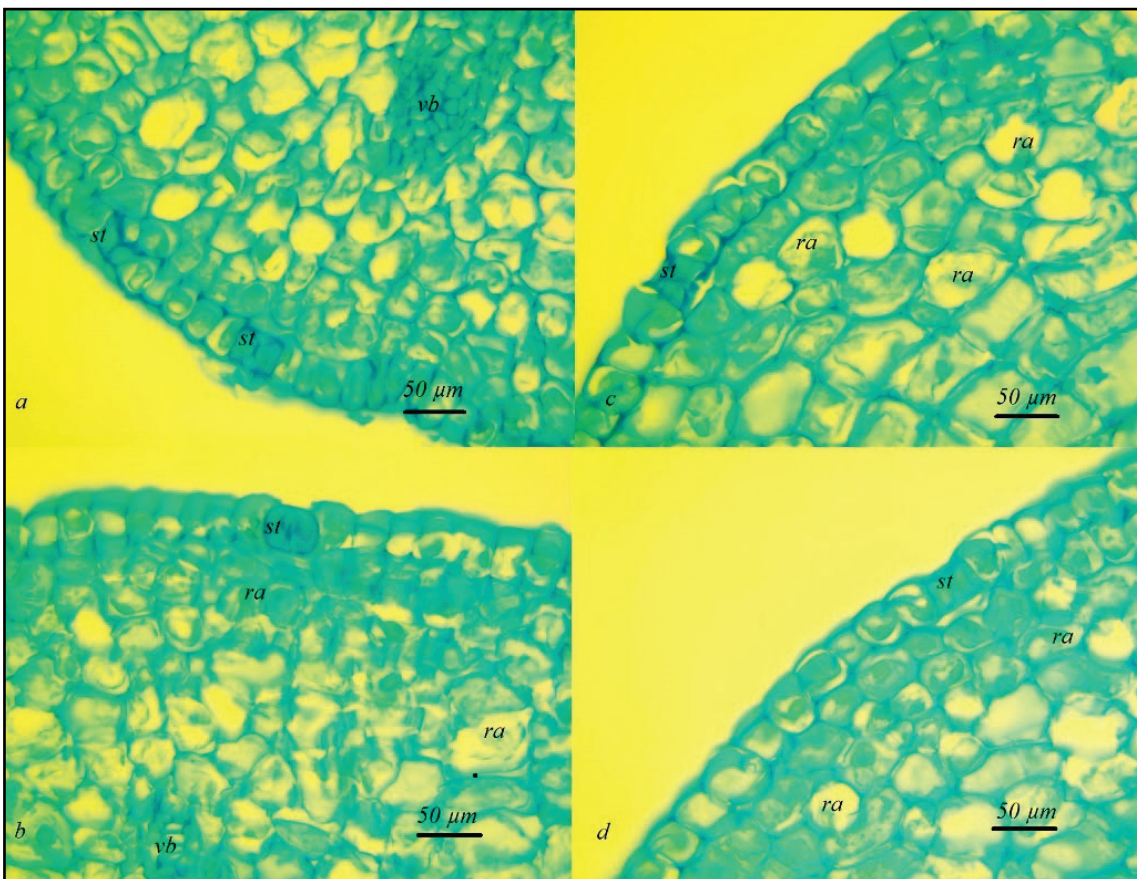


Fig. 3. Raphids and stomata in the distal parenchyma of the ovary wall of *Zephyranthes candida*: *ra* – raphids; *st* – stomata; *vb* – vascular bundle

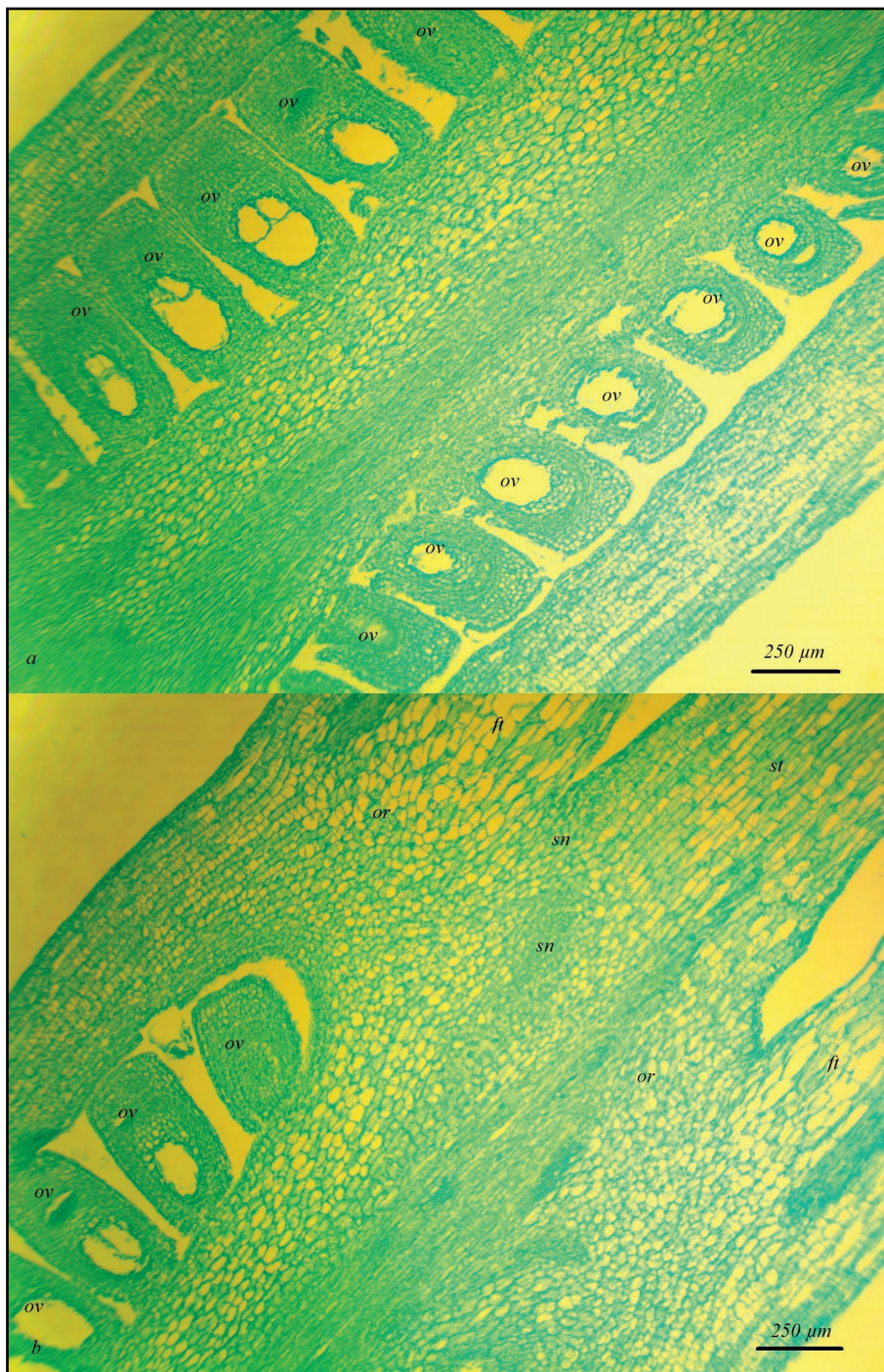


Fig. 4. Longitudinal sections of the ovary of *Zephyranthes candida*:
 ft – flower tube; ov – ovule; or – ovary roof; sn – septal nectary; st – style; on b septal nectary is visible

Above the locules, the ventral vascular bundles of the carpel, in the septa merge with the dorsal vascular bundles and form a dorsal vein (Fig. 1f). At the level of the flower tube there is a branching of the vascular bundles, as traces of the outer tepals and inner tepals (Fig. 1f, g). Traces of outer tepals have 10 vascular bundles, traces of inner tepals have 12 vascular bundles. Above, vascular bundles of the inner tepals are vascularized to form a continuous vascular tissue (Fig. 1h). Traces of stamens are branching off from traces of tepals, the trace of the stamen is single-bundle (Fig. 5b).

Discussion

The gynoecium consists of three united carpels in *Z. candida*, the style is slender, with punctiform, capitate, or 3-lobed stigma, ovary 3-locular, with from several to many ovules per locule. Nectaries are septal or

(Galantheae) perigonal (secreted from the distal part of the inner perianth segments). Ovules are anatropous or hemitropous, bitegmic or rarely (*Amaryllis* and *Nerine*) unitegmic or (*Crinum*) ategmic, crassinucellate or rarely (*Crinum*, *Narcissus*, *Zephyranthes*) tenuinucellate, mostly with parietal cell. Female gametophyte of *Polygonum* type, rarely of *Adoxa*-type (Takhtajan, 2009). Flowers are (sub)erect, actinomorphic, the tube short or long. Stamens are usually biseriate in length. The style is trifid or obscurely 3-lobed. Capsule papery with numerous or few, black flattened or compressed, D-shaped or wedge-shaped seeds (Meerow & Snijman, 1998).

Three species of *Zephyranthes* Herb. viz. *Z. candida*, *Z. carinata* Herb. and *Z. tubispatha* Herb. were cytotaxonomically studied to characterize and elucidate probable evolutionary relationship among them. These species were found to possess different chromosome number and karyotype formula (Dash et al., 2020). Megasporogenesis and megagametogenesis in *Z. candida* (Lindl.) Herb. (Amaryllidaceae) were

observed by means of conventional paraffin sections. The functional megaspore becomes a mononucleate embryo sac and develops through three subsequent mitotic divisions into a seven-celled/eight-nucleate embryo sac (Ao et al., 2016). The genus *Zephyranthes* Herb. is revised along with its pollination mechanism, seed germination and vegetative propagation. Detailed taxonomy of four *Zephyranthes* species occurring

in Bangladesh, namely, *Z. atamasco* (L.) Herb., *Z. candida*, *Z. carinata* and *Z. tubispatha* was studied with their updated nomenclature, important synonyms, phenology, specimens examined, habitat, distribution, economic value and mode of propagation. Pollination investigation reveals that all studied species of *Zephyranthes* are self-pollinated (Afroz et al., 2018).

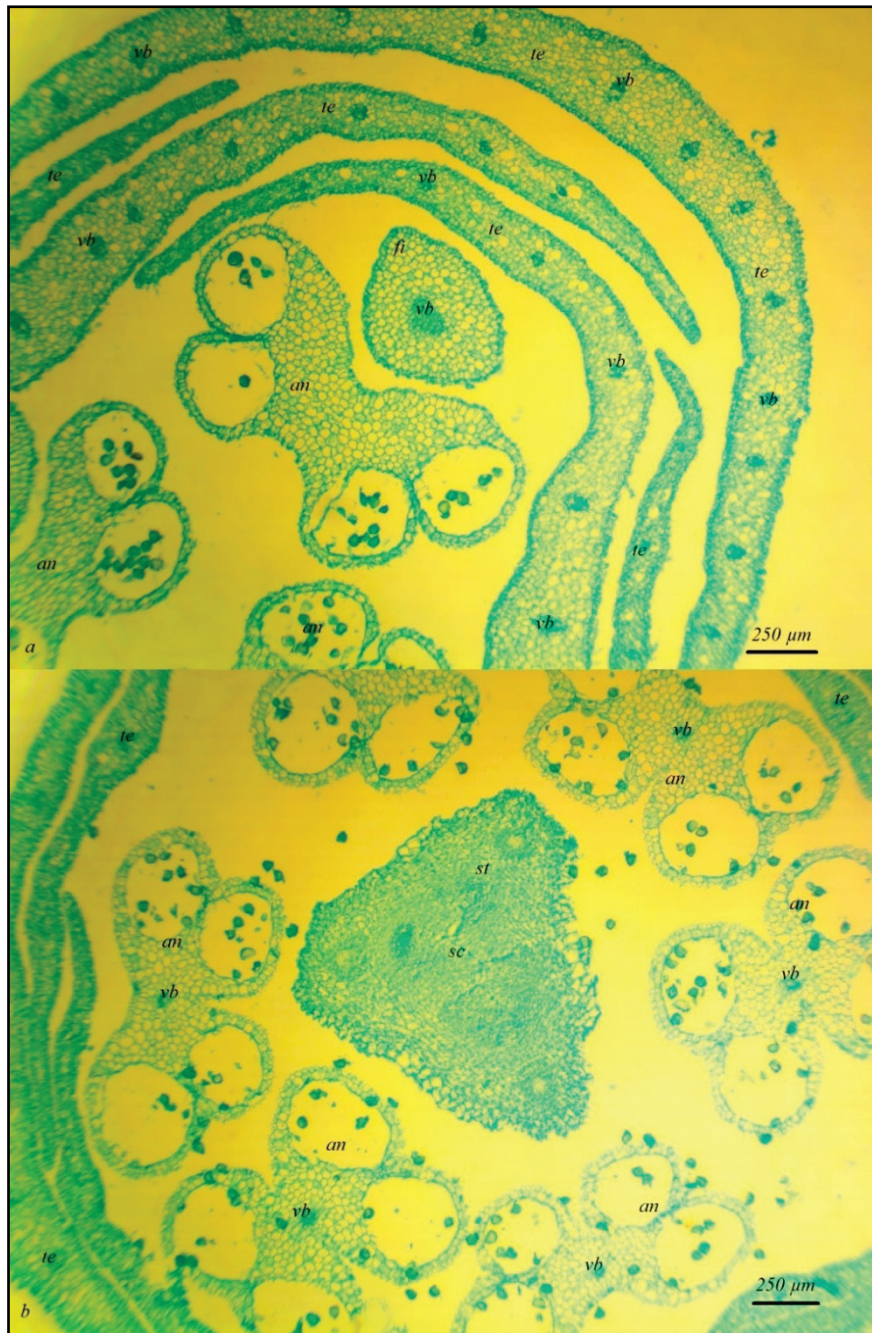


Fig. 5. Ascending series of transversal sections of the perigonium *Zephyranthes candida*: a – free tepals, filament and anthers; b – free tepals, anthers and style; an – anthers; fi – filament; sc – style channel; sv – septal vein; st – style; te – tepal; vb – vascular bundle

According to Daumann (1970), the genus *Zephyranthes* has an internal septal nectary. He established the presence of epidermal septal nectaries in *Z. candida*. In general, the family Amaryllidaceae is characterized by the presence of septal nectaries (Daumann, 1970; Meerow & Snijman, 1998; Takhtajan, 2009).

For monocotyledonous plants, common patterns of nectarines have been established – the absence of nectary flowers disks in superior ovary, nectary secretion through the cuticle rather than through nectary stomata, significant distribution of septal nectaries among lilioid monocotyledons and their frequent flowers from nectar-flower to pollen-flower (Smets et al., 2000). For the family Amaryllidaceae, central-angular placentation

is indicated (Meerow & Snijman, 1998). We found three vertical zones in the ovary of the studied species: a synascidiate structural zone (360 μm), a fertile symplicate structural zone (1560 μm) and a hemisymplicate zone (480 μm). Septal nectaries appear in the hemisymplicate zone and open with a nectary split at the base of the style, the total height of the septal nectary is 760 μm. The ovary roof is 280 μm. We consider the gynoecium of the studied species to be eusyncarpous in the sense of Leinfellner (1950), with symplicate and hemisymplicate fertile zones of the ovary. Shamrov (2010) came to similar conclusions in studying the development of the gynoecium in species of the genus *Allium*, which now belongs to the family Amaryllidaceae.

We found new features of the anatomical structure of the flower of *Z. candida*, the presence of raphids and stomata in the peduncle, at the base of the flower tube, in the stamens and in the wall of the inferior ovary and stomata in the wall of the ovary and a double trace of dorsal and septal vascular bundles, a large number of vascular bundles in the tepals. A double dorsal vein was also found by us in *Galanthus nivalis* and *Leucojum vernum* (Fishchuk & Odintsova, 2020). In *Hippeastrum striatum* traces of dorsal and septal bundles of the carpel are two-bundle too (Fishchuk, 2021).

Conclusion

The results of our research allowed us to deepen the knowledge about the micromorphological and anatomical features of the flower of *Z. candida*, in particular, the anatomical structure of the tepals, vertical zonality and type of gynoecium were specified. The anatomical structure of the ovary of *Z. candida* is characterized by a berry-like capsule with varying degrees lignified tissues reduction in the pericarpium. The juicy nature of the fruit is supported by the presence of numerous vascular bundles in the pericarpium, multi-bundle traces of tepals. The ovary revealed features of the early stages of fruit morphogenesis and adaptation to disclosure – differentiation of mesocarp and endocarp cells, bifurcated dorsal and septal bundles of carpels. We assume that the listed features of the flower structure are related to the offer of pollen as a reward to the pollinator. Because the ovary is the structural basis of the fruit, histological differentiation of the ovary wall reflects the features of the subsequent morphogenesis of the fruit. Also, the studied features can be used in taxonomy.

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