

## Flower and fruit micromorphology and anatomy in *Hippeastrum vittatum* (L'Hér.) Herb. (Amaryllidaceae)

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**Summary:** *Hippeastrum vittatum* is a member of the tribe Hippeastreae, subfamily Amaryllidoideae, Amaryllidaceae. Genera of the tribe are mostly distributed in South America and are often cultivated as ornamentals. The systematics of the tribe is equivocal, because of reticulated evolutionary history. New diagnostic characters are very desirable for a deeper understanding of the relations within the tribe. The flower and fruit micromorphology has been poorly studied in the Hippeastreae, that is why we examined the flower in *Hippeastrum vittatum* at preanthetic and postanthetic phases. The ovary of *Hippeastrum vittatum* contains symplicate and hemisymplicate vertical zones. The asymplicate zone with postgenitally connected carpels composes a style and a stigma. The ovary is trilocular, because of thick septa, which meet each other in the center and which are postgenitally connated. Ovules occur along carpel margins from the bottom to the top of each locule. Septal nectaries appear in the hemisymplicate zone and open at the base of the style by narrow tubular nectary channels. From the pedicel, many large vascular bundles enter the receptacle, arranged in a zonocyclic pattern. There are six compound veins in the ovary wall, three dorsal veins and three septal veins. Paired ventral carpel bundles arise near the locule base from the ring of vascular bundles of the receptacle. Ovule traces branch from the ventral bundles. In the ovary roof, the dorsal veins branch proximally into a dorsal carpel bundle, entering the style, and in the floral tube dorsal veins give rise to the outer stamen trace and the outer tepal trace. The septal veins branch into the inner stamen trace and inner tepal trace. Stamen traces are one-bundled, the outer tepal trace divides into 32 bundles and the inner tepal trace divides into 26 bundles. During fruit development, the ovary grows significantly in diameter and becomes spherical. The fruit wall is parenchymatous, small-celled. The inner ovary epidermis (endocarp) becomes lignified. Fruit dehiscence is defined as dorsiventral, perfect. The centrifugal development of dorsal slits in the fruit wall parenchyma was observed. The gynoecium structure was compared with the other studied Amaryllidoideae.

**Keywords:** *Hippeastrum*, Amaryllidoideae, Hippeastreae, gynoecium, flower, fruit, septal nectary, endocarp, fruit dehiscence

Amaryllidaceae is a large family of Asparagales that is now interpreted as being composed of three subfamilies, former recognized as separate families: Agapanthoideae, Allioideae and Amaryllidoideae (CHASE et al. 2016). The last subfamily is the largest and characterized by a typically bulbous life form, unique alkaloidal components, large epigynous flowers and a hollow style (MEEROW & SNIJMAN 1998). Fifteen tribes were recognized in Amaryllidoideae, strongly congruent with geographic distribution (MEEROW & SNIJMAN 1998). The American genera of Amaryllidoideae form two clades, the 'Hippeastroid'-clade with diploid members and extra-Andean distribution and the Andean tetraploid-derived clade (MEEROW et al. 2000, 2006). The 'Hippeastroid'-clade encompasses tribes Griffinieae and Hippeastreae, whereas the Andean tetraploid-derived clade is composed of the tribes Clinantheae, Eucharideae, Eustephieae and Hymenocallideae. Hippeastreae comprises 10–13 genera and about 180 species. The genera of Hippeastreae are often cultivated as ornamentals. Two subtribes were recognized within the tribe, Traubiinae with five genera and Hippeastrinae with 8 genera, without any diagnostic

morphological character (GARCIA et al. 2014, 2019). Reticulate evolution is supposed to be very common in the tribe, resulting in ambiguous views of the systematics of the tribe. Flower morphological characters are highly homoplastic in many clades of Amaryllidoideae, as it was revealed in the phylogenetic analysis in the genus *Cyrtanthus* (SNIJMAN & MEEROV 2010). New diagnostic characters may be useful in understanding the relations within the tribe.

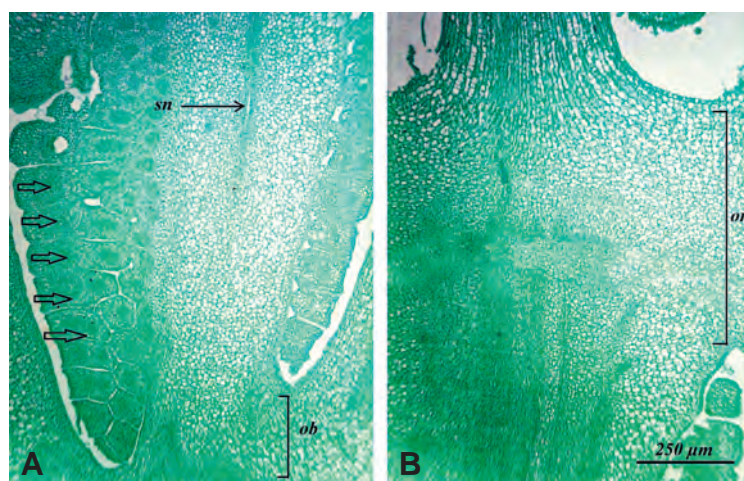
In Hippeastreae, the scape is usually hollow and the inflorescence 2–13 flowered. Flowers are zygomorphic and have a syntepalous funnel-formed perigonium. Stamens are usually declinate, free and not equal. Fruits are loculicidal capsules, seeds are flattened, winged or D-shaped with black phytomelaneous testa (MEEROW & SNIJMAN 1998). The flower and fruit micromorphology has been poorly studied in Hippeastreae, that is why we examined the flower in *Hippeastrum vittatum* at preanthetic and postanthetic phases.

We aimed to examine the structural zonality of the gynoecium with septal nectaries, vascular anatomy of the flower and fruit features in this member of the tribe Hippeastreae. The genus *Hippeastrum* Herb. comprises 50–60 species growing in Mexico, Argentina, Peru, eastern Brazil and Bolivia (MEEROV & SNIJMAN 2006). Roots of *Hippeastrum* are covered with velamen in the epiphytic species, scape is hollow, terete or slightly compressed, leaves are usually annual, sessile, wide. Hybridization is common among the species of *Hippeastrum* (MEEROV & SNIJMAN 1998). In *Hippeastrum*, paraperigonium occurs, composed of scales or fimbriae or a callose ring. *Hippeastrum vittatum* (L'Her.) Herb. has white tepals with dark rose streaks inside and grows mostly in sunny areas on rocky outcrops (DUTILH 2005). This species is native in western Bolivia to southern Brazil and northeast Argentina and introduced into the Dominican Republic, Haiti, Niue, Peru and the Venezuelan Antilles (POWO 2019).

Comparative flower and fruit morphology in some families of Asparagales was examined concerning the structure of septal nectaries and gynoecium zonality, as well as adaptations of the gynoecium and fruit for seed dispersal (ODINTSOVA et al. 2013; ODINTSOVA & FISHCHUK 2017; FISHCHUK & ODINTSOVA 2020; SKRYPEC & ODINTSOVA 2020). The concept of gynoecium vertical zonality by LEINFELLNER (1950) was used to analyze the internal structure of the gynoecium. According to this concept, in the eusyncarpous gynoecium several zones can be developed, namely: congenitally multilocular synascidiate zone, unilocular symplicate zone, transitional hemisymplicate zone and asymplicate (apocarpous) zone. If the fusion of carpels is incomplete, a hemisyncarpous gynoecium arises with hemisynascidiate, hemisymplicate and asymplicate zones. The approach of LEINFELLNER (1950) was somewhat elaborated for gynoecia of monocotyledons with septal nectaries by NOVIKOFF & ODINTSOVA (2008) and ODINTSOVA (2013). Fruit anatomy was analyzed according to BOBROV & ROMANOV (2019), fruit dehiscence was classified according to KADEN (1962).

## Materials and methods

Flowers, flower buds and fruits at different stages of development were collected in the A.V. Fomin Botanical Garden of the Taras Shevchenko National University of Kyiv, Ukraine in 2019–2021. Materials were fixed in 70% ethanol. For light microscope observations, flowers at the young preanthetic stage (with the ovary 5.2–5.5 mm long) were sectioned using standard methods of Paraplast embedding and serial sectioning at 20 µm thickness (BARYKINA et al. 2004). Sections were stained with Safranin and Astra Blau and mounted in Eukitt. The anatomical structure of



**Figure 1.** Preanthetic ovary of *Hippeastrum vittatum* in the tangential section. A – lower part; B – the upper part of the ovary. *ob* – ovary base; *or* – ovary roof; *sn* – septal nectary; *arrows* – ovules. Scale bar = 250  $\mu$ m (A, B).

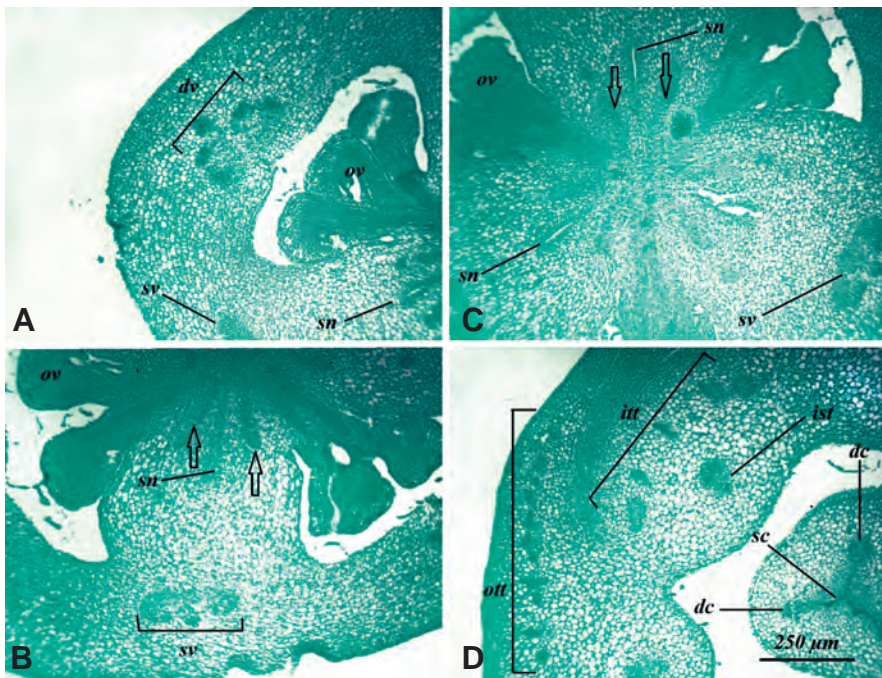
fruits was examined on transversal hand sections of the fixed materials made with a razor blade. Tissue lignification was determined using phloroglucinol reaction (BARYKINA et al. 2004). Digital photomicrographs were made using a microscope AmScope T490B-10M (USA) and microscope digital camera AmScope 10MP MU1000 (USA).

## Results

### Flower micromorphology

*Hippeastrum vittatum* flowers are 12–14 cm long, slightly zygomorphic, white, with red stripes. The scape is 29 cm long and 2.2 cm in diameter, there are 4 flowers per inflorescence. Bracts 2, cone-shaped, about 6.5–6.8 cm long, 1.8 cm wide and 2 cm at the base, leathery, light green. The pedicel is up to 1.3 cm long, about 0.6 cm in diameter. The flower tube is funnel-shaped, about 1.6 cm long, 0.9 cm in diameter. The outer tepals are 10.5–10.7 cm long and 5.5–5.6 cm wide, the inner tepals are 10.3–10.4 cm long and 3.5–4.3 cm wide. Filaments of all six stamens are dilated at the base, tapering to the apex, slightly unequal in length due to zygomorphy, outer stamens are 8.6–9.0 cm long, inner stamens are 8.7–8.8 cm long, filaments are 0.2 cm in diameter. Anthers are arcuate, introse, dorsifix, anthers of external stamens are 0.6 cm long, anthers of internal stamens are 0.55 cm long. Anthers attached to the filament at the middle height in the outer stamens and slightly above the middle height in the inner stamens. The inferior ovary is ovoid at anthesis, slightly triangular in section, 1.8 cm long and 0.6 cm in diameter. Style is subterminal, S-shaped, about 10 cm long and 0.15 cm in diameter, stigma lobes are 0.3 cm long.

The ovary is trilocular, with thick septa and thick ovary wall, base and roof (Figs 1; 2A–C). There are 42–63 ovules in each locule. Ovules are arranged in two rows along free carpel margins from the bottom to the top of each locule. In the examined preanthetic ovary, septa meet each other in the center and are postgenitally connated (Fig. 2C). In the ovary roof, the locules turn into tubular channels, entering the style (Fig. 3G,H). In the style of the preanthetic flower, a triradiate style channel occurs, covered by a small-celled secretory epidermis (Figs 2D; 3I,J; 4B,D). This channel provides a transmitting tract to the stigma surface.



**Figure 2.** Details of the floral structure of *Hippeastrum vittatum*. A – locule of the ovary; B – the septal region of the ovary; C – central region of the ovary; D – floral tube and style. *dc* – dorsal carpel bundle; *dv* – dorsal vein; *ist* – inner stamen trace; *itt* – inner tepal trace; *ott* – outer tepal trace; *ov* – ovule; *sc* – style channel; *sn* – septal nectary; *sv* – septal vein; *arrows* – ventral carpel bundles. Scale bar = 250 µm (A–D).

Near a quarter of the height of the locule, septal nectaries appear as three narrow cavities in the septa (Figs 1A; 2A–C; 3F,G). The nectaries are united by the postgenitally connated epidermis of carpels in the proximal part of the septa. The radial extension of nectaries is not large, about 150 µm in maximum.

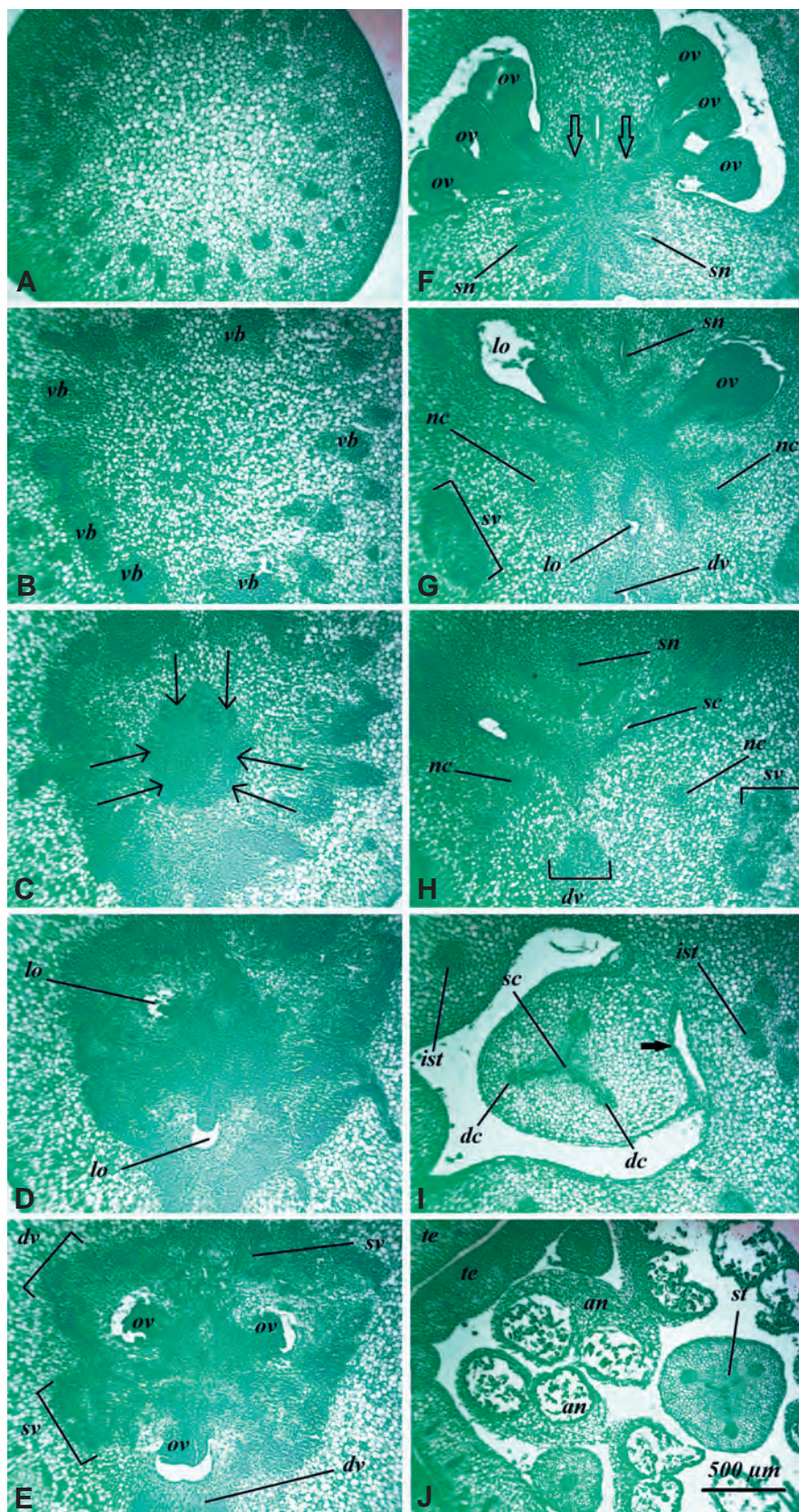
The secretory epidermis of the nectary slits is palisade, nectary parenchyma is not developed (Fig. 4C). In the ovary roof, septal nectaries turn into tubular nectary channels opening outside near the style base (Fig. 3I). Above the openings of the septal nectaries, carpels are united postgenitally up to the stigma.

### Flower anatomy

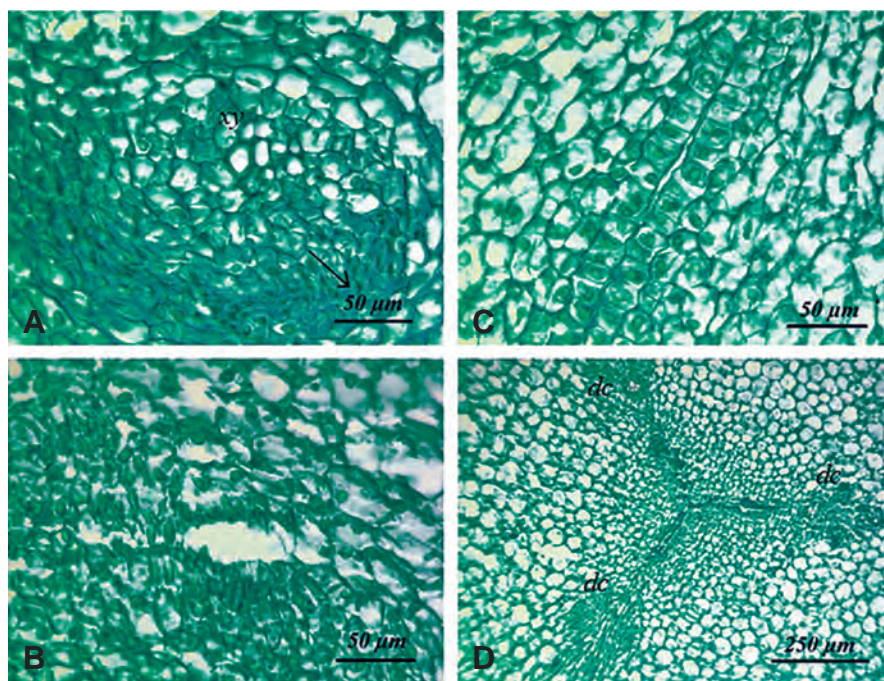
The floral parts at preanthetic and anthetic stages are fleshy, parenchymatous, composed of the solid undifferentiated parenchyma. There are numerous idioblasts with raphide inclusions in the upper part of the peduncle, receptacle, stamen filaments, ovary wall and free tepals. The raphides are absent in the connectives and style. The outer and inner epidermis of the ovary are small-celled and contain stomata. The parenchyma of the ovary wall is composed of approximately 30 cell layers, parenchyma of the septa of 40–50 cell layers. The cells of the parenchyma are slightly larger in the middle zone of the ovary wall (Fig. 2A,B).

**Figure 3.** Ascending series of transverse sections of the preanthetic flower of *Hippeastrum vittatum*. A, B – pedicel; C, D – receptacle; E–G – ovary locules; H – ovary roof; I – style base, J – free tepals and stamen. *an* – anther; *dc* – dorsal carpel bundle; *dv* – dorsal vein; *ist* – inner stamen trace; *lo* – ovary locule; *nc* – nectary channel; *ov* – ovule; *sc* – style channel; *st* – style; *sv* – septal vein; *te* – tepal; *vb* – the main ascending vascular bundle; ventral carpel bundles marked by arrows; black arrow – nectary channel exit to outside. Scale bars = 500 µm.









**Figure 4.** Secretory and vascular structures in the flower of *Hippeastrum vittatum*. A – inverted ventral carpel bundle (arrow points the direction towards the center of the flower); B – nectary channel in the ovary roof; C – septal nectary; D – tripartite style channel. *dc* – dorsal carpel bundle; *xy* – xylem. Scale bars = 50 µm (A–C); 250 µm (D).

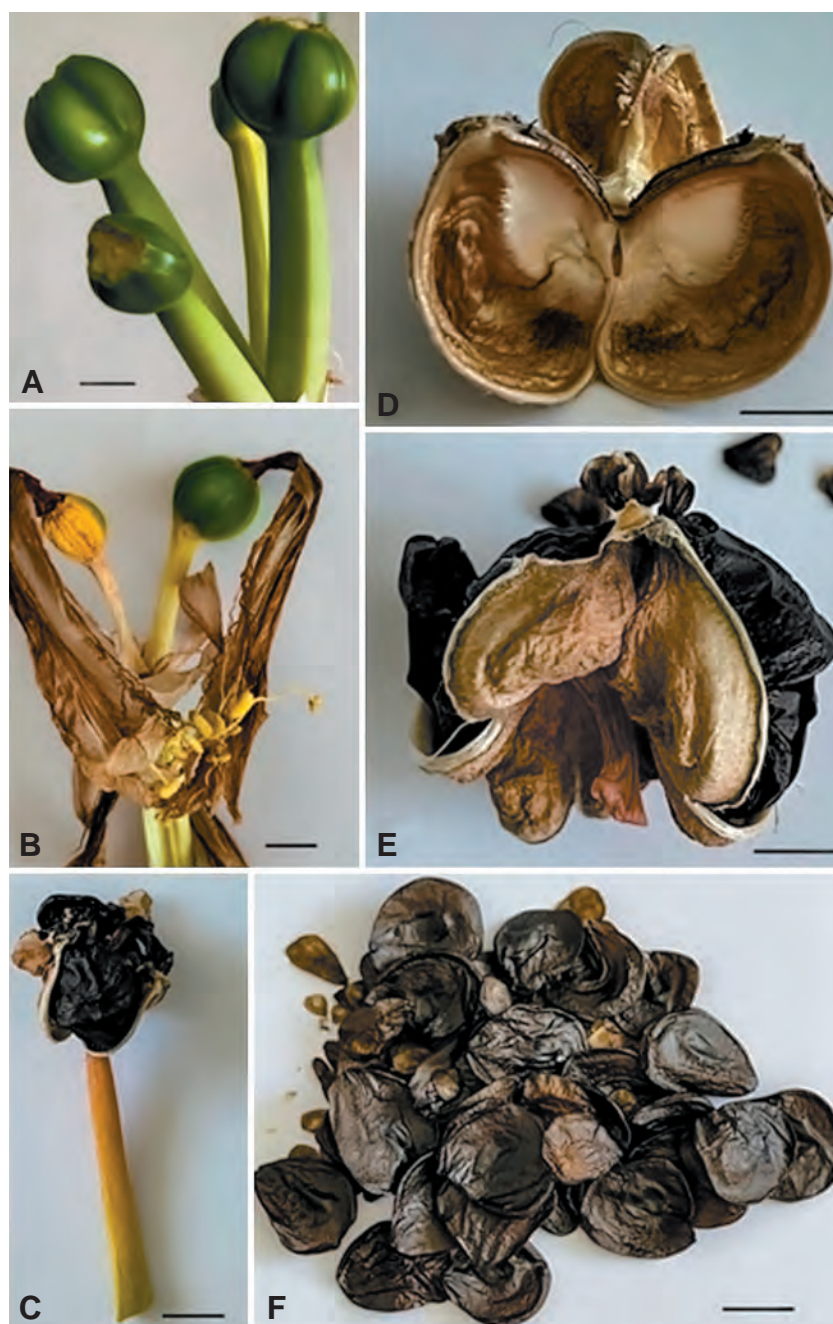
In the upper end of the pedicel of *Hippeastrum vittatum*, there are about 38 large ascending vascular bundles, arranged in zonocyclic pattern (Fig. 3A,B). In the receptacle, they are combined into a ring (Fig. 2C,D). Six vascular bundles branch from the ascending vascular bundles toward the center and form paired ventral carpel bundles (Fig. 3C). The xylem in the ventral carpel bundles is oriented outside (Fig. 4A). The ovules are supplied by one-bundled traces, branching from the ventral carpel bundles.

At the locule base, ascending bundles divide into six compound veins. Three of them are dorsal veins, located in the middle plane of the locules and composed of five bundles each. The other three veins are septal veins, located on the septa radii and composed of three vascular bundles each (Figs 2A,B; 3E).

In the ovary roof, the dorsal veins branch into a dorsal carpel bundle, entering the style and a stamen-tepal trunk bundle. The latter gives rise to outer stamen trace and outer tepal trace in the floral tube. The dorsal carpel bundles merge with the ventral carpel bundles before entering the style (Fig. 3G,H). The septal veins in the floral tube divide into the inner stamen trace and inner tepal trace. Stamen traces are one-bundled, the outer tepal trace divides into 32 bundles and the inner tepal trace divides into 26 bundles (Fig. 2D).

### Fruit anatomy and dehiscence

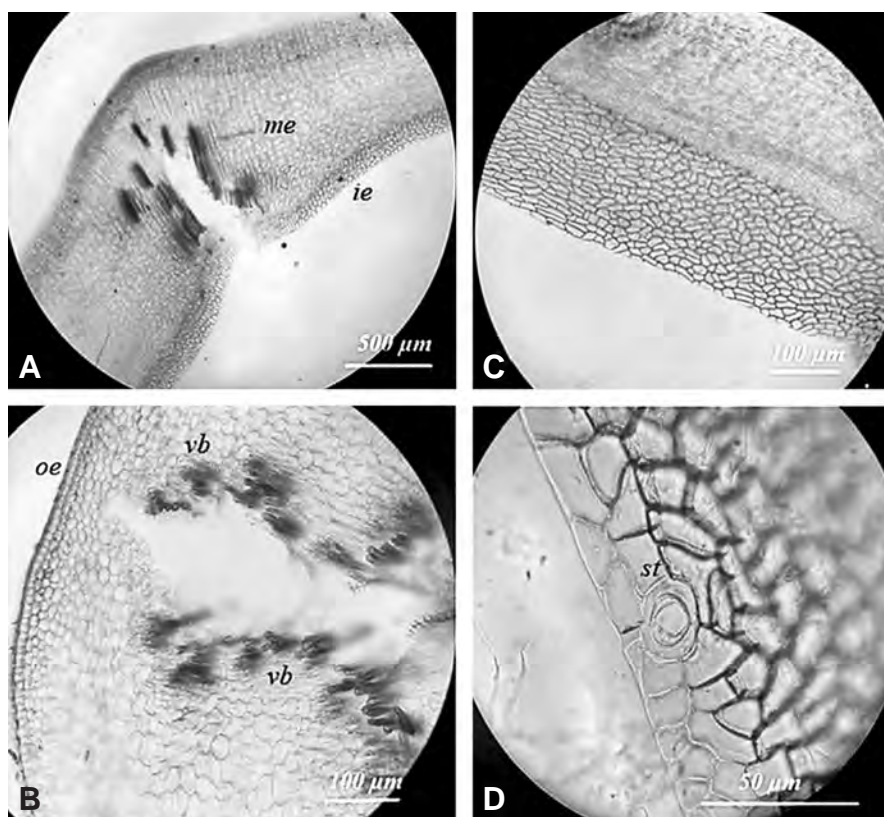
During fruit development, the ovary grows significantly in diameter and becomes spherical (Fig. 5A,B). The colour of the fruit changes from green to light brown. The fruit wall in the green fruit remains parenchymatous, small-celled. The outer fruit epidermis (exocarp) is unilayered, unignified (Fig. 6B). The mesocarp in the unripe fruit of perfect size is parenchymatous, thick,



**Figure 5.** Fruits and seeds of *Hippeastrum vittatum*: A, B – unripe fruit at subsequent stages; C–E – opened fruit with black seeds exposed; F – seeds and aborted ovules of one fruit. Scale bars = 10 mm.

contains 50–60 cell layers due to cell divisions (Fig. 6A,B). The inner ovary epidermis (endocarp) becomes lignified (Fig. 6C,D). Endocarp cells are polygonal and have different forms; open stomata occur among them (Fig. 6D).

Fruit dehiscence starts, when the fruit is ripe and dry. It proceeds from the fruit top, where the scar of the style is located. Three dorsal slits occur in the median plane of carpels from the fruit top to the fruit base (Fig. 5C). The centrifugal development of dorsal slits in the fruit



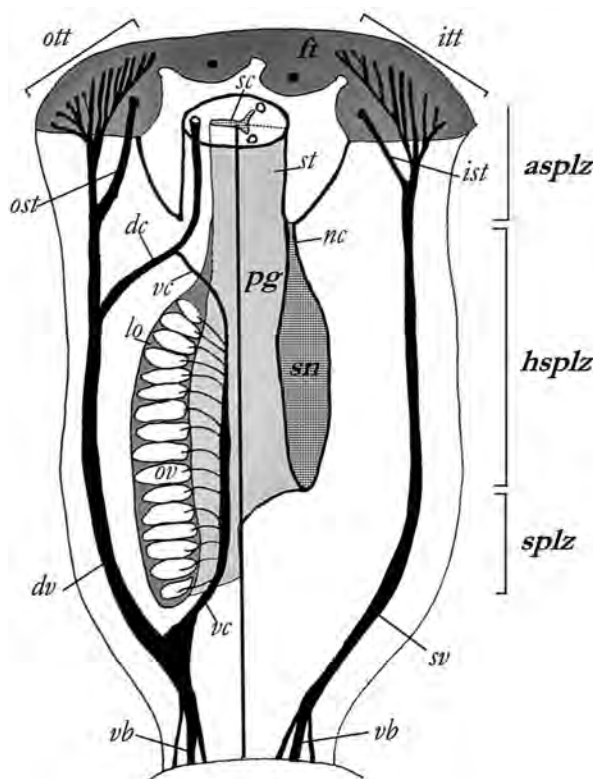
**Figure 6.** Fruit wall of *Hippeastrum vittatum*: A, B – split dorsal vein at the early stage of fruit dehiscence; C, D – the inner epidermis of the fruit wall (endocarp) in paradermal section. *ie* – inner epidermis, *me* – mesocarp, *oe* – outer epidermis, *vb* – vascular bundle, *st* – stoma.

wall parenchyma was observed in the green fruit (Fig. 6A,B). The dorsal slits dissect the inner parenchyma and dorsal vein toward the outside, when slits are not visible yet. Simultaneously, fruit septa detach from each other in the center allowing the fruit valves to turn outside (Fig. 5D). Black seeds and aborted ovules are exposed from the opened fruit and fall down (Fig. 5E,F).

## Discussion

The flower of *Hippeastrum vittatum* reveals the most common morphological traits for Amaryllidoideae, including multiovulate ovary and septal nectary. According to LEINFELLNER (1950), in *Hippeastrum vittatum* symplicate and hemisymplicate vertical zones occur in the gynoecium, both of them bear ovules (Fig. 7). The septal nectaries appear along the hemisymplicate zone and are composed of narrow secretory cavities and apical nectary channels. The asymplicate zone appears in the style, above the openings of the nectary channels. The carpel margins in the hemisymplicate and asymplicate zones are closed together by postgenital fusion of the epidermises. Due to the postgenital fusion of carpel margins, the ovary looks like having a synascidiate (multilocular) zone. The inner morphological structure of the gynoecium resembles the gynoecium of *Gladiolus imbricatus* (Iridaceae) with inferior ovary and septal nectary in the upper part of the ovary (SKRYPEC & ODINTSOVA 2020), except for the absence of the synascidiate zone. The interlocular septal nectaries in the upper part of the ovary are the most common type of nectaries in epigynous Amaryllidaceae (RUDALL 2002).





**Figure 7.** Patterns of floral vasculature and gynoecium micromorphology of *Hippeastrum vittatum*. *asplz* – asymplicate zone; *dc* – dorsal carpal bundle; *dv* – dorsal vein; *ft* – floral tube; *hsplz* – hemisymplicate zone; *ist* – inner stamen trace; *itt* – inner tepal trace; *lo* – ovary locule; *nc* – nectary channel; *ost* – outer stamen trace; *ott* – outer tepal trace; *ov* – ovule; *pg* – postgenitally fused carpal surfaces; *sc* – style channel; *sn* – septal nectary; *splz* – symplicate zone; *st* – style; *sv* – septal vein; *vb* – the main ascending vascular bundle; *vc* – ventral carpal bundles.

DAUMANN (1970) studied flower nectaries of the monocotyledons with special consideration of their systematic and phylogenetic importance. He examined nectaries in 27 genera of Amaryllidaceae and in most of them septal nectaries were found. In *Hippeastrum aulicum* Herb. and *H. reticulatum* (L'Hér.) Herb., DAUMANN (1970) described internal septal nectaries along with the whole ovary. However, he did not confirm that secretory tissue spreads to the opening of the nectary channel, and nectar is excreted by lifting and rupturing the strong cuticles covering the epidermal cells, as it was published earlier by SCHNIEWIND-THIES (1897). DAUMANN (1970) also denied that in *Hippeastrum vittatum* the basal parts of the inner tepals participate in nectar secretion. In the studied species of the genus *Hippeastrum*, septal nectaries are composed of secretory epidermis from the very base or higher, the cells of the secretory epidermis are isodiametric or slightly palisade, with convex external walls (DAUMANN 1970).

According to our data, there is an internal septal nectary in the *Hippeastrum vittatum* gynoecium, having a length from the ovary base to the ovary roof. The type of nectary is epidermal, the cuticle of the nectary epidermis is present. The nectaries are characterized by the absence of vascular bundles. The upper part of the septal nectary slit is free of nectar and forms a nectary channel, which could be narrowed like a tube (DAUMANN 1970). The septal nectary in *Hippeastrum vittatum* is non-labyrinthine and distinct (SCHMID 1985), with a postgenitally closed middle part, as in most Asparagales. The secretory activity of the nectaries was not evident in transverse

sections, because of the very young age of dissected floral buds. However, short radial extension and absence of vascular supply of the nectary confirms its low nectar production.

As in the other members of Asparagales, the vascular system in the flower of *Hippeastrum vittatum* is composed of a ring of ascending bundles in the ovary wall and paired ventral carpel bundles entering the ovary from the base (SHAMROV 2010; ODINTSOVA et al. 2013; FISHCHUK & ODINTSOVA 2020; SKRYPEC & ODINTSOVA 2020). Traces of tepals, stamens and dorsal carpel bundles arise from the ascending bundles (Fig. 7). Thus, each carpel is supplied by three bundles: a dorsal carpel bundle and a pair of ventral carpel bundles, developing ovule traces. The main ascending bundles in the ovary wall arrange into six complex veins, dorsal and ventral, differing from *Galanthus nivalis* and *Leucojum vernum* which have many additional vascular bundles, except six main veins in the ovary wall and double dorsal veins (FISHCHUK & ODINTSOVA 2020).

Fruit development in *Hippeastrum vittatum* is supported by the change of proportions of the ovary and increasing its size. The fruit wall parenchyma remains isodiametric, small-celled and solid, without aerial cavities found in the ovary of *Galanthus nivalis*, *Leucojum aestivum* and *Leucojum vernum* (RASMUSSEN et al. 2006; FISHCHUK & ODINTSOVA 2020). Stomata can be observed in the inner as well as in the outer epidermis in many capsules, however, their occurrence is more common in the outer fruit epidermis (ROTH 1977). The lignified endocarp was revealed in the green fruit that makes it possible to classify the capsule in *Hippeastrum vittatum* as a capsule of *Lilium*-type according to BOBROV & ROMANOV (2019). In the studied species of Amaryllidaceae (*Galanthus nivalis*, *Leucojum aestivum* and *Narcissus* cult.), the lignified endocarp was also revealed (RASMUSSEN et al. 2010), as in many other monocots with fleshy fruits (THADEO et al. 2015).

The fruit dehiscence in *Hippeastrum vittatum* proceeds by the formation of two kinds of longitudinal slits, dorsal and ventral. According to KADEN (1962), such mode of capsule dehiscence can be defined as dorsiventral and perfect (splitting all the fruit length). This mode of dehiscence is very common for monocot capsular fruits (KADEN 1962). Dorsal and ventral slits have different formations in the fruit wall; dorsal slits develop through the break of the fruit wall in the plane of dorsal veins which are divided into five bundles. Ventral slits develop between connected carpel margins. We observed a centrifugal development of dorsal slits in the fruit wall, which means that the endocarp and inner mesocarp layers break first.

The present research of micromorphology and anatomy of flower and fruit in *Hippeastrum vittatum* allows to obtain new data on the structure of the gynoecium and fruit wall. It also enables to compare these structures with other species Amaryllidaceae.

## Conclusion

The flower and fruit micromorphology and anatomy in *Hippeastrum vittatum* were studied using light-microscopic methods to reveal gynoecium zonality and adaptations for seed dispersal. No synascidiate zone was detected in the ovary. The hemisyncarpic zone is the longest. Style and stigma are composed of the asyncarpic zone. The septal nectary is distinct, 'liliod' -type, opens apically in the ovary roof. Fruit is an inferior, trilocular, multi-seeded capsule with a pericarp of the *Lilium*-type. Fruit dehisces by two types of longitudinal slits, dorsal and ventral. Centrifugal development of dorsal slits was detected for the first time. The gynoecium inner structure and anatomy differ from the other members of Amaryllidaceae.

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