Thaiszia - J. Bot., Košice, 28 (2): 125-143, 2018
http://www.bz.upjs.sk/thaiszia

THAISZIA
JOURNAL OF
BOTANY

Flower morphology and vascular anatomy in some representatives of Urgineoideae (Hyacinthaceae)

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Dyka O. (2018): Flower morphology and vascular anatomy in some representatives of Urgineoideae (Hyacinthaceae). – Thaiszia – J. Bot. 28 (2): 125-143. – ISSN 1210-0420.

Abstract: The flower morphology and vascular anatomy in *Bowiea volubilis*, *Geschollia anomala* and *Fusifilum physodes* have been studied. It was shown that the perigonium and androecium in the studied species are very similar. Each of tepals, and each stamen is supplied by a single vascular bundle. Some significant differences are recognized in the inner structure of the ovary, vertical zonality of septal nectary, as well as gynoecium venation in the studied species. Accordingly to W. Leinfellner concept of the gynoecium vertical zonality, it was established that the gynoecium of *B. volubilis* consists of hemisynascidiate, hemisymplicate and asymplicate zones, and the gynoecium of *G. anomala* and *F. physodes* consists of synascidiate, symplicate, hemisymplicate and asymplicate zones. The septal nectary of all studied species have a nectary cavity and nectary split which opens to the exterior. In the septal nectary we detected three vertical zones: the zone of the distinct nectary at the symplicate zone in *F. physodes*; the zone of the common nectary at the hemisynascidiate, and hemisymplicate zones in *B. volubilis*, and at the hemisymplicate zone in *G. anomala* and *F. physodes*; the zone of the external nectary (nectary splits) in all studied species at the asymplicate zone in the ovary roof. The gynoecium of *B. volubilis* can be determined as hemisyncarpous with common septal nectary, and those of *G. anomala* and *F. physodes* – as eusyncarpous with common septal nectary. The gynoecium vasculature of *F. physodes* is the most complicated, each carpel showing one dorsal, two ventral and two septal bundles.

Keywords: floral tube, gynoecium, vertical zonality, septal nectary

Introduction

The subfamily Urgineoideae Speta [alternatively – tribe Urgineeae, subfamily Scilloideae, family Asparagaceae sensu APG III (2009), CHASE et al. (2009), APG IV (2016)] within the family Hyacinthaceae includes about 100 species (SPETA 1998; PFOSSER & SPETA 1999; MANNING et al. 2004), which are distributed in South Africa, around the Mediterranean basin, Arabia, India, and Burma. Researches of the taxonomy and phylogenetical relationships within the Hyacinthaceae have been actively carried out on the basis of molecular data (PFOSSER & SPETA 1999; PFOSSER et al. 2003; MANNING et al. 2004; MARTINEZ-AZORIN et al. 2011; PFOSSER et al. 2012), but the list of species within the subfamily Urgineoideae and delimitation of genera are still actively debated (STEDJE 2001a, 2001b; WETSCHNIG et al. 2007; MARTINEZ-AZORIN et. al. 2013; PINTER et. al. 2013; KNIRSCH et al. 2015).

Anatomical and morphological investigations of the flower are important for the phylogenetical analysis of Urgineoideae (STEDJE 2001a, 2001b; PFOSSER et al. 2006; WETSCHNIG et al. 2007; MANNING et al. 2014). The comparative morphology of gynoecium is widely used in Monocot taxonomy and developmental morphology (DAUMANN 1970; SMETS et al. 2000; RUDALL 2002; REMIZOVA et al. 2006; REMIZOWA et al. 2010; SOKOLOFF et al. 2012; ODINTSOVA et al. 2013; ODINTSOVA et al. 2017).

As shown for the families Asparagaceae (ODINTSOVA et al. 2013; ODINTSOVA et al. 2017), Bromeliaceae (NOVIKOV & ODINTSOVA 2008), Tofieldiaceae, Petrosaviaceae, Nartheciaceae (REMISOVA et al. 2006) among the morphological features of the flower the most important are provided by the gynoecium, in particular, vertical zonality, septal nectary structure, placement of obturators. For the Hyacinthaceae, these features were studied only for individual representatives, in particular, for *Ornithogalum caudatum* Ait. (NOVIKOV 2008), *Hyacinthoides non-scripta* (L.) Chouard ex Rothm. (DEROIN 2014), *Hyacinthoides italica* (L.) Rothm. (Zalko & Deroin 2018), *Ledebouria socialis* (Bak.) Jessop, *Drimiopsis maculata* Lindl. ex Paxt., *Barnardia japonica* (Thunb.) Schult. & Schult., *Scilla bifolia* L., *Galtonia viridiflora* I. Verd., *Dipcadi brevifolium* (Thunb.) Fourc., *Ornithogalum fimbriatum* Willd., *Ornithogalum dubium* Houtt. and *Ornithogalum orthophyllum* subsp. *kochii* (Parl.) Zahar. (DYKA 2011a, 2011b, 2011c, 2013, 2014, 2018) from the subfamilies Hyacinthoideae and Ornithogaloideae. Therefore, our aim was to extend the examination to the subfamily Urgineoideae.

Materials and methods

Flowers and developed floral buds of *Bowiea volubilis* Harv. ex Hook. f. were sampled by Natalya Demchuk in the Botanical Garden of Ivan Franko National University of Lviv (Ukraine), while flowers of *Geschollia anomala* (Baker) Speta (02508-01), *Fusifilum physodes* (Jacq.) Speta (52277-01) were collected by Michael Pinter in the Botanical Garden of the Karl-Franzens University of Graz

(Austria). Plant material was fixed in FAA (10:1:2:7 of ethanol (96 %), glacial acetic acid, formalin, water). The material was embedded in Histomix®, cut at 10µm or 20µm and stained with Safranin and Astra Blue (BARYKINA 2004). Figures were drawn by mean of the microscopes 'MBS-9'(USSR) and 'Lomo Mikmed-1' (USSR) and camera lucida 'Lomo RA-1' (USSR). Digital microphotographs were made using a microscope 'Lomo Mikmed-1' and AMScope 3.7 Digital Camera. Size of the gynoecium vertical zones was estimated after the calculation of the transverse sections of the pistil. We determine the gynoecium type based on the concept of vertical zonality of the gynoecium after LEINFELLNER (1950) and the nectary pattern – we analyzed after DAUMANN (1970), SCHMID (1985) and ODINTSOVA (2013b).

Results

Flower morphology

All studied species have actinomorphic trimerous flowers (Fig. 1) with six tepals, six stamens adnate to the tepals and tricarpellate gynoecium with septal nectary.

Flowers of *Bowiea volubilis* are stellate, 9−10 mm in diameter. The tepals are located in two whorls of three, fused together at the bottom and with the base of the ovary (Fig. 1. A). Filaments are short and extended in the base. Anthers are small, dorsifixed. The ovary is semi-inferior, pear-shaped, with longitudinal septal grooves (Fig 1. B, C). There are a few ovules in two rows in each ovary locule. The *Bowiea volubilis* carpels are fused from the bottom to the top of the column. The ovary is fused with tepals at the ⅓ of the height (Fig. 1. B, C).

Flowers of *Geschollia anomala* are 7−8 mm in diameter. The tepals form a short floral tube (Fig. 1. D). The outer tepals are wider than inner tepals. The tepals have convolute apexes (Fig. 1. D, E). There are two whorls of three stamens attached to the base of the floral tube (Fig. 1. E). The filaments are cylindrical at the bottom and gradually tapering to the top, gaining rounded-triangular shape. The anthers are elongated and dorsifixed. The carpels are opposite to outer whorl stamens. The ovary is superior, elongated, with six longitudinal grooves. Three of grooves are septal and lie on the radii of ovary septa, extending higher through the style and stigma (Fig. 1. F). The other three grooves are opposite to the ovary locules and disappear at the base of the style. There are 14−20 ovules in each ovary locule. The ovary base is fused with floral tube at a certain height.

Flowers of *Fusifilum physodes* are 6–7 mm in diameter, similar to those of *Geschollia anomala* with some differences noted below. Outer tepals are narrower than inner ones (Fig. 1. G). The filaments are cylindrical at the base, gradually expanding, getting rhomboid shape and then narrowed to the top (Fig. 1. H). The ovary is superior, pear-shaped, with six longitudinal grooves (Fig. 1. I). There are 10−15 ovules in each ovary locule.

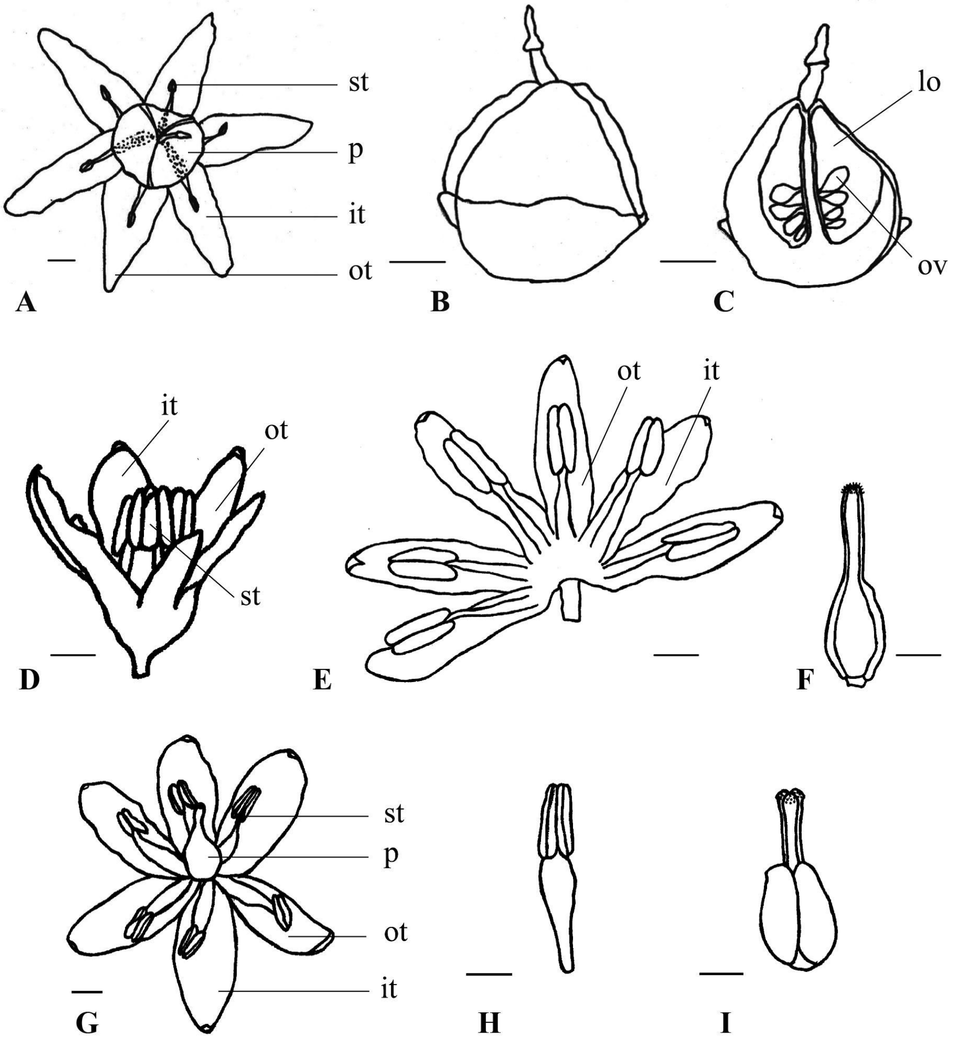


Fig. 1. General view of the flower and flower details of Hyacinthaceae (Urgineoideae). *Bowiea volubilis* (A–C). A, flower; B, pistil; C, pistil's longitudinal section. *Geschollia anomala* (D–F). D, flower; E, dissected perigonium with androecium; F, pistil. *Fusifilum physodes* (G–I). G, flower; H, stamen; I, pistil. it – inner tepal, lo – ovary locule, ot – outer tepal, ov – ovule, p – pistil, st – stamen. Scale bars: 1 mm.

Gynoecium micromorphology

The gynoecium of *Bowiea volubilis* (Tab. 1) has a short sterile part with isolated locules at the base. The size of this part is 3,8 % of the total ovary height. Above is the fertile part, which represents 6,3 % of the total ovary height. Three nectary cavities appear in septa of the ovary at the bottom of the locules, they exhibit congenitally fused external walls, but are postgenitally closed at the center of the ovary. These both parts form hemisynascidiate structural zone (Fig. 4. C). Just above the septal nectary cavities are – as well as ventral splits of carpels – postgenitally closed at the center and visible as two rows of epidermal cells (Fig. 4. D, E). This part forms the hemisymplicate structural zone, and represents 62 % of the total ovary height (fertile part: 41,8 % and sterile part: 20,3 %). Still higher ovary locules are gradually narrowing, ventral splits of carpels appear, building a triradiate style channel (Fig. 4. H). Septal nectary cavities unite distally with the septal grooves at the ovary roof forming nectary splits, which act as the septal nectary deferent channels (Fig. 4. F). Above the opening level of the septal nectary channels there is the epidermal fusion carpels zone. This is a sterile part and it continues higher through the ovary roof (15,2 % of the total ovary height), style and stigma. It belongs to the asymplicate structural zone (Fig. 4. G−I).

Tab. 1. Parts of the ovary and structural zones of the gynoecium in studied species and their respective percentages along the ovary.

Parts of the ovary	Structural zones		*Bowiea volubilis*	*Geschollia anomala*	*Fusifilum physodes*
Ovary roof	Asymplicate	sterile part	15,2 %	18,3 %	8,0 %
Ovary locules	Hemisymplicate	sterile part	20,3 %	14,8 %	37,0 %
		fertile part	41,8 %	36,1 %	26,1 %
	Symplicate	fertile part	–	4,7 %	15,9 %
	Hemisynascidiate	fertile part	6,3 %	–	–
		sterile part	3,8 %	–	–
	Synascidiate	fertile part	–	4,7 %	–
		sterile part	−	18,3 %	9,4 %
Ovary base	Septal nectaries are absent		12,6 %	3,1 %	3,6 %

The gynoecium of *Geschollia anomala* (Tab. 1) has sterile part with isolated locules at the base (Fig. 5. C−E), representing 18,3 % of the total ovary height. Above is a fertile part, whose size is 4,7 % of the total ovary height (Fig. 5. F). These both parts form a synascidiate structural zone. At the upper level ventral splits of carpels are postgenitally closed and outlined by two rows of epidermal cells (Fig. 5. G). This part is fertile, belongs to the symplicate zone, and represents 4,7 % of the total ovary height. Above this part three septal nectary cavities appear, with a congenitally fused external wall, but postgenitally closed toward the center and then visible as two rows of epidermal cells. This is hemisymplicate zone (Fig. 5. H, I). At this level ventral splits of carpels are postgenitally closed too. The size of this zone is 50,9 % of the total ovary height (fertile part: 36,1 % and sterile part: 14,8 %). Above ovary locules are gradually narrowing and form three style channels (Fig. 5. J, K). Septal nectary cavities unite distally with the septal grooves at the ovary roof and form nectary splits which are the septal nectary deferent channels (Fig. 5. J). The zone of epidermal fusion of carpels is found above the level of septal nectary channels opening. This is a sterile part and continues higher through the ovary roof (18,3 % of the total ovary height), style and stigma. It belongs to the asymplicate structural zone (Fig. 5. G−L).

The zonality of the gynoecium of *Fusifilum physodes* (Tab. 1) is similar to that of *Geschollia anomala*. The ovary is trilocular and has a short sterile part with isolated locules at the base (Fig. 6. E, F), representing 9,4 % of the total ovary height and forming a synascidiate structural zone. At the upper level ventral splits of carpels are postgenitally closed (Fig. 6. G−I). This part is fertile and belongs to the symplicate zone. It represents 15,9 % of the total ovary height. At this level three septal nectary cavities appear, with congenitally fused external and internal walls (Fig. 6. H). The hemisymplicate zone is above. In this zone three septal nectary cavities have a congenitally fused external wall but it is postgenitally closed at its center and ventral splits of carpels are postgenitally closed too (Fig. 6. J, K). The height of this zone is 63,1 % of the total ovary height (fertile part – 26,1 % and sterile part − 37,0 %). Above ovary locules gradually narrow and form three style channels (Fig. 6. L−N). These channels unite at stigmas. Septal nectary cavities unite distally with the septal grooves at the ovary roof and form nectary splits which are the septal nectary deferent channels (Fig. 6. L). Above the level of septal nectary channels opening there is the epidermal fusion carpels zone. This is sterile part and continues higher through the ovary roof (8,0 % of the total ovary height), style and stigma. It belongs to the asymplicate structural zone (Fig. 6. L−N).

We have identified three main parts of the ovary in the studied species: ovary base, ovary locules and ovary roof (Tab. 1; Fig. 2). Ovary base is located below its locules. At this zone in studied species septal nectaries are absent. Zone of ovary locules is the main part of the ovary with three locules. At the ovary septa there are septal nectaries at the different heights. Ovary roof is located above the locules where style channels are present. The style channels are located apically. At the ovary roof there are septal nectary deferent channels − nectary splits.

The gynoecium inner structure in the studied species differs by the number of gynoecium zones and structure of septal nectary (Fig. 2). In accordance with the concept of the gynoecium vertical zonality (LEINFELLNER 1950), we found three gynoecium vertical zones in *B. volubilis*: hemisynascidiate, hemisymplicate and asymplicate zones. And in *G. anomala* and *F. physodes* we found four gynoecium vertical zones: synascidiate, symplicate, hemisymplicate and asymplicate zones.

After our data the gynoecium of *B. volubilis* is hemisyncarpous and the gynoecium of *G. anomala* and *F. physodes* is eusyncarpous. In the studied species above the nectary splits the carpels are postgenitally fused thus the style and stigma are formed as a result of functional connation of carpels.

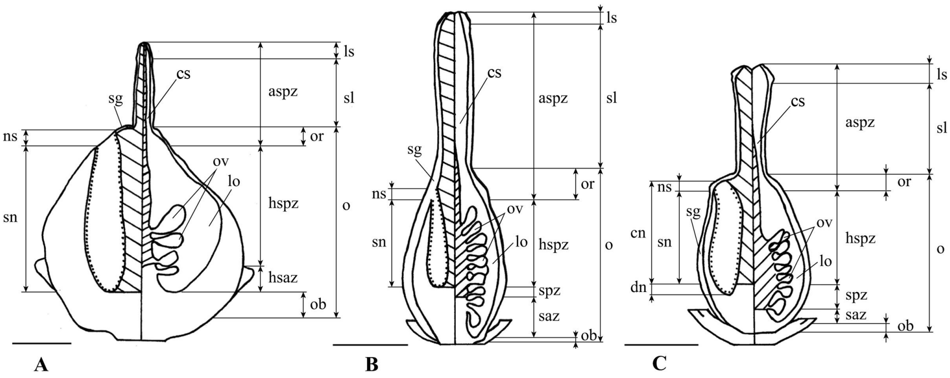


Fig. 2. Vertical zonality of the gynoecium and septal nectary of *Bowiea volubilis* (A), *Geschollia anomala* (B) and *Fusifilum physodes* (C): aspz – asymplicate zone, cn – zone of common nectary, cs – style channel, dn – zone of distinct nectary, hsaz – hemisynascidiate zone, hspz – hemisymplicate zone, lo – ovary locule, ls – stigma lobe, ns – nectary split, o – ovary, ob – ovary base, or – ovary roof, ov – ovule, saz – synascidiate zone, sg – septal groove, sl – style, sn – septal nectary cavity, spz – symplicate zone, postgenitally fused surfaces are hatched. Scale bars: 1 mm.

Septal nectary is represented by three cavities in the ovary septa in studied species (Fig. 3). The walls of the septal nectaries of *Bowiea volubilis* and *Geschollia anomala* are entirely covered by a secretory epidermis while in *Fusifilum physodes* secretory epidermis covers only the nectary cavity but nectary split do not have it. On cross-section the septal nectary cavities of the investigated species are not labyrinthine, and in *B. volubilis* (Fig. 3. A, B) and *G. anomala* (Fig. 3. C, D) they have smooth surface and in *F. physodes* (Fig. 3. E, F) they have gibbous surface. The septal nectary of all studied species have a nectary cavity and nectary split which open to the exterior (Fig. 2). Septal nectary height of *Bowiea volubilis* is 86,1 %, *Geschollia anomala* – 57,4 % and *Fusifilum physodes* – 76,1 % of the total ovary height. Septal nectary in *Bowiea volubilis* is available at the level of the hemisynascidiate, hemisymplicate and asymplicate zones, in *Geschollia anomala* is available at the level of the hemisymplicate and asymplicate zones, in *Fusifilum physodes* is available at the level of the symplicate, hemisymplicate and asymplicate zones.

In studied species obturators are formed at the base of the funiculus and on the tip of each carpel margin (Fig. 3. A, C, E). According to the defininitions by TILTON and HORNER (1980, 1983) these obturators are of placental-funicular type.

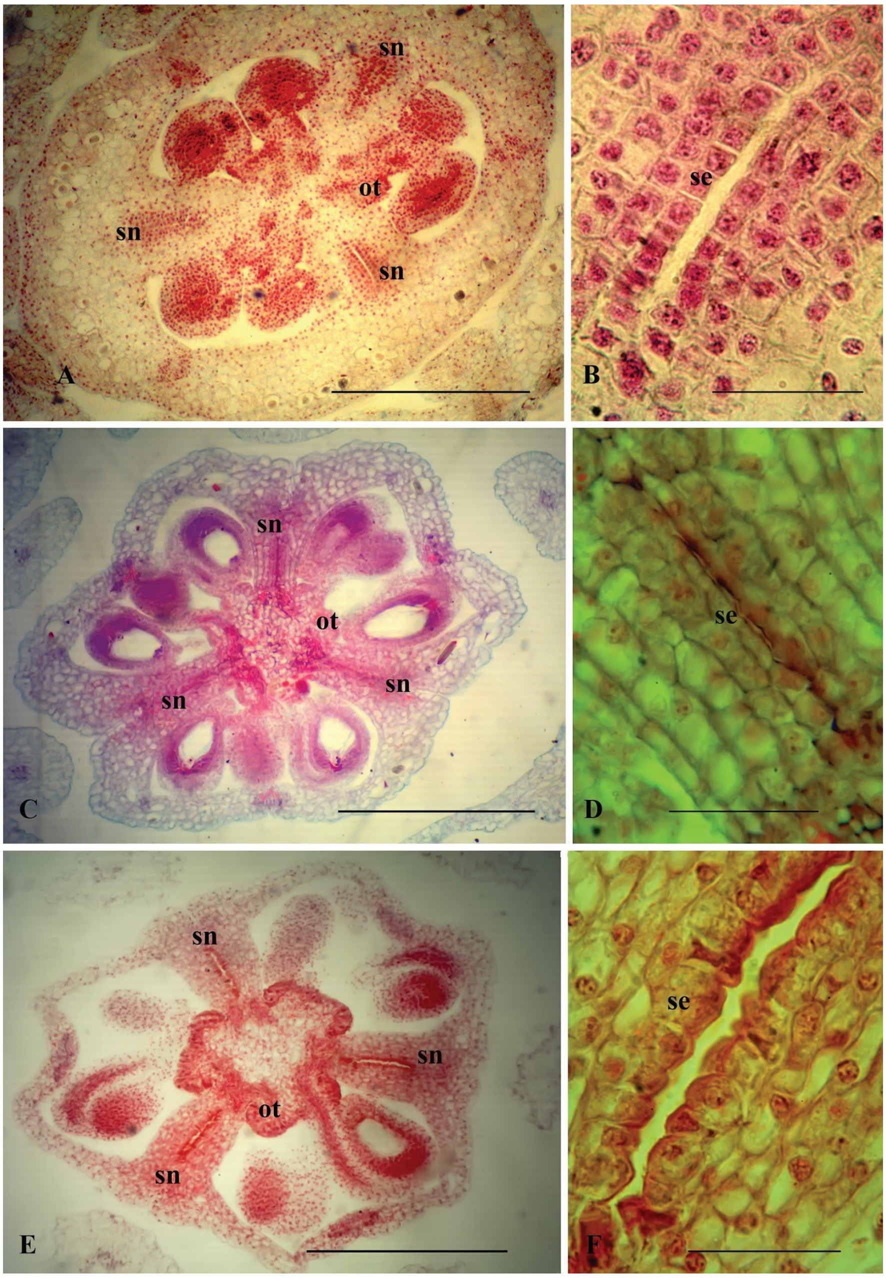


Fig. 3. Cross-section through the middle heighth of the ovary and septal nectary of *Bowiea volubilis* (A, B), *Geschollia anomala* (C, D), *Fusifilum physodes* (E, F): ot – placental obturator, se – secretory epidermal cell, sn – septal nectary cavity. Scale bars: 500 µm (A, C, E), 50 µm (B, D, F).

Flower vascular anatomy

Bowiea volubilis. The vascular system of pedicel is composed of six collateral bundles, three of them are located on the radii of ovary locules and three – on the septa radii (Fig. 4. A). All bundles branch out in upward direction, forming a large number of small bundles which form a ring. Of the vascular cylinder

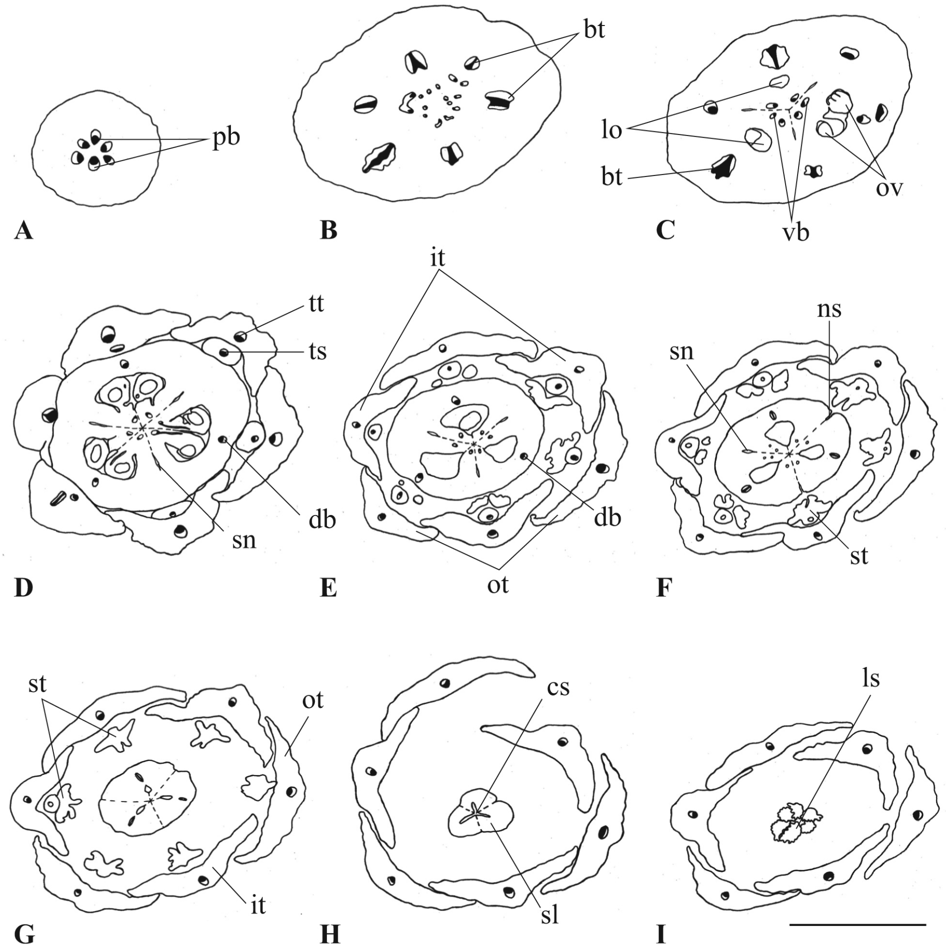


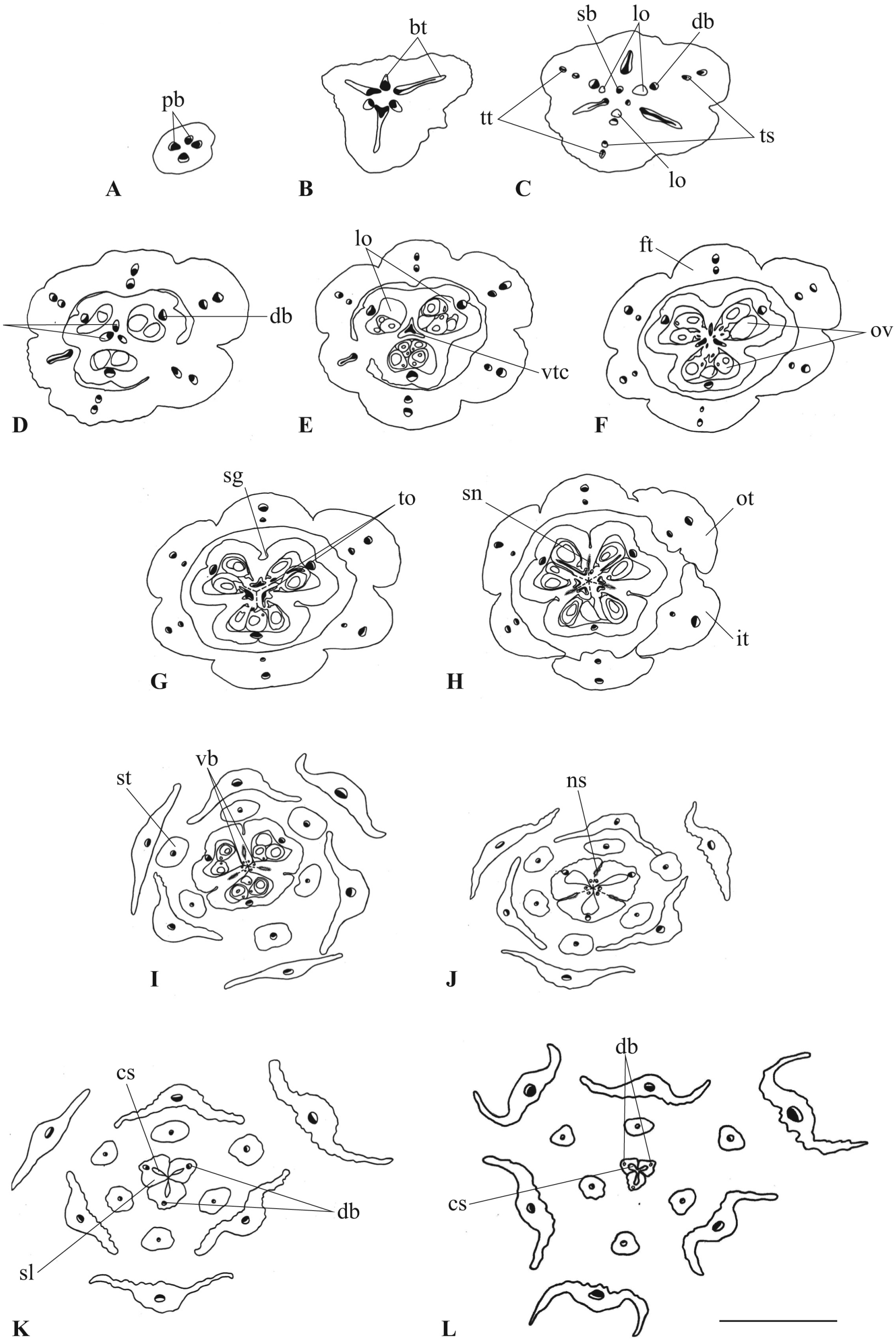
Fig. 4. Ascendent series of the cross-sections through the flower of *Bowiea volubilis* (A–I): bt – trunk bundle, cs – style channel, db – dorsal bundle of the carpel, it – inner tepal, lo – ovary locule, ls – stigma lobe, ns – septal split, ot – outer tepal, ov – ovule, pb – pedicel bundle, sl – style, sn – septal nectary cavity, st – stamen, ts – stamen trace, tt – tepal trace, vb – ventral bundle of the carpel. Scale bar: 1 mm.

horizontal branch off six trunk bundles to outwards of the bottom of flower (Fig. 4. B). Three trunk bundles branch on outer tepal trace, stamen trace and dorsal carpellary bundle (Fig. 4. C, D). Other three trunk bundles branch on inner tepal trace and stamen trace. There is a large number of small bundles in the center, uniting at the bottom of ovary locules in six ventral carpel bundles (Fig. 4. C). The ventral bundles run up and branch off ovule traces at different levels. The ventral carpel bundles have blindly ending at the ovary roof. The dorsal vascular bundles lie in the ovary wall opposite the ovary locules, run to the ovary roof that continues into the style and blindly ending in ½ style length (Fig. 4. F−H).

Geschollia anomala. Unlike the *Bowiea volubilis*, the vascular system of pedicel of *Geschollia anomala* has three collateral bundles. Close to the bases of the perianth each of them divides and forms six trunk bundles (Fig. 5. A, B). Three trunk bundles branch on outer tepal trace, stamen trace and dorsal carpellary bundle on the radii of ovary locules (Fig. 5. C, D). Other three trunk bundles branch on inner tepal trace, stamen trace and septal carpellary bundle on the radii of septa. The septal bundles fuse together at the center and form a triangular ventral complex (Fig. 5. E). At the placenta level three septal bundles separate again. Each of them reorganize and forms two ventral carpellary bundles, belonging to different carpels (Fig. 5. F–J). The ventral bundles run up and branch off ovule traces at different heights and blindly end at the ovary roof. Dorsal vascular bundles round outward the ovary locules, run to the ovary roof, continue into the style and blindly ending too (Fig. 5. K, L).

Fusifilum physodes. Similar to *Geschollia anomala* the vascular system of pedicel of *Fusifilum physodes* has three collateral bundles and each of them branch out two in upward direction (Fig. 6. A, B). In the receptacle are six trunk bundles (Fig. 6. C). Three of them branch on outer tepal trace and stamen trace on the radii of ovary locules (Fig. 6. D). Other three trunk bundles branch on inner tepal trace and stamen trace on the radii of septa. In the center remains the vascular cylinder. At the ovary base vascular cylinder bundles divide to form three rings of bundles (Fig. 6. E). Outer ring forms three dorsal bundles which round outward the ovary locules, run to the ovary roof, continue into the style and blindly ending (Fig. 6. E–M). Median ring forms three septal bundles which lie in the ovary septa. Inner ring forms three ventral median veins which lie in the center on the radii of ovary locules. At the placenta level ventral median bundles divide in two, run up and branch off ovule traces at the different heights and blindly ending at the ovary roof (Fig. 6. H–L). The septal bundles branch out and fuse with two ventral bundles which belong to different carpels (Fig. 6. J).

Fig. 5 (on the right). **Ascendent series of the cross-sections through the flower of *Geschollia anomala* (A–L): bt – trunk bundle, cs – style channel, db – dorsal bundle of the carpel, ft – floral tube, it – inner tepal, lo – ovary locule, ns – septal split, ot – outer tepal, ov – ovule, pb – pedicle bundle, sb – septal bundle, sg – septal groove, sl – style, sn – septal nectary cavity, st – stamen, to – ovule trace, ts – stamen trace, tt – tepal trace, vb – ventral bundle of the carpel, vtc – ventral complex. Scale bar: 1 mm.**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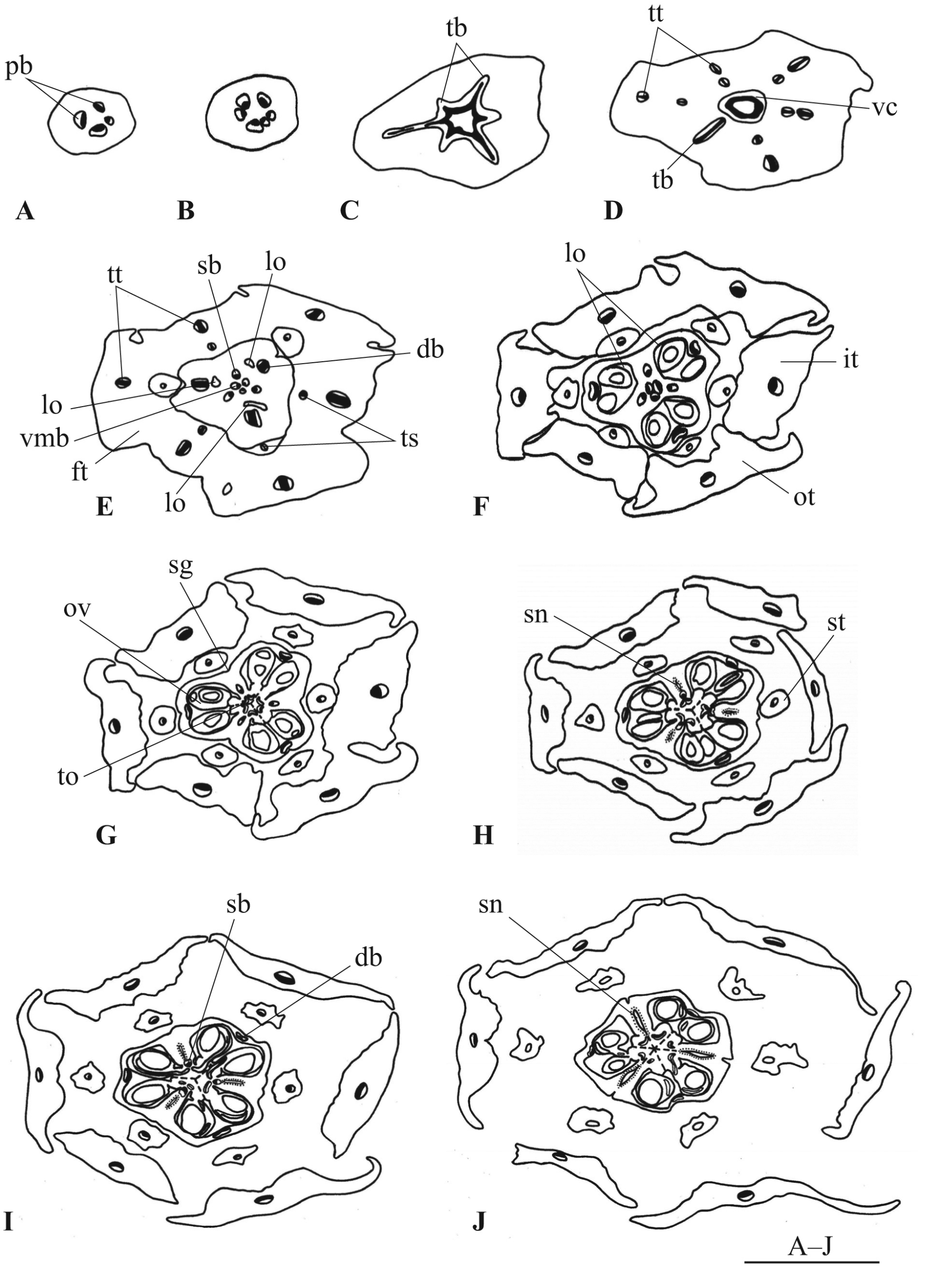
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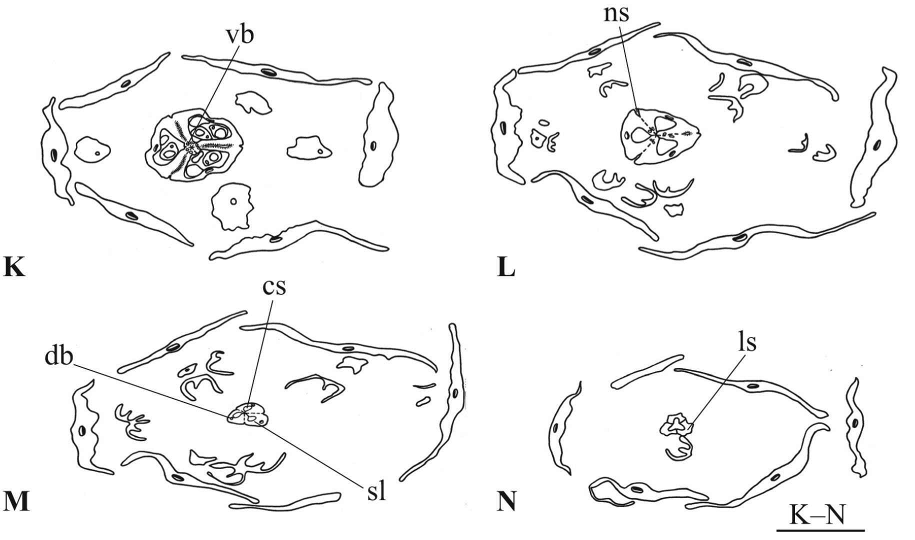

Fig. 6. Ascendent series of the cross-sections through the flower of *Fusifilum physodes* (A–N): bt – trunk bundle, cs – style channel, db – dorsal bundle of the carpel, ft – floral tube, it – inner tepal, lb – lateral bundle of the carpel, lo – ovary locule, ls – stigma lobe, ns – septal split, ot – outer tepal, ov – ovule, pb – pedicle bundle, sg – septal groove, sl – style, sn – septal nectary cavity, st – stamen, to – ovule trace, ts – stamen trace, tt – tepal trace, vb – ventral bundle of the carpel, vc – vascular cylinder, vmb – ventral median bundle. Scale bar: 1 mm.

Discussion

The flowers of studied species are trimerous-pentacyclic and have typical monocot groundplan (Remizowa et al. 2010). The outer and inner tepals are equal in shape and outer ones are slightly longer. The tepals of these species are fused together at the bottom and with the base of the ovary. The tepals of *Geschollia anomala* and *Fusifilum physodes* form a short floral tube. Syntepaly in monocots is related to pollination strategies restricting rewards to long-tongued pollinators, so that nectaries are hidden deep in the flower and ovaries are better protected (Ronse de Craene 2010). The outer and inner stamens are equal in all species. The filaments of *Bowiea volubilis* are fused with tepals while those of *Geschollia anomala* and *Fusifilum physodes* are fused with the floral tube. The anthers are dorsifixed and introrse. Our study confirms the observations of ovary by Speta (1998), which is semi-inferior in *Bowiea volubilis*, and superior in *Geschollia anomala* and *Fusifilum physodes*.

All studied species have ovary base, ovary locules and ovary roof. Unlike the representatives of Asparagaceae s. l. (*Dracaena*, *Sansevieria* and *Polygonatum* species) (Odintsova et al. 2013; Fishchuk & Odintsova 2014; Odintsova & Fishchuk 2017) ovary base and roof of studied species are not thickened (only in *Bowiea volubilis* occurs a massive ovary base).

All studied species have tricarpellate gynoecia as is common in monocots (RUDALL 2002; REMIZOWA et al. 2006; REMIZOWA et al. 2010). The ovary is three-locular with axile placentation in the lower portion and parietal placentation in the upper portion on *Bowiea volubilis*, *Geschollia anomala*, and parietal placentation on *Fusifilum physodes*.

Obturators (or transmitting tissue) are recognized in the gynoecium of different members of Hyacinthaceae (TILTON & HORNER 1980; KOMAR 1985; SHAMROV 1990) They are varied in anatomy and morphology. In *Albuca transvaalensis*, *Bowiea volubilis*, *Dipcadi montanum*, *Ornithogalum caudatum*, funicular obturators are found (SHAMROV 1990). According to TILTON and HORNER (1980, 1983) the obturator of *Ornithogalum caudatum* belongs to the placental-funicular type, which is also the case for the species we studied here.

The septal nectary of all studied species have a body (inner septal nectary after DAUMANN (1970)) and nectary split which opens outside (outer septal nectary after DAUMANN (1970)). Following the descriptive classification of SCHMID (1985) the septal nectaries of studied species can be interpreted as “liliad” type (non-labyrinthine distinct type) by the shape of nectary cavity on the cross-sections and as combined type by the vertical structure, which includes inner and outer (nectary splits) septal nectaries after DAUMANN (1970).

Comparative structural analysis of the septal nectaries was carried out according to the concept of vertical zonality (ODINTSOVA 2013a, 2013b). In the nectary of the studied species some vertical zones that correspond to different descriptive types of nectaries after DAUMANN (1970) and SCHMID (1985) may be identified: zone of distinct nectary with congenitally closed nectary cavities at the symplicate zone in *F. physodes*; zone of “liliad” common nectary with postgenitally closed central part of the nectar at the hemisynascidiate, and hemisymplicate zones in *B. volubilis*, and at the hemisymplicate zone in *G. anomala* and *F. physodes*; zone of external nectary (nectar split) in all studied species at the asymplicate zone in the ovary roof.

The gynoecium of *B. volubilis* with hemisynascidiate, hemisymplicate and asymplicate zones may be defined as hemisyncarpous sensu Leinfellner (1950). The gynoecium of *G. anomala* and *F. physodes* with synascidiate, symplicate, hemisymplicate and asymplicate zones should be defined as eusyncarpous sensu Leinfellner (1950). All studied species have common septal nectary after ODINTSOVA (2013a, 2013b).

According to the figures and authors descriptions we can determine that among Hyacinthaceae the hemisyncarpous gynoecium with common septal nectary type is in *Ledebouria socialis* (Bak.) Jessop (DYKA 2011a), *Drimiopsis maculata* Lindl. ex Paxt. (DYKA 2011b) and *Hyacinthoides italica* (L.) Rothm. (ZALKO & DEROIN 2018), the eusyncarpous gynoecium with common septal nectary type is in *Scilla bifolia* L. (DYKA 2013), *Galtonia viridiflora* I. Verd. (DYKA 2014), *Hyacinthoides non-scripta* (L.) Chouard ex Rothm. (DEROIN 2014), *Dipcadi brevifolium* (Thunb.) Fourc., *Ornithogalum fimbriatum* Willd., *Ornithogalum dubium* Houtt. and *Ornithogalum orthophyllum* subsp. *kochii* (Parl.) Zahar. (DYKA 2018), the eusyncarpous gynoecium with distinct septal nectary type is in *Ornithogalum caudatum* Ait. (NOVIKOV 2008) and *Barnardia japonica* (Thunb.) Schult. & Schult. (DYKA 2011c).

The perigonium and androecium vascular systems are similar, while the carpel vasculature is different in the species studied here. Tepal and stamen traces are one-bundled and unbranched.

In *B. volubilis* and *G. anomala*, the carpel vascular system consists of one dorsal and two ventral bundles, and in *F. physodes* – of one dorsal, two ventral and two septal bundles. The investigated species differ by types of ventral carpel bundles. The carpels ventral bundles in *B. volubilis* are formed from receptacle bundles. *G. anomala* has three gynoecium septal bundles, which make anastomoses with each other above and form the ventral complex, and higher they separate again and form two ventral veins which belong to different carpels. The receptacle vascular system of *F. physodes* continues into the three gynoecium vascular bundles to become the ventral-median carpels bundles which lie on ovary locules radii. At the placenta level ventral-median bundles divide to form two ventral veins which belong to one carpel.

The question of the carpel and ovule morphological nature is not clearly interpreted in the literature. It is focused on whether carpel and ovule are axial structures, phylloms, or organs of a special type that are not related to other organs of the flower (EAMES 1964; TAKHTAJAN 1964; ESAU 1980; SHAMROV 2008). Anatomical confirmation of the foliar nature of the ovule is the fact that in almost all cases it receives its vascular supply from the ventral bundles of carpel. We do not support the concept of the axial nature of ovules, and accordingly we consider all ovules to be carpellary and supplied straight by carpel in the studied species. They are supplied straight by carpel unlike *Hyacinthoides italica* (L.) Rothm. ovules are supplied straight by the floral stele (ZALKO & DEROIN 2018) and *Hyacinthoides non-scripta* (L.) Chouard ex Rothm. ovules are supplied by the floral stele and by carpel (DEROIN 2014).

The branches of the vascular bundles that innervate the septal nectary were not detected in any species. This may be due to the fact that the investigated flowers are preanthetical, small in size (2,1–2,7 mm in diameter) and these bundles have not yet developed.

The results of this study suggest that the most advanced characters are found in *B. volubilis*: the semi-inferior ovary, few ovules per carpel and simplified vascular system. We can assume the reversion of the floral tube and synascidiate zone. In *F. physodes* we deduced the most complicated gynoecium vascular system, the zone of the distinct nectary and the non-secretory nectary split. The longest flower tube and the highest ovules number per carpel are discovered in *G. anomala*.

Conclusions

Our data show that the perigonium and androecium in the studied species are very similar. Tepal and stamen traces are one-bundled and unbranched. The investigated species differ mainly by their carpel venation.

In accordance with concepts of vertical zonality of gynoecium (LEINFELLNER 1950) and septal nectary (ODINTSOVA 2013a, 2013b), the gynoecium of *B. volubilis* is hemisyncarpous with common septal nectary type and the gynoecium of *G. anomala* and *F. physodes* are eusyncarpous with common septal nectary type.

New inner features of gynoecium structure are revealed, which can be used in the comparative morphological analysis of the flower among Hyacinthaceae.

Acknowledgements

I would like to thank PhD Andriy Prokopiv and Natalya Demchuk (Ivan Franko National University of Lviv, Ukraine), Prof. Dr. Wolfgang Wetschnig and Mag. Michael Pinter (Karl-Franzens-University Graz, Austria) for fixed plant material. And I would like to thank Prof. Dr. Lidiya Tasenkevych and PhD Anastasiya Odintsova (Ivan Franko National University of Lviv, Ukraine) for critical comments and correction of the text.

References

APG III. (2009): An update of the Angiosperm Phylogeny Group Classification for the orders and families of flowering plants: APG III. – Bot. J. Linn. Soc. 161: 105-121. https://doi.org/10.1111/j.1095-8339.2009.00996.x

APG IV. (2016): An update of the Angiosperm Phylogeny Group Classification for the orders and families of flowering plants: APG IV. – Bot. J. Linn. Soc. 181: 1-20. https://doi.org/10.1111/boj.12385

BARYKINA R.P., VESELOVA T.D., DEVIATOV A.G. et al. (2004): Spravochnik po botanicheskoy mikrotehnike. [Handbook of the botanical microtechniques]. Moscow: Moscow University Press. [In Russian]

CHASE M.W., REVEAL J.L., FAY M.F. (2009): A subfamilial classification for the expanded asparagalean families, Amaryllidaceae, Asparagaceae and Xanthorrhoeaceae. – Bot. J. Linn. Soc. 161: 132-136.

DAUMANN E. (1970): Das Blütennektarium der Monocotyledonen unter besonderer Berücksichtigung seiner systematischen und phylogenetischen Bedeutung. – Feddes Repert. 80 (7-8): 463-590.

DEROIN T. (2014): Vascular anatomy of the flower of *Hyacinthoides non-scripta* (L.) Chouard ex Rothm. A new insight about a complex placentation pattern in Asparagaceae. – Modern Phytomorphol. 5: 9-14.

DYKA O.O. (2011a): Morfolohiya i vaskulyarna anatomiya kvitky *Ledebouria socialis* (Bak.) Jessop (Hyacinthaceae) [Morphology and vascular anatomy of the flower *Ledebouria socialis* (Bak.) Jessop (Hyacinthaceae)]. – Visnyk of L'viv Univ. Series Biology. 56: 60-64. [In Ukrainian]

DYKA O.O. (2011b): Morfolohiya ta vaskulyarna anatomiya kvitky *Drimiopsis maculata* Lindl. & Paxt. (Hyacinthaceae) [Floral morphology and vascular anatomy of *Drimiopsis maculata* Lindl. & Paxt. (Hyacinthaceaea)] // Fundamental and applied research in biology: Abstracts of the IInd International conference of young scientists (Donetsk, 19-22 September 2011). – Donetsk: 17-18. [In Ukrainian]

DYKA O.O. (2011c): Morfolohiya i vaskulyarna anatomiya kvitky *Barnardia japonica* (Thunb.) Schult. & Schult. (Hyacinthaceae) [Morphology and vascular anatomy of the flower *Barnardia japonica* (Thunb.) Schult. & Schult. (Hyacinthaceaea)]. –

Scientific herald of Chernivtsy university. Biological system. 3 (4): 379-383. [In Ukrainian]

DYKA O.O. (2013): Morfolohiya ta vaskulyarna anatomiya kvitky *Scilla bifolia* L. (Hyacinthaceae) [Morphology and vascular anatomy of *Scilla bifolia* L. (Hyacinthaceae) flower]. – Studia biologica. 7 (1): 123-130. [In Ukrainian]

DYKA O.O. (2014): Morfolohiya ta vaskulyarna anatomiya kvitky *Galtonia viridiflora* I. Verd. (Hyacinthaceae) [Morphology and vascular anatomy of *Galtonia viridiflora* I. Verd. (Hyacinthaceae) flower]. – Studia biologica. 8 (3-4): 209-220. [In Ukrainian]

DYKA O.O. (2018): Porivnialna morfolohiia hinetseiu deiakykh vydiv pidrodyny Ornithogaloideae (Hyacinthaceae) [The gynoecium comparative morphology of some representatives of Ornithogaloideae (Hyacinthaceae)]. – Studia biologica. 12 (1): 87-98. [In Ukrainian]. DOI: 10.30970/sbi.1201.549

EAMES A. (1964): Morfologiya tsvetkovykh rasteniy. [Morphology of the angiosperms]. Moscow. [In Russian]

ESAU K. (1980): Anatomiya semennykh rasteniy. [Anatomy of seed plants]. Moscow. [In Russian]

FISHCHUK O, ODINTSOVA A. (2014): Morfolohiya ta vaskulyarna anatomiya kvitok *Dracaena surculosa* Lindl. i *Sansevieria aethiopica* Thunb. (Asparagaceae Juss.) [Morphology and vascular anatomy of the flower in *Dracaena surculosa* Lindl. and *Sansevieria aethiopica* Thunb. (Asparagaceae Juss.)]. – Visnyk of the Lviv University. Series Biology. 64:113-123. [In Ukrainian]

KNIRSCH W., MARTINEZ-AZORIN M, PFOSSER M. et al. (2015): The reinstatement and rediagnosis of the Madagascan genus Rhodocodon (Asparagaceae, Scilloideae), with validation and remarks on H. Perrier's taxa. – Phytotaxa 195 (2): 101-134. http://dx.doi.org/10.11646/phytotaxa.195.2.1

KOMAR G.A. Liliaceae. (1985) – In: // Takhtajan A. (ed.): Sravnitelnaya anatomiya semyan. [Anatomia Seminum Comparativa]. Vol. 1: p. 71-77. – Leninopoli: Nauka. [In Russian]

LEINFELLNER W. (1950): Der Bauplan des synkarpen Gynözeums. – Österr. Bot. Zeitschr. 97 (3-5): 403-436. https://doi.org/10.1007/BF01763317

MANNING J., DEACON J., GOLDBLATT P. (2014): A review of the *Schizobasis* group of *Drimia* Jacq. (Hyacinthaceae: Urgineoideae), and the new species *D. sigmoidea* from Western Cape, South Africa. – S. African J. Bot. 94: 263-269. http://dx.doi.org/10.1016/j.sajb.2014.07.011

MANNING J.C., GOLDBLATT P., FAY M.F. **(**2004): A revised generic synopsis of Hyacinthaceae in sub Saharan Africa based on molecular evidence, including new combinations and the new tribe Pseudoprospereae. – Edinburgh J. Bot. 60: 533-568.

MARTINEZ-AZORIN M., CRESPO M.B., DOLD A.P. et. al. (2013): Sagittanthera (Hyacinthaceae, Urgineoideae), a new buzz pollinated genus from the Eastern Cape Province of South Africa. – Phytotaxa 98 (2): 43-54. http://dx.doi.org/10.11646/phytotaxa.98.2.2

MARTINEZ-AZORIN M., CRESPO M.B., JUAN A. et al. (2011): Molecular phylogenetics of subfamily Ornithogaloideae (Hyacinthaceae) based on nuclear and plastid DNA regions, including a new taxonomic arrangement. – Ann. Bot. 107: 1-37. DOI: 10.1093/aob/mcq207

NOVIKOV A.V. (2008): Morfolohiya ta vaskulyarna anatomiya kvitky *Ornithogalum caudatum* Ait. (Hyacinthaceae) [Floral morphology and vascular anatomy of *Ornithogalum caudatum* Ait. (Hyacinthaceae)]. – Studia Biologica. 2 (1): 87-94. [In Ukrainian]

NOVIKOV A.V., ODINTSOVA A. (2008): Some aspects of comparative gynoecium morphology in three bromeliad species. – Wulfenia 15: 13-24.

ODINTSOVA A., FISHCHUK O. (2017): The flower morphology in three Convallariaceae species with various attractive traits. – Acta Agrobot. 70 (1): 1705. https://doi.org/10.5586/aa.1705

ODINTSOVA A.V. (2013a): Vertykal'na zonal'nist' septal'nykh nektarnykiv odnodol'nykh [Vertical zonality of septal nectaries of Monocots]. – Modern Phytomorphol. 4: 317-318. [In Ukrainian]

ODINTSOVA A.V. (2013b): Dva osnovnykh typy septal'nykh nektarnykiv odnodol'nykh [Two principal models of Monocots' septal nectaries]. – Visnyk of L'viv Univ. Biology Series. 61: 41-50. [In Ukrainian]

ODINTSOVA A., FISHCHUK O., SULBORSKA A. (2013): The gynoecium structure in *Dracaena fragrans* (L.) Ker Gawl., *Sansevieria parva* N. E. Brown and *Sansevieria trifasciata* Prain (Asparagaceae s. l.) with special emphasis on the structure of the septal nectary. – Acta Agrobot. 66 (4): 55-64. https://doi.org/10.5586/aa.2013.051

PFOSSER M., KNIRSCH W., PINTER M. et al. (2012): Phylogenetic relationships of Malagasy Hyacinthaceae. – Pl. Ecol. Evol. 145: 65-72. https://doi.org/10.5091/plecevo.2012.590

PFOSSER M., SPETA F. (1999): Phylogenetics of Hyacinthaceae based on plastid DNA sequences. – Ann. Missouri Bot. Gard. 86: 852-875. DOI: 10.2307/2666172

PFOSSER M., WETSCHNIG W., SPETA F. (2006): *Drimia cryptopoda*, a new combination in Hyacinthaceae from Madagascar. – Linzer Biol. Beitr. 38 (2): 1731-1739.

PFOSSER M., WETSCHNIG W., UNGAR S. et al. (2003): Phylogenetic relationships among genera of Massonieae (Hyacinthaceae) inferred from plastid DNA and seed morphology. – J. Plant Res. 116: 115-132. DOI: 10.1007/s10265-003-0076-8

PINTER M., CRESPO M.B., ILG I. et al. (2013): Mucinaea (Hyacinthaceae-Urgineoideae) a remarkable new genus from Namaqualand (Northern Cape Province, South Africa). – Phyton (Horn) 53 (2): 289-304.

PURI V. (1951): The role of floral anatomy in the solution of morphological problems. – Bot. Rev. 17 (7): 471-553.

REMIZOVA M., SOKOLOFF D., RUDALL P.J. (2006): Evolution of the monocot gynoecium: evidence from comparative morphology and development in *Tofieldia*, *Japonolirion*, *Petrosavia* and *Narthecium*. – Pl. Syst. Evol. 258: 183-209. DOI 10.1007/s00606-005-0397-3

REMIZOWA M., SOKOLOFF D., RUDALL P. (2010): Evolutionary history of the monocot flower. – Ann. Missouri Bot. Gard. 97: 617-645. https://doi.org/10.3417/2009142

RONSE DE CRAENE L.-P. (2010): Floral diagrams. An aid to understanding flower morphology and evolution. Cambridge: Cambridge University Press.

RUDALL P.J. (2002): Homologies of inferior ovaries and septal nectaries in monocotyledons. – Int. J. Pl. Sci. 163: 261-276.

SCHMID R. (1985): Functional interpretations of the morphology and anatomy of septal nectaries. – Acta Bot. Neerl. 34 (1): 125-128.

SHAMROV I.I. (2008): Semyazachatok tsvetkovykh rasteniy: stroeniye, funktsii, proiskhozhdeniye. [Ovule of flowering plants: structure, functions, origin]. Moscow: KMK Scientific Press Ltd. [In Russian]

SHAMROV I.I. Liliaceae. (1990) – In: // Batygina T.B., Yakovlev M.S. (ed.): Sravnitelnaya embriologiya tsvetkovyih rasteniy. [Comparative Embryology of Flowering Plants]. Vol. 5: p. 63-74. – Leningrad: Nauka. [In Russian]

SMETS E.F., RONSE DECRAENE L.-P., CARIS P. et al. (2000): Floral nectaries in Monocotyledons: distribution and evolution. In: Wilson K.L., Morrison D.A. (ed.). Monocots: systematics end evolution, p. 230-240. – Melbourne: CSIRO.

SOKOLOFF D.D., REMIZOVA M.V., RUDALL P.J. (2012): Evolyutsiya ginetseya odnodolnykh i vysshikh dvudolnykh rasteniy: vsegda li apokarpiya vtorichna? [Gynoecium evolution in Monocots and Eudicots: is apocarpy always a derived condition?] In: Timonin A.K. (ed.) Leonid Vasilyevich Kudryashov. Ad memoriam: Collection of articles, p. 208-231. – Moscow: MAX Press. [In Russian]

SPETA F. (1998): Hyacinthaceae. In: Kubitzki K. (ed.): The Families and Genera of Vascular Plants. Vol. 3: 261-285. – Springer, New York.

STEDJE B. (2001a): Generic delimitation of Hyacinthaceae, with special emphasis of sub-Saharan genera. – Syst. Geogr. Pl. 71: 449-454. DOI: 10.2307/3668693

STEDJE B. (2001b): The generic delimitation within Hyacinthaceae. A comment on works by F. Speta. – Bothalia 31 (2): 192-195.

TAKHTAJAN A. (1964): Osnovy evolyutsionnoy morfologii pokrytosemennykh. [Foundations of the evolutionary morphology of angiosperms], Moscow and Leningrad. [In Russian]

TILTON V.R., HORNER H.T. (1980): Stigma, style, and obturator of *Ornithogalum caudatum* (Liliaceae) and their function in the reproductive process. – Amer. J. Bot. 67: 1113-1131.

TILTON V.R., HORNER H.T. (1983): Carpel development, anatomy, and function in the reproductive process in *Ornithogalum caudatum* (Liliaceae). – Flora, 173: 1-31.

WETSCHNIG W., KNIRSCH W., ALI S.S. et al. (2007): Systematic position of tree little known and frequently misplaced species of Hyacinthaceae from Madagascar. – Phyton (Horn), 47: 321-337.

ZALKO J., DEROIN T. (2018): Floral anatomy and micromorphology of *Hyacinthoides italica* (L.) Rothm. A case of complete stachyospory in Asparagaceae. – Modern Phytomorphol. 12: 81-93. https://doi.org/10.5281/zenodo.1313005

Received: December 21st 2017
Revised: December 7th 2018
Accepted: December 10th 2018