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THE GYNOECIUM STRUCTURE IN *Dracaena fragrans* (L.) Ker Gawl., *Sansevieria parva* N.E. Brown AND *S. trifasciata* Prain (Asparagaceae) WITH SPECIAL EMPHASIS ON THE STRUCTURE OF THE SEPTAL NECTARY

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Abstract

In the gynoecium of *Dracaena fragrans*, *Sansevieria parva* and *S. trifasciata*, the vertical zonality of the ovary, the structural zonality of the gynoecium following Leinfellner, and the zonality of the septal nectary were studied. The ovary structure is characterised by a high parenchymatous ovary base and ovary roof as well as a long septal nectary that can be extended in both of them and opens with secretory nectary splits. The gynoecium of these species has a short synascidiate zone, a fertile hemisynascidiate zone with a median ovule attached, a hemisymlicate zone (only in *D. fragrans*) and an asymplicate zone (with postgenitally fused carpels) that comprises the ovary roof, common style and stigma. In the septal nectary, we detected three vertical zones: the basal zone of the distinct nectary in the ovary base or/and the synascidiate zone, the zone of the common nectary (in the hemisynascidiate and hemisymlicate zones) and the zone of the external nectary (the nectary splits in the asymplicate zone). The gynoecium structure in the studied species shows differences in the length of the gynoecium and septal nectary zones and also in the interrelationships of all these three types of vertical zonality.

Key words: *Dracaena, Sansevieria,* gynoecium morphology, gynoecium vertical zonality, ovary structure, septal nectary zonality

INTRODUCTION

The monocot gynoecium is the subject of numerous new studies regarding the monocot phylogeny and evolution of the flower [1,2,3,4,5]. The *Dracaena* and *Sansevieria* species are closely related [6,7]; they were previously included in the families of Agavaceae [6,8], Convallariaceae [1], Dracaenaceae [7, 9], Ruscaceae [10], but finally they are regarded as members of the large and heterogeneous family Asparagaceae *sensu lato* [11]. The gynoecium structure in some *Dracaena* and *Sansevieria* species was investigated by Wunderlich [6] who conducted a developmental study. Van Heel [12] carried out a SEM study of the gynoecium development of one of *Dracaena* and *Sansevieria* species, while Rudall et al. [1] performed a cladistic analysis of the morphological characters of the flower, including the gynoecium characters. All these researchers confirmed the great resemblance of the two genera, with no diagnostic feature in the gynoecium structure for either of them.

Our aim was to precisely analyse the inner gynoecium structure in *Dracaena* and *Sansevieria* species according to some approaches that have not been previously applied to these genera. To the gynoecium structure, we applied the concept of vertical zonality of the gynoecium after Leinfellner [13]. According to this concept, there are two types of syncarpous gynoecium: eusyncarpous and hemisyncarpous. The latter one is characterised by congenital fusion only in the lateral part of pistil, while the innermost part of the common ovary has a cavity or is postgenitally (dermally) closed. Such a gynoecium has three vertical zones: hemisynascidiate, hemisymplicate and asymplicate, and often a septal nectary.

The septal nectary is an essential feature of the gynoecium in Asparagaceae. It was studied according to the typological approach [2,14,15] and we intended to analyse it with regard to its vertical zonality, too [16,17].

MATERIALS AND METHODS

Flowers of *Dracaena fragrans* Ker Gawl., *Sansevieria parva* N.E. Brown, *S. trifasciata* Prain were collected in the A. V. Fomin Botanical Garden of the Taras Shevchenko National University of Kyiv and fixed in 70% alcohol. For light microscopy observations, the material was sectioned using standard methods of Paraplast embedding and serial sectioning at 20 μm thickness [18]. The sections were stained in Safranin and Astra Blau and mounted in Canada balm. Digital photomicrographs were made using a LABOVAL 4 microscope of CARL ZEISS (Jena) and a CANON 1000 D camera. The height of the gynoecium vertical zones was obtained after the calculation of the transverse sections of the pistil.

RESULTS

Gynoecium structure

The gynoecium of the studied species is trimerous. The ovary is superior, obovate, crumpled, with longitudinal septal grooves**.** In *Dracaena fragrans*, the ovary is 2.0–2.2 mm, in *Sansevieria parva* – 1.3–1.6 mm, in *S. trifasciata* – 2.0–3.8 mm long, about 1.5–1.7 mm in diameter at anthesis. The ovary is trilocular, with one median anatropous ovule in each locule and a long septal nectary. Each ovule has a well-developed funicular obturator (Figs 1 C; 2 B; 3 B). The style is apical (*D. fragrans, S.trifasciata*) or somewhat excentric (*S. parva*), 13–14 mm (*S. parva, D. fragrans*) to 19–26 mm (*S. trifasciata*) long and about 0.2–0.5 mm in diameter. Three channels go through the style (Figs 1 E; 2 E; 3 D). The stigma is trilobate, with closed channels (Figs 1 F; 2 F; 3 E).

As in the previously studied species of *Dracaena-Sansevieria* – the group of Asparagaceae [19, 20, 21], we found three main parts of the ovary of the studied species:

Ovary base – a parenchymatous bottom of the locules, potentially with a septal nectary (Figs 1 A; 2 A). Septal nectaries are present in the upper part of the ovary base in *S. parva* and *S. trifasciata.*

Ovary locules – the main part of the ovary with three cavities covered with the inner epidermis of the carpels and the cavity of the septal nectary. The ovule is attached in the middle part of the locule, the funiculus is short and directed upwards. The micropyle is directed downwards and composed only of the inner integument (Fig. 4 A–C).

Ovary roof – the closed part above the locules where the style channels are present, continuing up to the level where the nectaries disappear and the style structure is available. The ovary roof structure differs from the style structure in a much greater diameter and the presence of the septal nectaries – two features that are characteristic of the ovary structure (Figs 1 D; 2 D; 3 C). In *S. parva* the style channels are not located apically but are shifted about 140 μm to the ventral side of the locule.

In the studied species, the maximal height of the ovary base and ovary roof is found in *S. trifasciata*, but the locules are maximal in *D. fragrans* (Table 1). Due to a considerable size of the ovary base and roof, the locule height is only about ½ of the total ovary height (between 42% in *S. trifasciata* and 57% in *D. fragrans*) (Table 1).

In accordance with the concept of vertical zonality of the gynoecium [13], we found four gynoecium vertical zones in the studied species:

synascidiate zone – the shortest gynoecium zone (60–180 μm) with three disconnected locules. In the studied species, it is non-typical because of the presence of distinct septal nectary cavities (Fig. 1 B). As in the case of the locules, the nectary cavities here have no common epidermis and in this zone there are in fact six distinct cavities – three locules and three nectaries.

hemisynascidiate zone – a zone with three disconnected locules and triradial fissure in the centre. The distal parts of this fissure form septal nectary cavities, but the central part is postgenitally closed and visible as two rows of epidermal cells. This zone is long (Table 1) and a median ovule is attached to the cross-zone of each carpel (Figs 1 C; 2 B; 3 B).

hemisymplicate zone – a zone of partly fused carpels where ventral splits of carpels appear but postgenitally closed and visible as two rows of epidermal cells. In this zone, the septal nectary is also available as in the hemisynascidiate zone and it has a congenitally fused external wall. This zone is present in the upper part of the locules and in the ovary roof in *D. fragrans.*

asymplicate zone – this zone after Leinfellner [13] has no congenital fusion between carpels. We distinguish the functionally asymplicate zone with no fusion between carpels and the structurally asymplicate zone with postgenital fusion due to which the common style and stigma arise. In the studied species, the carpels in this zone are fused postgenitally. This zone begins at the level where each septal nectary cavity unites distally with the septal groove (Figs 1 D; 2 C; 3 C). In *D. fragrans* it occurs at the top level of the ovary roof, in *S. parva* – at the upper part of the locules, in *S. trifasciata* – at the level where the style channels occur (Fig. 5). The asymplicate zone continues higher through the ovary roof, style and stigma.

In the ovary of *Dracaena-Sansevieria* species, the hemisynascidiate zone is the most stable in length (Table 1), perhaps because of its functional value (ovule bearing).

Table 1
Height of the gynoecium structures
in *Dracaena* and *Sansevieria* species

Height, µm \ Species	*D. fragrans***	*S. parva*	*S. trifasciata*
Locule	1000–1250	800	720–800
Ovary base	340	480	500
Ovary roof	420	180	700
Synascidiate zone	180	100	60
Hemisynascidiate zone	520–880	480	660
Hemisymplicate zone	360	–	–
Asymplicate zone at the ovary level	100	400	700
Septal nectary total*	1250	1100	1530
Nectary split	108	385	700
Nectary split to septal nectary total*, %	9	35	46
Ovary base – locules – roof to ovary, in %	19–57–24	33–55–12	26–42–32
Septal nectary total* to ovary, in %	62–71	75	76
Septal nectary total to locule height	1,0–1,2	1,4	1,9–2,1

*Note. Septal nectary total includes the height of the nectary cavity and nectary split
** Note. The parameters were defined for the floral bud and anthetic flowers and can be slightly different.

Septal nectary structure

The septal nectary cavities are available throughout the ovary; they are covered with secretory epidermis from the very base and do not have a defending channel, as was presumed by D a u m a n n [14] for all species with the septal nectary. On the contrary, they have apically located secretory nectary splits, often of considerable length, located in the ovary roof (Figs 1 D; 2 C, D; 3 C). The walls of the splits are covered with the same secretory epidermis as the walls of the septal nectary cavities and this makes them well visible in the stained sections.

Following the descriptive classification of S c h m i d [15], the septal nectary in all studied species is distinct, not labyrinthine, but in the upper part sometimes slightly labyrinthine (in *Sansevieria* species). After D a u m a n n [14], they are inner in the lower part and outer (external) in the upper part (nectary splits).

To the studied species, we applied the concept of vertical zonality of the septal nectary [16,17]. According to it, one can distinguish some vertical zones in the structure of a typical septal nectary analogously with the vertical gynoecium zones described by Leinfellner [13].

These zones are as follows:

1) zone of **distinct nectary** (not in Schmid's sense) – where there are three epidermally disconnected nectariferous cavities located in the ovary base beneath the locules (Fig. 2 A) and in the synascidiate zone.
2) zone of **common nectary** – a zone with three nectary cavities united in the ovary centre by a common epidermal surface, with a postgenitally closed central part of the nectary. This zone is available at the level of the hemisynascidiate (Fig. 3 A) and hemisymplicate zones of the gynoecium and above.
3) zone of **external nectary** – the upper part of the previous zone at the level where the septal grooves fuse with the nectariferous cavities (the base of the asymplicate zone). Here, the septal nectary is presented as slightly flexuosus (in *S. parva, S. trifasciata*) or straight (*D. fragrans*) **nectary splits,** opened to the exterior (Figs 1 D; 2 D; 3 C). In *Sansevieria* species, the splits reach about half of the ovary roof radius, while in *D.fragrans* they are short in radial direction.

The total height of the septal nectary includes the height of the septal nectary cavity and the height of the nectary split. The total septal nectary height exceeds twice the locule height in *S. trifasciata* and is about $^{2}/_{3}$ of the ovary height (Table 1). In *D. fragrans* the nectary split to total septal nectary is about $^{1}/_{10}$, while in *Sansevieria* species it reaches $^{1}/_{3}$ to $^{1}/_{2}$ (Table 1; Fig. 5).

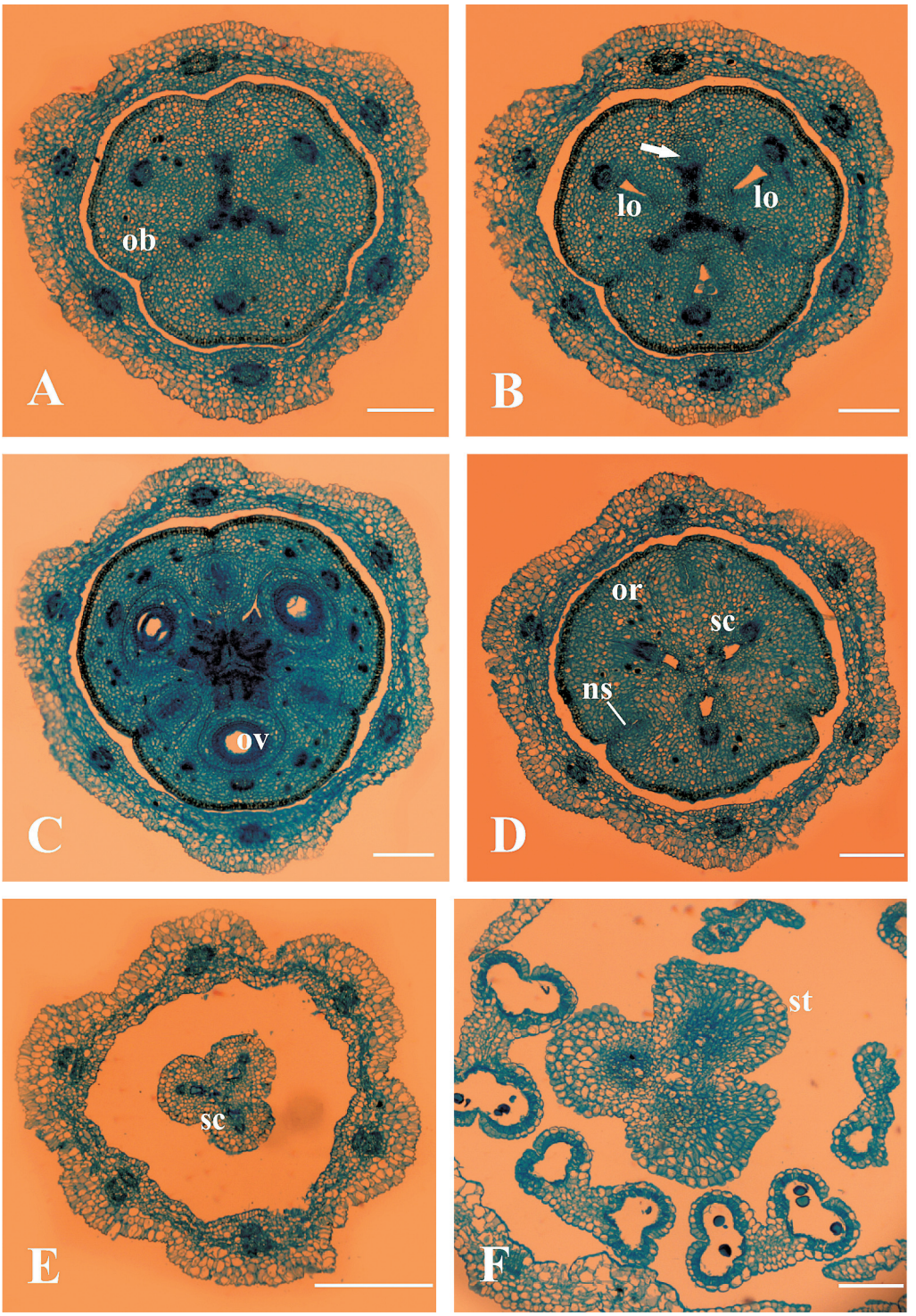

Fig. 1. Transverse sections of *Dracaena fragrans* gynoecium zones. Scale bars 250 μm.
ob – ovary base, lo – ovary locule, ov – ovule, ns – nectary split, or – ovary roof, sc – style channel, st – stigma. Arrow in B shows the distinct septal nectary bottom.

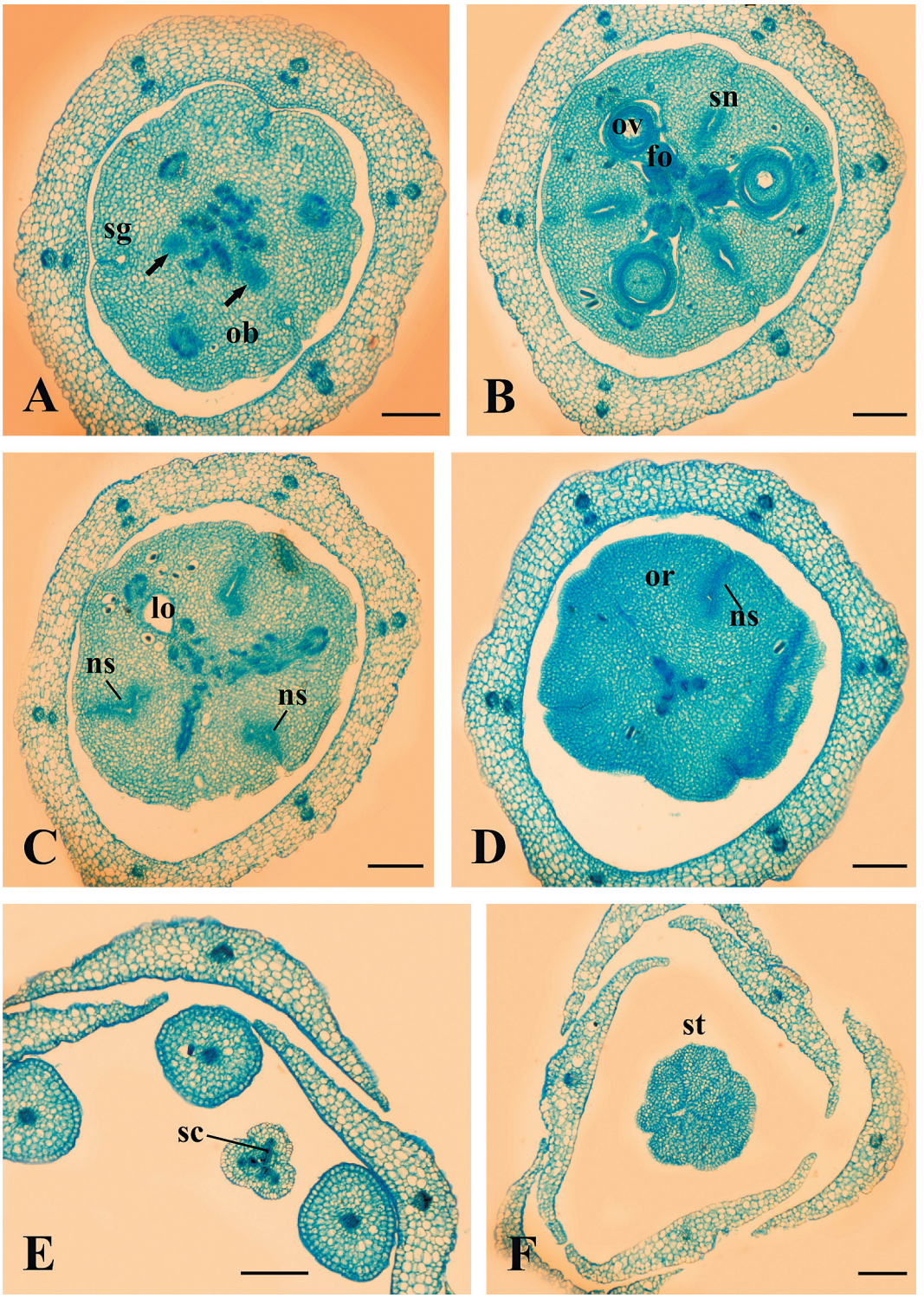

Fig. 2. Transverse sections of *Sansevieria parva* gynoecium zones. Scale bars 250 μm.
sg – septal groove, ob – ovary base, ov – ovule, fo – funicular obturator, sn – septal nectary cavity, ns – nectary split, lo – ovary locule, or – ovary roof, sc – style channel, st – stigma.
Arrows in A show the distinct septal nectary bottom.

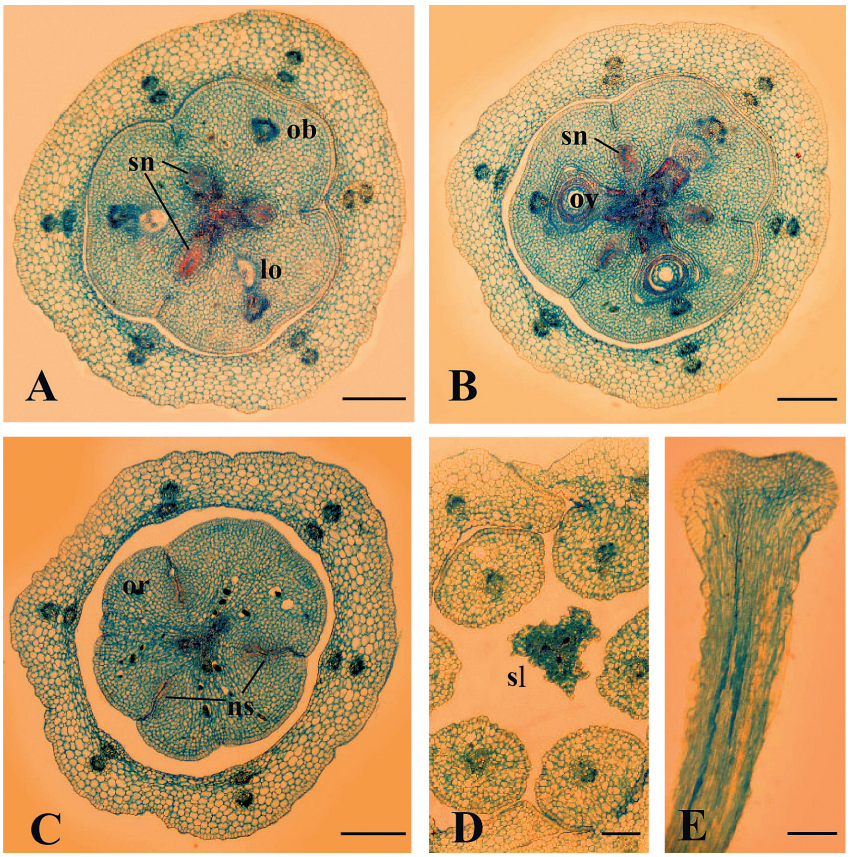

Fig. 3. A – D – Transverse sections of *Sansevieria trifasciata* gynoecium zones, E – longitudinal section of style and stigma. Scale bars 250 μm.
sn – septal nectary cavity, ob – ovary base, lo – ovary locule, ov – ovule, or – ovary roof, ns – nectary split, sl – style.

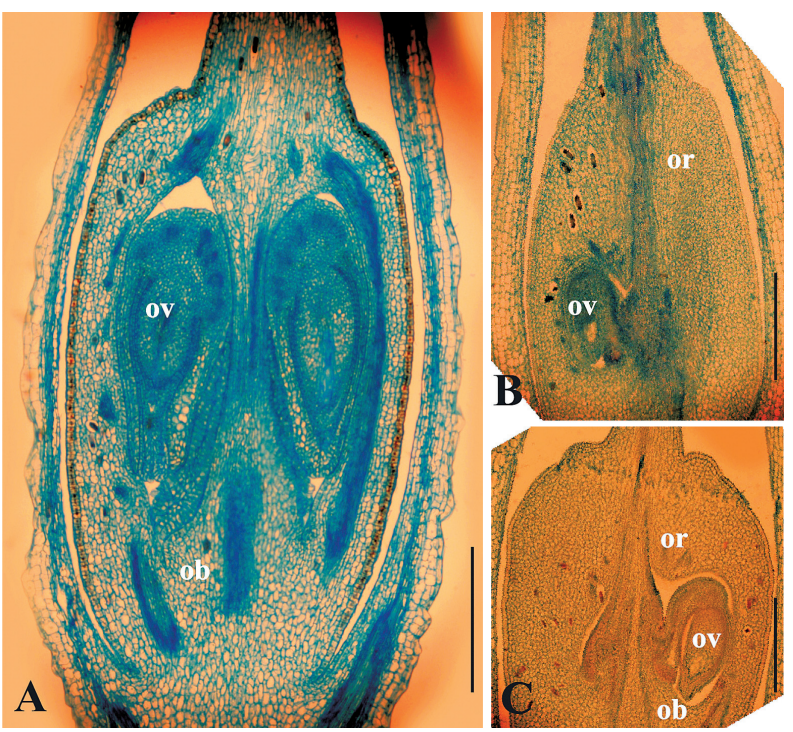

Fig. 4. Longitudinal sections of gynoecium *Dracaena fragrans* (A), *Sansevieria trifasciata* (B), *S. parva* (C). Scale bars 250 μm.
ob – ovary base, ov – ovule, or – ovary roof.

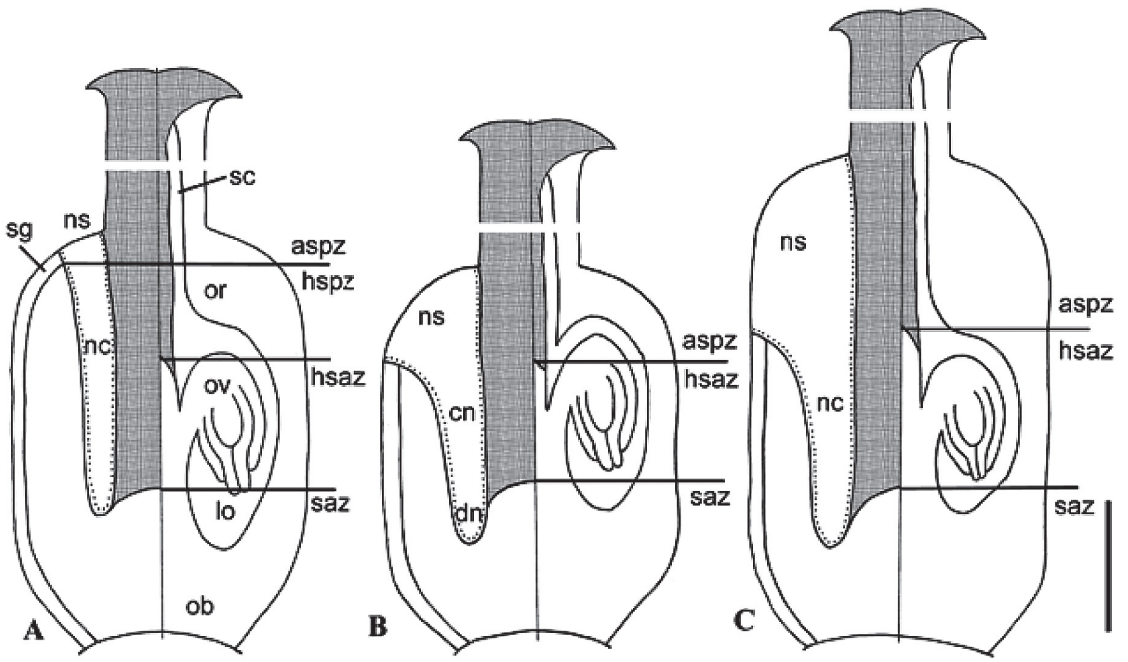

Fig. 5. Vertical zonality of the gynoecium of *Dracaena fragrans* (A), *Sansevieria parva* (B) and *S. trifasciata* (C). Scale bar 0.5 mm. aspz – asymplicate zone, cn – zone of common nectary, dn – zone of distinct nectary, hspz – hemisymplicate zone, hsaz – hemisynascidiate zone, lo – ovary locule, nc – nectary cavity, ns – nectary split, ob – ovary base, or – ovary roof, ov – ovule, saz – synascidiate zone, sg – septal groove, sc – style channel, postgenitally fused surfaces are hatched.

DISCUSSION

Our study has revealed many common features of the gynoecium structure in *Dracaena-Sansevieria* species. The first of them is the presence of a massive ovary base and roof with the prolongation of the septal nectary in both of them (only in the ovary roof in *D. fragrans*). Wunderlich [6] was the first who noted the prominent ovary base in *Sansevieria* species. She also revealed the median location of the ovule to the long cross-zone of the carpel.

We assume that two reasons explain the fact that the locule height is about ½ of the total ovary height:

1) The ovary base and roof provide the greated height of the septal nectary (up to twice longer that locule). In the ovary base distinct or common nectary zones are located. In *D. fragrans* with the lowest height of the ovary base, the septal nectary occurs only at the level of the locules. In the ovary roof, the external nectary zone (nectary splits) is located; in *Sansevieria* species it is prominent and long (400–700 μm). In *S. parva* the external nectary zone is shifted to the locule level and the ovary roof height is less than in other species. In *S. trifasciata* both the ovary base and the roof are prominent (overall, they account for about 60% of the ovary height) and the septal nectary height is the greatest.
2) The parenchymatous ovary base and roof can provide succulent parts of the berry-like fruit of these species, while the ovary wall remains thin.

The second common feature of the gynoecium is the presence of the synascidiate zone in the hemisyncarpous gynoecium of *Dracaena-Sansevieria* species. The synascidiate zone in these species contains three cavities of carpels and three cavities of septal nectaries (zone of distinct nectary). We consider these six cavities arised in similar way during the differential growth of the base of pistil with septal nectary. The occurrence of the synascidiate zone in the hemisyncarpous gynoecium makes it necessary to expand Leinfellner's [13] gynoecium classification, especially for monocot taxa [22].

As was noted by van Heel [12], the degree of carpel fusion in *Dracaena-Sansevieria* species is not great. In *S. parva* the asymplicate zone begins at the locule level and in *S.trifasciata* it begins at the locule apex.

The third common feature of the gynoecium of *Dracaena-Sansevieria* species is a considerable height of the septal nectary and its vertical zonality. The septal nectary is divided into the nectary cavity (distinct and common portions) and the nectary splits.

We consider the mentioned unique features to be characteristic for the *Dracaena-Sansevieria* group of the Asparagaceae family. Our approach gives us the possibility to differentiate the species and perhaps genera based on the location and presence of various vertical zones in the gynoecium, and in the nectary particularly. The gynoecium structure in the studied species shows differences in the length of the gynoecium and

septal nectary zones and also in the interrelationships of all these three types of vertical zonality.

In general, the following traits are characteristic of *D. fragrans*: the least total height of the ovary base and roof, the presence of the hemisymplicate zone, the least developed septal nectary, especially the nectary split. Opposite features are characteristics for both *Sansevieria* species. The nectary split in *D. fragrans* has the least vertical and radial extent and a straight surface. This fact and the least ratio of total nectary height to ovary and locule height are evidence of the lowest nectar production in this species.

CONCLUSIONS

1. In the gynoecium of the studied species, the ovary base and ovary roof are found to be high. This gynoecium is hemisyncarpous *sensu lato*, because it comprises hemisynascidiate and hemisymplicate zones, but it also has a synascidiate zone that is characteristic of the eusyncarpous type of gynoecium. In *Sansevieria* species, the hemisymplicate zone is absent. The style is composed of the asymplicate zone.
2. The total septal nectary height considerably exceeds the locule height, because there are secretory nectary splits in the ovary roof above the locules and a distinct nectary in the ovary base (in *Sanseviria*). Such type of gynoecium zonality has not been previously revealed for *Dracaena* and *Sansevieria* species. The presence and height of various vertical zones of the ovary, gynoecium and septal nectary as well as the interrelationships of all these three types of vertical zonality gives the possibility to differentiate the studied species more precisely.

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Author's contributions:

Concept of the study: AO, microscopical analysis OF, AO, photographs OF, AS, drawing figure AO, analysis of research results AO, OF, AS, writing of the manuscript AO, OF, AS.

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Struktura słupków *Dracaena fragrans* (L.) Ker Gawl., *Sansevieria parva* N. E. Brown i *S. trifasciata* Prain (Asparagaceae) ze szczególnym uwzględnieniem budowy nektarników przegrodowych

Streszczenie

W słupkach *Dracaena fragrans*, *Sansevieria parva* i *S. trifasciata* badano pionową strefowość zalążni, strukturalną strefowość słupka w ujęciu Leinfellner'a oraz strefowość nektarników przegrodowych. Zalążnia słupków tych taksonów charakteryzuje się wysoką podstawą utworzoną z tkanki miękiszowej, jak również wysoką częścią apikalną. Długi przegrodowy nektarnik może rozciągać się w obu tych częściach i otwiera się szczelinami nektarnikowymi. Słupki analizowanych taksonów posiadają krótką strefę określaną jako synascidiate, płodną strefę z centralnym zalążkiem (hemisynascidiate), strefę wyróżnioną jako hemisypmlicate (tylko u D. *fragrans*) oraz strefę nazwaną asymplicate ze zrośniętymi owocolistkami, która obejmuje górną część zalążni, szyjkę i znamię. W nektarniku przegrodowym zarejestrowano trzy pionowe strefy: bazalną strefę nektarnika u podstawy zalążni lub/i strefę określoną jako synascidiate typowego nektarnika w strefie hemisynascidiate i hemisypmlicate zalążni oraz zewnętrzną strefę nektarnika (szczeliny nektarnikowe w strefie asymplicate). Słupki badanych gatunków różnią się długością, wysokością stref obejmujących nektarniki przegrodowe, a także powiązaniami między trzema typami wertykalnej strefowości.

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