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## INVITED ORIGINAL RESEARCH PAPER

# The flower morphology in three Convallariaceae species with various attractive traits

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**Abstract**

The general morphology and micromorphology of the flower in *Polygonatum multiflorum*, *Maianthemum bifolium*, and *Convallaria majalis* were studied using light microscopy methods. Among the studied species, *P. multiflorum* and *C. majalis* have sympetalous and trimerous flowers, and in *M. bifolium* flowers are the most reduced: they are dimerous, pentacyclic, and with free tepals. Only in *P. multiflorum* stamens are considerably adnate to the floral tube. The gynoecium of *P. multiflorum* consists of synascidiate, hemisymphicate, and asymplicate zones. In the gynoecium of *M. bifolium* and *C. majalis*, synascidiate, symplicate, and asymplicate vertical zones were revealed. In *P. multiflorum* and *M. bifolium*, the style is composed of postgenitally connated carpels, while in *C. majalis* the style is formed by congenitally fused carpels (symplicate gynoecium zone). A common pattern of the venation of the floral parts was revealed in all the species.

The external flower morphology and the gynoecium inner structure are different in all three species, providing adaptations for the pollination mode. Attractive elements observed in the flower of *P. multiflorum* are the long septal nectary in the ovary and epidermal trichomes on the inner perigonium surface and on the filaments. In *M. bifolium*, a rudimentary external septal nectary was observed for the first time. No nectaries or other morphologically distinct secretory structures were found in the *C. majalis* flower, allowing considering the *C. majalis* flowers as pollen flowers.

**Keywords**

*Polygonatum multiflorum*; *Maianthemum bifolium*; *Convallaria majalis*; flower adaptations; gynoecium structure; vertical zonality; septal nectary

**Introduction**

The monocot family Convallariaceae (17/130) [1], with the Eurasian – North American distribution, is now placed within the heterogeneous family Asparagaceae s. l. as a part of Ruscaceae s. l. [2,3], basically on the ground of molecular data, and from this point of view, it is the object of morphological and phylogenetical studies [4–6]. The flower morphology of some Convallariaceae (Convallariaceae: *Aspidistra*, *Rohdea*, *Tupistra*, *Convallaria*) reveals the absence of septal nectary – a characteristic structure of the gynoecium in most of Asparagaceae s. l. [5].

In the flora of Ukraine, three genera of Convallariaceae occur (excluding *Streptopus amplexifolius* that is now placed in Liliaceae): *Polygonatum* (six species), *Maianthemum* (one species), *Convallaria* (one species) [7], and in the latest source [8] they are seen as members of the Ruscaceae s. l. All three genera are perennial forest herbs with underground rhizomes, on which generative shoots arise. Flowers are grouped in racemose inflorescences. Fruits are berries, dispersed presumably by birds; clonal

reproduction by means of fragmentation is also effective, especially in *Maianthemum* and *Convallaria* [9–13]. Although *Polygonatum* and *Maianthemum* (tribe Polygonateae) are closer related than both of them to *Convallaria* (tribe Convallarieae) [1,5], the structural and functional adaptations of flowers are different in all of them. While for *Polygonatum* the homogamy (absence of dichogamy), septal nectaries [14,15], and a great amount of nectar are reported [16], *Convallaria* flowers are proterandrous [9], and *Maianthemum* flowers are slightly protogynous [10]. Both latter genera are nectarless [14]. For *Polygonatum*, “buzz-pollination” is showed [1,17].

This study is focused on two aspects of the flower structure of Convallariaceae members: the recognition of conservative, evolution-significant traits of the flower, common for Convallariaceae and the other Asparagaceae s. l., and secondly, identification of the morphological flower traits adaptive for insect or self-pollination.

## Material and methods

### Studied species

For this study, three species were selected: *Polygonatum multiflorum* (L.) All., *Maianthemum bifolium* (L.) F. W. Schmidt, and *Convallaria majalis* L. *Polygonatum multiflorum* has unbranched thick sympodial rhizomes with the arcuate generative upper parts of sympodia, bearing fascicles of 3–5 flowers in axils of assimilative leaves. Stamens are epitepalous [1,16]. *Maianthemum bifolium* has long plagiotropous unbranched rhizomes and erect generative shoots with two assimilative leaves. The inflorescence is a compound bracteose raceme of 2–5-flowered umbels, totally 4–23 flowers per inflorescence are reported [10]. *Convallaria majalis* has branched monopodial rhizomes with erect fragments bearing two assimilative leaves and axillary inflorescence – a bracteose raceme of 3–11 flowers [9].

### Material treatment

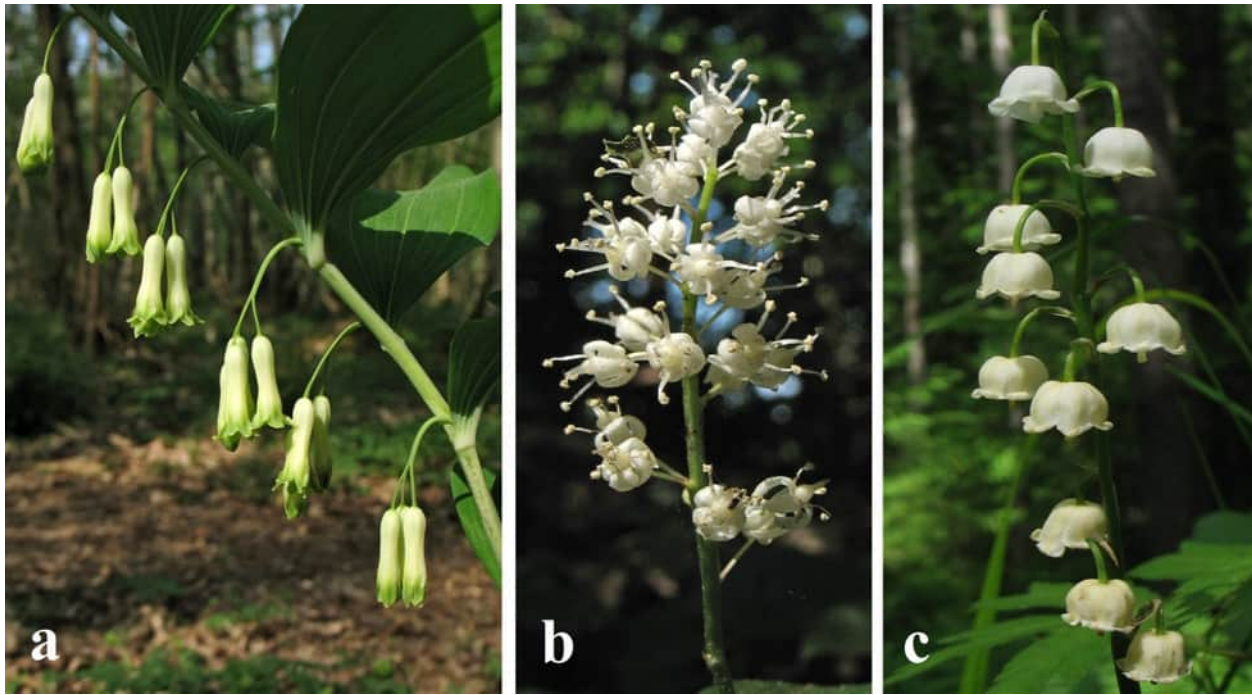
Flower buds and anthetic flowers were collected in Lviv and Volyn regions, Ukraine, in 2014–2015, in natural conditions. Material was fixed in 70% ethanol or acetic alcohol. Flower buds just before anthesis were embedded in Paraplast using standard method and serial-sectioned at 20 µm thickness [18]. Sections were stained with safranin and Astra Blue and mounted in Canada balm. Photos of the flowers were made using a SZ 61 microscope and a SC 30 camera (Olympus, Germany) as well as an XS-2610 microscope (MICROMED, China) and an AmScope-3.7 digital ocular (AmScope, USA).

The inner gynoecium structure was analyzed based on the concept of the gynoecium vertical zonality by W. Leinfellner [19]. The septal nectary structure was analyzed according to the terminology by Daumann, Schmid, and Odintsova; all the concepts are explained in [14,20,21], respectively, a review in [22]. The absolute and relative height of the gynoecium zones was calculated from the number of transversal serial-sections of five flowers of each species.

## Results

### General flower morphology and venation of floral organs

***Polygonatum multiflorum*.** Flowers are pendulous, tubular, 19 mm long; the pedicel is up to 13 mm long (Fig. 1a). The floral tube is about 3.2 mm in diameter, white (Fig. 2a). Free parts of the perigonium are about 3 mm long, obtuse triangulate, with a pubescent tip, greenish, slightly declined at anthesis. The inner surface of the floral tube on its upper part and free tepals are densely covered with pear-shaped papillae (Fig. 3a, Fig. 4h–j), the other epidermal cells of the inner surface of the floral tube



**Fig. 1** Flowering shoot of *Polygonatum multiflorum* (a), *Maianthemum bifolium* (b), *Convallaria majalis* (c) (photos by Andriy Kovalchuk, with permission).

are small, convex and densely stained (Fig. 4b,g, Fig. 7a). Stamens are erect, adnate to the floral tube with their filaments (Fig. 4h). Filaments are pubescent above the middle-height of its length with short simple trichomes with striate surface (Fig. 3b,c, Fig. 4i). The trichomes are longer and bicellular on the upper part of the filament and connective. Anthers are located on the short free filament parts near the upper margin or the floral tube; inner stamens are slightly longer (Fig. 2b). Anthers are 3.2 mm (inner stamens) to 3.5 mm long (outer stamens), oblong, introse, dorsifix, attached to the filament on its lower part. The anther base is bilobed, and the anther apex is whole. The ovary is ellipsoid, 1.8–2.1 mm in diameter and 3.0–3.2 mm long (Fig. 2c). The style is erect, terminal, about 7–9 mm long, and it elongates during anthesis: at the beginning the stigma exposes below anthers (Fig. 2b, Fig. 3h), while at the end of anthesis it reaches the anther apex (Fig. 2a). Stigmatic lobes are short, bifurcate at the apex, covered with long unicellular papillae (Fig. 4h).

From the receptacle, six common vascular bundles enter the floral tube and each one divides at once into the tepal trace and stamen trace, both one-bundled and unbranched (Fig. 4a). In the gynoecium, three dorsal carpellary veins and three pairs of ventral veins are formed (Fig. 4a,b). The latter fuse in pairs into three V-shaped septal bundles (Fig. 4c) from which ovule traces arise. In the upper part of the ovary above placentae, no vascular bundles are evident. Only dorsal carpellary veins extend through the ovary and style (Fig. 4c–g). The septal nectary obtains no distinct vascular supply.

***Maianthemum bifolium*.** Flowers are erect, born on pedicels about 3.5 mm long (Fig. 1b). Tepals are free, 3.5 mm long, 1.4 mm wide, white, recurved below at anthesis (Fig. 2d). Stamens are attached to the receptacle (Fig. 5a), erect, equal in length to each other and to the pistil, declined at anthesis (Fig. 1b, Fig. 2d). Anthers are ca. 1 mm long, widely ovoid (Fig. 2e), dorsifix, attached to the filament on its lower part. The anther base is bilobed (Fig. 5g) and the anther apex is whole. The ovary is spheroid, 1.0–1.2 mm in diameter, with a narrow base (Fig. 2f). The style is 1.5 mm long; the stigma is bilobed, oblique (Fig. 2d,f), covered dorsally with short papillae (Fig. 5h). Flowers are fully glabrous.

Each tepal and stamen of *M. bifolium* obtain one unbranched trace immediately from the receptacle (Fig. 5a). In the gynoecium, two dorsal carpellary veins are formed as well as a central vascular strand (the stele) (Fig. 5b), dividing into two septal





**Fig. 2** Anthetic flower and flower details of Convallariaceae. **a–c** *Polygonatum multiflorum*. **a** Flower in longitudinal section at late anthesis. **b** Fragment of the floral tube with stamens, stigma is visible below the anthers. **c** Ovary with septal grooves visible. **d–f** *Maianthemum bifolium*. Flower (**d**), stamen (**e**), pistil (**f**). **g–i** *Convallaria majalis*. **g** Flower in longitudinal section; apically open anthers are visible. **h** Stamen adnate to the floral tube. **i** Pistil. Scale bars: **a–d, f–i** 1 mm; **e** 200  $\mu$ m.

bundles supplying the ovules (Fig. 5c,d). Four ventral veins are visible in placenta above the ovules (Fig. 5e).

***Convallaria majalis***. Flowers are pendulous, campanulate, 8 mm long, 7.5 mm in diameter (Fig. 1c, Fig. 2g). The pedicel is up to 15 mm long. The flower tube is 5.5 mm long, 7.5 mm in diameter, free parts of the perigonium are 2.0–2.5 mm long and 2.6 mm wide, white. Flowers are somewhat monosymmetric: some stamens are born at the base of the floral tube (Fig. 2h), while the other stamens are attached to the receptacle (Fig. 6a). Stamens are significantly shorter than the style; filaments are cylindrical, two times shorter than anthers. Anthers are dorsifix, oblong, 2.5 mm long, attached to filament on its lower part (Fig. 2h). The anther base is bilobed (Fig. 6b,c) and the anther apex is whole (Fig. 6h). Anther opening begins apically (Fig. 2g). The pistil is about 5 mm long. The ovary is ovoid, 2.0 mm in diameter (Fig. 2i), and it gradually transforms into the style. The stigma is trilobate, with unequal lobes, covered with long papillae (Fig. 2i, Fig. 6j). Flowers are fully glabrous.

As in *M. bifolium*, all tepal and stamen traces in *C. majalis* are formed in the receptacle, sometimes from the short common bundles (Fig. 6a). Three dorsal carpellary veins and the central group of about nine bundles enter the ovary (Fig. 6b, Fig. 7b). Among them, there are three pairs of ventral veins supplying the lower ovules and three bundles which enter the incomplete septae of the ovary and supply the uppermost ovules (Fig. 6d).

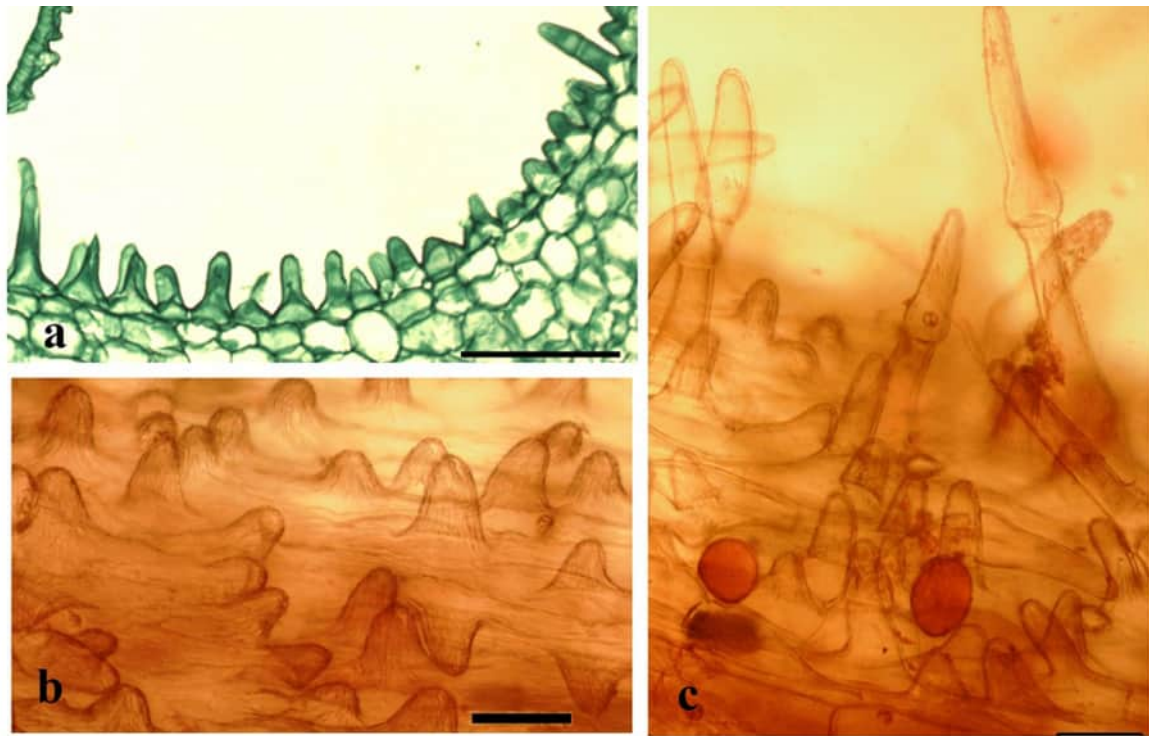
#### Gynoecium micromorphology

***Polygonatum multiflorum***. The ovary is trilocular on most of its length, with two ovules in each locule placed one above another. In the ovary, three vertical structural and functional zones are present: ovary base (Fig. 4a,b), ovary

locules (Fig. 4c–e), and ovary roof (Fig. 4f). The locule height covers about 2/3 of the ovary height (Tab. 1, Fig. 7a). Above the ovules, locules merge together and form a common three-lobed cavity of the ovary (Fig. 4e), continuing into the style as a cylindrical style channel (Fig. 4f,g). Funicular collar-like obturators are formed on the ovules (Fig. 4d), and also placental obturators on the incomplete septae composed of secretory papillate epidermises (Fig. 4e).

The gynoecium of *P. multiflorum* contains three vertical zones sensu Leinfellner [19] (Tab. 1): sterile synascidiate zone in which the lower ovules hang (Fig. 4c), hemisymphic zone that is fertile in the lower portion (Fig. 4d,e) and asympic zone (Fig. 4g,h) that forms the ovary roof and continues into the style and stigma. Placentation is, therefore, parietal (hemisymphic zone is fertile).

The septal nectary of *P. multiflorum* is located throughout the ovary from the synascidiate zone up to the style base (Fig. 4c–f, Fig. 7a). In the transversal sections, the septal nectary looks like three separate slits (“lilioid” septal nectary sensu Schmid [20]). Nectary epidermis is glandular on the whole of the nectary surface. In its lower



**Fig. 3** Epidermal trichomes of *Polygonatum multiflorum*. **a** Tepaline papillae, note a bicellular papilla in the upper right corner of the photo. **b** Short trichomes on the lower part of the filaments with striate surface of the papillae. **c** Long multicellular trichomes on the upper parts of the filaments, with pollen grains attached. Scale bars: **a** 250  $\mu\text{m}$ ; **b,c** 50  $\mu\text{m}$ .

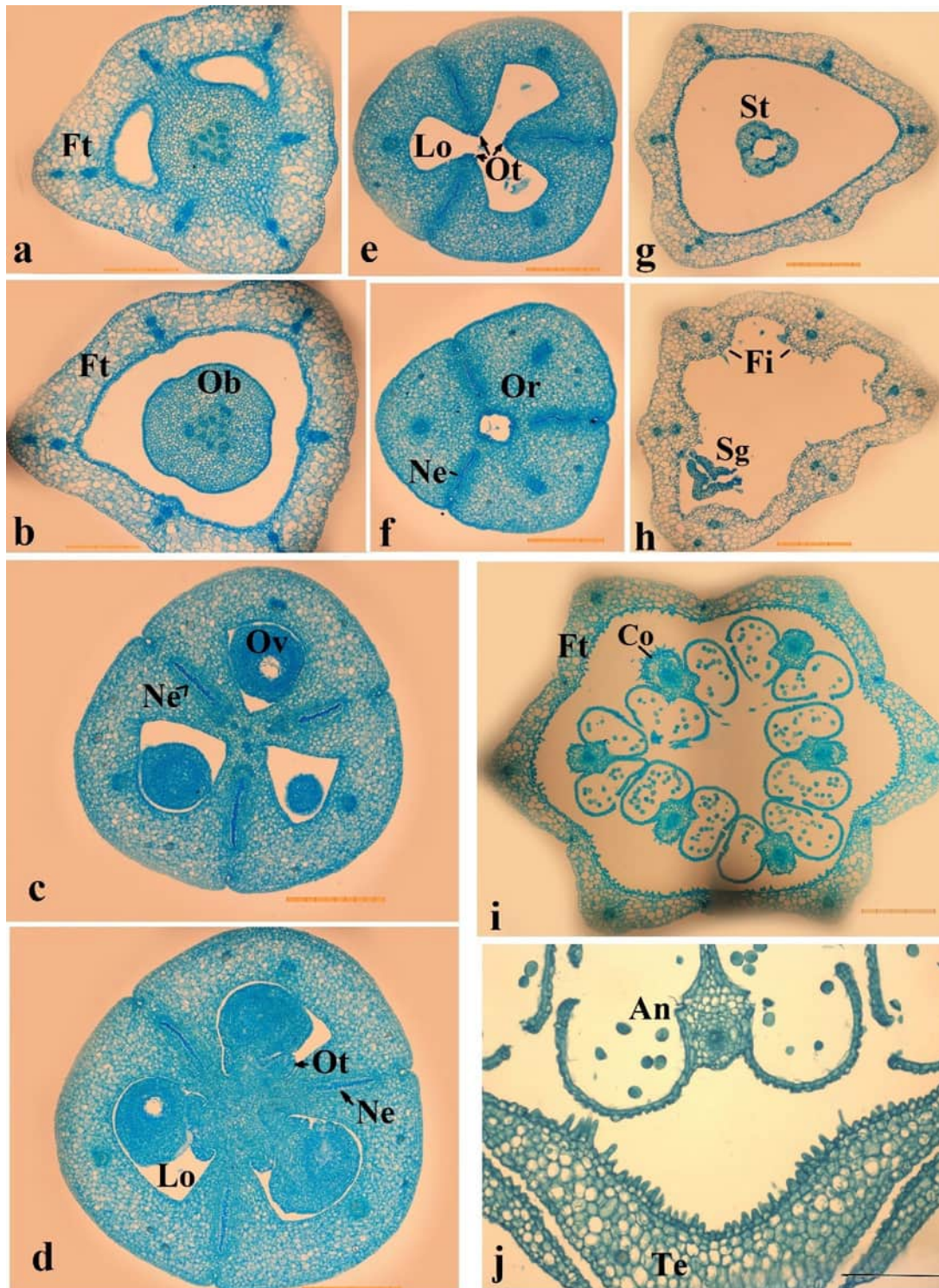
portion (in the synascidiate zone), it has no common epidermis (Fig. 4c), while above (in the hemisymphic and asymphic zones) three nectary cavities are united with the non-secretory epidermis in the center of the ovary (Fig. 4d-f). The septal nectary comprises two structures: the septal nectary body (the inner nectary sensu Daumann [14]) and the nectary split where nectar can be released outside (the outer nectary sensu Daumann [14]) (Tab. 1). The septal nectary body reaches half of the ovarian radius; in the ovary roof the septal body becomes slightly undulate (Fig. 4f). Narrow septal grooves on the ovary surface are connected with the nectary splits in the ovary apex (Fig. 2c, Fig. 4c-f).

***Maianthemum bifolium*.** The ovary is bilocular, with two ovules in every locule (Fig. 5c). The ovary base (Fig. 5a,b) and ovary roof (Fig. 5g) are not prominent; ovary locules prevail in the ovary height (Tab. 1). Both funicular and placental obturators are formed (Fig. 5c-e). The ovary locules continue into the style as two narrow channels that soon vanish (Fig. 5g,h). In the ovary roof, carpels are separated centripetally from each other with their epidermises, but still remain connected postgenitally.

The *M. bifolium* gynoecium contains three vertical zones sensu Leinfellner [19]: synascidiate (Fig. 5b,c), symplicate (Fig. 5d,e), and asymphic; the latter occupies the upper part of the ovary and forms the style and stigma (Fig. 5g-i). The hemisymphic zone is not formed. The ovules are attached at the boundary between the synascidiate and symplicate zones, with most part of the funiculi attached on the symplicate zone (Fig. 5c,d). The placentation is presumably defined as parietal. In the upper part of the ovary septal grooves covered with secretory epidermis were sporadically found, at most about 220  $\mu\text{m}$  in height (Fig. 5e), which are considered as a rudimentary outer septal nectary.

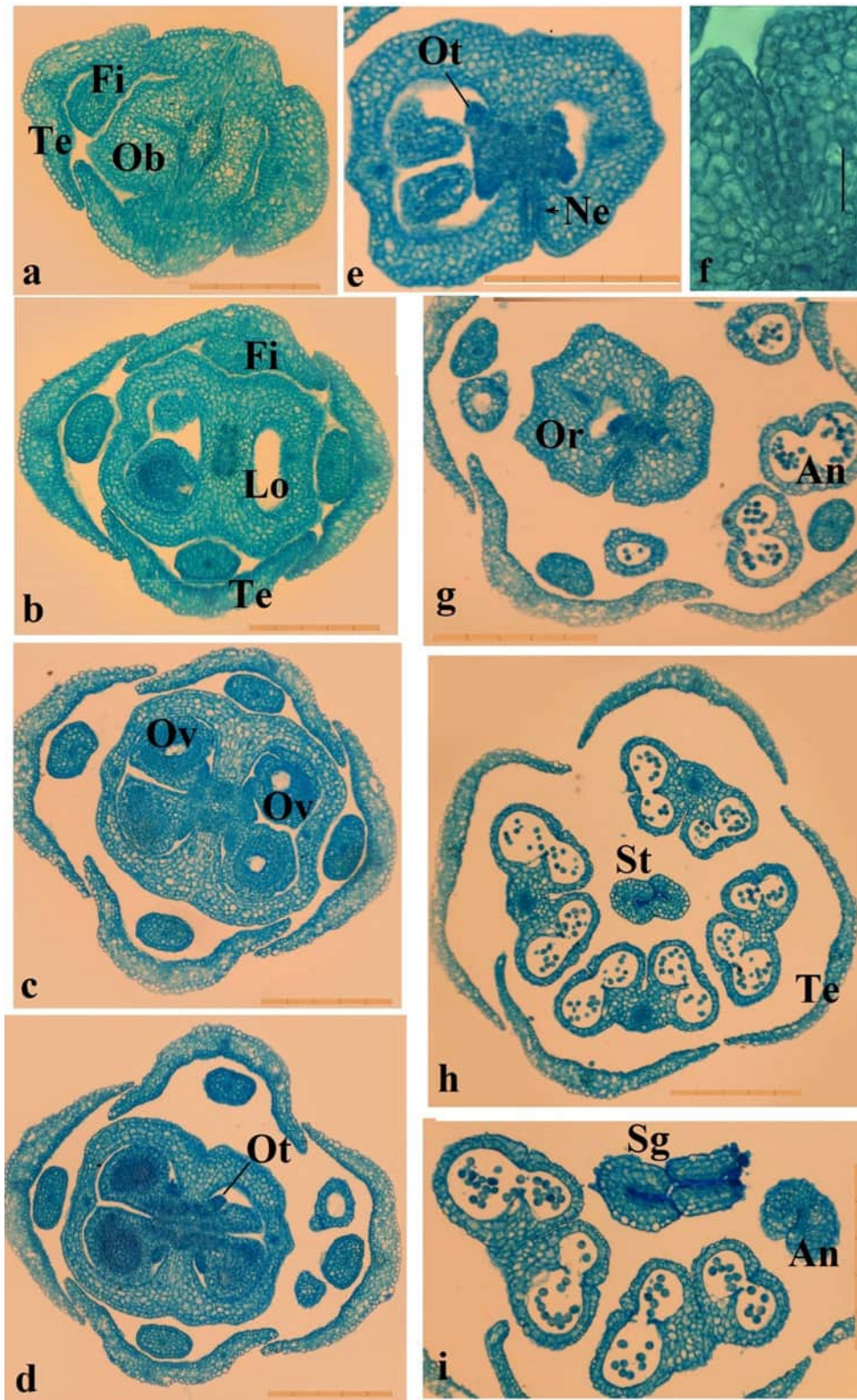
***Convallaria majalis*.** The ovary is mostly trilocular, with six ovules in each locule placed in three pairs (Fig. 7b). The height of the ovary locules (Fig. 6c-g) is greater than the height of the ovary base (Fig. 6b) and ovary roof together (Tab. 1). Funicular obturators (Fig. 6c) and also placental obturators are formed on the incomplete septa (Fig. 6d-g). The style channel is triradiate and triangular in the proximal and distal portion, respectively (Fig. 6h,i).





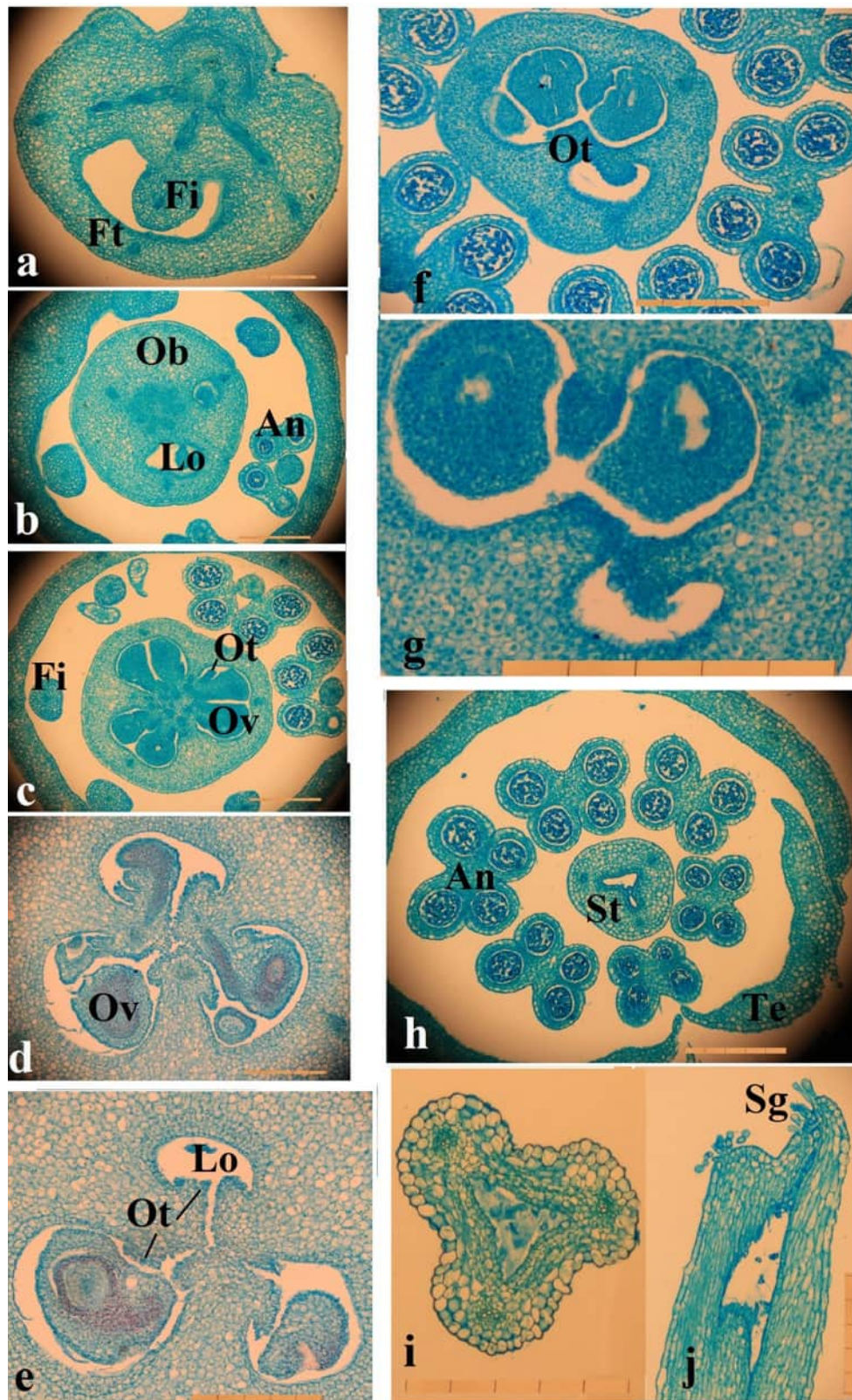
**Fig. 4** Ascending series of transversal sections of the flower of *Polygonatum multiflorum*. In **c,d,e,f**, only the ovary is shown. **j** Fragment of the tepal and stamen. An – anther; Co – connective; Fi – filament; Ft – floral tube; Lo – ovary locule; Ne – septal nectary; Ob – ovary base; Or – ovary roof; Ot – obturator; Ov – ovule; Sg – stigma; St – style; Te – tepal. Scale bars: 500  $\mu$ m.





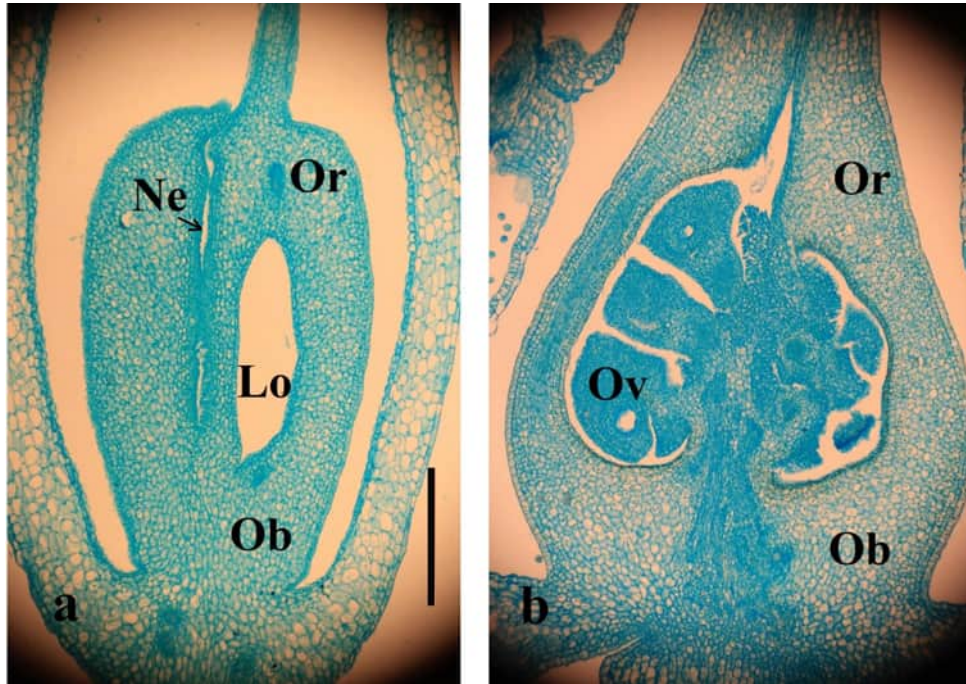
**Fig. 5** Ascending series of transversal sections of the flower of *Maianthemum bifolium*. **e** Only the ovary is present. **f** Fragment of the ovary with nectary epidermis. An – anther; Fi – filament; Lo – ovary locule; Ne – septal nectary; Ob – ovary base; Or – ovary roof; Ot – obturator; Ov – ovule; Sg – stigma; St – style; Te – tepal. Scale bars: **a–e,g–i** 500  $\mu\text{m}$ ; **f** 50  $\mu\text{m}$ .





**Fig. 6** Ascending series of transversal sections of the flower of *Convallaria majalis* (a-c,f,h), the central part of the ovary enlarged (d-g), style (i), stigma in LS (j). An – anther; Fi – filament; Ft – floral tube; Lo – ovary locule; Ne – septal nectary; Ob – ovary base; Or – ovary roof; Ot – obturator; Ov – ovule; Sg – stigma; St – style; Te – tepal. Scale bars: 500  $\mu$ m





**Fig. 7** Longitudinal sections of the ovary of Convallariaceae: *Polygonatum multiflorum* (a), *Convallaria majalis* (b). Lo – ovary locule; Ne – septal nectary; Ob – ovary base; Or – ovary roof; Ov – ovule. Scale bars: a 1 mm; b 500  $\mu$ m.

**Tab. 1** Height ( $\mu$ m) of the gynoecium structures of the Convallariaceae species.

	<i>Polygonatum multiflorum</i>	<i>Maianthemum bifolium</i>	<i>Convallaria majalis</i>
Locule	1900	680	900
Ovary base	560	120	360
Ovary roof	260	40	300
Synascidiate zone	680	160	520
Hemisyndascidiate zone	-	-	-
Hemisymplicate zone	1220	-	-
Symplicate zone	-	420	380
Asymplicate zone at the ovary level	260	40	0
Septal nectary total*	1760	0–220	0
Nectary split	260	0–220	0
Ovary base – locules – roof to ovary, in %	21–70–9	14–81–5	23–58–19

\* Septal nectary total comprises the height of the nectary cavity and nectary split.

In the gynoecium of *C. majalis*, there are three vertical zones sensu Leinfellner [19]: synascidiate zone (Fig. 6c), symplicate zone (Fig. 6d–h) – both are fertile, and asymplicate zone. The hemisymplicate zone is absent. Locules are distinct in the synascidiate zone and become united in the symplicate zone. Placentation is axillar in the lower portion (Fig. 6c) and parietal in the upper portion (Fig. 6d). Septal nectaries are absent and carpels remain fused up to the stigma (Fig. 6j). Therefore, the style is composed by the symplicate zone and only the stigma is composed by the asymplicate zone.

## Discussion

### General flower morphology and adaptations

The flowers of the studied species represent different functional types [23,24]: *Polygonatum* flower is tubular, *Convallaria* flower is campanulate, and *Maianthemum* flower is disc-shaped. From the ecological point of view, disc-shaped blossoms seem to be most primitive, as they are two-dimensional, adapted for generalized pollinators, with open access to pollen or nectar. The campanulate and tubular flowers are tri-dimensional, with hidden nectar or pollen. Evolutionary, the disc-shaped and small flower of *Maianthemum* is seen to be derived from the syntepalous flowers of the Convallariaceae as a result of flower reduction and oligomerization [25,26]. In spite of dimery, the common pentacyclic ground plan of the monocot flowers is maintained in *Maianthemum*, resembling the tetramerous flower [26]. Another aspect of flower reduction in *Maianthemum* is the loss of stamen adnation to the floral tube. Interestingly, this feature occurs also in *Convallaria*, supporting the hypothesis that syntepaly in *Polygonatum* and *Convallaria* is convergent.

The evolutionary type of stamens is common for the studied species. Anthers in all studied species are adaxial (dorsifix), introse opened, sagittal (no connective present below where the filament joins the anther) [27]. Additional functions of stamens can be detected in *P. multiflorum* where epidermal trichomes are present. Short papillae on the lower portion of filaments as well as papillose trichomes on the adaxial surface of tepals of this species have striated cuticle, resembling tepaline osmophores in other members of the order Asparagales: *Asphodelus aestivus* [28], *Galanthus nivalis* [29], and *Crocus vernus* [30]. Papillose osmophores with striate cuticle were also found on the ovary in some *Allium* species [31–33]. The long trichomes in the upper portion of the filaments in *P. multiflorum* can prevent nectar outflowing from the pendant flower, as was presumed in *Asphodelus albus* with erect flowers [34], or they can provide sites for secondary pollen load.

All species studied are considered as cross-pollinated by insects [9,10,16]. In *P. multiflorum* and *C. majalis*, a different character of herkogamy was revealed. In *P. multiflorum* at the beginning of anthesis, reverse herkogamy is possible (anthers are more distally located than the stigma) changing into approximative herkogamy at the end of the anthesis due to the elongation of the style (the stigma is more distally located than anthers). Contrastingly, in *C. majalis* the conditions of approximative herkogamy are unchanged during the anthesis. In *M. bifolium* with flowers open for visitors, herkogamy is less expressed because of equal length of stamens and pistil.

The pendant flower position and introse anthers, forming a reasoning chamber, are considered to be significant for the buzz-pollination syndrome in *P. multiflorum* [17]. Filamentous osmophores, an elongating style and apically dehiscent poricidal anthers were also shown in *Solanum* flowers, which are adapted for buzz-pollination [35]. This pollination mode is also possible with longitudinally dehiscent anthers that open first in the apex [36]. A very similar condition occurs in *C. majalis* with anthers opening apically. Obviously, both species, *P. multiflorum* and *C. majalis*, are morphologically adapted for offering pollen grains as a floral reward for pollinators by buzzing. In *P. multiflorum*, both kinds of floral reward are offered: nectar and pollen, similarly to the other Asparagaceae s. l. species pollinated by bumblebees [37].



## Gynoecium micromorphology and general considerations

All studied species have fused carpels and a narrowed ovary base. The relative height of the ovary base is significant as in the other studied genera of Asparagaceae s. l. – *Dracaena* and *Sansevieria* [22,38] and is more than 1/5 of the ovary height in *P. multiflorum* and *C. majalis*. The ovary roof height is shorter in the studied species. All metric parameters of the ovary zones, both absolute and relative, are minimal in *M. bifolium* and maximal in *P. multiflorum*.

In *P. multiflorum*, 1–3 ovules per carpel have been reported [1,16], in *C. majalis* – 4–8 ovules per carpel [9], in *M. bifolium* – only 2 ovules per carpel [10], which corresponds to our data. As was shown in this work, the ovule number per carpel in *M. bifolium* is the most constant and the lowest.

In the gynoecium of different members of Asparagaceae s. l., placental and funicular obturators are commonly found [22,37,39,40]. Obturators (called also transmitting tissue) are the fragments of the secretory epidermis of the carpels and ovules facilitating the pollen tube growth toward the embryo sac. In the studied species, the most prominent placental obturators are located in the upper sterile part of the locules on the septa margins; funicular obturators are also formed. In *Ophiopogon wallachianus*, the rudimentary proximally open nectary splits on the incomplete septae were referred as the placental obturator [5].

Septal nectaries in *P. multiflorum* were described earlier [14] as an inner nectary, located along the entire ovary, having nectariferous parenchyma and epidermis, with a non-secretory basal part of the septal cavity, with palisade epidermal cells, covered with cuticle, supplied with no vascular bundles. Following Schmid's classification [20], the septal nectary in *Polygonatum* is of non-labyrinthine, distinct type ("lilioid-type"). After the concept of the vertical zonality of the septal nectary [21], in the lower part of the septal nectary of *P. multiflorum* (in the synascidiate zone) it has a zone of the distinct nectary. Above, in the hemisymphicate zone, the common nectary with the postgenitally closed proximal part is formed. The outer nectary is formed in the upper part of the common nectary, where the nectary splits are open outwards and the asymplicate zone occurs. The septal grooves running along the ovary in *P. multiflorum* function as nectar ducts, and such grooves are also common in *Asparagales* having a septal nectary [15].

After Daumann [14], there is no nectary tissue in the flowers of *Convallaria* and *Maianthemum*. However, our study revealed the rudimentary outer nectary in *M. bifolium*. The loss of nectaries is related with the shift to pollen flowers and buzz-pollination. A septal nectary can be replaced by tepaline glands or elaiophores in *C. majalis* [1], but they are not differentiated morphologically.

The gynoecium of *P. multiflorum* with synascidiate, hemisymphicate, and asymplicate vertical zones, with the inner common septal nectary, can be defined as hemisyncarpous sensu Leinfellner [19]. The gynoecium of *C. majalis* and *M. bifolium* with synascidiate, symplicate, and asymplicate zones, with mostly (*M. bifolium*) or fully reduced (*C. majalis*) septal nectaries, should be defined as eusyncarpous gynoecium sensu Leinfellner [19]. *Polygonatum multiflorum* and *M. bifolium* with a septal nectary have one more common feature: the style composed of the asymplicate zone of the gynoecium (carpels are fused only postgenitally), while in *C. majalis* it is composed of congenitally fused carpels.

The vascular system of the flower is simple and uniform in the species studied here. Tepal and stamen traces are one-bundled and unbranched, while carpel traces are initially three-bundled. Septal veins (arising from the stele or ventral veins) supplying ovules are evident in all the species. In comparison with the data of another genera included in Asparagaceae s. l. – *Dracaena* and *Sansevieria* [38], the vascular system of the Convallariaceae flower is poor (there are no branches of tepal traces, no lateral carpellary veins, no ventral complex).

The data collected in this study suggest that anther structure and flower organ venation are the most stable flower characters in the Convallariaceae, while perigonium morphology and gynoecium inner morphology are distinct in the studied species. From this point of view, we must consider that the gynoecium inner structure is not always more conservative than the other flower traits.

Close evolutionary relations between *Polygonatum* and *Maianthemum* are not obviously deduced from the flower morphology because of a significant shift in floral construction in the latter genus exemplified in flower reduction and despecialization. The new common characters for both genera revealed in our study are the presence of a septal nectary (rudimentary in *M. bifolium*) and a postgenitally composed style.

## Conclusions

The general flower construction and gynoecium inner structure support that the *P. multiflorum* flower potentially functions as a xenogamous nectar and pollen flower, while *M. bifolium* and *C. majalis* flowers are pollen flowers. The disc-shaped flowers of *M. bifolium* are morphologically adapted for generalist pollinators and self-pollination. In the inner gynoecium structure, some new traits were detected, among them, the zone of the distinct septal nectary in *P. multiflorum* and the rudimental outer nectary in *M. bifolium*. The gynoecium micromorphology is regarded to be quite different in the studied Convallariaceae species.

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### Morfologia kwiatu u trzech gatunków Convallariaceae o różnych cechach powabni

#### Streszczenie

W pracy opisano morfologię i mikromorfologię kwiatów *Polygonatum multiflorum*, *Maianthemum bifolium* i *Convallaria majalis*. W badaniach stosowano metody mikroskopii świetlnej. Wśród badanych gatunków *M. bifolium* posiada najbardziej zredukowane kwiaty o pięciokółkowym okwiecie 4-krotnym, z wolnymi członami okwiatu. Kwiaty *P. multiflorum* i *C. majalis* są zrosłocłonowe i trzykrotne. Tylko u *P. multiflorum* pręciki są zrosnięte z rurkowatym okwiatem. Słupkowie u *P. multiflorum* składa się z trzech stref (ang. *synascidiate*, *hemisymphlicate*, *asymphlicate*). W słupkowie *M. bifolium* i *C. majalis* wyróżniono w pionie także trzy strefy, jednak o odmiennych cechach (ang. *synascidiate*, *symplicate*, *asymphlicate*). W kwiatach *P. multiflorum* i *M. bifolium* zalążnia jest złożona z owocolistków zrastających się po zapyleniu, natomiast w zalążni *C. majalis* owocolistki są połączone przed zapyleniem (*symplicate* strefa zalążni). U wszystkich badanych gatunków stwierdzono występowanie takiego samego wzoru nerwacji w poszczególnych częściach kwiatu.

W pracy wykazano, że zewnętrzna morfologia kwiatu oraz struktura wewnętrzna słupka różni się u wszystkich trzech gatunków, zapewniając adaptacje dla zapylenia. W zalążni *P. multiflorum* występuje jeden nektarnik przegrodowy z trzema podłużnymi szczelinami i trichomy epidermalne na wewnętrznej powierzchni perigonium i na nitkach pręcików. W przypadku *M. bifolium* po raz pierwszy opisano zewnętrzny nektarnik przegrodowy, mający szczątkową formę. Nektarniki nie występują w kwiecie *C. majalis*. Ogólna budowa kwiatu i struktura wewnętrzna zalążni potwierdzają pogląd, że kwiat *P. multiflorum* funkcjonuje jako obcopylny kwiat nektarowy i pyłkowy, podczas gdy u *M. bifolium* i *C. majalis* kwiaty są pyłkowe.