

Comparative flower morphology of the *Anthericum liliago* and *Cordyline fruticosa* (Asparagaceae)

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Article info

Received 21.07.2025

Received in revised form
19.08.2025

Accepted 08.09.2025

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*Fishchuk, O. S., & Kostruba, N. S. (2025). Comparative flower morphology of the *Anthericum liliago* and *Cordyline fruticosa* (Asparagaceae). *Regulatory Mechanisms in Biosystems*, 16(4), e25165. doi:10.15421/0225165*

The structure of *Anthericum liliago* and *Cordyline fruticosa* flowers was studied on permanent cross-sectional and longitudinal sections using a light microscope. The genus *Anthericum* belongs to the subfamily Agavoideae, the family Asparagaceae, which is characterized by the capsular spherical to three-faced fruit. The flowers are pollinated by hymenopterans, while the seeds are distributed by the wind and flowering period extends from June through August. The genus *Cordyline* belongs to the subfamily Lomandroideae, the family Asparagaceae and has small white to mauve flowers formed on panicles. Flowering occurs from September to October. Fruit is an orange-red berry, ripening from December to March. This species propagates easily from seeds, suckers or stem cuttings. Micromorphological studies of the flower are considered as a way for detection of unknown plant features, adjustment of plants to specialized ways of pollination and determining the first stages of morphogenesis of fruit, and further use of these features in taxonomy. 15 flowers of *A. liliago* and *C. fruticosa* were sectioned using standard methods of Paraplast embedding and serial sectioning at 20 micron thickness. Sections were stained with safranin and Astra Blau and mounted in Eukitt. It was found that in the studied species the tepals have three-bundle traces. The vascular system of *A. liliago* consists of three dorsal bundles of the carpel and three pairs of smaller vascular bundles – roots of the ventral complex, which branch higher and form twelve bundles of the carpel (ventral complex) at the level of the ovary base. The outer vascular bundles form three-bundle traces of the outer and inner tepals, the other vascular bundles merge and form a continuous central cylinder. The trace of the ovules is single-bundle. For the first time, the following gynoecium zones were detected in *A. liliago*: sterile synascidiate with a height of about 360 µm, symplicate 180 µm, fertile hemisymplicate with a height of 1100 µm – the middle part of the ovary with two ovules and asympicate. The total height of the septal nectary is 1580 µm. The vascular system of *C. fruticosa* forms a circle of seven vascular bundles, from which three dorsal carpel bundles extend and, in the center, there remain three vascular bundles on the radii of the septa – the roots of the ventral complex. Each of the three ventral bundles of the gynoecium divides into two, forming six ventral vascular bundles, which are located in the ovary septa and form the traces of the ovules. The trace of the ovules is single-bundle. In the gynoecium of *C. fruticosa* there are three vertical zones: a short sterile synascidiate with a height of about 220 µm, fertile hemisymplicate with a height of 1540 µm – the middle part of the ovary and asympicate. The total height of the septal nectary is 1720 µm. The ovary roof is 200 µm in *A. liliago* and 320 µm in *Cordyline fruticosa*. Triple dorsal bundles of carpels in *C. fruticosa* have been identified, which could be considered as adaptation of different stages of morphogenesis of fruit to dehiscence. The new data obtained by the vascular anatomy of the flower and the presence of different ovary zones are a significant addition to information about anatomical and morphological features of the studied species, which can be further used in the taxonomy of the family Asparagaceae.

Keywords: Anthericum liliago; Cordyline fruticosa; ovary; flower morphology; gynoecium; septal nectary.

Introduction

According to molecular taxonomy, the Asparagaceae family includes 7 subfamilies: Agavoideae, Aphyllanthoideae, Asparagoideae, Scilloideae, Lomandroideae, Nolinoideae, Brodiaeoidae (APG, 2016). The gynoecium micromorphology in *Polygonatum multiflorum*, *Maianthemum bifolium*, *Convallaria majalis*, *Dracaena fragrans* and *Sansevieria parva*, which belong to the subfamily Nolinoideae, was previously studied using a series of ovary sections and light microscopy (Fishchuk, et al., 2014; Odintsova & Fishchuk, 2017). New species of the Asparagaceae family are increasingly being encountered and studied in China and Vietnam (Lin et al., 2024), and based on new research, the subfamily Nolinoideae (Asparagaceae) is proposed in APG III to be replaced with Convallarioideae (Tanaka & Nguyen, 2023). This study highlights the importance of integrating morphological and molecular data, presenting a solid basis for future phylogenetic studies within the genera *Anthericum*, *Cordyline* and related taxa. The study of phylogenetic relationships in the family Asparagaceae is quite relevant, for example, for species of the genus *Bellevalia* (Asparagaceae), determined on the basis of morphology and molecular systematics, namely, fifteen morphological characteristics were recorded, the most important of which are the flower, leaf margin cilia, inflorescence shape and capsule shape. The results identified two major clades in this genus and provide new phylogenetic

data (Roudsari et al., 2025). Also, the results of study of phylogenetic relationships of Convallarioideae are compared with morphological characters from the perspective of evolutionary aspects (Le et al., 2024).

The classification of *Yucca* (Asparagaceae, Agavoideae) is based on morphological characters, mainly fruit type, stem, leaf margin and inflorescence type. To investigate the evolution of these features and their potential taxonomic significance as synapomorphies for some groups within *Yucca* a phylogenetic analysis was conducted with 44 *Yucca* species and eight outgroup species. Divergence times were estimated to provide a suitable phylogenetic basis for studying the evolution of morphological characters (Ayala-Hernández et al., 2025).

Genome structure and phylogenetic data for the heterogeneous subfamily Convallarioideae (Asparagaceae) have been studied by Wu et al. (2025) inferred from plastome data. Despite its importance, chloroplast genome data of Convallarioideae remain limited, hindering a comprehensive understanding of the structural evolution of their genome and phylogenetic relationships. This study provides a detailed characterization of chloroplast genome features and conducts a robust phylogenetic analysis of this subfamily using an expanded chloroplast genome dataset (Wu et al., 2025).

The epidermis morphology of some members of the family Asparagaceae has been studied and analyzed in detail and its systematic significance has been assessed. No consistent characteristics were

found at the family level, but the anticlinal wall and stomata morphology provided systematic information of different tribes, especially Ophiopogoneae and Polygonateae. Therefore, the epidermis may have systematic significance for Asparagaceae (Chao et al., 2022).

Also, the study of micromorphological ovary features has been linked to the ecology of pollination and fruit dispersal in members of Asparagaceae. Within the clade *Sansevieria* (genus *Dracaena*, Asparagaceae), although there are consistent signs of pollination by lepidopterans, the floral biology of these plants remains largely unexplored. A study comprehensively describes the biology of the flora and reproduction of *Dracaena trifasciata*, a widely cultivated species in this group. This study included the characterization of floral flowering and morphometry, the process of nectar secretion, testing the effects of nectar removal and evaluation of the reproductive system. The results show that the floral features of *D. trifasciata* are strongly consistent with the phalaenophilic syndrome (i.e. pollination by lepidopterans), characterized by white flowers, a short floral tube and nocturnal flowering. The species' nectar accumulates at the base of the floral tube by continuous secretion, persisting throughout the night (Primo et al., 2025).

Molecular-phylogenetic analysis allows the division of families, subfamilies and genera by molecular characteristics, and scientists do not always use such important features of vascular anatomy and structure of septal nectaries, the presence and height of ovarian zones, although the basis for taxonomic systems may also be signs of flower micromorphology. The integration of data from molecular phylogenetics and evolutionary comparative flower morphology is a promising direction for the construction of modern evolutionary taxonomy. The study of micromorphology and vascular anatomy of monocotyledonous flowers and fruits is a modern direction in the study of evolutionary morphology (Odintsova & Fishchuk, 2017; Skrypec & Odintsova, 2020; Odintsova & Khomei, 2023). Molecular-phylogenetic reconstructions of the family Asparagaceae were carried out by many scientists Chase et al. (2009), Meng et al. (2021), Lu et al. (2022), Le et al. (2023).

The objects of our study were *A. liliago* L. and *C. fruticosa* (L.) A. Chev. They belong to the subfamilies Agavoideae and Lomandroideae, Asparagaceae family, in accordance with Chase et al., (2009; APG IV).

Anthericum is one of many genera in the ancient lily family (Liliaceae) (Cronquist, 1981), which, along with its closest relatives, has been treated very differently by taxonomists over the past twelve years. Those who preferred to distinguish numerous small families (e.g., Reveal's system of 1993–1999) have placed the family Anthericaceae J. Agardh. in the order Agavales (Reveal, 1993). In early versions of the APG system (1998, 2003) the genus was included in the family Agavaceae, which was demoted to a subfamily in the 2009 version (www.mobot.org/MOBOT/research/APweb).

A. Takhtadjan refers the genus *Anthericum* to the order Amaryllidales and the family Anthericaceae, which includes twenty-seven genera (Takhtajan, 2009). Molecular studies have shown that the genus can remain monophyletic only if it is restricted to European species. These species form a sister clade to a lineage that includes African species of *Anthericum* and members of the genus *Chlorophytum* according to the Angiosperm Phylogeny website (updated APG IV system from 2016). The genus *Anthericum* situated the the subfamily Agavoideae in the family Asparagaceae s.l. Within the subfamily, it comprises a group of eight genera, forming a sister clade with two genera, *Herreria* and *Herrerriopsis*. In the APG I and APG II systems, the genus was classified within the family Agavaceae.

The genus *Anthericum* has been widely studied by scientists. A set of polymorphic nuclear microsatellite loci was developed and tested for use in population genetic analyses of *Anthericum ramosum* (Agavaceae) and related species. This newly developed set of polymorphic nuclear microsatellite markers will be useful for population genetic investigation of *A. ramosum* and closely related species (Vít et al., 2020). Morphological variation in Scandinavian populations of the diploid-tetraploid species pair *A. ramosum* and *A. liliago* (Anthericaceae) was studied (Rosquist & Prentice, 2001). Speciation in the genera *Anthericum* and *Chlorophytum* (Asparagaceae) in Ethiopia – a

molecular phylogenetic approach was investigated. The relationships between sister groups of Ethiopian *Anthericum* and *Chlorophytum* species, as well as patterns of variation within the *C. gallabatense* and *C. comosum* complexes, were studied using molecular phylogenetic analysis, morphometrics, and scanning electron microscopy of the seed surface. The results show that molecular data largely support previous morphological inferences, and that speciation occurred in Ethiopia at least three times within *Anthericum* and repeatedly within different *Chlorophytum* clades (Bjorå et al., 2017).

Three species of the genus *Anthericum* and 32 species of the genus *Chlorophytum* are recognized in Ethiopia and Somalia. Nine new species of the genus *Chlorophytum* are described, illustrated and mapped: *C. applanatum*, *C. filifolium*, *C. hiranense*, *C. littorale*, *C. nervosum*, *C. pendulum*, *C. petraeum*, *C. pterocarpum* and *C. ramosissimum* (Nordal & Thulin, 2008).

Plant extracts remain an endless source of biologically active chemicals and an inexhaustible resource for the discovery of new drugs of natural origin. Therefore, a study focused on the analysis of 29 ethanol extracts (E1-E29) from selected flora of Poland to evaluate their antioxidant, anti-inflammatory and acetylcholinesterase inhibitory properties in relation to the chemical profiles of phenolic compounds. This study is the first to report the phytochemical and pharmacological analysis of *Anthericum ramosum* and *Lysimachia europaea* extracts (Jakimiuk et al., 2023).

The genus *Cordylina* is assigned to the extremely broad family Liliaceae as part of the order Liliiflorae with a hypogenous, pentacyclic and trimerous flower, classic for monocots. In early phylogenetic systems, both ascending (Engler, 1892; Wettstein, 1901) and descending (Hallier, 1912; Bessey, 1915) orders and families were described very broadly, according to such traditionally important features in the systematics of dicots as the number of whorls in a flower and flower members in a whorl, and the position of the ovary. A revolutionary step was the creation of the system by Hutchinson (1934). The order Liliiflorae of previous authors and even the family Liliaceae s.l. are divided into many orders and families. The genus *Cordylina* was placed in the family Asteliaceae along with the genera *Astelia*, *Millisamia* and *Cohnia* on embryological grounds. These ideas dominated the classical systems that were revived in the 20th century, although some authors adopted broader family boundaries (Thorne, 1992). With the development of molecular genetic and cladistic approaches to monocot taxonomy (Chase, 2004; Kim et al., 2010), the ideas of Huber and Dahlgren have been fully confirmed, although the positions of certain genera and approaches to family boundaries are controversial.

In the first version of the APG system (1998), the genus *Cordylina* is assigned to the family Laxmanniaceae of the order Asparagales. Convallariaceae (incl. *Dracaena*, *Sansevieria*, *Ruscus*, etc.), Agavaceae, etc. are presented as separate families here. At the same time, "Laxmanniaceae" is the correct name of the family established with the inclusion of *Cordylina* according to molecular genetic analysis under the name Lomandraceae (Chase, et al. 1996). The correct name of the family "Convallariaceae" in this volume is Ruscaceae, Asparagaceae. Subsequent versions of the APG system (APG, 2003, 2009) revealed a tendency to increase the volume of monophyletic families. A. Takhtadjan refers the genus *Cordylina* to the order Orchidales and the family Asteliaceae, which includes five genera (Takhtajan, 2009). The genus *Cordylina* is assigned to the subfamily Lomandraideae, family Asparagaceae s. l. including 7 subfamilies including the subfamily Nolinoideae (incl. *Convallaria*, *Dracaena*, *Ruscus* etc.) (Chase et al., 2009; APG, 2016).

The genus *Cordylina* has been widely studied by scientists in various aspects. *In vitro* reproduction was performed and preliminary results of *Agrobacterium*-mediated genetic transformation of *Cordylina fruticosa* have been analysed. A method for *in vitro* propagation by axillary shoot proliferation and induction of accessory shoots have been applied, as well as *Agrobacterium*-mediated transformation of *Cordylina fruticosa*. A rapid and efficient method for obtaining transgenic plants by *Agrobacterium*-mediated transformation has been developed for *Cordylina* (Dewir et al., 2015).

Two new steroidal saponins were isolated and elucidated from the roots of *Cordylina fruticosa* (L.) A. Chev. Their structures were

established by interpretation of spectroscopic data (1D and 2D NMR) and mass spectrometry (HR-ESI-MS) (Nguyen et al., 2022). One new steroidal saponin from the leaves of *C. fruticosa* (L.) A. Chev was studied (Tan et al., 2023).

A study was conducted to determine the effect of transpiration on leaf anatomy, particularly leaf thickness, in six species of ornamental monocotyledons, namely: *Rhoeo discolor* (L. Her.) Hance ex Walp., *Hymenocallis littoralis* (Jacq.) Salisb., *Cordyline fruticosa* (L.) A. Chev., *Chlorophytum laxum* R. Br., *Dracaena reflexa* Lam. and *Aglaonema commutatum* Schott. The study procedures were carried out using a factorial completely randomized design (factorial CRD) with an experimental approach. The first factor was plant type, and the second was the condition before and after transpiration. The obtained data were analyzed using analysis of variance (ANOVA), followed by LSD and Pearson correlation tests. The results showed that the factor plant type significantly affects the thickness of leaf tissues. The conditions before and after transpiration also significantly affected all leaf tissues except the lower epidermis (Febriyani et al., 2023).

Research has been conducted on the antibacterial activity of *C. fruticosa* leaf extracts and its endophytic fungi extracts (Elfita et al., 2019) and green synthesis of silver nanoparticles using five varieties of *Cordyline fruticosa* sp. leaves and reviewing their antimicrobial, antioxidant and photocatalytic properties (Amasha et al., 2024). Molecular evaluation of *C. fruticosa* (L.) A. Chev. behavior affected by different chemical mutagens was investigated (Fathy & Tawfik, 2021).

Consequently, the issues of taxonomy and *in vitro* micropropagation, antibacterial activity, effect of transpiration on leaf anatomy and steroidal saponins in the genera *Anthericum* and *Cordyline* have attracted considerable attention among modern researchers, but the issues of vascular anatomy of the flower, the gynoeceum structure remain poorly studied. The aim of our study is to elucidate the flower morphology features and the internal structure of the gynoeceum and identify its vertical zonality in members of the family Asparagaceae for further use in the taxonomy of the family.

Material and methods

Ten *A. liliago* and *C. fruticosa* flower buds were collected in the A. V. Fomin Botanical Garden of the Taras Shevchenko National University of Kyiv, Ukraine, in 2019–2021 and fixed in 70% alcohol. Flower buds were dehydrated in t-butanol series (20%, 30%, 50%, 70%, 100% – 2 h each, the last one 24 h) and stored in 100% t-butanol and paraplast in the ratio 1:1. Infiltration was performed in Paraplast (Merck®) according to the described method (Soukup & Tylová, 2019). Transverse and longitudinal sections thickness were obtained with manual rotary microtome, the thickness of the slide was 20 µm (MPS – 2 (USSR)). Then it was stained in safranin (Sigma-Aldrich®) and Astra Blau (Merck®). Slides were mounted in “Eukitt®” (Sigma-Aldrich®) and images were made with an Amscope 10MP digital camera attached to an Amscope T490B-10M (USA) microscope.

For the morphological analysis, measurements were made of at least 20 fresh *A. liliago* and *C. fruticosa* flowers. The concept of gynoeceum vertical zonality by Leinfellner (1950) was used to analyze the gynoeceum's internal structure. This concept considers only the congenital fusion of the carpels. The congenital multilocular synascidiate, unilocular simplicate, transitional hemisimplicate, and asymplicate zones could be formed in the syncarpous gynoeceum according to this concept when carpels are grown together. In terms of incomplete fusion of carpels, only in their outer part was there a hemisyncarpous gynoeceum with hemisynascidiate, hemisimplicate, and asymplicate zones formed; later, this method was improved for monocots (Odintsova & Fishchuk, 2017).

Results

Flowers of *A. liliago* are up to 22 mm long, up to 3 mm in diameter. Bract posterior is up to 11 mm long, 1 mm at the base, then ex-

panded to 1.3 mm and twisted at the apex. The pedicel is up to 15 mm long, has a joint at 1/3 of the length.

Perigonium is simple, not fused, saucer-shaped, 1.5 mm in diameter. At the base, the perigonium tepals are lanceolate, 6 mm wide and up to 22 mm. The androecium consists of six stamens about 6 mm long, the diameter of the stamen filament is 0.3–0.4 mm (Fig. 2b), the outer stamens are formed from the receptacle somewhat lower than the inner ones. The anthers are linear, basifixed, 5.2 mm long, 1.6 mm in diameter (Fig. 1e).

The ovary is globose, with three distinct nectar grooves, 2.8 mm high, 2.7 mm in diameter. The style is up to 14.5 mm high and 0.5 mm in diameter. The stigma is three-lobed, blades about 0.7 mm long, with a large number of villi. The ovary has three vertical structural and functional zones: ovary base 280 µm, nests 1740 µm and ovary roof 200 µm. The style channels are ventral, separated by septa, merge into one continuous channel above (Fig. 1f). The ovules are placed two by two in the locule, horizontally deflected, micropyle directed outwards, placentation is parietal (Fig. 2a). The ovules are anatropous, crassinucellate, laid on centrally angular placentas (Fig. 3a). In the gynoeceum of *A. liliago*, there are four structural zones according to Leinfellner (1950): sterile synascidiate with a height of about 360 µm (Fig. 1a), symplicate 180 µm (Fig. 1b), fertile hemisymphlicate with a height of 1100 µm – the middle part of the ovary with two ovules (Fig. 1c, 1d) and asymplicate (Fig. 1e).

Raphides are present in the pedicel, the base of the floral tube, the tepals, the stamen filaments, and along the entire height of the ovary and in the style (Fig. 1a, 1b). The septal nectary in *A. liliago* is located from the base of the synascidiate zone of the ovary to its roof (Fig. 3c), in the form of three narrow cavities that open with nectary slits (Fig. 2b, 2c). The height of the nectary slit is 200 µm. The total height of the septal nectary is 1580 µm (Fig. 3b).

At the base of the pedicel there are six vascular bundles, which become more massive higher up and are divided into a large number of large and small vascular bundles (Fig. 1a) arranged according to the atactostelle type: the larger ones give rise to the outer and inner traces of the tepals, and the smaller ones merge to form a continuous vascular cylinder with the xylem outwards (Fig. 1b). Above, six vascular bundles – traces of stamens – separate from this cylinder (Fig. 1b), and in the center there remain three large bundles, which, deflecting, form three dorsal bundles (Fig. 2a, 2c) of the carpel and three pairs of smaller vascular bundles – roots of the ventral complex, which branch higher and form twelve bundles of the carpel (ventral complex) at the level of the ovary base (Fig. 1b, 1c). The outer vascular bundles form three-bundle traces of the outer and inner tepals, the other vascular bundles merge and form a continuous central cylinder.

Above the central cylinder, single-bundle traces of stamens depart (at the same level), after which the lacunae in the central cylinder close. Subsequently, the central cylinder is reorganized into a triangular cross-section group of nine vascular bundles, of which three dorsal vascular bundles and six vascular bundles are the roots of the ventral complex, which are divided above into a group of small conducting bundles – the ventral complex (Fig. 2a). Then six of them merge into three large ventral septal bundles, which are located on the radii of the ovary septa, and six smaller ones end blindly (Fig. 1b). At the level of the fertile part of the ovary, the septal bundles of the gynoeceum are divided into two in the ovary septa and feed the ovules with their branches. The trace of the ovules is single-bundle (Fig. 1c). Above the ovules, 12 small ventral carpel bundles remain (Fig. 2c). Dorsal carpel bundles form blind lateral branches in the ovary wall (Fig. 1e). Above the locule, they all merge with the dorsal carpel bundles, forming a dorsal vein that does not branch until the receptacle (Fig. 3d).

The flowers of *C. fruticosa* are collected in panicle inflorescences, bisexual, actinomorphic, three-membered, 8–11 mm in diameter, 10–15 mm long. The flowers are located in the axils of lanceolate leathery bracts. The pedicel is short, 0.5–0.7 mm long, simultaneously under the flower with a clear articulation. At the base of the pedicel is a broadly trapezoidal in outline, leathery, bidentate at the apex, posterior bract with two keels. The flower is easily separated at the point of articulation of the pedicel so that its lower part together with the bract remains on the axis of the inflorescence.

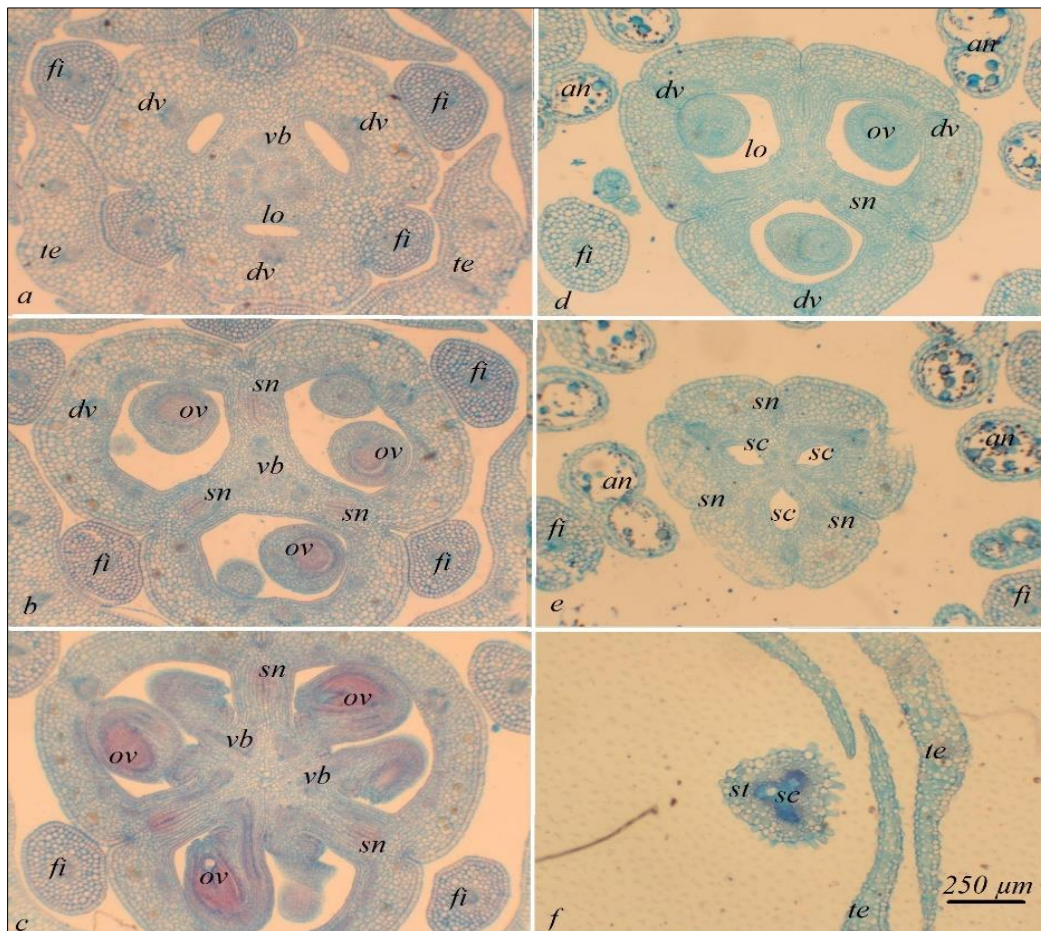


Fig. 1. Ascending series of transversal sections of the flower *Anthericum liliago*: *a* – synascidiate zone, *b* – symplicate zone; *c-d* – hemisymplicate zone; *e* – asymplicate zone; *d-e* – ovary roof, *f* – free tepals and style; *an* – anther; *dv* – dorsal vein; *fi* – filament; *lo* – ovary locule; *ov* – ovule; *sc* – style channel; *sn* – septal nectaries; *st* – style; *te* – tepal; *vb* – vascular bundle

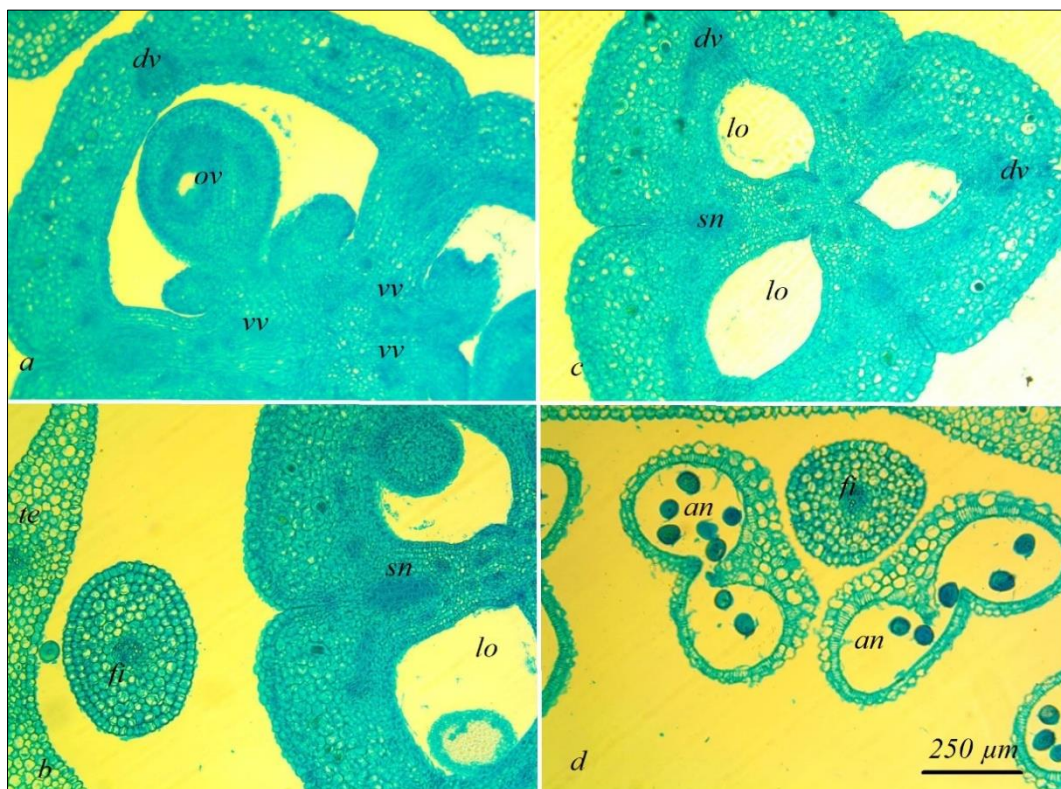


Fig. 2. Floral parts of *Anthericum liliago*: *a* – ovary wall in the median part of the carpel, dorsal vein; *b* – ovary wall with septa attached, septal nectary is visible; *c* – upper part of the ovary with septal nectaries; *d* – anther and filament; *an* – anther; *dv* – dorsal vein; *fi* – filament; *lo* – locule; *ov* – ovule; *te* – tepal; *sn* – septal nectaries; *vv* – ventral vein

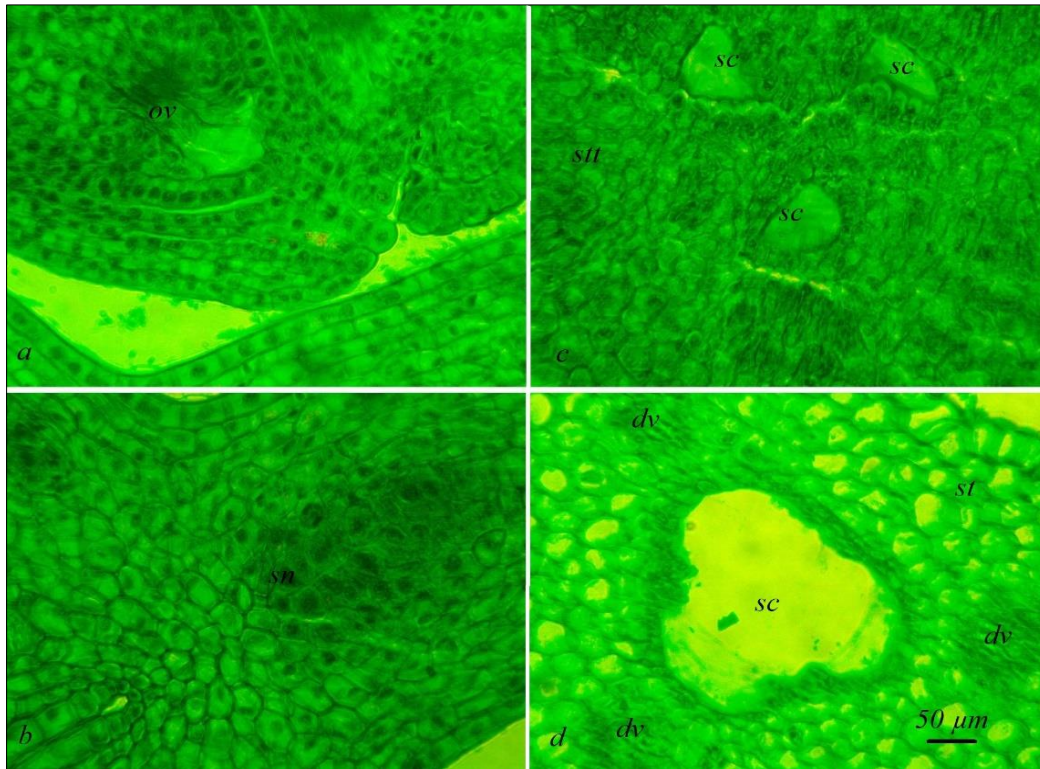


Fig. 3. Gynoecium parts of *Anthericum liliago*: *a* – anatropous, crassinucellate ovule which laid on centrally angular placentas; *b* – septal nectary is visible; *c* – central part of the ovary roof; *d* – triradial style channel is visible; *dv* – dorsal vein; *ov* – ovule; *sc* – style channel; *sn* – septal nectaries; *st* – style

The perigonium and androecium are united at the base by a short flower tube (Fig. 4a). Tepals and stamens are separated from each other almost at the same level (Fig. 4f). The perigonium is white or light pink, with 6 identical bent, obovate tepals. Two tepals of the outer circle are anterior diagonal, and one is posterior medial. The outer tepals of the perigonium form a tessellated shape, and the inner one forms a valve (Fig. 4e).

Cordyline fruticosa has six stamens. The stamen filaments are expanded at the base, tapering towards the apex and standing cylindrical, introrse, dorsifixed. The pistil has an ovoid, narrowed at the apex, convex-triangular ovary in cross section, which gradually turns into a straight, cylindrical style (Fig. 5d) with a short-tridentate stigma.

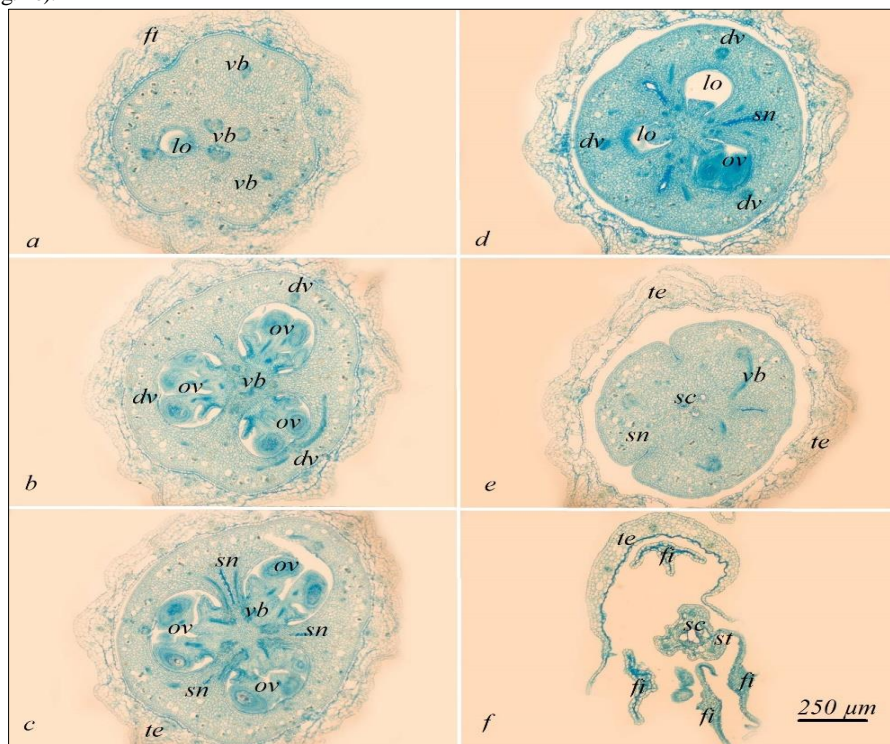


Fig. 4. Ascending series of transversal sections of the flower *Cordyline fruticosa*: *a* – synascidiate zone; *b-d* – hemisymphiccate zone; *e* – asympiccate zone; *f* – free tepals, anthers and style; *dv* – dorsal vein; *fi* – filament; *ft* – flower tube; *lo* – ovary locule; *ov* – ovule; *sc* – style channel; *st* – style; *sn* – septal nectaries; *te* – tepal; *vb* – vascular bundle

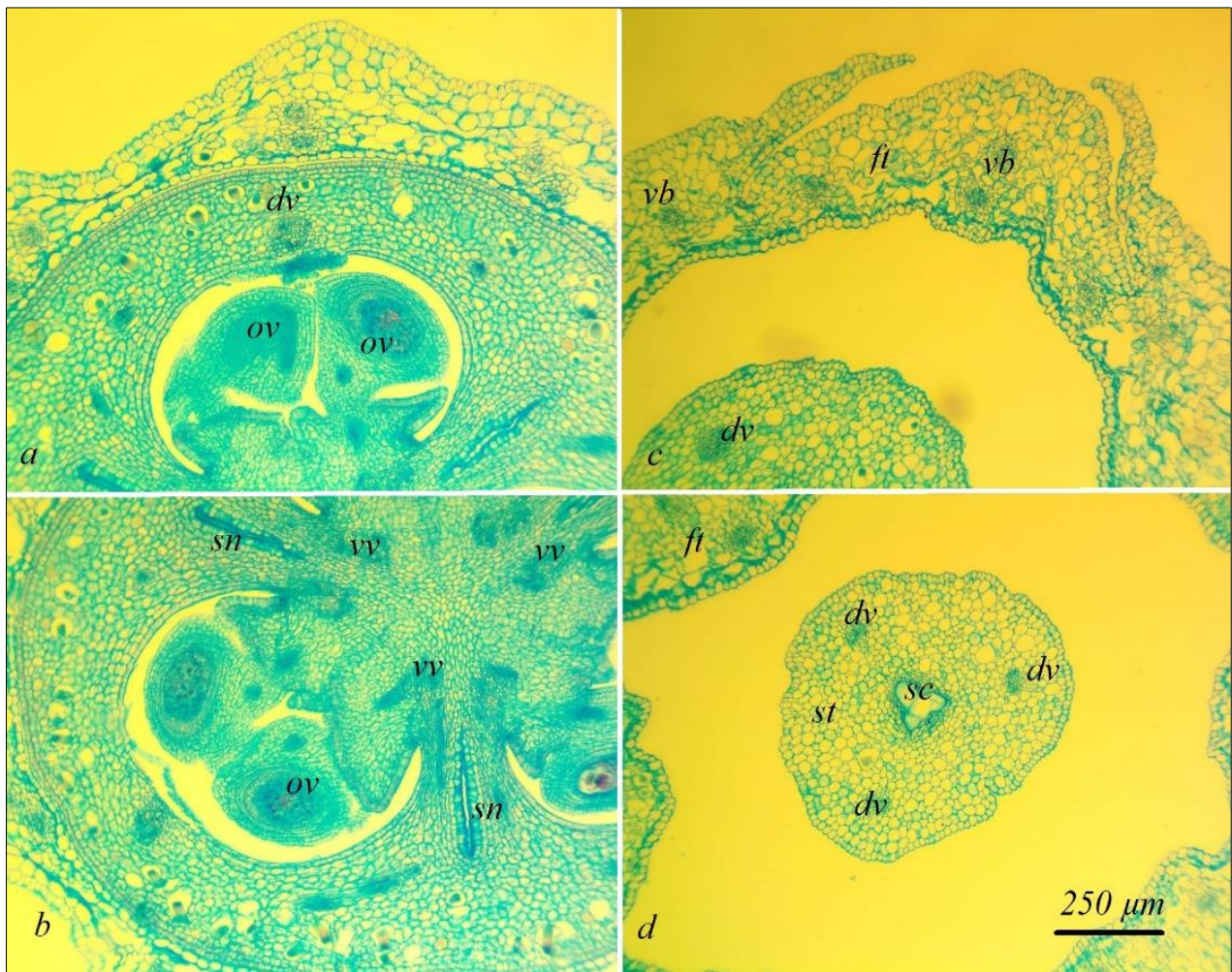


Fig. 5. Floral parts of *Cordyline fruticosa*: *a* – ovary wall in the median part of the carpel, dorsal vein is visible; *b* – central part of the ovary with septal nectaries; *c* – flower tube is visible; *d* – style and style channel are visible; *dv* – dorsal vein; *ov* – ovule; *sn* – septal nectaries; *ft* – flower tube; *sc* – style channel; *st* – style; *vb* – vascular bundle; *vv* – ventral vein

In the pedicel of *C. fruticosa*, at the base of the receptacle, at the base of the floral tube, in the free tepals, along the entire height of the ovary, in floral filament and style are cellular inclusions – raphides (Fig. 7a, 7b).

There are three vertical structural and functional zones in the ovary of *C. fruticosa*: the base of the ovary 340 μm, the locules 1860 μm and the roof of the ovary 320 μm (Fig. 4e). There are several ovules in the locule (Fig. 5a), located in the middle part of the ovary in pairs on incomplete septa, deviated horizontally, the micropyle is directed outwards, the placentation is parietal, the obturator is funicular (Fig. 5b, 6a). The locule contains up to six ovules in total. The style channels are ventral, separated (Fig. 6d), later merging into one (Fig. 5d).

In the gynoecium of *C. fruticosa* there are three vertical zones according to W. Leinfelner: short sterile synascidiate (Fig. 1a) with a height of about 220 μm, fertile hemisymphicate (Fig. 4b, 4c) with a height of 1540 μm – the middle part of the ovary and asymplicate (Fig. 1e). The septal nectary in *C. fruticosa* is located at the beginning of the hemisymphicate zone (Fig. 4b) of the ovary to the roof of the ovary (Fig. 5b), in the form of three narrow cavities that open with nectary slits (Fig. 6c). It appears at the fertile level of the ovary, 140 μm above the beginning of the hemisymphicate zone (Fig. 4d). The nectary slit is straight, glandular, elongated, 220 μm high. The total height of the septal nectary is 1720 μm (Fig. 6b).

The vascular system of the pedicel *C. fruticosa* consists of five vascular bundles, which merge above and form three massive vascular bundles on the radii of the outer tepals. Eighteen vascular bundles extend outward from these bundles: nine on the radii of the outer tepals somewhat lower and nine on the radii of the inner tepals, high-

er, immediately in the perigonium they divide radially into a stamen trace (Fig. 4a). Above the formation of the perigonium traces and androecium, the vascular system of the flower forms a circle of seven vascular bundles, from which three dorsal carpel bundles extend, and in the center there remain three vascular bundles on the radii of the septa – the roots of the ventral complex (Fig. 4a).

Each of the three ventral bundles of the gynoecium divides into two, forming six ventral vascular bundles, which are located in the ovary septa and form the traces of the ovules (Fig. 4b). The trace of the ovules is single-bundle (Fig. 4c). The dorsal bundles of the carpel do not branch above the locules (Fig. 4b). They merge with the ventral bundles and form the dorsal vein (Fig. 5c, 5d), which does not branch to the receptacle.

Discussion

Flowers in the genus *Anthericum* are hypogynous and hermaphroditic. There are 6 tepals, free or basally fused into a tube, perianths of various lengths. Tepals with 1–7 veins, usually marcescent and persistent. There are 6 stamens, attached to tepals. The filaments in genus *Anthericum* are free or fused, glabrous or scabrid and introrse. The anthers can be either basifixed and introrse or dorsifixed and usually versatile. The gynoecium is syncarpous and three locular. The style is filiform with a minute capitate or three-lobed stigma. The stigmatic surface is dry in all genera examined and generally papillate with unicellular papillae. Septal nectaries are present. The placentae are axile and there are 2–numerous ovules per locule. The ovules are anatropous, campylotropous or rarely hemianatropous.

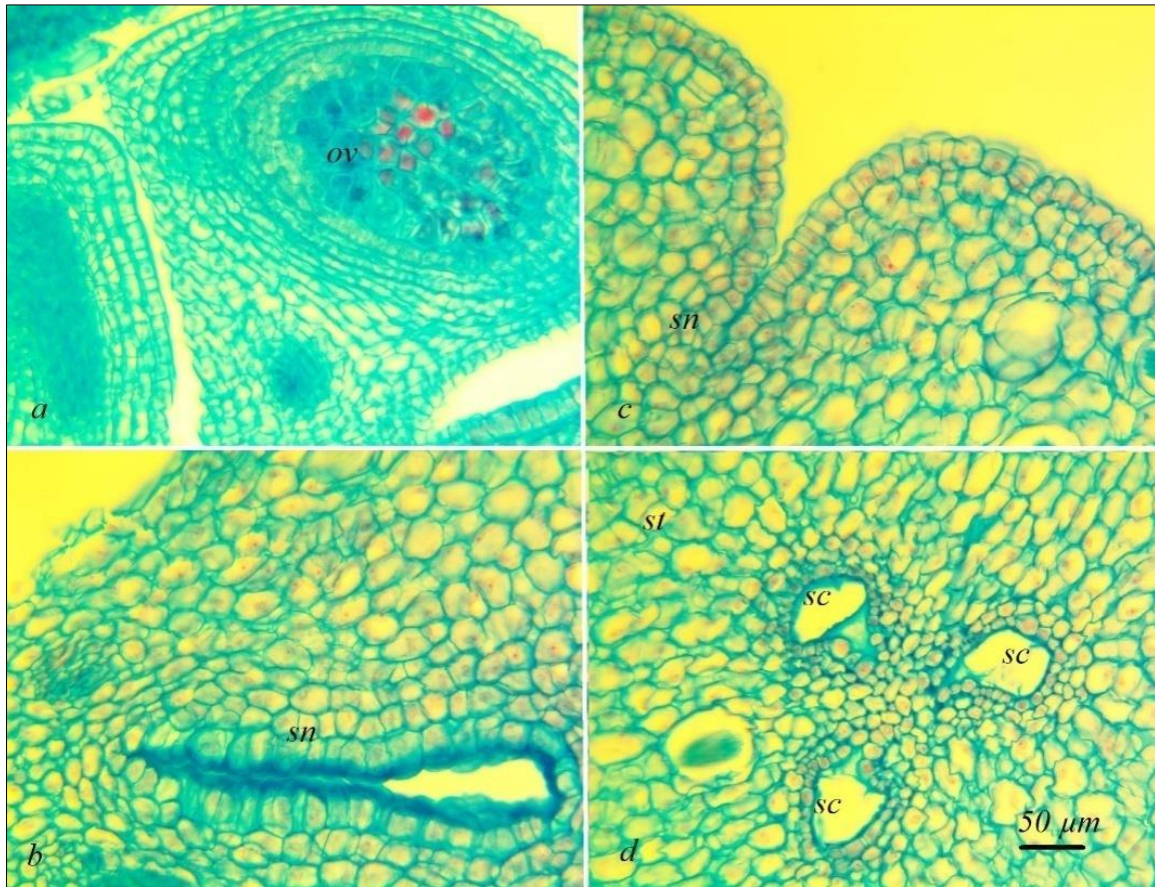


Fig. 6. Gynoecium parts of *Cordyline fruticosa*: *a* – ovule with parietal placentation, the obturator is funicular; *b* – central part of the ovary, septal nectary is visible; *c* – upper part of the ovary with septal nectaries; *d* – ovary roof; *ov* – ovule; *sn* – septal nectaries; *sc* – style channel; *st* – style

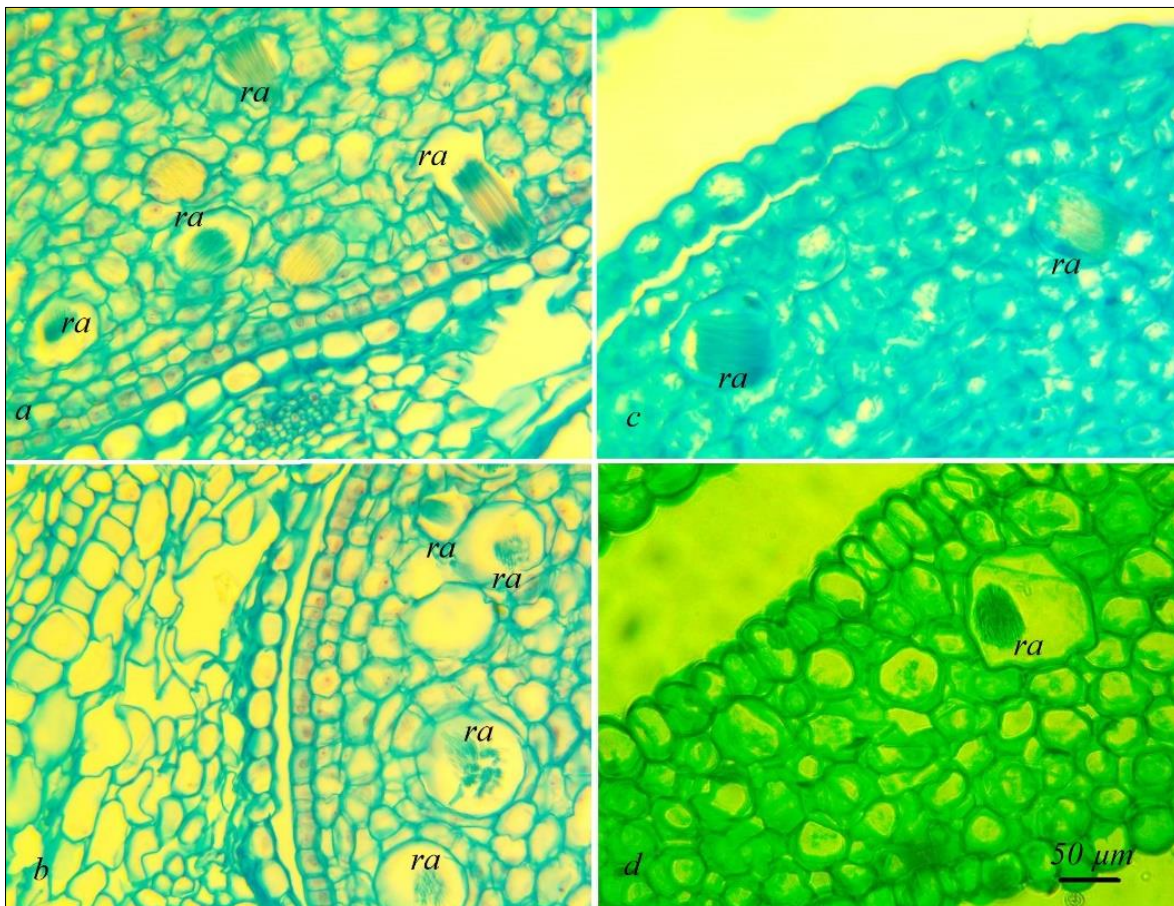


Fig. 7. Raphides in the distal parenchyma of the ovary wall of *Cordyline fruticosa* (*a, b*) and *Anthericum liliago* (*c, d*): *ra* – raphides

The fruit is an elongated to ovoid or trilete, loculicidal, three-valved, sometimes angled, or deeply 3-lobed capsule, dehiscent apically, with few-numerous seeds. The seeds are black, and angular (most genera), round in outline and vertically flattened, discoid and thin, or flat on one side. The outer layer of the seed coat contains phytomelan. The epidermal cells are tabular and flattened, convex rounded, more or less hexagonal and sometimes variously papillate. In *Anthericum*, the testa is multilayered at maturity and the outer cell layers are thickened along their periclinal walls, with the inner cell layers thin-walled. The endosperm walls in *Anthericum* have round to elliptic pits, with no distinct size differences. Copious fats, oil and some reserve starches are stored in the endosperm of *Anthericum* (Conran, 1998).

Flowers in the genus *Cordylina* are in terminal or lateral racemose or spicate panicles, pedicels not articulated. Flowers are single per node, subtended by several bracts. Tepals are free or united basally, white, pinkish, mauve-purple or dark purple-grey. Anthers are introse, free, medifixed, inserted on tepal bases, filaments hairless. The ovary is small and ovoid, ovules 2-numerous per locule. The style is shortly filiform. The stigma is capitate or trifid. The capsule is ovoid, seeds few, rounded, black, smooth (Conran, 1998).

Flowers in Anthericaceae have various kinds of inflorescences, usually pedicellate, subtended by single to numerous bracts, not articulated or articulated along the pedicels, bisexual, actinomorphic or zygomorphic. The perianth segment of six in two more or less similar cycles is petaloid, membranous, scarious or papery, often with fimbriate margins, persistent, free or connate. There are six or fewer, often three, stamens, all fertile or three staminodial; filaments are free or (*Echeandia*) basally connate; anthers are basifixed or dorsifixed, dehiscent longitudinally or by apical pores, introrse or rarely latrorse or extrorse. Pollen grains are 2-celled, 1-colpate or rarely trichotomocolpate or tetrachotomocolpate. Septal nectaries are present. Gynoecium of three carpels is sessile or (*Chlorophytum*) stipitate. The style is filiform, rarely (*Tricoryne*) gynobasic, with small, capitate or 2–3-lobed stigma; ovary superior, 3-locular; ovules single to numerous per locule. The fruits are loculicidal or septicidal capsules, nuts or schizocarps (*Tricoryne*). The seeds are testal, sometimes arillate, the endosperm is fleshy, embryo cylindrical, straight to curved inwards; testae are encrusted with phytomelan. Chelidonic acid, saponins / sapogenins are present (Takhtajan, 2009).

In the genus *Cordylina* seeds are black, glabrous. This genus is represented by perennial herbs (dwarf to large), shrubs or trees (to 10 m tall, often rhizomatous or tuberous, occasionally epiphytic (on trees). Raphides are present. Secondary thickening is anomalous (*Cordylina*) or absent. Vessels are only in roots, with scalariform perforations. Leaves are alternate, spiral or distichous, mesomorphic to leathery and stiff, linear to broadly lanceolate, mostly keeled, sheathing at base, usually densely pubescent, at least when young; the trichomes are scalelike or stellate, multicellular and arising from a multicellular base (Takhtajan, 2009).

The genera *Anthericum* and *Cordylina* have an internal septal nectary. In general, the family Asparagaceae is characterized by the presence of septal nectaries (Daumann, 1970; Conran, 1998; Takhtajan, 2009).

The studied genera are also widely researched in other areas. Both members of the diploid-tetraploid species pair *Anthericum ramosum* L. and *A. liliago* L. occur as geographically separated isolates at the northern limits of their range in Scandinavia. Variation in floral morphology was studied in 33 populations of *A. ramosum* from four geographical regions and 25 populations of *A. liliago* from seven regions of Scandinavia. Tepal shape was characterized using moment invariants, and intra- and interspecific variation in style and filament length was investigated. Significant interregional and interpopulation variation in shape, style and filament length was observed within both species. However, despite the geographical divergence of the distribution of both species, there was considerable overlap in tepal shape between populations from different regions. The hierarchical distribution of tepal shape diversity was similar in the two species. Most of the total diversity was explained by regional and interpopulation components of diversity (48% and 35%, respectively, in *A. ramosum*

and 61% and 22%, respectively, in *A. liliago*). The two species were clearly distinguished in tepal shape and style, as well as in the length of the outer filaments. The southern Swedish population, which contained triploid hybrids between *A. ramosum* and *A. liliago*, did not differ from other Scandinavian populations of *A. liliago* in tepal shape. However, the (probably hybrid) Danish population of *A. liliago* was intermediate between these two species in tepal shape (Rosquist & Prentice, 2001).

The reproductive output (seeds per ramet) was only highly correlated ($P < 0.001$) with the proportion of flowering ramets in a population, which could be caused by a more effective pollination in large populations which are more attractive to specialized pollinators. The specialized *A. liliago* pollinator *Merodon rufus* (Syrphidae) and high abundances of solitary bees could only be found in *A. liliago* populations with more than 10,000 individuals. Genetic differentiation among the investigated *A. liliago* populations may have been caused by limited seed and pollen dispersal and a mixed mating system permitting a high selfing rate. The differentiation among the small and isolated populations lacking main pollinators seems to be caused by genetic drift (Peterson et al., 2008).

The study of pre-European Māori agriculture in New Zealand is complicated by the lack of direct evidence in the form of plant remains. Results have been obtained of pollen and phytolith analyses from three archaeological sites on the Auckland Isthmus, Cambridge and north Taranaki. All sites show evidence of human disturbance of the landscape and the presence of pollen from the introduced Māori cultigen *Cordylina* cf. *fruticosa* (ti), suggesting that the species had a wide geographical range, extending well beyond what is considered to be a range climatically restricted by early ethnographic records. *C. fruticosa* pollen can be identified in the Pacific Islands, including New Zealand, where there are several endemic *Cordylina* species. A study describes this pollen type and reviews the locations and types of *C. fruticosa* macro- and microfossils previously reported in the Pacific Islands region (Horrocks et al., 2022).

There is a study of floral morphology and morphometry, nectar secretion, testing the effects of nectar removal, and evaluation of the reproductive system in *D. trifasciata*. The results show that the floral characteristics of *D. trifasciata* are strongly consistent with the phalaenopsis syndrome (i.e., lepidopteran pollination), characterized by white flowers, a short floral tube, and nocturnal flowering. The species' nectar is accumulated at the base of the floral tube by continuous secretion, persisting throughout the night (Primo et al., 2025).

The relationships between the sister groups of Ethiopian *Anthericum* and *Chlorophytum* species, as well as the patterns of variation within the *C. gallabatense* and *C. comosum* complexes, were studied using molecular phylogenetic analysis, morphometrics and scanning electron microscopy of the seed surface. The results show that the molecular data largely support previous morphological conclusions, and that speciation occurred in Ethiopia at least three times within *Anthericum* and repeatedly within different *Chlorophytum* clades. Areas particularly rich in endemic species are the lowlands around the Bale Mountains in southeastern Ethiopia and the Beninshangul-Gumuz regional state in western Ethiopia near the Sudanese border. A new species, *Chlorophytum mamillatum* Elden & Nordal, is described, and the names *C. tordense* and *C. tetraphyllum* are reinstated (Bjorå et al., 2017). New features of the anatomical structure of the flower *A. liliago* and *C. fruticosa* which we found are the presence dorsal carpel bundles forming blind lateral branches in the ovary wall of *A. liliago* and dorsal carpel bundles which do not branch above the ovary locules. In *C. fruticosa*, we discovered the presence of ventral complex roots, the presence of a high ovary base and the ovary roof, the presence of synascidiate, symplicate (only in *A. liliago*) a hemisymplicate and asymplicate gynoecium structural zones. Also, the heights of the ovary zones in the studied species and the length of septal nectaries are very different.

Conclusion

The new data allowed us to deepen the knowledge of the micro-morphological and anatomical features of the *A. liliago* and *C. fruti-*

cosa flowers, in particular, the anatomical structure of tepals, gynoeium vertical zonality and vasculature of the flower as a whole were studied. The septal nectary in *A. liliago* is located from the base of the synascidiate zone of the ovary to its roof, in the form of three narrow cavities that open with nectary slits. The height of the nectary slit is 200 µm. The total height of the septal nectary is 1580 µm. There are three vertical structural and functional zones in the ovary: the ovary base 280 µm, the locules 1740 µm, and the ovary roof 200 µm. The septal nectary in *C. fruticosa* is located at the beginning of the hemisymphicate zone of the ovary to the roof of the ovary, in the form of three narrow cavities that open with nectary slits. It appears at the fertile level of the ovary, 140 µm above the beginning of the hemisymphicate zone. The nectary slit is straight, glandular, elongated, 220 µm high. The total height of the septal nectary is 1720 µm. There are three vertical structural and functional zones in the ovary of *C. fruticosa*: the base of the ovary 340 µm, the locules 1860 µm and the roof of the ovary 320 µm. The features of micromorphology and vascular anatomy obtained during the study will be further used in the taxonomy by morphological features of the family Amaryllidaceae.

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