

## MICROMORPHOLOGY, ANATOMY AND ULTRASTRUCTURE OF NECTARIES IN TWO TYPES OF FLOWERS OF *Citrus limon* CV. 'PONDEROSA'

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**Abstract.** Trees of the genus *Citrus* can bloom all year round and are an abundant source of nectar for honey bees. Nectar production largely depends on nectary structure. The aim of this study was to investigate the structure of nectariferous tissues in hermaphrodite and functionally male flowers of the so-called Skierniewice lemon (*Citrus limon* cv. 'Ponderosa'), which enjoys great popularity in Europe, using light microscopy as well as scanning and transmission electron microscopy. The nectary glands in both types of flowers differed in shape and size, but their structure and the pathways of nectar transport were similar. The intrastaminal nectary in the lemon flowers is composed of a massive ring-like located below the base of the ovary. Nectar is secreted through few modified stomata and probably through the microchannels in the cuticle. Numerous branches of vascular bundles, with phloem elements, penetrate the nectariferous tissue and reach the subepidermal layers. The high content of endoplasmic reticulum, vesicles and Golgi bodies in the nectary cells indicates that the nectar is transferred by granulocrine secretion. The intercellular transport of nectar occurs using two ways: the symplast and apoplast pathway. The different regions of the nectary function asynchronously.

**Key words:** lemon, flower nectaries, microstructure, SEM, TEM

### INTRODUCTION

The lemon, native to south-east China, was brought to Europe by Arabs in the 11th century [Szwejkowska and Szwejkowski 2003]. The flowers of this species, 3 cm in

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diameter, grow singly or in small clusters. Their whitish corolla consists of 5 fleshy, intensely fragrant petals. The androecium of numerous stamens surrounds the pistil with a superior ovary. The lemon flowers and produces fruit all year round [Rönnerblom 2003].

The floral nectaries of species of the family *Rutaceae* are classified as receptacular and intrastaminal [Bernardello 2007]. They are formed from the receptacle tissues, taking on various forms. In accordance with the division proposed by Smets [1986], this type of nectary is included in “nectaria persistentia”, because it is connected to the persistent floral parts. In *Dictamnus* and *Cneorum*, the floral nectaries are formed as outer layers of the lower part of the gynophore [Weryszko-Chmielewska et al. 2001, Caris et al. 2006]. In *Ruta*, a fleshy nectary disc forms at the ovary base, with its diameter much exceeding the width of this part of the pistil [Weryszko-Chmielewska et al. 2003]. The nectary type in *Metrodorea nigra*, which is a 5-lobed disc in shape located on the upper edge of the receptacle, is similar to that found in rue. The epidermis of the upper part of the gland in this species additionally forms outgrowths resembling trichomes and the nectary color changes from yellow to pink or red as the anthesis proceeds [Pombal et al. 2000, Souza et al. 2004].

The nectary gland found in lemon flowers forms a characteristic ring-like located below the ovary base. Due to its morphological and topographic characteristics, Fahn [1952, 1979] classified the nectary of this species as toral nectary (torus type), developing on the receptacle. The above-mentioned author described few anatomical features of the *Citrus limon* nectary, drawing attention to the presence of orbicular stomata through which the nectar is secreted. Some features of the nectary microstructure in other *Citrus* species were studied by Rachmilevitz and Fahn [1973] (in *C. sinensis*) and Xiao [2000] (in *C. reticulata*). Many authors think that the location and structure of nectaries are important characteristics that provide important taxonomic significance and can elucidate the origin and evolution of various plant groups [Smets et al. 2000, Bernardello 2007, Konarska 2015].

*Citrus limon* cv. ‘Ponderosa’, the so-called Skierniewice lemon is not a commercially grown cultivar, but in Europe it enjoys great popularity, since it enters the flowering and fruiting period early and its fruit has a taste similar to the fruit of other cultivars of this species [Pieniżek 1983]. This study on the nectary of *C. limon* is a continuation of our research on the structure of floral nectaries in various representatives of the family *Rutaceae*. Because few data were found in the literature concerning the structure of the *C. limon* nectary and these data did not allow us to conclude whether the nectary structure in this species differs from the model typical of previously studied *Citrus* species compared to other *Rutaceae*, the aim of the present study was to carry out detailed observations of the structure of the tissues of the nectar-secreting gland in hermaphrodite and functionally male flowers of *Citrus limon* cv. ‘Ponderosa’, with special attention to the characteristics of secretory epidermis.

## MATERIALS AND METHODS

Fresh nectar-secreting lemon flowers at the closed- and open-bud stages, belonging to two types: hermaphrodite and functionally male, were collected in October 2013 in the

UMCS Botanical Garden in Lublin, Poland (51°15'44"N, 22°30'48"E) and were examined and viewed under a stereoscopic light microscope SMT 800 (SLM) coupled with a NIKON COOLPIX 4500 camera. Having removed the perianth and filaments, flower portions containing nectaries collected from flowers in the open-bud stage were fixed and analyzed using light, scanning and transmission electron microscopy.

**Scanning electron microscopy (SEM).** The plant material was fixed in 2% glutaraldehyde with 2.5% paraformaldehyde in 0.75 M phosphate buffer with a pH of 6.8 for 12 hours at a temperature of 4°C. Subsequently, the samples were washed twice with the buffer for 15 seconds at room temperature and with distilled water also for 15 seconds. The specimens were dehydrated in HCl-acidified 2,2-dimethoxypropane [Muller and Jacks 1975]. After dehydration, the material was critical-point dried in liquid CO<sub>2</sub> and sputter-coated with gold using a CS-100 Sputter Coater. The examination was carried out at an accelerating voltage of 30 kV using a BS – 300 Tesla scanning electron microscope. The measurements of the length (n = 10) and number (n = 5) of nectarostomata per mm<sup>2</sup> surface area of the nectary were taken using morphology software coupled with SEM.

**Light microscopy (LM).** The flower samples were fixed in 2.5% glutaraldehyde with 2.5% paraformaldehyde in 0.75 M phosphate buffer with a pH of 7.4 at room temperature for 2 hours and then kept for 12 hours at 4°C [Glauert 1974]. Next, after the material was treated with 1% osmium tetroxide and dehydrated in ethanol and acetone series, it was embedded in Spurr Low Viscosity resin. The collected samples were used to prepare 0.5 µm semi-thin sections which were stained with 1% methylene blue with 1% azure II in a 1% aqueous solution of sodium tetraborate. Observations and photographs were made with a Jenaval Contrast microscope. Hand-cut longitudinal sections of the nectary from flowers at the closed- and open-bud stages were stained with IKI (iodine/aqueous potassium iodide solution) in order to detect starch.

**Transmission electron microscopy (TEM).** Flower portions containing the nectaries were fixed in 2% paraformaldehyde and 2.5% glutaraldehyde as well as 0.1 M cacodylate buffer with a pH of 7.4. After the samples were rinsed in 0.1 M cacodylate buffer and postfixed in 1% OsO<sub>4</sub>, they were stained in a 0.5% aqueous solution of uranyl acetate. Subsequently, the material was dehydrated in an alcohol series and propylene oxide, and embedded in Spurr Low Viscosity resin [Spurr 1969]. 60 nm thin sections, obtained using a Reichert Ultracut S ultramicrotome, were treated with an 8% solution of uranyl acetate in 0.5% acetic acid and lead citrate [Reynolds 1963]. Observations and documentation were made using a BS – 500 Tesla electron microscope.

## RESULTS

**Morphological characteristics of the nectary.** The intrastaminal, a greenish yellow colour nectary in hermaphrodite and functionally male flowers of *C. limon* 'Ponderosa' is located on the receptacle between the ovary base and the base of the filaments, which form a single whorl (fig. 1 a, b). Nectar droplets were observed on the nectary surface in

both types of flowers in the closed- and open-bud stages. The flattened and fused filaments (in 2–3) as well as the fleshy petals prevent the nectar released by the nectary tissues from flowing out of the nectary. When viewed from above, it has a spherical shape in the hermaphrodite flowers and most frequently a polygonal shape in the functionally male flowers (fig. 1 c–e). Its upper surface shows irregular folds, while the lateral part is characterized by distinct ribs (fig. 1 b, c, f). The diameter of the annular nectary in the hermaphrodite flowers reaches 7–8 mm and its height 1–1.5 mm, whereas in the functionally male flowers its diameter is 5–6 mm and its height 0.5–0.8 mm. Unlike in the sepals, the petals as well as the ovary and the style, we did not find any essential oil cavities in the nectary.

**Nectary micromorphology.** The nectary surface in *C. limon* cv. ‘Ponderosa’ in both types of flowers differed distinctly from the ovary surface (fig. 2 a–f). In the outer layers of the ovary, quite regularly arranged depressions could be seen, at the bottom of which essential oil cavities were found (fig. 2 a, b). No such depressions were observed on the nectary surface. The surface of the degenerated ovary in functionally male flowers was characterized by strong undulation, and the cells of the ovary epidermis were very irregularly shaped (fig. 2 c). The upper surface of the nectary showed a number of small projections (fig. 2 d), whereas the lateral walls of the gland were characterized by the occurrence of numerous groove-like depressions, arranged in a wavy pattern in the vertical direction (fig. 2 e, f), which facilitated the downward movement of the nectar.

Stomata were observed in the nectaries of both types of flowers and they were located primarily on the upper surface of the nectary, but few stomata also occurred on the lateral walls of the gland (fig. 3 a–f). It was calculated that in the epidermis of the upper part of the nectary there were about 45 stomata per mm<sup>2</sup>. In dorsal view, the nectarostomata had a shape close to spherical (fig. 3 c–f). Small outer cuticular ledges, located far apart from each other, surrounded a large outer stomatal chamber of the stoma leading to a permanently open stomatal aperture. Most frequently, the stomata were situated at the level of the other epidermal cells. Only some of them were located above the epidermis surface. The stomata were surrounded by 7–8 epidermal cells that did not differ from the other cells of this tissue. Therefore, they can be classified as anomocytic. Some epidermal cells were covered with striated cuticle, but most cells were characterized by a layer of smooth cuticle (fig. 3 c–e). A slight wax coating and a spongy substance, which could have been nectar residues, were observed in the vicinity of the stomata or on their surface (fig. 3 c–e). Two stomata being in contact with each other through their guard cells were found sporadically (fig. 3 d). Some stomata were sealed with a cuticular plug. The nectarostomata differed in size compared to the leaf stomata (fig. 3 f, g). The length of the nectarostomata ranged from 20.6 µm to 23.1 µm, their width reached larger dimensions, ranging between 24.9 and 26.7 µm, whereas the leaf stomata had a similar length to that of the nectarostomata, but their width was smaller by 27% (21.7 × 18.9 µm).

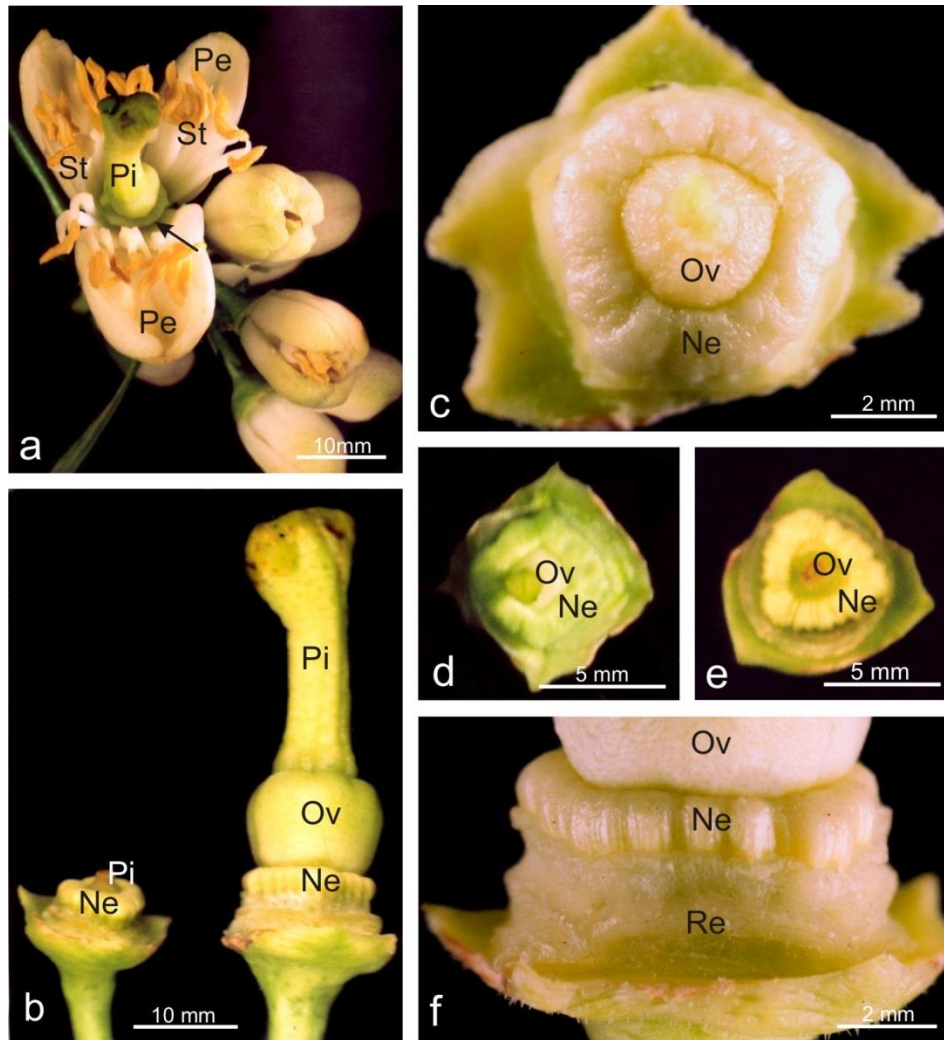


Fig. 1. Flowers and nectaries of *Citrus limon*. SLM images: a – flowers with nectaries (arrow); b – nectary in a functionally male flower (with a short vestigial pistil) and in a hermaphrodite flower (with a long pistil); c–e – different shaped nectaries in dorsal view in functionally male flowers; f – lateral view of the hermaphrodite flower's nectary; Ne – nectary, Pe – petal, St – stamen, Pi – pistil, Ov – ovary, Re – receptacle

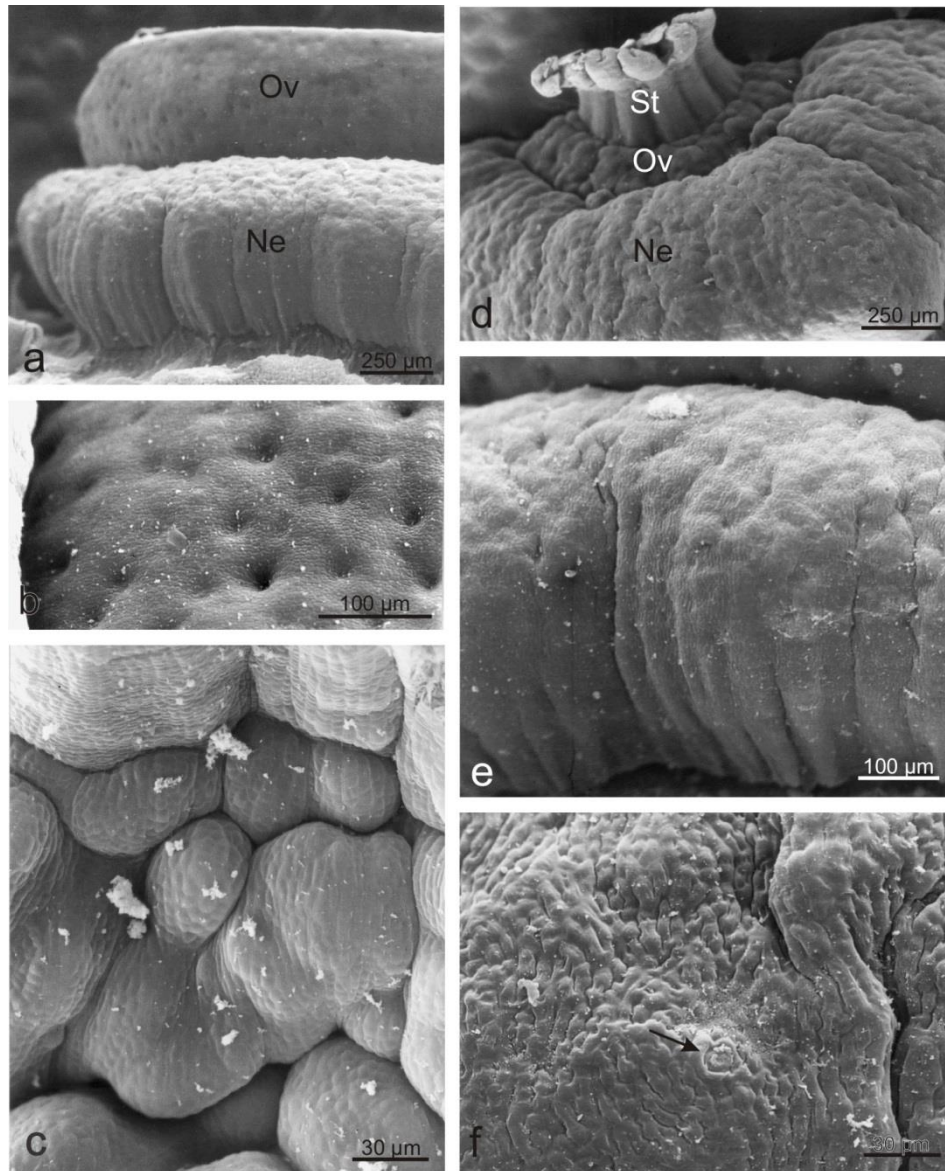


Fig. 2. Surface of the ovary and nectary of *C. limon*. SEM images: a – fragment of the ovary of a long pistil with the nectary in lateral view; b – surface of the ovary of a long pistil with depressions containing oil glands; c – visible epidermal cells of the ovary of a short pistil; d – folded upper surface of the nectary from a flower with a short pistil; e – ribbed lateral surface of the nectary from a flower with a long pistil; f – fragment of the lateral strongly folded nectary surface with a stoma (arrow) from a flower with a short pistil; Ne – nectary, St – style, Ov – ovary

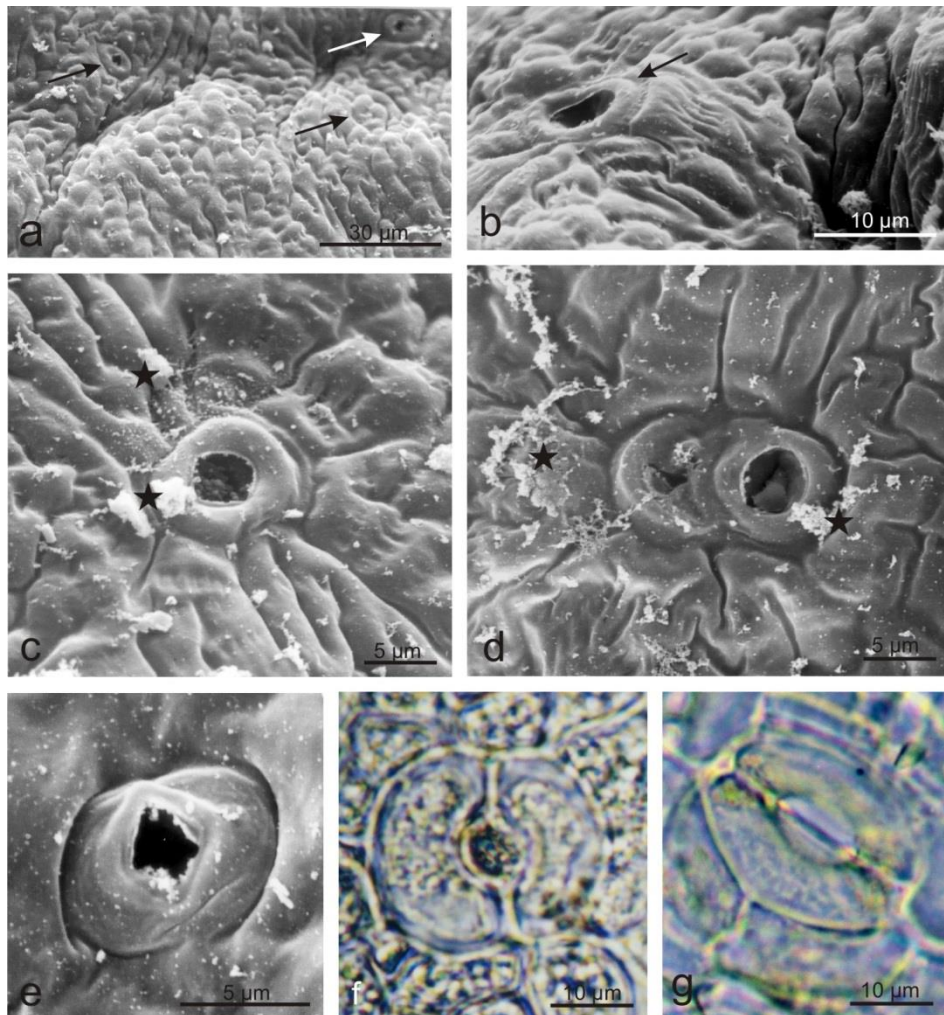


Fig. 3. Nectarostomata of *C. limon* visible on the upper nectary surface. SEM and LM images: a, b – fragments of the folded surface of the nectary epidermis with stomata (arrows); c–e – open stomata (arrows) on the nectary epidermis surface; f – stoma from the nectary epidermis; g – stoma from the lower epidermis of a *C. limon* leaf; stars – dried flocculent secretion

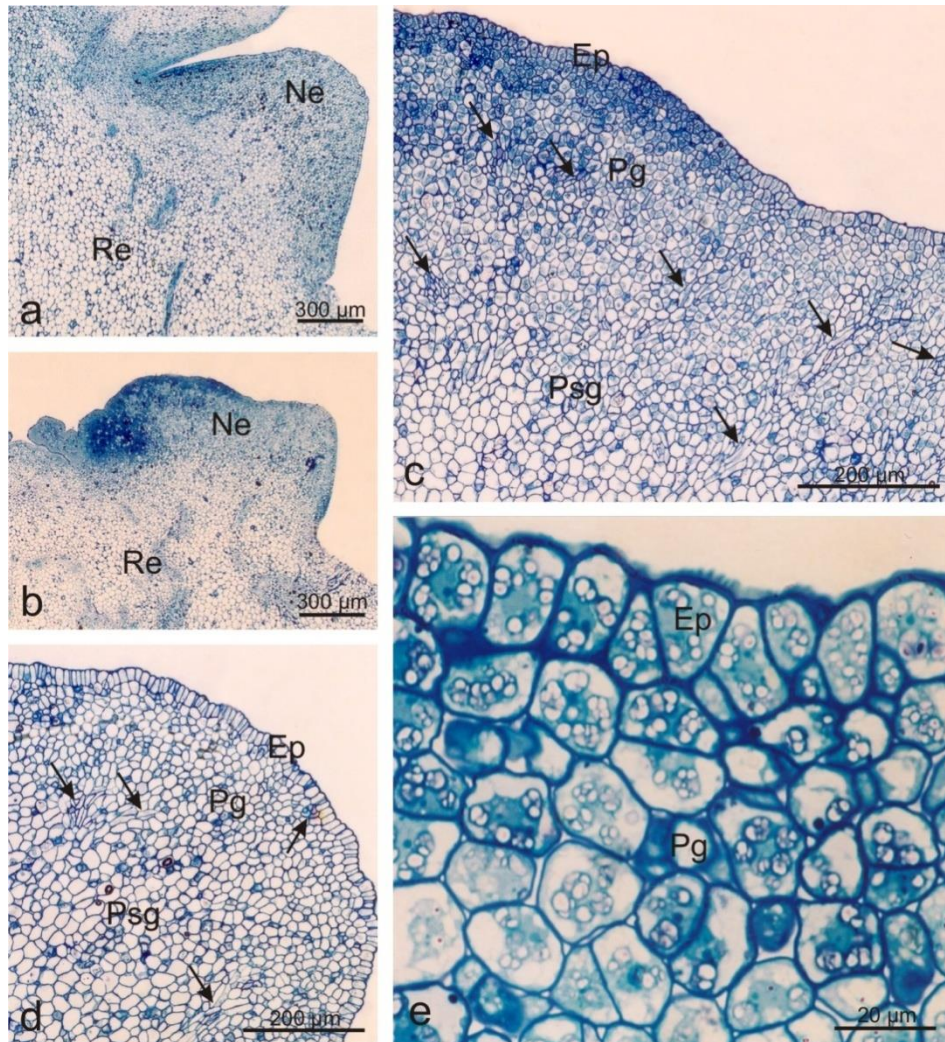


Fig. 4. Partial longitudinal sections of the nectary gland and receptacle in *C. limon*flowers. LM images. Note the darker color of the nectary cells in the upper part of the gland compared to the cells making up its lateral parts: a – partial section of the receptacle with the nectary in a hermaphrodite flower; b – partial section of the receptacle with the nectary in a functionally male flower. c–e – partial section of the *C. limon*nectary in a hermaphrodite flower (c, e) and in a functionally male flower (d) with numerous vascular bundles (arrows); e – visible epidermal cells and glandular parenchyma cells containing numerous starch grains; Ne – nectary, Re – receptacle, Ep – epidermis, Pg – glandular parenchyma, Psg – subglandular parenchyma



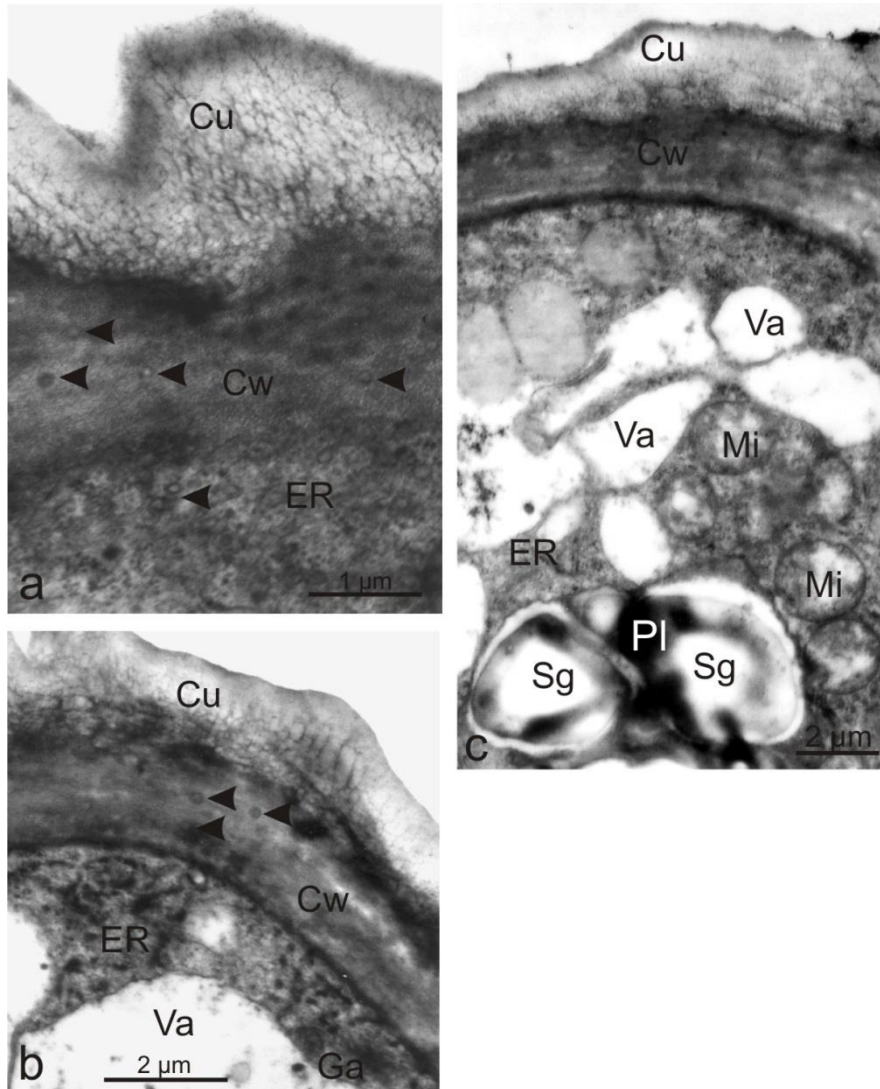


Fig. 5. Fragments of secretory epidermal cells with cuticle. TEM images: a, b – visible a thick cuticle with a reticulate structure containing numerous microchannels and the cytoplasm of the epidermal cells containing ER tubules terminating in vesicles with dark contents as well as numerous small vesicles with dark contents. Similar vesicles were observed in the outer cell wall (arrow-heads); c – visible cytoplasm containing numerous mitochondria and ribosomes, Golgi, as well as plastids filled with starch grains; Cu – cuticle, Cw – cell wall, Mi – mitochondria, Pl – plastid, Sg – starch grains, Go – Golgi, Va – vacuoles, ER – endoplasmic reticulum

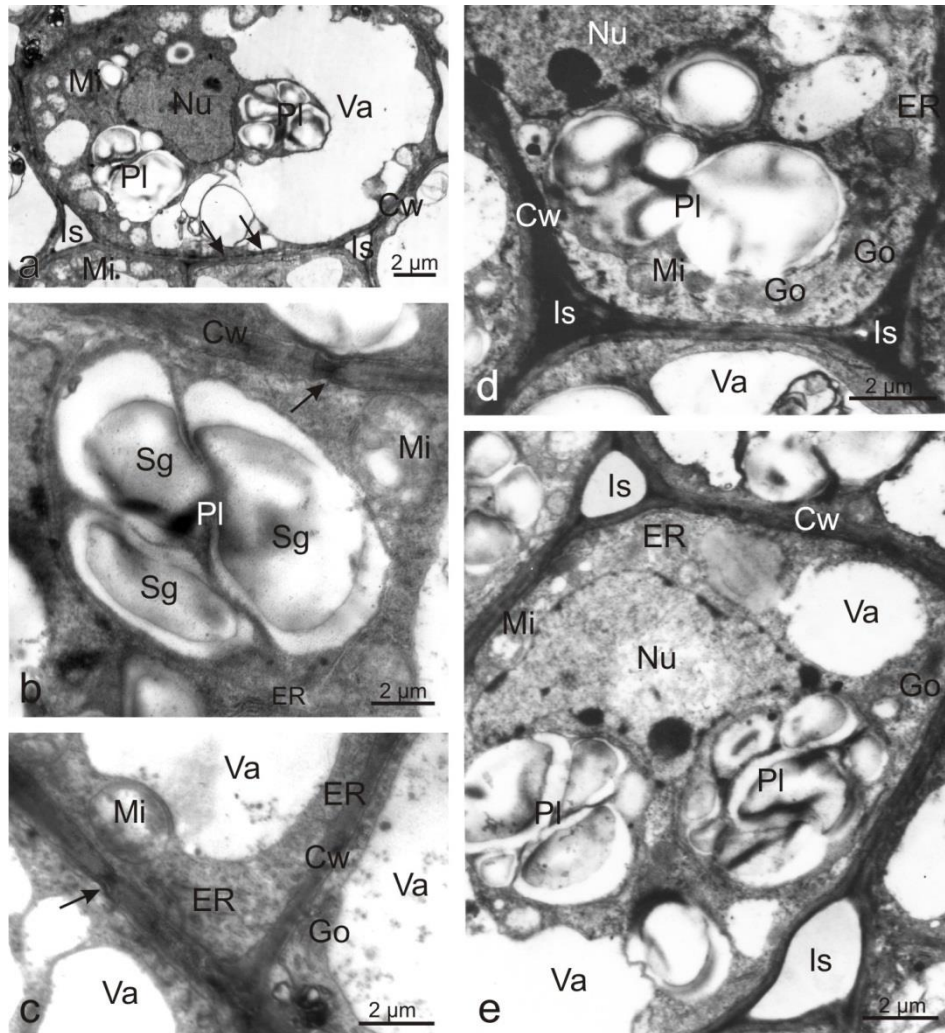


Fig. 6. Fragments of glandular parenchyma cells. TEM images. In the cells, visible are lobed nuclei and plastids filled abundantly with starch grains (a, b, d, e) as well as mitochondria (a–e) and Golgi bodies (c–e). b–d – note numerous ER tubules with dark contents, a large number of different sized vesicles, and ribosomes. Visible thin and electron dense cell walls with plasmodesmata (arrows) (a–c) and electron transparent intercellular spaces (a,e); d – subepidermal layers of the nectary with large intercellular spaces filled with dark contents are visible; Cw – cell walls, Va – vacuoles, Pl – plastids, Sg – starch grains, Nu – nucleus, Mi – mitochondria, Go – Golgi, ER – endoplasmic reticulum, Is – intercellular spaces

**Nectary anatomy.** In both types of flowers, the nectary cells were more intensely colored and had smaller dimensions than the neighboring cells of the receptacle (fig. 4 a–c). The nectary surface was covered with a single-layered epidermis which formed folds in the upper part of the nectary, corresponding to the surface irregularities observed in SEM. In longitudinal section, it was difficult to find stomata, probably due to their small number. The epidermal cells were radially elongated (fig. 4 c–e). In most epidermal cells the cytoplasm with the nucleus and numerous plastids containing starch grains were located centrally, while the vacuoles most frequently occupied positions adjacent to the tangential walls (fig. 4 e).

The glandular tissue consisted of a dozen or so layers of cells which had different sizes and exhibited varying degrees of vacuolation depending on their position in the nectary (fig. 4). In the nectaries of both flower types, in the closed-bud stage, the results of the IKI reaction indicated the presence of starch grains in all cells of the secretory parenchyma. More starch grains were present in the central (upper) region of the nectary, than in the lateral region of the gland. In the open-bud stage, two differently functioning secretory parenchyma regions differing in the content of starch grains were observed. The cells located in the upper region of the nectary were small and strongly colored (fig. 4 b), with numerous starch grains in the plastids (fig. 4 e). On the other hand, the cells located on the lateral walls of the gland were much brighter, with well-developed vacuoles and often without starch (fig. 4 d). Small intercellular spaces were found in the nectariferous tissue, much smaller than those in the subglandular tissue. The nectariferous tissue is penetrated by numerous branches of vascular bundles which contain xylem and phloem elements (fig. 4 c–e). Numerous small phloem branches reached the subepidermal layers

**Nectary ultrastructure.** The outer walls of the secretory epidermal cells were much thicker than the radial and periclinal walls, which were in contact with the glandular tissue. Their surface was covered with a layer of cuticle of varying thickness, strongly folded at some places, which was penetrated by a network of polysaccharide fibrils forming specific microchannels (fig. 5 a–c). Plasmodesmata occurred in the tangential walls of the epidermal and nectariferous parenchyma cells (not shown). Plastids containing different sized starch grains were located in the cytoplasm, most frequently situated peripherally and less frequently in the central part of the cell (fig. 5 b). Numerous mitochondria were found near the plastids and in the peripheral part of the cytoplasm (fig. 5 b). Endoplasmic reticulum tubules terminating in vesicles with dark contents and numerous small vesicles with dark contents were observed in the cytoplasm located next to the outer cell wall (fig. 5 a, c). Similar vesicles were observed in the outer cell walls. Very numerous ribosomes were also present. The vacuoles formed bright regions in the cell (fig. 5 b, c).

The cell walls of glandular parenchyma were relatively thin and electron dense (fig. 6 a–e). Plasmodesmata were observed in them (fig. 6 a–c). In turn, relatively large intercellular spaces in the subepidermal layers of the nectary were filled with dark contents (fig. 6 d), but in the deeper layers they were electron empty (fig. 6 a, e). The degree of vacuolation was higher in the deeper located glandular tissue layers. The nuclei were lobed (fig. 6 a, e). Plastids abundantly filled with starch grains and mitochondria were located near the nuclei (fig. 6 a, b, d, e). Numerous ER tubules with dark contents, a large number of

different sized vesicles and ribosomes were also present (fig. 6 b–e). Golgi bodies were also observed (fig. 6 c–e).

## DISCUSSION

The present study found that the nectary glands occurring in the hermaphrodite and functionally male flowers of *C. limon* ‘Ponderosa’ differed only in shape and size, whereas their structure was similar. Guardiola [1997] reports that flowers of most citrus species having both pistil and stamens are perfect; however, staminate flowers, having only a rudimentary pistil, are formed sometimes in a variable proportion. In *Cneorum tricoccon* belonging to the family Rutaceae, in turn, two types of flowers were likewise described by Caris et al. [2006].

SEM examination shows that few stomata with permanently open apertures occur in the nectary epidermis in *C. limon*. Their number per 1 mm<sup>2</sup> of this gland’s epidermis is almost 5 times lower than in the nectary of *Dictamnus* (Rutaceae) [Weryszko-Chmielewska et al. 2001]. Stomatal pores are possible sites of nectar secretion and the nectar is released along this pathway in an uncontrolled way, similarly as in typical “nectarostomata” described by many authors in other species [Konarska 2014, Zini et al. 2014, Denisow et al. 2015]. Similar stomata in the nectaries of *C. limon* were previously presented in drawings by Fahn [1952]. But nectar release through stomata was also found in other Rutaceae [Xiao 2000, Weryszko-Chmielewska et al. 2001, 2003, Souza et al. 2003, Caris et al. 2006]. In turn, ultrastructural examination of the epidermal cells of the *C. limon* nectary reveals that strongly developed microchannels forming a characteristic reticulum are found in the cuticle layer present on the surface of this tissue. Their presence and the small number of nectarostomata suggest the possibility of nectar release in this species not only through the stomatal pores, but also through the cuticle. A strongly thickened cuticle is also found near the stomata and perhaps the nectar emission regions are located there. Nectar secretion through polysaccharide microchannels present in the cuticle was previously described in *C. reticulata* by Xiao [2000] as well as in other taxa from various families by numerous researchers [Koteyeva 2005, Buzatto et al. 2012, Antoń and Kamińska 2015].

Epidermis, parenchymatous tissue with vascular bundles and subglandular tissue were distinguished in the anatomical structure of the *C. limon* nectary. A similar nectary structure in *Citrus reticulata* was presented by Xiao [2000], while in *Pilocarpus pennatifolius* (Rutaceae) by Souza et al. [2003]. The anatomical observations of the *C. limon* nectary revealed that within the gland its different regions exhibit varying activity. The lateral parts of the nectary probably begin to function earlier and terminate the activity during the functioning of the central part of the gland. This is confirmed by the presence of nectar and the lower content of starch grains in the plastids of the nectary tissue in the lateral regions of the nectary than in its central part in the closed-bud stage. Furthermore, the absence of starch in the nectary tissue cells in the lateral parts of the gland in the open-bud stage indicates earlier starch hydrolysis and utilisation of its components for nectar production. The centrally located upper regions, whose cells contained a greater amount

of starch grains in the closed-bud stage, probably become active later, because the nectariferous cells of this nectary region exhibited the presence of plastids with many starch grains in the open-bud stage, too. In turn, similar asynchronous functioning of cells in the nectaries of other species was observed by Gaffal et al. [2007] and Konarska [2011]. According to many authors, the presence of many starch grains in the nectary suggests that pre-nectar, which reaches the nectary parenchyma through phloem, originates from photosynthesis taking place in other floral or leaf/stem parts and before anthesis it is converted into starch which is hydrolyzed to sugars immediately before secretion [Stolar and Davis 2010, Giuliani et al. 2012, Abedini et al. 2013]. This type of nectar development leads to the production of a large amount of nectar with a high sugar concentration in a short time [Durkee et al. 1981, Nepi 2007]. Thanks to the asynchronous function of the various parts of the *C. limon* nectary, nectar secretion proceeds over time and the nectar is available to flower-visiting insects for a longer period. Moreover, ultrastructural examination showed the presence of nectar in the intercellular spaces of the subepidermal layers of the nectary's active region, whereas the spaces in the lower layers were empty. This may be evidence of the existence of two types of space, pneumatic and hydraulic, which were described by Gaffal et al. [1998] in *Digitalis*.

During the study, it was found that the nectary of *C. limon* is equipped with its own vascular system which consists of xylem and phloem and includes numerous small phloem branches, reaching even the epidermis, which provide good inflow of nutrient compounds necessary for nectar synthesis. In the secretory tissue in other representatives of Rutaceae, phloem elements that supplied the nectary were also observed by Xiao [2000] and Souza et al. [2003, 2004].

Due to the presence of a large number of ER cisterns, Golgi bodies and numerous vesicles near the cell walls in *C. limon*, it can be concluded that the transfer of nectar from the protoplasts outside the nectariferous parenchyma cells occurs through "granulocrine secretion". This type of nectar transfer was also observed by Rachmilevitz and Fahn [1973] in the nectary of *C. sinensis*, where an active ER and numerous Golgi bodies were found in the glandular parenchyma cells. Granulocrine secretion in nectaries of various taxa was also described by other researchers such as Melo et al. [2010] and Kowalkowska et al. [2015].

Plasmodesmata were observed in the cell walls of the glandular parenchyma in *C. limon*, whereas in the intercellular spaces of this tissue a secretion was visible, which indicates the existence of two ways of intercellular nectar transport in this species: via the symplast and apoplast pathway. Likewise, both types of nectar transport were described in *C. reticulata* by Xiao [2000].

## CONCLUSIONS

The nectaries in the hermaphrodite and functionally male flowers of *Citrus limon* have different sizes, but their microstructure is very similar. These glands are characterized by the occurrence of many similarities to the nectaries described in other *Citrus* species and various representatives of Rutaceae. However, the nectary microstructure in the family

Rutaceae has been described for the first time in such a comprehensive and detailed manner. It has been found that the common features characterizing nectaries in the described representatives of Rutaceae are their location, vascularization, granulocrine secretion of nectar, and the presence of modified stomata. On the other hand, the variable traits include nectary type, asynchronous functioning of different regions of the nectary, and mode of nectar exudation, which occurs only through stomata or simultaneously through stomata and probably through the cuticle.

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### MICROMORFOLOGIA, ANATOMIA I ULTRASTRUKTURA NEKTARNIKÓW W DWÓCH TYPACH KWIATÓW *Citrus limon* CV. 'PONDEROSA'

**Streszczenie.** Kwitnące przez cały rok drzewa należące do rodzaju *Citrus* są obfitym źródłem nektaru dla pszczoły miodnej. Produkcja nektaru w znacznym stopniu zależy od struktury nektarnika. Celem pracy było zbadanie struktury tkanki nektarnikowej w obupłciowych i funkcjonalnie męskich kwiatach cenionej w Europie cytryny skierniewickiej (*Citrus limon* cv. 'Ponderosa') przy zastosowaniu mikroskopu świetlnego oraz elektronowego: skaningowego i transmisyjnego. Gruczoły nektarnikowe w dwóch typach kwiatów różniły się kształtem i wielkością, natomiast ich struktura i drogi transportu nektaru były podobne. Intrastaminalny nektarnik w kwiatach cytryny tworzy masywny pierścień zlokalizowany poniżej podstawy zalążni. Sekrecja nektaru odbywa się przez nieliczne zmodyfikowane aparaty szparkowe oraz prawdopodobnie przez mikrokanaliki w kutykuli. Liczne odgałęzienia wiązek przewodzących zawierających łyko przenikają tkankę nektaronośną i docierają do warstw subepidermalnych. Znaczna zawartość retikulum endoplazmatycznego, pęcherzyków i aparatów Golgiego w komórkach nektarnika wskazuje na „granulocrine” transfer nektaru. Międzykomórkowy transport nektaru odbywa się dwoma sposobami: symplastem i apoplastem. Różne rejony nektarnika funkcjonują asynchronicznie.

**Słowa kluczowe:** cytryna, nektarniki kwiatowe, mikrostruktura, SEM, TEM

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