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CHARACTERISTICS OF FLOWER NECTARIES OF *Hedera helix* L. (Araliaceae)

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Abstract. The structure of floral nectaries of ivy (*Hedera helix*) was investigated under light, scanning, and transmission electron microscopes. The nectar of ivy is located on top of the inferior ovary forming a distinct undulating disc between the base of petals and the style. The ivy nectary represents open and persistent nectaries. During consecutive days of anthesis, nectaries change their colour from green to brown. The secretory epidermis is covered with a thick, deeply striated cuticle, and nectar is released by nectarostomata. Epidermal cells exhibited plastids with plastoglobules and a few starch grains as well as vacuoles containing anthocyanins, the content of which increased during the successive days of anthesis and nectar secretion. Multi-layered glandular parenchyma and, underneath, subglandular tissue are located under the epidermis. The nectary was supplied by vascular bundles with phloem and xylem. Numerous chloroplasts were visible in the cytoplasm of the external layers of glandular parenchyma; they were either typical with small starch grains or untypical with circular arrangement of thylakoids. Amyloplasts containing storage starch grains and numerous small vacuoles were present in the cells of deeper layers of the nectar-bearing tissue. Druses, flocculent residue, myelin figures and spherical deposits of unknown origin were visible in the gland parenchyma vacuoles.

Key words: *Hedera helix*, floral nectaries, nectarostomata, micromorphology, anatomy, ultrastructure.

INTRODUCTION

Hedera helix L. (Araliaceae) is an evergreen climber living several hundred years. In nature, it occurs in Europe, Asia Minor, and the Caucasus. Its flowers appear in autumn on 8–10-year-old fertile shoots, which are climbing shoots at the same time [Kołtowski 2006, Witkowska-Żuk 2008]. The protogyneous ivy flowers clustered in semi-circular umbels are intensively visited by insects (mainly bees, wasps, and flies) providing the pollinators mainly with nectar [Bottema 2001, Metcalfe 2005, Jacobs et al. 2010]. Ivy nectar is composed mainly of glucose but also contains sucrose and fructose [Vezza et

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al. 2006]. The sugar content fluctuates within a wide range (25–81%) and depends on relative air humidity and the phase of nectary avtivity [Kołtowski 2008].

The specifically scented, pentapetalous ivy flowers live for about a week; they have inconspicuous, serrulate sepals, fleshy, greenish petals, and five stamens with yellow anthers. A large, disc-shaped nectary gland is located on top of the inferior ovary [Erbar and Leins 1988, 2010, Vezza et al. 2006]. The ivy nectary is classified as the open-type nectary, i.e. easily accessible for insect pollinators, and it is a persistent nectary [Smets 1986, Pacini et al. 2003]. Nectar is secreted through modified nectarostomata, and carbohydrates, which are indispensable for nectar production, are produced in the photosynthetic process that takes place in nectary cells [Vezza et al. 2006].

The relatively long period of ivy flowering which takes place in late autumn as well as the high content of sugars in the plant nectar render the species a productive honey-bearing plant and an important link in the food chain for honeybees. Given this fact and due to the incomplete information about the characteristics of the floral nectaries in this plant species, the aim of the present study was to investigate the structure of secretory glands of *H. helix* using light, scanning and transmission electron microscopes.

MATERIAL AND METHODS

Flowers of *Hedera helix* growing in a sunny place in the Botanical Garden of the Maria Curie-Skłodowska University in Lublin were collected on 25–29 September 2011, at full bloom and in full nectar production. The structure of the nectary gland was analysed under the light microscope (fresh and fixed material) and scanning and transmission electron microscopes on the second day of nectar secretion.

Scanning electron microscopy (SEM). Ovaries with nectary disc were fixed in 2% solution of glutaraldehyde with 2.5% paraformaldehyde in 0.75 M phosphate buffer (pH 6.8) at temperature of 4°C for 12 h. Subsequently, the samples were dehydrated in an ethanol series and dried at the critical point in liquid CO_2. Using the sputter coater EMITECH K 550x, they were coated with gold. The length of nectarostomata (guard cells) was measured and the number of stomata per mm^2 of nectary epidermis was counted using the Morphology software coupled with SEM. The preparations were examined under a TESCAN/VEGA LMU scanning electron microscope at an accelerating voltage of 30 kV**.**

Light microscopy (LM). For preliminary examinations of the size and structure of nectary glands, preparations from 10 ivy flower specimens were hand-made and mounted in slides with glycerine jelly. Nectary length and height, nectary thickness in its mid-length, the height of epidermal cells, and cuticle thickness on the epidermis surface were measured in the cross sections of the nectary tissue under a Nikon SE 102 light microscope; additionally, the number of the secretory parenchyma layers was counted. Furthermore, changes in nectary colour and the occurrence of pigments in the epidermis and glandular parenchyma were observed during the anthesis.

The anatomical observations of the nectaries were based on semithin longitudinal sections, which were scanned under a Jenaval Contrast microscope. The sections were cut at 0.9 μm thick using a Reichert Ultracut-S ultramicrotome with a glass knife and

were stained with 1% methylene blue with 1% azur II in 1% aqueous solution of sodium tetraborate. The material was fixed and embedded in Spurr resin with the standard method used in transmission electron microscopy.

Transmission electron microscopy (TEM). Flower fragments with nectaries were fixed in 2% paraformaldehyde and 2.5% glutaraldehyde buffered at pH 7.4 in 0.1 M cacodylate buffer. Fixation was performed at room temperature for 2 h, followed by 12 h at 4°C. When fixed, the samples were rinsed with 0.1 M cacodylate buffer at 4°C for 24 h and then treated with 1% OsO_4. Subsequently, the samples were transferred to redistilled water and stained with 0.5% aqueous solution of uranyl acetate. After passage through increasing concentrations of propylene oxide in ethanol and finally through pure propylene oxide, the samples were embedded for 12 h in Spurr low-viscosity resin at 70°C [Spurr 1969]. Ultrathin sections (60 nm thick) were treated with 8% solution of uranyl acetate in acetic acid and with lead citrate [Reynolds 1963]. Images were observed and recorded using the FEI Technai G2 Spirit Bio TWIN transmission electron microscope at an accelerating voltage of 120 kV. Images were captured using a Megaview G2 Olympus Soft Imaging Solutions camera.

RESULTS

The nectary gland in *Hedera* flowers is located on top of the inferior ovary forming a conspicuous nectary disc between the style and the base of petals (fig. 1a–d). Nectar secretion from the ivy flowers started on the second day of anthesis and persisted until the end of this period (7 days). In the initial phase of secretion, the nectary gland was green, but during the successive days of flowering and nectar secretion, it gradually turned brown. It was observed under the stereoscopic microscope that drops of nectar were still visible on the brown staining nectaries.

The ivy nectary observed under the SEM was characterised by an undulated surface (fig. 1d, e), and the nectary epidermis was covered by cuticle exhibiting distinct, massive striae (fig. 1g, h, 2a–c). T-shaped non-glandular trichomes were sporadically visible on the nectary surface (fig. 1f). Nectar secretion proceeded through epidermal stomata, which were open and had massive cuticular ledges. Active nectarostomata were located above the epidermal cells and frequently were filled with dried secretion inside (fig. 1g, 2a–c). The non-functional stomata covered with the cuticular epithelium located below the level of adjacent epidermal cells were also present in the nectary epidermis of ivy (fig. 1h).

Based on the observations of the cross sections of the ivy nectary, it was found that the gland is made up of single-layered epidermis covered with a massive cuticle and several layers of secretory parenchyma composed of tiny, compactly arranged cells (fig. 3a, b, tab. 1) containing chloroplasts and druses. A layer of subglandular tissue with larger and more loosely arranged cells and vascular bundle formed by phloem and xylem was visible under the secretory parenchyma (fig. 3a). From the second day of nectar secretion, anthocyanins were present in the epidermal cell vacuoles and appeared in the glandular parenchyma cells as well during the successive days of anthesis (fresh material, not shown).

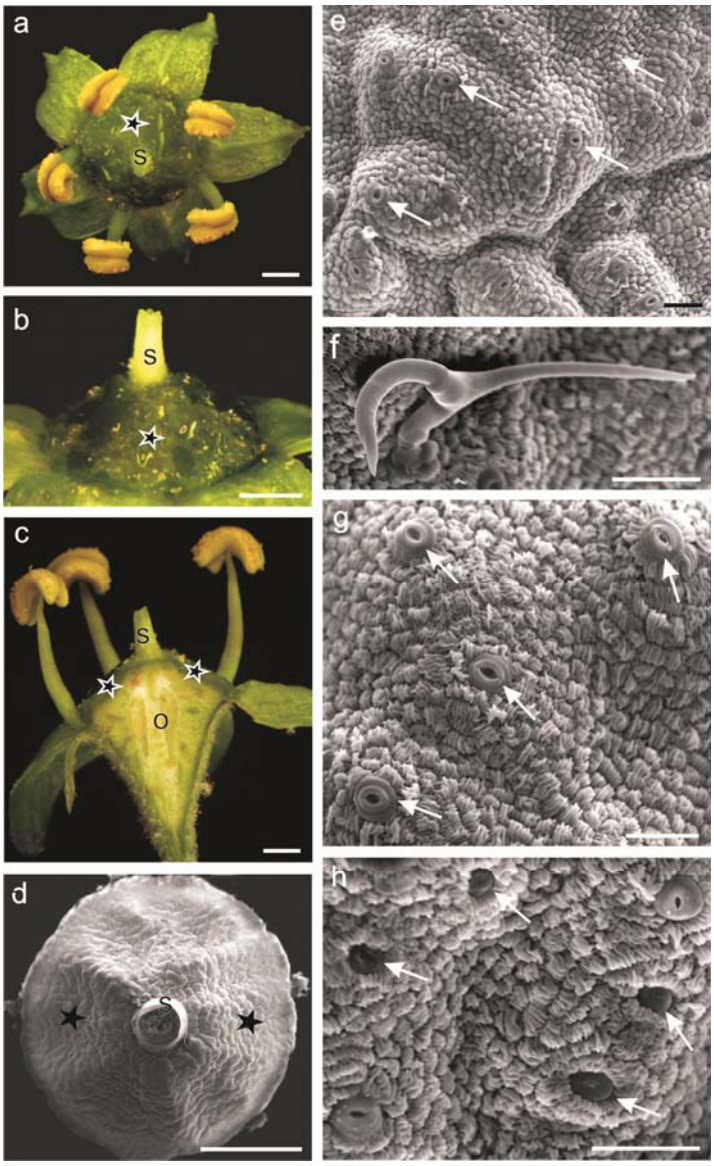

Fig. 1. LM and SEM images. Nectary of *Hedera helix* in secretory stage. (a–c) Flowers with a nectary (asterisks) on top of the inferior ovary. (a) top view; (b) side view; (c) longitudinal section. (a, b) Note the glossy secretion on the nectary surface. (d) Visible ivy nectary with an undulated surface. (e) fragment of a strongly undulated nectary surface with numerous stomata (arrows). Bars = 1 mm. (f) non-glandular, T-shaped trichome on the nectary surface (g) Fragment of the nectary surface with open, active nectarostomata (arrows) located at the level or above the level of epidermis. (h) Fragment of nectary surface with non-functional stomata (arrows), located below the epidermis level. Note the strongly striated cuticle. Bars = 50 µm. o – ovary, s – style

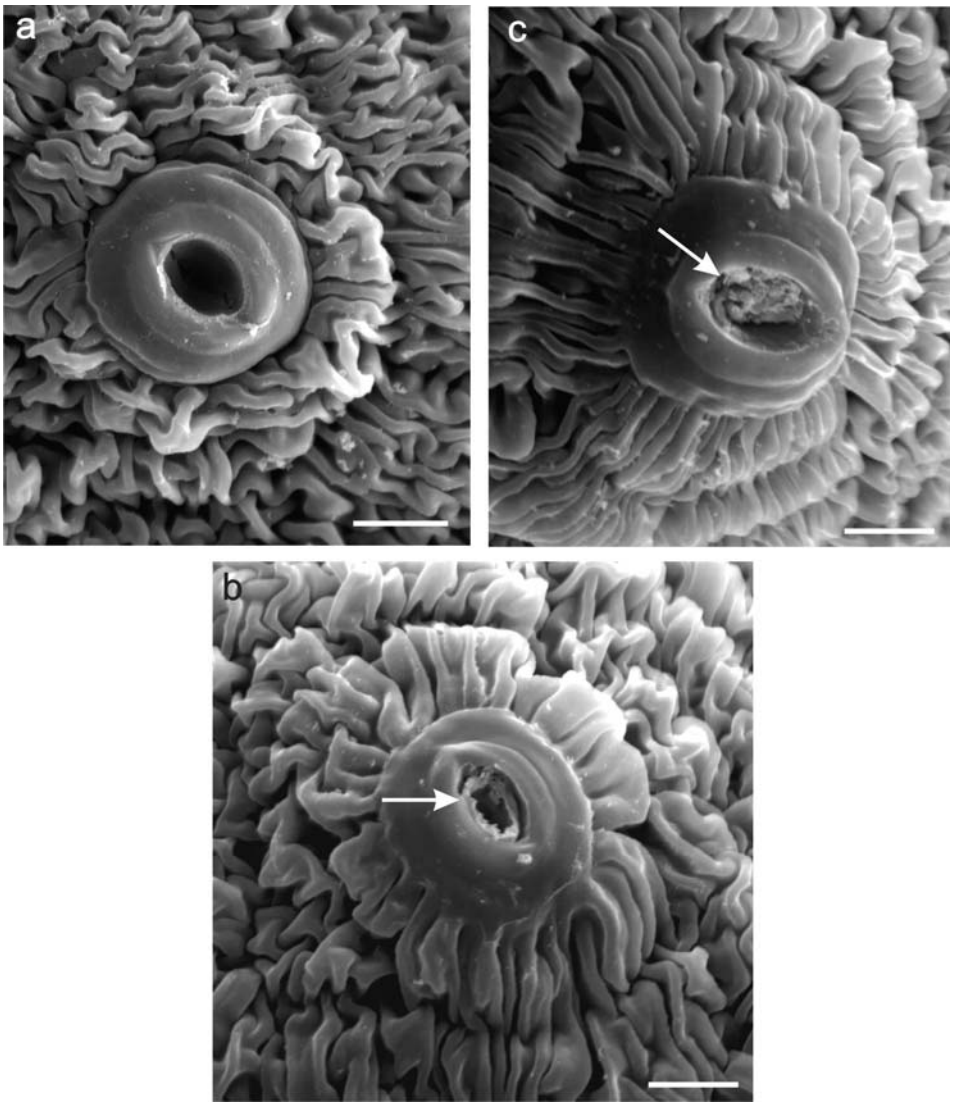

Fig. 2. SEM images. (a–c) Fully developed, active stomata of the surface of *H. helix* nectary surrounded by a cuticle with massive cuticular striae. (b, c) Note the secretion in the stomatal pores (arrows). Bars = 10 µm

The nectary epidermal cells were characterised by presence of cytoplasm containing variously shaped plastids with plastoglobules and/or few starch grains and by the presence of numerous vacuoles with cell sap darker than the content of the vacuoles of the glandular parenchyma cells (fig. 4a–c). In the cells of the outer parenchyma layers, there were numerous small vacuoles containing flocculent material, more or less spherical electron-dense deposits, myelin figures (myelin-like multilamellar bodies), and cyto-

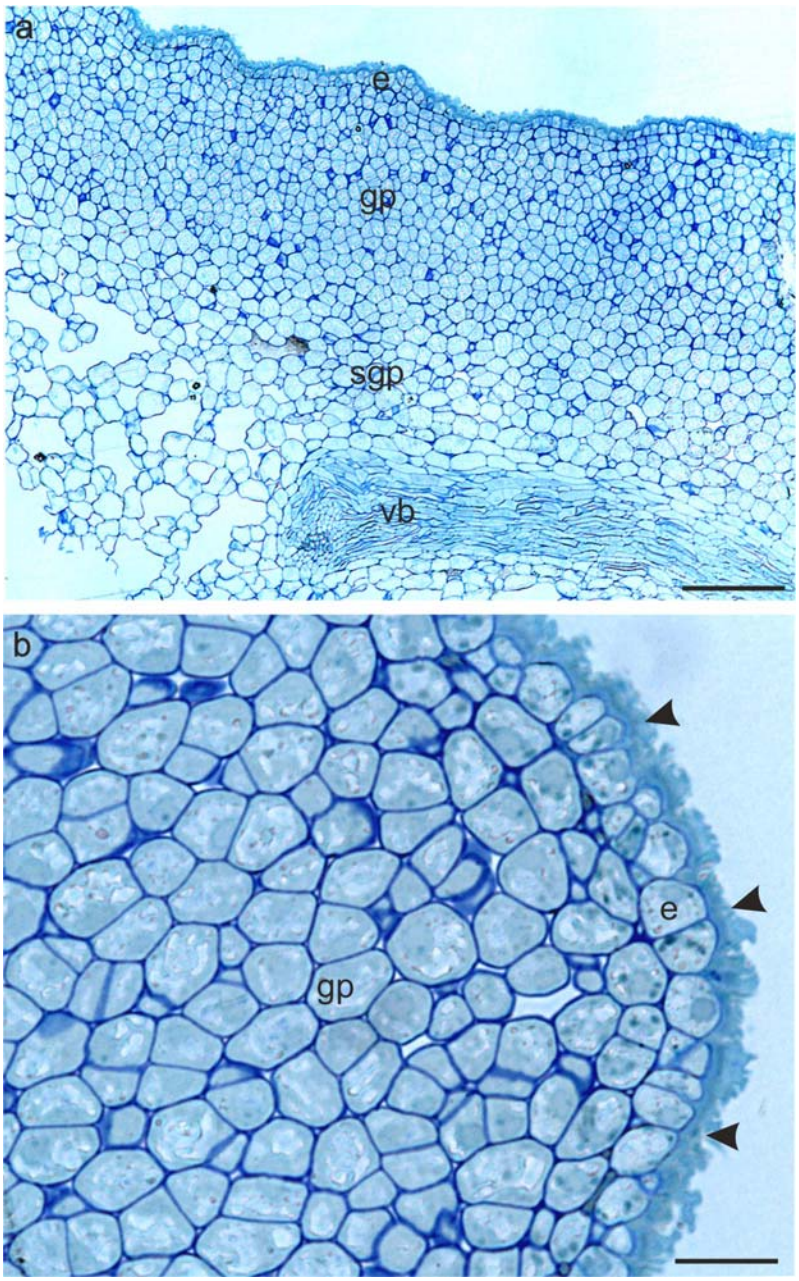

Fig. 3. LM images. (a, b) Fragments of cross sections through the *H. helix* nectary tissue. Visible single-layered epidermis covered by a striated cuticle (arrowheads), multi-layered glandular parenchyma and subglandular tissue with the collateral vascular bundle. Bars: (a) = 100 µm; (b) = 20 µm. e – epidermis, gp – glandular parenchyma, sgp – subglandular parenchyma, vb – vascular bundle

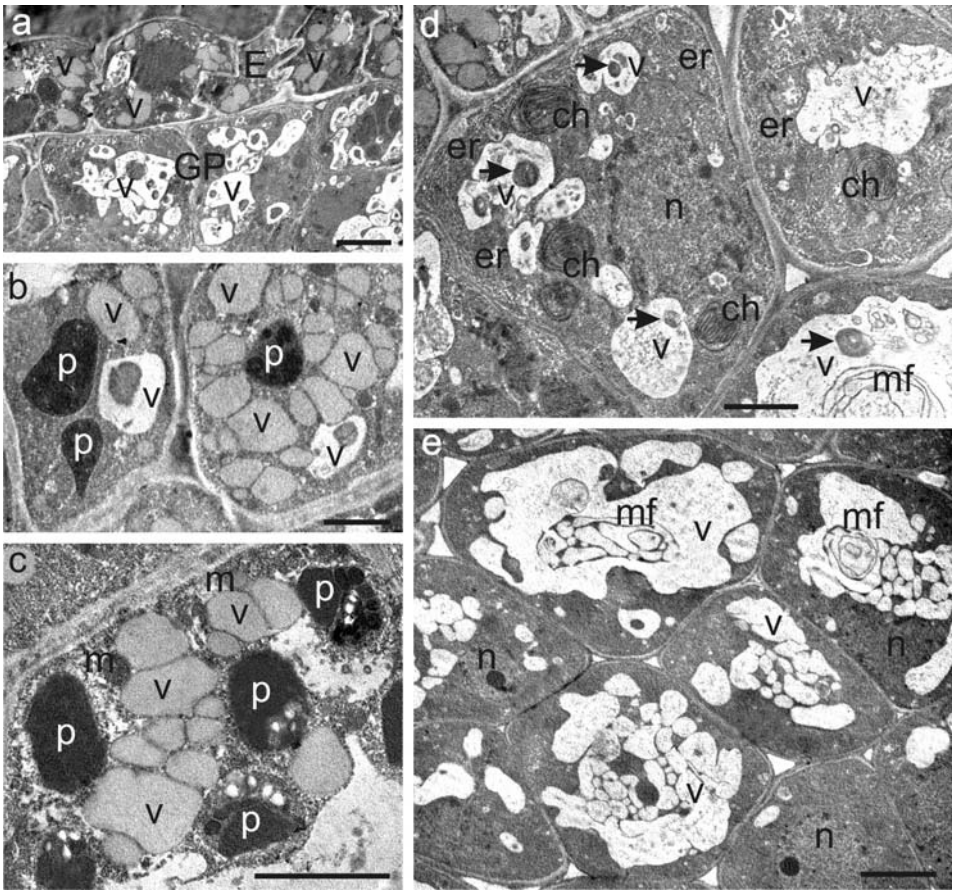

Fig. 4. TEM images. (a) Cells of the secretory epidermis and glandular parenchyma of the ivy nectary. Note the darker colour of the vacuoles of the epidermis (E) in comparison to the colour of glandular parenchyma (GP) vacuoles. Bar = 5 µm. (b, c) Cells of the secretory epidermis. Visible numerous small and dark coloured vacuoles and variously shaped plastids with plastoglobules (b) and starch grains (c). (d) Cells of the first layer of glandular parenchyma with visible chloroplasts, cell nucleus, rich endoplasmic reticulum and small vacuoles containing flocculent sediment, spherical deposits (arrows) and myelin figures. Bars = 2 µm. (e) Cells of the 3rd, 4th, and 5th layer of the glandular parenchyma with numerous fused vacuoles containing myelin figures. Bar = 10 µm. n – nucleus, p – plastids, ch – chloroplasts, m – mitochondria, er – endoplasmic reticulum, v – vacuoles, mf – myelin figures

plasm with cell nuclei, rich endoplasmic reticulum, and oval or irregularly shaped chloroplasts (fig. 4d, e). Two types of chloroplasts were distinguished: organelles with regular arrangement of thylakoids and few small starch grains and untypical chloroplasts that were devoid of starch grains, exhibited circular thylakoid arrangement, and contained plastoglobules (fig. 5a–f). Sometimes etioplasts with prolamellar bodies were

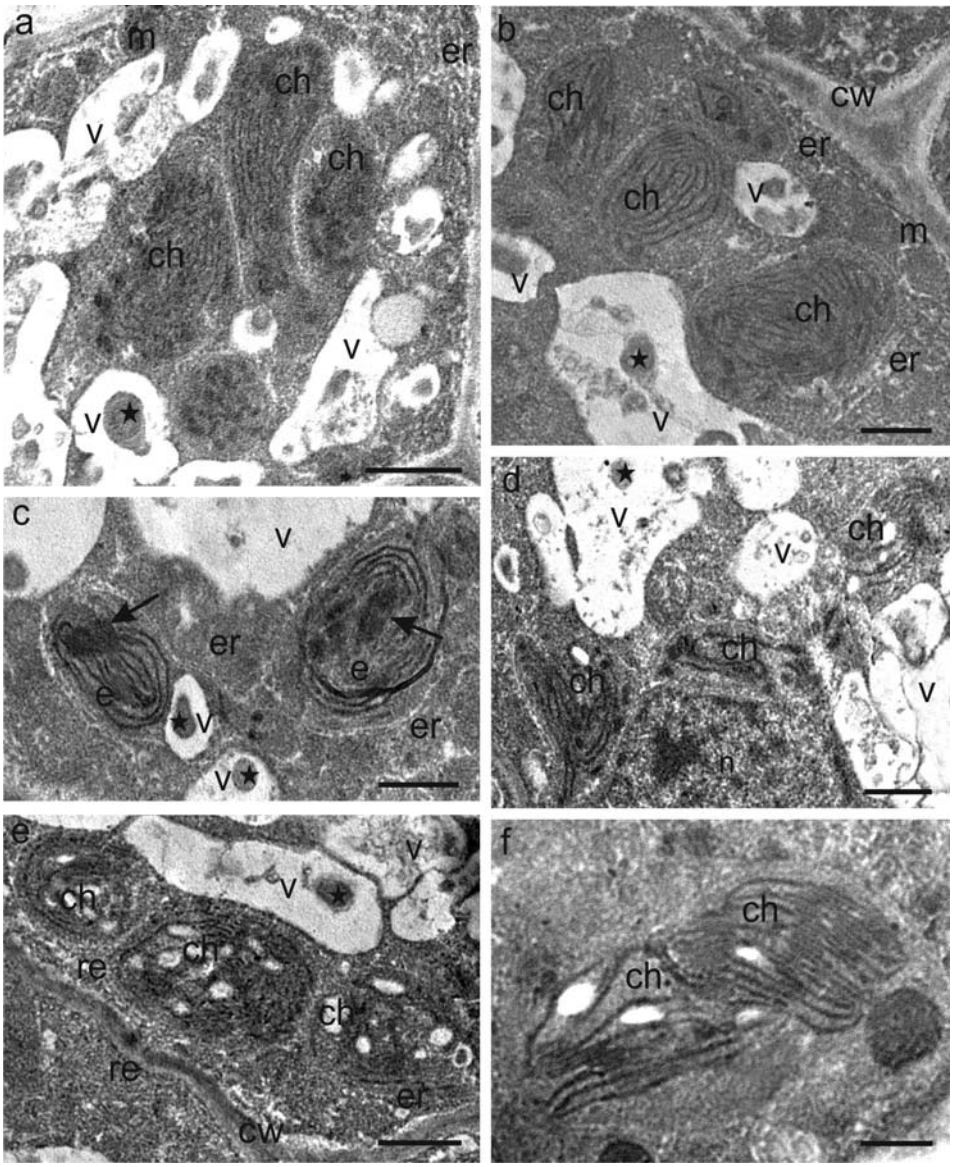

Fig. 5. TEM images. Fragments of glandular parenchyma cells in the *H. helix* nectary with different types of chloroplasts. (a) chloroplasts with typical arrangement of thylakoids (lamellae) and plastoglobules. (b) chloroplasts with untypical, circular arrangement of thylakoids. (c) etioplasts with circular arrangement of thylakoids and prolamellar bodies (arrows). (d–f) chloroplasts with visible thylakoids and small starch grains. Mitochondria, rich endoplasmic reticulum, and small vacuoles with spherical deposits visible in the cells (asterisks). Bars = 1 μm. ch – chloroplasts, e – etioplasts, m – mitochondria, er – endoplasmic reticulum, v – vacuoles, cw – cell walls

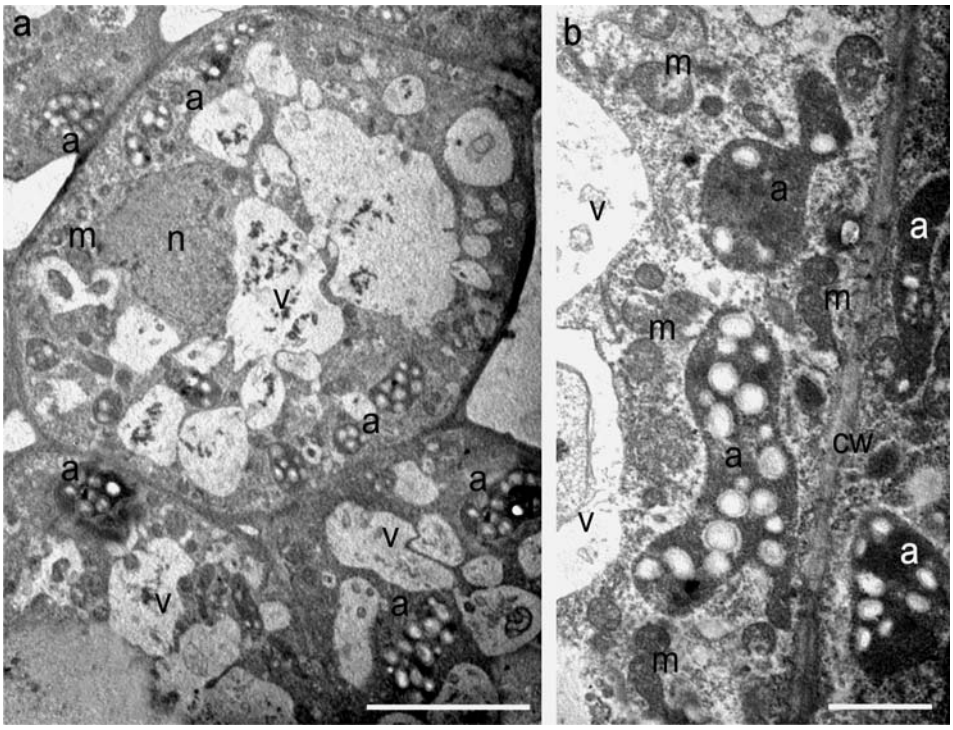

Fig. 6. TEM images. (a, b) Fragments of cells of deeper layers of glandular parenchyma with variously shaped amyloplasts filled with starch grains. Visible numerous mitochondria and vacuoles with inclusions of unknown origin. Bars: (a) = 10 µm; (b) = 2 µm. a – amyloplasts, m – mitochondria, n – nucleus, v – vacuoles, cw – cell walls

Table 1. Characteristics of *Hedera helix* nectaries (n = 10)

Number of stomata (per mm^2)	22 ±4	Thickness of nectary (µm)	267 ±72.3
Length of guard cells (µm)	25 ±0.7	Number of the secretory parenchyma cell layers	13 ±3
Length of nectary (mm)	2.1 ±0.3	Height of epidermal cells (µm)	10.5 ±1.3
Height of nectary (mm)	2.3 ±0.4	Thickness of cuticle (µm)	6.9 ±1.5

observed in the cells of the secretory parenchyma (fig. 5c). In the cells of deeper parenchyma layers, irregularly shaped amyloplasts filled with storage starch grains, mitochondria, and vacuoles with inclusions of unknown origin were observed (fig. 6a, b).

DISCUSSION

In Poland, ivy plants bloom rather infrequently in nature; however, flowering specimens produce numerous flowers, which provide honeybees and other insect pollinators with pollen and primarily nectar flow. The late (IX–XI) and long flowering time of *H. helix* is an important advantage of this climber plant, given the limited number of nectar-secreting taxa during this season of the year. It seems probable that the relatively long phase of nectar secretion results not only from the photosynthesizing type of nectaries but mainly because, that nectaries were supplied by phloem cells, which deliver additional carbohydrates required to continue the production of nectar. Pacini et al. [2003] reported that nectar may be produced in persistent and photosynthesizing nectaries for a long time, even after the end of the stigma receptivity period during fruit formation and seed maturation.

There are two types of stomata in the epidermis of the ivy nectary: typical, open nectarostomata and non-functional stomata. Modified stomata through which nectar is secreted have been reported from other plant species as well [Davis and Gunning 1992, Wist and Davis 2006, Weryszko-Chmielewska and Dmitruk 2009, Almeida et al. 2013, Dmitruk i Weryszko-Chmielewska 2013]; however, non-secreting stomata in nectaries of some species of Disa (Orchidaceae) were observed by Hobbhahn et al. [2013].

The author of the present study observed that as early as on the 2nd day of nectar secretion anthocyanins appeared in the vacuoles of the gland epidermal cells and the nectary was still active and was characterised by green colour. During the following days of anthesis, anthocyanins were accumulated in the vacuoles of deeper layers of secretory tissue, which was accompanied by continuous nectar secretion. Probably at this time, photosynthesis does not contribute to sugar production but carbohydrates needed for the production of nectar are provided by the phloem cells. Vezza et al. [2006] suggest that anthocyanins accumulation in secretory parenchyma cells in ivy, particularly in the final stage of nectar secretion, may protect the ovary and the developing embryo against solar radiation and elevated or decreased temperature; they may also provide information for insect pollinators about changes in the composition and increased density of nectar. In 2011, during ivy flowering, the author reported a rapid, short-term cooling, which probably accelerated the production of anthocyanins as a plant defense reaction against the low temperatures. Other authors have also described accumulation of anthocyanins in nectary cells of other plant species. They suggest that anthocyanins protect against UV and low temperatures [Mohr and Schopfer 1995], inform insect pollinators about changes in the nectar composition [Baker and Baker 1983], or signal the end of secretion and/or loss of insect floral attractiveness [Belmonte et al. 1994, O'Brien et al. 1996, Konarska 2011, Lippi et al. 2011, Giuliani et al. 2012].

Although ivy nectaries represent the open type with a structure promoting uncontrolled flow of nectar and its quick drying and crystallisation, it seems that the strongly undulated gland surface, the presence of massive cuticle with deep striae, as well as a few non-glandular trichomes on the nectary surface may, even to a small extent, prevent nectar flow and limit its drying.

The present study has demonstrated that ivy nectaries represent the photosynthesizing; hence, assimilates that are indispensable for nectar production are mainly produced

in the gland by chloroplasts of secretory parenchyma cells. Produced carbohydrates are utilised almost fully and continuously for secretion production. Plastids containing storage starch grains, which are specific short-term reservoirs for accumulation of excess sugars, were present only in the deepest layers of the glandular tissue. Vezza et al. [2006] obtained similar results concerning the mode of synthesis of prenectar components in ivy plants. Photosynthesizing nectaries in other species have been described by numerous other researchers [Vesprini et al. 1999, Pacini et al. 2003, Cawoy et al. 2008, Weryszko-Chmielewska and Sulborska 2011, Nocentini et al. 2012]. Vesprini et al. [2012] considered that, the contribution of the nectar itself reduces the cost associated with flower functions and, more generally, with reproduction.

In the secretory stage, two types of chloroplasts differing in the arrangement of thylakoids and content of starch grains were observed in the cells of the glandular parenchyma. Classic chloroplasts with typical arrangement of lamellae were located close to those that exhibited abnormal, circular thylakoid arrangement. Typical chloroplasts were found in glandular tissue cells of nectaries in other plant species [Zer and Fahn 1992, Razem and Davis 1999, Fahn and Simony 2001, Vesprini et al. 2012]. In turn, the abnormal thylakoid arrangement in ivy chloroplasts may imply initiation of destructive and degenerative processes in lamellae, which may constitute initial symptoms of transformation of chloroplasts to chromoplasts, as described by O'Brien et al. [1996] and Paiva [2012]. Moreover, this hypothesis seems to be confirmed by the presence of β-carotene and decreased chlorophyll content in the ivy nectary parenchyma in the final stage of nectar secretion previously reported by Vezza et al. [2006]. Furthermore, nectary cells may exhibit structural heterogeneity, since changes within them do not have to proceed synchronously [Gaffal et al. 2007, Nicolson et al. 2007 and references therein, Konarska 2011].

The author of the present study found calcium oxalate crystals in the form of druses as well as various types of deposits (multiform inclusions) and myelin figures in the vacuoles of the epidermis and secretory parenchyma in the ivy. Many researchers have emphasized the fact that, from the initial phase, through the full secretion phase, to the final stage of nectar secretion, glandular parenchyma vacuoles may contain a variety of inclusions resulting from rupture or degradation of the tonoplast or originating from pinching off of plasmatic evaginations into the vacuole [O'Brien et al. 1996, Wist and Davis 2006, Gaffal et al. 2007, Gui and Liu 2013]. In turn, other authors have observed granular or irregularly shaped protein bodies in nectary vacuoles [Durkee 1982, Horner et al. 2003, Stpiczyńska et al. 2003]. Wist and Davis [2006] have reported that the content of deposits, primarily multilamellar and multitubular bodies, increased together with progression of nectary senescence.

CONCLUSIONS

1. The photosynthesizing type of nectaries and presence of phloem cells supplying carbohydrates in nectar composition contribute to extension of the nectar secretion period.

2. Appearance of anthocyanins and initiation of destruction and degeneration of chloroplasts in the nectaries cells does not imply the end of the nectar secretion process. The supply of nectaries with phloem cells, which deliver carbohydrates, facilitates continuation of nectar production.

3. The undulating nectary surface, strongly striated cuticle, and T-shaped non-glandular trichomes may limit uncontrolled nectar flow and drying to some extent.

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CHARAKTERYSTYKA NEKTARNIKÓW KWIATOWYCH *Hedera helix* L. (Araliaceae)

Streszczenie. Strukturę nektarników kwiatowych *H. helix* badano w mikroskopie świetlnym oraz elektronowym skaningowym i transmisyjnym. Gruczoł nektarnikowy bluszczu znajduje się na szczycie zalążni dolnego słupka i tworzy pokaźny, pofałdowany dysk między nasadą płatków korony a szyjką słupka. Nektarniki bluszczu należą do typu otwartych i trwałych, a w kolejnych dniach antezy charakteryzują się zmianą barwy z zielonej na brunatną. Epiderma sekrecyjna pokryta jest głęboko prążkowaną grubą kutykulą, a sekrecja nektaru odbywa się przez zmodyfikowane aparaty szparkowe. Pod epidermą znajduje się kilkunastowarstwowa parenchyma gruczołowa, a poniżej tkanka podgruczołowa. Nektarnik zaopatrzony jest w wiązki przewodzące zawierające łyko i drewno. W komórkach epidermy zaobserwowano plastydy z plastoglobulami i nielicznymi ziarnami skrobi oraz wakuole zawierające antocyjany, których zawartość wzrastała w kolejnych dniach antezy i sekrecji nektaru. W cytoplazmie zewnętrznych warstw parenchymy gruczołowej występowały liczne chloroplasty; typowe, mogące zawierać niewielkie ziarna skrobi oraz nietypowe, odznaczające się kolistym przebiegiem tylakoidów. W komórkach głębszych pokładów tkanki nektaronośnej obecne były amyloplasty z ziarnami skrobi zapasowej oraz drobne, liczne wakuole. W wakuolach parenchymy gruczołowej widoczne były druzy oraz kłaczkowaty osad, figury mielinowe i sferyczne depozyty niewiadomego pochodzenia.

Słowa kluczowe: *Hedera helix*, nektarniki kwiatowe, aparaty szparkowe, mikromorfologia, anatomia, ultrastruktura

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