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DIVERSITY IN THE STRUCTURE OF THE PETAL EPIDERMIS EMITTING ODOROUS COMPOUNDS IN *Viola* × *wittrockiana* Gams.

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Abstract. The flowers of *Viola* × *wittrockiana* Gams. emit odorous compounds. The glands found in the flowers, responsible for the production of essential oils, are most frequently distributed on the petals of the corolla. They include papillae – conical epidermal cells. The structure of the epidermis and the internal tissues of the petals of *V.* × *wittrockiana* were examined using light, fluorescence and scanning electron microscopy. Papillae were found to occur in the epidermis on both sides of all the petals (spurred, lateral and upper), but they were much longer in the adaxial epidermis. Different-sized droplets of lipid nature, which are essential oils, were present in the papillae. They were also observed on the outer surface of the walls of these cells. Moreover, in the adaxial epidermis there were areas of flattened cells with a characteristic structure, being probably secretory glands. The present study shows that differently-structured cells of both the abaxial and adaxial epidermis participate in the release of odorous compounds by the flowers of *V.* × *wittrockiana*. These different structures may produce varied scents in terms of their quality.

Key words: *Viola* × *wittrockiana*, petals, epidermis, papillae, osmophores

INTRODUCTION

Pansy or garden pansy (*Viola* × *wittrockiana* Gams.) [Erhardt et al. 2002] is a popular ornamental plant differing in the size and colour of flowers depending on the variety. These plants are used for ground cover plantings in green spaces and for pot culture [Oszkinis 1994, Startek 2003]. Research is carried out on the introduction of an optimal substrate for growing pansies [Zawadzińska and Janicka 2007 a, b]. These plants are also found in a wild-growing form in natural stands. They bloom from early spring to late autumn (III – X) [Rutkowski 2003].

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Putative parental species of *Viola* × *wittrockiana* Gams. are *Viola altaica* Ker-Gawl., *V. lutea* Huds. and *V. tricolor* L. [Oszkinis 1994, Rutkowski 2003]. Both *Viola tricolor* and *Viola* × *wittrockiana* are mentioned among 100 plant species whose flowers are edible. These flowers are recommended for salads, soups, desserts, snacks, and drinks. On the market, they can be found in special packaging [Barash 1998, Kelley et al. 2003].

Large zygomorphic flowers of pansy with a diameter of up to 10 cm are characterized by multicoloured petals. Five corolla petals and sepals are free. The lower petal forms a spur up to 7 mm long, in which nectar accumulates. The pistil with a superior ovary is surrounded by 5 stamens [Szweykowska and Szweykowski 2003]. The drying corolla remaining in overblown flowers may play an essential role in fruit and seed formation [Herrera 2010].

The flowers of *V. tricolor*, with weakly scented petals, produce nectar guides marked in the form of dark stripes and light spots that emit a more intense scent than the other parts of the petals [Kugler 1970]. These guides, most contrasted in the central part of the flower next to the generative elements, are attractants for insects visiting flowers and are visible from a large distance. There is also characteristic deep green spot on the style below the stigma playing the role of additional guide. The coloured circumferential sections of petals of different *Viola* species reflect UV rays, whereas the parts located at the mouth of the corolla absorb these rays and form a darker area, well visible for insects, which indicates the location of food [Beattie 1969].

Similarly as wild-growing species of *Viola*, pansy flowers are also visited by bees, bumblebees, and other insect species that find nectar and pollen in them [Beattie 1969, Maurizio and Grafl 1969, Proctor et al. 1996]. Humans do not always can smell the scent of flowers that is intense and attractive to insects, which is also the case for *Viola* × *wittrockiana* [Proctor et al. 1996].

The aim of the present study was to determine the structure of the epidermis in the petals of *Viola* × *wittrockiana*, in particular the structures producing and emitting odorous compounds [osmophores].

MATERIAL AND METHODS

Flowers (buds, first day of blooming, full blooming = third day of blooming) of two cultivars of *Viola* × *wittrockiana* Gams. were selected for microscopic observations: cv. 'Delta F_1 Premium Yellow with Blotch' and cv. 'Saint Tropez Mix F_2'. All petals of the corolla (spurred, lateral and upper) were investigated.

For light microscopy (LM) examination, transverse and tangential sections were cut from fresh petals, in which special attention was paid to the structure of the epidermal cells. Papillae of adaxial epidermis from the middle part of spurred petals were measured (n = 20 × five petals). Neutral red was used to detect secretory cells [Stern et al. 1987]. Saturated ethanolic solution of Sudan III as histochemical test to detect lipids and Sudan III in chloral hydrate solution to detect essential oil were applied [Broda 1971]. Starch grains in the plastids were visualised with IKI.

Sections of petals were placed in a drop of 0.01% fluorochrome auramine O solution. The tissue samples were examined using a Nikon Eclipse 90i fluorescence microscope (FITC filter, excitation wavelength 465–495 nm, emission wavelength 515–555 nm).

The micromorphology of the adaxial and abaxial epidermis of spurred and upper petals was studied using scanning electron microscopy (SEM). The petal segments were fixed in 4% glutaraldehyde and 0.1 M phosphate buffer with a pH of 7.0, at a temperature of 4°C. After dehydration in ethanol and acetone series, the plant samples were critical-point dried in liquid CO_2 and coated with gold. Observations and photographic documentation were made with a Tescan Vega II LMU scanning electron microscope.

RESULTS

The anatomical structure of the petal (Lm)

Adaxial epidermis. We found conical papillae in the adaxial epidermis of all the petals (spurred, lateral and upper) in the two investigated *Viola* × *wittrockiana* cultivars. The vacuoles in the papilla cells were coloured red after neutral red treatment (fig. 1E), which indicates on secretory function of these cells. In cross section of the spurred petal in the variety 'Delta F_1 Premium Yellow with Blotch' (fig. 1A), conical papillae (fig. 1C, D, 2A, C), 50–94 μm in height (on average 85.6 μm) and 20–44 μm width at the base (on average 40.6 μm) were observed in the adaxial epidermis. The papillae on the same petal of 'Saint Tropez Mix F_2' cultivar were 28–56 μm in hight (on average 54 μm) and width at the base 20–28 μm (on average 31.5 μm). The walls of papilla cells were thin, covered by a layer of cuticle forming parallel striae (figs 5B, C; 6A–C)

Papilla cells of the adaxial epidermis were polarised with the nucleus surrounded by the cytoplasm rich in plastids in the basal part and a large vacuole in the upper part (fig. 1D, 2A–C). In the papillae of the petals in the buds, we observed chloroplasts (fig. 1 B) and chromoplasts (fig. 1D; 2A) in fully developed, opened flowers. In the protoplast of many papilla cells, different-sized yellow-green droplets were visible (fig. 1E, 2C), which were probably essential oil. After the treatment with Sudan III these droplets were orange colour (fig. 1D, 2B), whereas Sudan III in chloral hydrate stained the droplets red (fig. 1 F). Droplets of the substance stained with Sudan III were visible in the lower part of the papillae adjacent to the chromoplasts (fig. 1D–F; 2A), and sometimes they were surrounded by numerous chromoplasts (fig. 1D). Many droplets were concentrated in the upper part of some conical papillae (Fig. 2 B, C). The secreted material was also visible on the surface of papilla cuticle (fig. 2A, C–E). We observed luminous light green droplets of secretion inside and outside the papilla cells with the use of fluorescence microscopy (fig. 2F). In many papillae, we observed vacuoles with a light luminous substance (fig. 2H).

The mesophyll formed 4–5 layers in the petals and was composed of irregularly branched cells with large intercellular air spaces between them (fig. 1C). These cells did not contain coloured plastids or anthocyanins in the vacuoles. Their cell walls were thin.

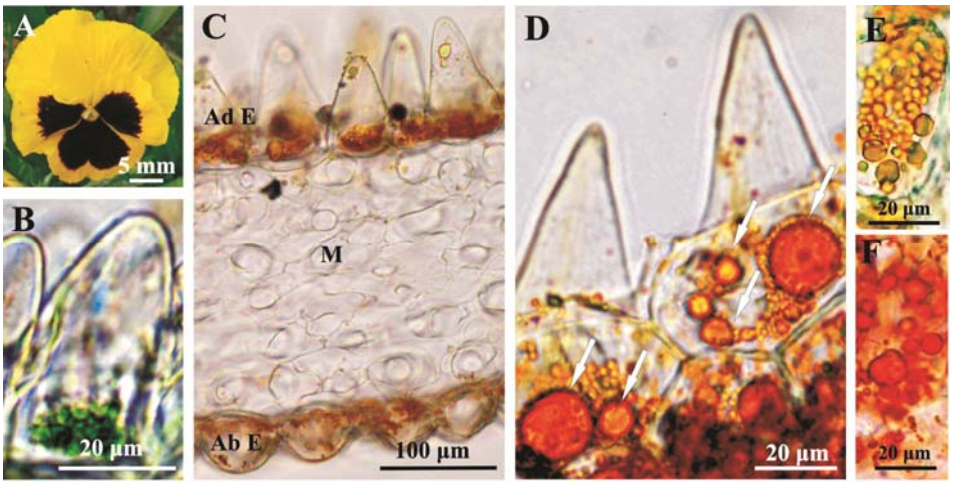

Fig. 1. Flower and tissues of *Viola* × *wittrockiana* petals: A – flower of the 'Delta F_1 Premium Yellow with Blotch' cultivar; B – papilla of the adaxial epidermis of the upper petal in the bud; chloroplasts are visible in the basal part of the protoplast; C – cross section of the spurred petal with the conical papillae in the adaxial epidermis (AdE), mesophyll (M) with large intercellular spaces and the abaxial epidermis (AbE) with smaller papillae; D – papilla cells of the adaxial epidermis of the spurred petal with numerous chromoplasts and lipid droplets of different size after the Sudan III treatment (arrows); E, F – chromoplasts and lipid droplets in the basal part of conical papillae: E – without staining; F – after the treatment with Sudan III with chloral hydrate

Fig. 1. Kwiat i tkanki płatków korony *Viola* × *wittrockiana*: A – kwiat odmiany 'Delta F_1 Premium Yellow with Blotch'; B – papilla epidermy doosiowej górnego płatka z pąka kwiatowego; w bazalnej części widoczne są chloroplasty; C – fragment przekroju poprzecznego przez ostrogowy płatek z widocznymi papillami w epidermie poosiowej (AdE), miękiszem (M) o dużych przestworach międzykomórkowych oraz epidermą dolną (AbE) z mniejszymi papillami; D – komórki papilli epidermy doosiowej ostrogowego płatka korony z licznymi chromoplastami i kroplami lipidowymi różnej wielkości (strzałki), barwienie Sudanem III; E, F – chromoplasty i krople lipidowe zlokalizowane w dolnej części papilli. E – bez barwienia, F – po traktowaniu roztworem Sudanu III z wodzianem chloralu

The collateral vascular bundles located in the middle of the petal mesophyll were composed of annular and spiral tracheary elements in the xylem part (fig. 4C).

The abaxial epidermis was composed of cells with wavy anticlinal walls forming ingrowths (figs 2I; 3D; 4B, E). These cells in the middle part of the petals had asymmetrically convex outer walls visible as short papillae (fig. 1C; 2I). The surface of the outer cell walls was covered with striated cuticle (figs 2I; 3A; 5E–G), which had orange colour after the Sudan III treatment (fig. 3B). Stomata appeared in the abaxial epidermis (fig. 3A, B; 4A).

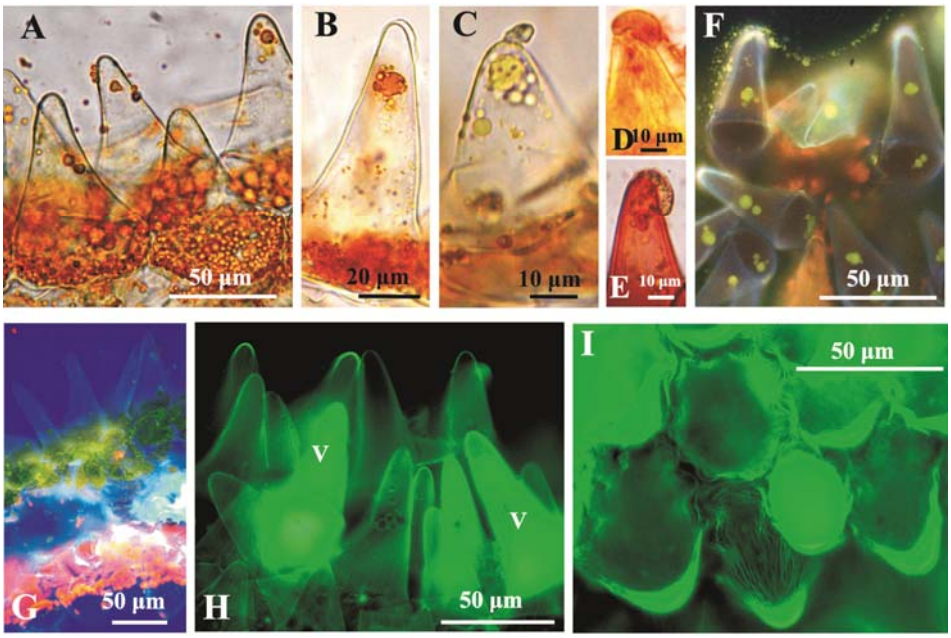

Fig. 2. Papillae on the surface of *Viola* × *wittrockiana* petals: A, B, C, D – conical papillae of the adaxial epidermis of the spurred (A, C, D) and upper (B) petals with visible chromoplasts and lipid droplets in the cells and on their surface. B – after the Sudan III treatment, D – after the treatment with Sudan III with chloral hydrate; E – papilla of the adaxial epidermis of the upper petal with visible red coloured vacuole and secreted material on the top; after neutral red treatment; F – light green autoflurescence of the lipid droplets inside and outside the papillae; G – chromoplasts in the conical papillae of the adaxial epidermis showing green autofluorescence and chloroplasts in the abaxial epidermis showing red autofluorescence (first day of blooming); H – fluorescence of the cuticle and vacuoles (V) in the conical papillae of the adaxial epidermis of the upper petal after staining with auramine O; I – papillae of the abaxial epidermis showing fluorescence of the cuticle and lipid substances in vacuoles after staining with auramine O

Fig. 2. Papille na płatkach *Viola* × *wittrockiana*: A, B, C, D – papille epidermy doosiowej ostrogowego (A, C, D) i górnego (B) płatka z widocznymi chromoplastami i kroplami lipidowymi wewnątrz komórek oraz na ich powierzchni. B – barwienie Sudanem III, D – barwienie roztworem Sudanu III z wodzianem chloralu; E – papilla epidermy adaksjalnej górnego płatka. Widoczna czerwono wybarwiona wakuola i substancja wydzielnicza na szczycie; barwienie czerwienią obojętną; F – jasnozielona autofluorescencja kropli tłuszczowych zlokalizowanych wewnątrz papilli i na ich powierzchni; G – chromoplasty w papillach z epidermy górnej wykazują zieloną autofluorescencję, natomiast w chloroplastach z papilli dolnych widoczna jest czerwona autofluorescencja chlorofilu (pierwszy dzień kwitnienia); H – fluorescencja kutykuli i wakuol (V) komórek papilli epidermy adaksialnej górnego płatka po traktowaniu auraminą O; I – papille skórki dolnej wykazują fluorescencję kutykuli i substancji lipidowych zlokalizowanych w wakuoli po traktowaniu auraminą O

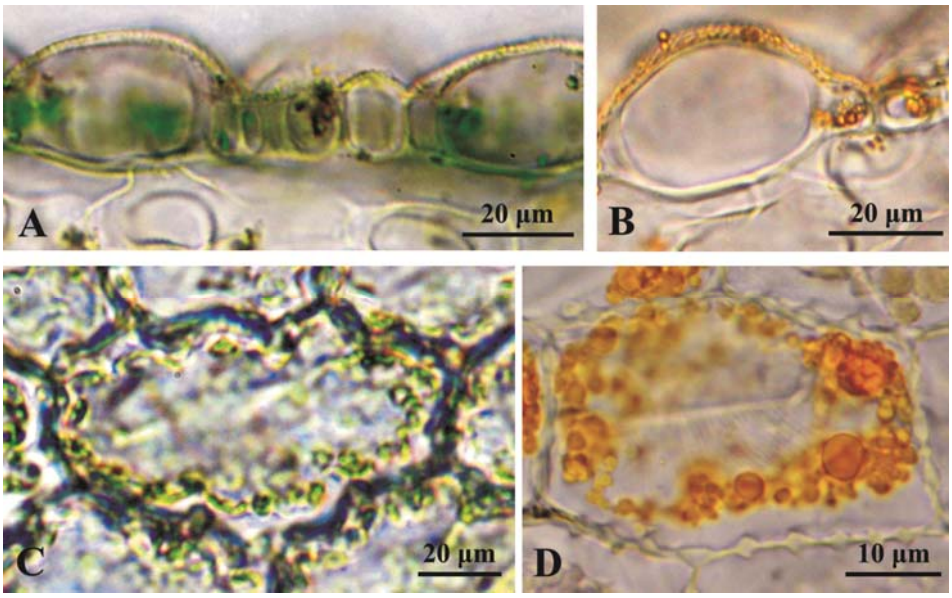

Fig. 3. Cells of the abaxial epidermis of *V.* × *wittrockiana* cv. 'Delta F_1 Premium Yellow with Blotch': A, B – stomata and common adaxial epidermis cells in the cross section of the upper petal; B – orange-stained cuticle after the Sudan III treatment; C – cells with folded walls and chloroplasts on the first day of blooming; D – epidermis cell with characteristic ingrowths in the cell walls and chromoplasts in the stage of full blooming; visible green-orange lipid droplets in the protoplast

Fig. 3. Komórki abaksjalnej epidermy *V.* × *wittrockiana* 'Delta F_1 Premium Yellow with Blotch': A, B – aparaty szparkowe i typowe komórki epidermy na przekroju poprzecznym górnego płatka korony; B – pomarańczowo zabarwiona kutykula po traktowaniu Sudanem III; C – komórki z pofałdowanymi ścianami i chloroplastami (pierwszy dzień kwitnienia); D – komórka epidermy z charakterystycznymi wrostami ściany komórkowej i chromoplastami w fazie pełni kwitnienia; widoczne są zielono-pamarańczowe krople lipidowe

In the petals of the cultivar 'Delta F_1 Premium Yellow with Blotch', chromoplasts occurred in the cytoplasm of the abaxial and adaxial epidermis (figs 1C; 3D; 4B, E). On the first day of blooming, the cells of the adaxial epidermis in the petals matured earlier than the cells of the abaxial epidermis. At that time, we observed chromoplasts visible in fluorescence microscopy as a green structures in the cells of the adaxial epidermis, while in the abaxial epidermis chloroplasts were still present (fig. 3C), in which chlorophyll showed red autofluorescence (fig. 2G). In the chloroplasts, we detected starch grains after the treatment with IKI (fig. 4D). In the stage of full blooming, big green-yellow droplets of the secretion were visible in the cells of the abaxial epidermis (fig. 3D; 4F), which had a red colour after the treatment with Sudan III in chloral hydrate solution (fig. 4E).

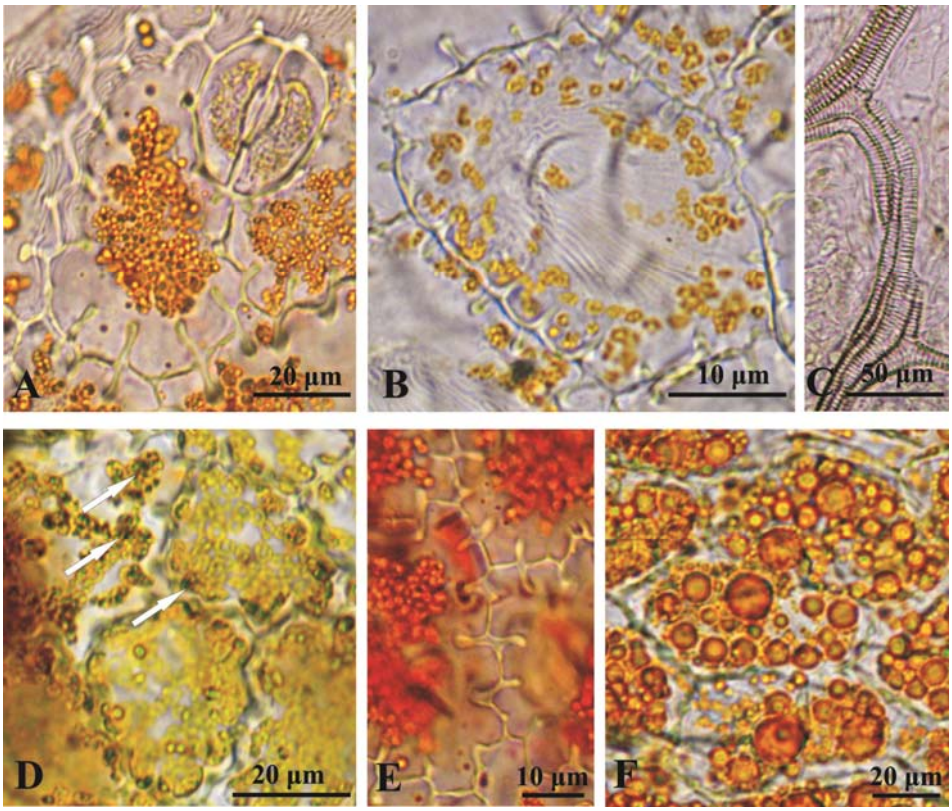

Fig. 4. Cells of the abaxial epidermis of *V.* × *wittrockiana* cv. 'Delta F_1 Premium Yellow with Blotch': A, B – epidermis cells with characteristic ingrowths in the cell walls and chromoplasts in the stage of full blooming; A – fragment of the epidermis with a stoma; C – Branched vascular bundles in the petal mesophyll; D – epidermis cells with numerous chloroplasts and dark starch grains after the IKI treatment (arrows); E – red coloured lipid droplets and chromoplasts after the treatment with Sudan III in the chloral hydrate solution; F – numerous green-orange lipid droplets of different size in the epidermis cells in the full blooming stage

Fig. 4. Komórki abaksjalnej epidermy *V.* × *wittrockiana* 'Delta F_1 Premium Yellow with Blotch': A, B, – komórki epidermy z charakterystycznymi wrostami ściany komórkowej i chromoplastami w fazie pełni kwitnienia; A – fragment epidermy z aparatem szparkowym; C – rozgałęzione wiązki przewodzące w miękiszu płatka korony; D – komórki epidermy z licznymi chloroplastami i ciemnymi ziarnami skrobi po barwieniu JKJ (strzałki); E – czerwono wybarwione krople lipidowe i chromoplasty po zastosowaniu roztworu Sudanu III w wodzianie chloralu; F – liczne, zielono-pomarańczowe krople lipidowe różnej wielkości w komórkach epidermy (faza pełni kwitnienia)

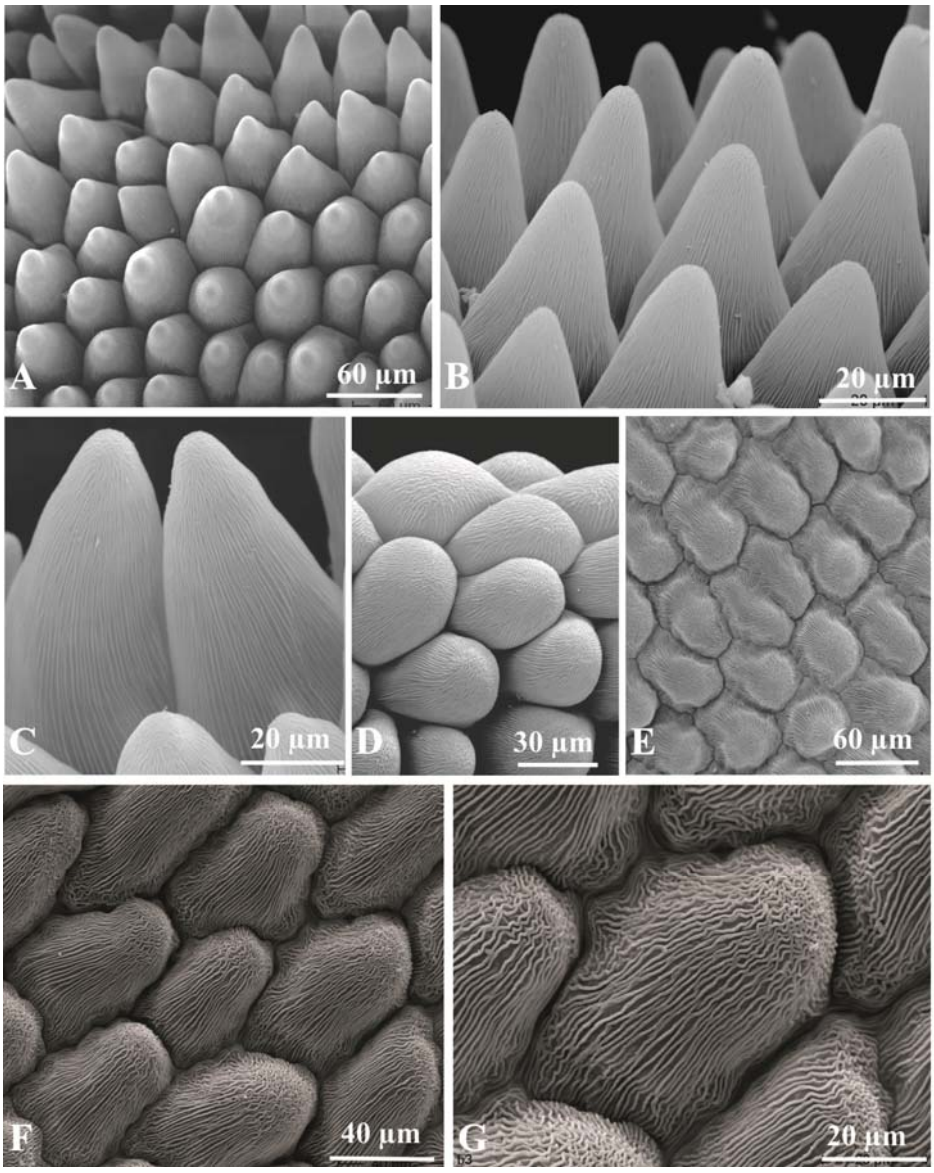

Fig. 5. Surface of *Viola* × *wittrockiana* petals ('Delta F_1 Premium Yellow with Blotch' cultivar) in SEM: A, B – adaxial epidermis of the petals with numerous papillae; C – papillae with striated cuticle; D – papillae on the rand of the petal; E–G – surface of the abaxial epidermis cells with characteristic cuticular striation

Fig. 5. Powierzchnia płatków korony *Viola* × *wittrockiana* (odmiana 'Delta F_1 Premium Yellow with Blotch') oglądana w SEM: A, B – górna epiderma płatków korony z licznymi papillami; C – papille z prążkowaną kutykulą; D – papille w brzeżnej części płatka korony; E–G – powierzchnia epidermy odosiowej z charakterystycznym kutykularnym prążkowaniem

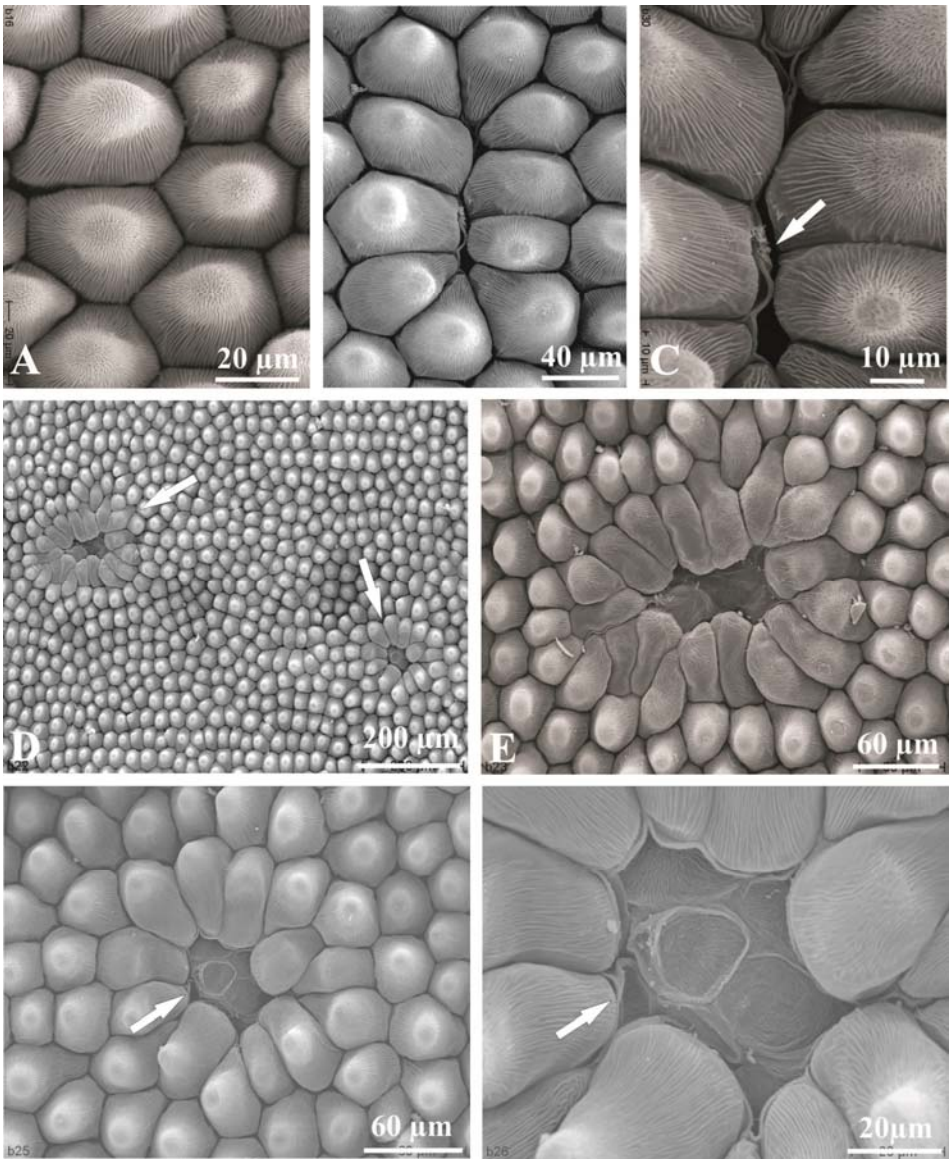

Fig. 6. Adaxial epidermis of *Viola* × *wittrockiana* ('Saint Tropez Mix F_2' cultivar) petals: A, B – upper view of the papillae; C – the hollow between epidermis cells (arrow); D – distribution of the secretory glands between the papillae; E–G – surface of the secretory glands (arrows)

Fig. 6. Doosiowa epiderma płatków korony *Viola* × *wittrockiana* (odmiana 'Saint Tropez Mix F_2'): A, B – papille widziane z góry; C – zagłębienie między komórkami epidermy (strzałka); D – rozmieszczenie gruczołów wydzielniczy między papillami; E–G – powierzchnia gruczołów wydzielniczych (strzałki)

Micromorphology of epidermal cells (SEM)

Conical papillae of the adaxial epidermis were covered by a cuticle showing regular striation. The striae concentrated at the tip of the papillae and ran radially downwards (figs 5B, C; 6A–C). Swellings and lighter areas were observed at the tip of some papillae (figs 5A; 6A–C); their presence was probably associated with their secretory activity. In these parts, droplets of secretion were observed on the surface.

Some structures with radially arranged, slightly flattened and elongated epidermal cells, surrounding depressions, were sparsely distributed between the papillae; cells with flat tangential walls could be seen in these structures (fig. 6D–G). Strips of protruding anticlinal cell walls and traces of secretion were observed in the central part of them. We observed small hollows between some epidermis cells too (fig. 5C). It seems that the above described structures might be secretory glands.

The rands of the petals were covered by the flattened papillae (fig. 5D). The abaxial epidermal cells were irregularly shaped due to small folds of the anticlinal walls. Their tangential walls formed small, asymmetrically arranged papillae that were covered with a striated cuticle (fig. 5E–G).

DISCUSSION

The floral structures emitting the scent are most frequently associated with the epidermis of the petals [Vogel 1990, Stpiczyńska 1993, 2001, Weryszko-Chmielewska and Chwil 2010, Whitney et al. 2009, 2011a, b, Antoń et al. 2012]. Weberling [1992] finds that the cells of the upper epidermis of these organs are often transformed into papillae. In our earlier study, we showed that papillae could also be located on the surface of stamen filaments [Weryszko-Chmielewska et al. 2006]. Ciccarelli et al. [2008] found papillae on the surface of the ovary.

The tissue structure observed in the cross section of the petal of *Viola* × *wittrockiana* differs to some extent from the structure presented by Weberling [1992] for this species. We observed papillae not only in the adaxial epidermis, but also in the abaxial epidermis. The mesophyll of the petal in the investigated plants was composed of many-branched cells, which is in agreement with the description given by Weberling [1992]. The cells of abaxial epidermis had strongly undulating and thickened walls forming ingrowths, which was probably related to their reinforcing function.

We observed stomata in the abaxial epidermis of the petal of *V. wittrockiana*, contrary to the description given by Weberling [1992] who claims that generally stomata are not present in flower petals. Previously, we also observed numerous stomata in the tepals in *Galanthus nivalis* [Weryszko-Chmielewska and Chwil 2010] as well as single stomata in the epidermis of the petals of *Ruta graveolens* [Weryszko-Chmielewska 2003].

The research of other authors shows that in some species of *Viola* (*V. kizildaghenzis*) there are no papillae on the upper surface of the petals [Dinç et al. 2007]. The papillae formed by the epidermis of *V.* × *wittrockiana* are covered by a regularly striated cuticle. Kuta et al. [2012] described a similar structure of the papillae in the adaxial epidermis in

Viola lutea and *V. tricolor* petals. These authors claimed that the cells of the abaxial epidermis of the investigated taxa were not papillate.

A similar arrangement of cuticular striae is found on the long hairs on the lower petals in some *Viola* species [Gil-Ad 1998]. The presence of papillae with striate cuticular ornamentation contributes to the formation of the velvety surface of the petals [Kugler 1970, Weberling 1992], which is of great significance as it is one of the attractants in pollination ecology [Proctor et al. 1996]. The function of the ornamented cuticle is also to reflect and refract the sun's rays, which protects the surface of the petals and other floral structures against excessive heating [Juniper and Jeffree 1983].

Our observations carried out under the fluorescence microscope have demonstrated that the papillae of the adaxial and abaxial epidermis *V.* × *wittrockiana* function asynchronously, since only some of them exhibited presence of a brightly fluorescent substance when treated with auramine O. Additionally, we have found that maturation of adaxial epidermis cells in the petals of *V.* × *wittrockiana* occurs earlier than in the abaxial epidermis, which was demonstrated by concurrent presence of chromoplast in the adaxial epidermis and chloroplasts in the abaxial epidermis. On the first day of blooming, we detected starch grains in the chloroplasts of the adaxial and abaxial epidermis cells of *V.* × *wittrockiana* petals. Presence of starch grains in osmophore cells has been reported in many plant species, which is a typical characteristic of osmophores as starch can be a source of energy required for production of odorous compounds [Stern et al. 1987, Vogel 1990, Weryszko-Chmielewska et al. 2006, Antoń et al. 2012].

In the adaxial epidermis, we observed some areas of partially flattened, radially arranged cells surrounding recessed areas between the papillae, where there were 4–6 cells with slightly sunken external walls. Perhaps these cells were associated with the emission of others substances and formed glands with a specific structure. Ciccarelli et al. [2008] described similar epidermal secretory structures in petals, sepals, stamens, and the style of *Myrtus communis* flower, which were cavities capped by 2–4 modified epidermal cells that were surrounded with normal epidermal cells characterized by numerous cuticular strations.

In the cytoplasm of the papillae of *V.* × *wittrockiana*, we observed lipid droplets of different size, which were essential oil. Such droplets were also found on the surface of the papillae. Their presence allows us to conclude that the papillae in *Viola* × *wittrockiana* perform the function of osmophores. Other authors have observed tiny lipid droplets penetrating into the surface of the cells of the osmophores in other plant species [Vogel 1990, Stern et al. 1987, Ascensão et al. 2005, Weryszko-Chmielewska et al. 2006].

CONCLUSIONS

1. The papillae of the adaxial and abaxial *Viola* × *wittrockiana* epidermis differing in the size and shape participate in the release of odorous substances.
2. Multi-celled structures functioning probably as additional secretory structures are found in the adaxial epidermis.
3. The papillae covered by a striated cuticle, which are present in the adaxial and abaxial epidermis, produce the effect of "velvet petals".

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RÓŻNORODNOŚĆ STRUKTURY EPIDERMY PŁATKÓW KORONY *Viola* × *wittrockiana* Gams. EMITUJĄCEJ ZWIĄZKI ZAPACHOWE

Streszczenie. Kwiaty *Viola* × *wittrockiana* Gams. emitują związki zapachowe. Gruczoły występujące w kwiatach, odpowiedzialne za wytwarzanie olejków eterycznych, rozmieszczone są najczęściej na płatkach korony. Do struktur tych należą papille – stożkowate komórki epidermy. Badano budowę epidermy oraz wewnętrznych tkanek płatków *V.* × *wittrockiana* przy użyciu mikroskopii świetlnej, fluorescencyjnej i skaningowej elektronowej. Stwierdzono, że po obu stronach płatków (ostrogowego, bocznych i górnych) występują w epidermie papille, z tym, że w epidermie adaksjalnej są one znacznie dłuższe. W papillach oraz na zewnętrznej powierzchni ich ścian obecne były różnej wielkości krople o charakterze lipidów. Wyniki badań histochemicznych potwierdziły, że w obserwowanych kroplach występują olejki eteryczne. Ponadto w epidermie adaksjalnej znajdowały się strefy spłaszczonych komórek o charakterystycznej budowie, stanowiące prawdopodobnie gruczoły wydzielnicze. Z badań wynika, że w wydzielaniu związków zapachowych przez kwiaty *V.* × *wittrockiana* uczestniczą zarówno komórki epidermy adaksjalnej, jak i abaksjalnej o różnej budowie. Być może te zróżnicowane struktury wytwarzają niejednorodne pod względem jakościowym zapachy.

Słowa kluczowe: *Viola* × *wittrockiana*, płatki korony, epiderma, papille, osmofory

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