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# CHARACTERISTICS OF THE SURFACE OF THE EPIDERMIS IN FLORAL NECTARIES AND THE RECEPTACLE OF MOUNTAIN ASH (*SORBUS AUCUPARIA* L.)

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S u m m a r y

The structure of receptacular surfaces of floral nectaries at two flowering stages and the structure of the outer surface of the receptacle of *Sorbus aucuparia* were investigated using scanning electron microscopy. Changes in the development of the cuticular epithelium of the nectary epidermis and differences in the degree of aperture of stomata were observed. Increased undulation of the gland surface was found during flower development. Numerous stomata were situated slightly below the level of epidermal cells of the nectary. At the pollination stage, open pores or pores surrounded by the cuticular epithelium were observed, as well as covered by dried secretion. Dried nectar in the form of patches was also visible on the surface of the gland. Stomata of the outer surface of the receptacle were located on protrusions and surrounded by the cuticular epithelium.

Key words: nectaries, epidermis, cuticle, stomata, *Sorbus aucuparia*

## INTRODUCTION

Mountain ash (rowan) is the most popular species from the genus *Sorbus* found in Poland on the whole lowland and in the mountains, as far as the mountain pine zone. At natural stands, it is encountered in bright forests and in-field tree stands. It is also often used in urban plantings due to ornamental values of its leaves, flowers and fruit, high resistance to air pollution and low soil type requirements (S z w e y k o w s c y , 2003). Small creamy white flowers of rowan contain a lot of organic acids as well as carotenoids, bitter substances, tannins, sugar compounds and a lot of vitamin C. Despite the occurrence of essential oils in trace amounts, the scent of rowan flowers is intensive, not very pleasant, rather sweet, but choking (it contains trimethylamides). It can be smelt from a distance of many meters (P r o c t o r and Y e o , 1973).

The part of the receptacle between the stamen filaments and the base of the styles is occupied by nectariferous tissue (W e r y s z k o - C h m i e l e w s k a et al. 1996, 1997; R a s p é , 1998;). Many authors consider *S. aucuparia* to be quite a good source of nectar and pollen (P r o c t o r and Y e o , 1973; S z k l a n o w s k a , 1978; S i m o n e t t i et al. 1989; F r i t z , 1990), and the high sugar content in nectar (about 27%) makes it attractive for pollinating insects (W e r y s z k o - C h m i e l e w s k a et al. 1996). As reported by B a n a s z a k (1987), honey yield of rowan is on the average 8 kg from 1 ha, max. up to 20 kg. Under Belgian conditions, main pollinators of rowan flowers are insects from the Diptera order (87-89%), while the others are honey bees and bumble bees (R a s p é , 1998).

The amount of nectar produced is determined not only by the size of nectary glands, but also by their structure (O r o s z - K o v á c s et al. 1990; D a v i s and G u n n i n g , 1992, W e r y s z k o - C h m i e l e w s k a et al. 1997). Even though the anatomy of nectaries of rowan has been studied thoroughly (W e r y s z k o - C h m i e l e w s k a and K o n a r s k a , 1996; W e r y s z k o - C h m i e l e w s k a et al. 1996), but no information has been found in literature on the structure of their surface on which, among other things, the speed of drying and the mode of nectar secretion are dependent, thereby the availability of secretion for pollinators.

In this study, the micromorphology of the surface of floral nectaries of *Sorbus aucuparia* was investigated using scanning electron microscopy (SEM). In addition, in order to observe dependencies between the structure of the epidermis and its function, the surface of the receptacle in the flower of *Sorbus aucuparia* was also analysed.

## MATERIALS AND METHODS

The material comprised flowers of *Sorbus aucuparia* L. collected at two development stages:

I. Bloom initiation – flowers with stamens with closed anthers, no visible nectar,

II. Full bloom – flowers with pollinating anthers with visible nectar.

The surface of the nectary glands and the outer surface of the receptacle were observed using scanning electron microscopy (SEM), having fixed flower fragments in 4% glutar aldehyde in 0.1M phosphate buffer with a pH of 7.2 and having treated them with 1% osmium tetroxide. Then, the sections were dehydrated in acetone series and critical point dried in liquid $CO_2$, subsequently they were coated with gold using the CS 100 Sputter Coater. Observations were made using the BS- 300 Tesla scanning microscope.

## RESULTS

Rowan flowers which live about 3 days are clustered in branched corymbs. The perianth of rowan flowers is composed of five white corolla petals surrounded by five hairy green sepals. The androecium is composed of 20 stamens with creamy white filaments and yellow anthers. Fifteen of them, with long stamen filaments, form the outer whorl, whereas the remaining five, with shorter filaments bent in the direction of the pistil, make up the inner whorl. The lower pistil has 4 or 5 styles which are surrounded by filiform hairs growing from the receptacle, partially protecting the nectary and the upper part of the ovary (Figs 1, 2).

The nectary gland of rowan belongs to the receptacular type, and in the receptacle it forms a wide, thick layer between the styles of the lower pistil and the base of the stamen filaments (Fig. 2). The surface of the nectary is slightly wavy (Fig. 2).

In the upper part, the nectary is surrounded by a bulging belt bordering with the base of the stamen filaments, composed of cells with larger dimensions and an elongated shape. Only few of the cells were marked by cuticular striation (Fig. 3). In the studied development stages, no differences were found in the structure of the epidermis of the above-nectary region.

Cells of the secretory epidermis of the nectary were polygonally shaped, and their outer walls formed slight bulges. The surface of the cuticle covering the epidermal cells of the gland was devoid of striae on the whole area of the nectary (Figs 4, 5). At places, secretion and wax coating in the form of flocculent or lumpy clusters were observed (Figs 4, 5).

Clear differences between the studied stages were noted in the arrangement of the surface of the nectary epidermis. Clearer folds on the surface of the epidermis were observed at the secretion stage than at bloom initiation. On the surface of the gland's epidermis, at many places dried secretion was visible, forming uneven patches frequently masking the presence of pores (Figs 6, 7). A stronger development of the cuticle was also noticed, which at places created characteristic "chimneys" or rings above the stomata (Fig. 7). Nectar secretion took place through the pores, quite numerous and evenly distributed over the whole surface of the gland (Figs 4-7). They were located in small hollows and surrounded by several epidermal cells (Figs 4-7).

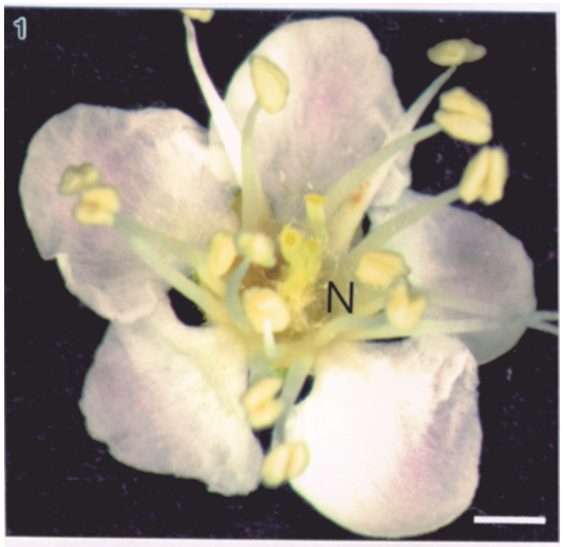
At the pre-secretion stage, the pores were closed, with quite clearly developed cuticular ledges (Figs 5, 8, 9). In the secretion period, open pores were observed (Fig. 10), as well as stomata masked by dried nectar or surrounded by specific cuticular rings of significant height (Figs 7, 11, 12).

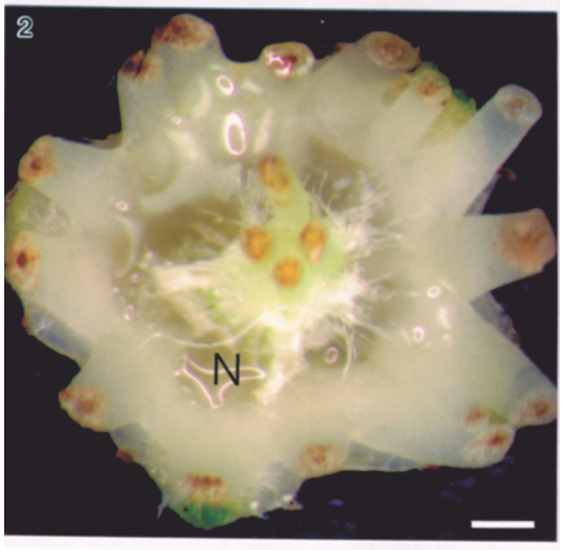
The epidermis of the outer part of the receptacle, not adapted to nectar secretion, looked entirely different (Figs 13, 14). The surface of the epidermis was slightly wavy and composed of small oval-contoured cells. Its outer convex walls were characterised by a smooth non-striated cuticle (Figs 13, 14). The stomata were situated on quite large protrusions and they had a protective cover of the strongly developed cuticle around them (Figs 13, 14). In the studied development stages, no clear differences were found in the structure of the epidermis of this part of the receptacle.

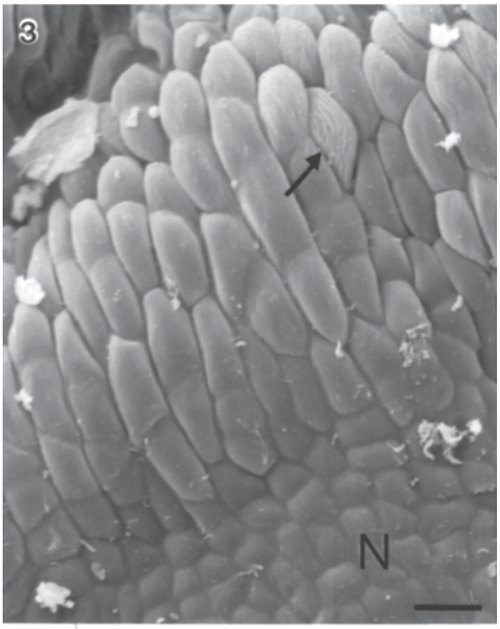
## DISCUSSION

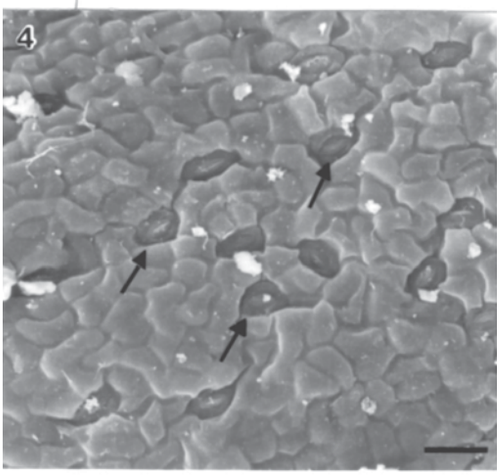
The location of nectaries in flowers of mountain ash is typical for the whole subfamily Pomoideae (Weryszko-Chmielewska and Konarska, 1995; 1996; Weryszko-Chmielewska et al. 2004; Weryszko-Chmielewska and Konarska, 2006). Due to the location of nectaries on the uncovered surface of the receptacle, nectar of most species is easily accessible for pollinating insects, in spite of large differences in the rate of nectar production (Szklanowska, 1978; Ferrazi and Priore, 1987; Gadawski and Smith, 1992; Weryszko-Chmielewska et al. 2003a; b; Konarska et al. 2005). The result of such exposure of the nectary is that secretion is exposed to quick evaporation and drying. Quite numerous filiform hairs, covering the nectary in the lower part of the gland, probably prevent it partially. Similar hairs were observed in *Prunus persica* by Radice and Galati (2003), and they suggested their protective role against the drying of nectar. Hairs of similar type were also found in other species from the subfamily Pomoideae (Weryszko-Chmielewska et al. 2004; Weryszko-Chmielewska and Konarska, 2006).

The surface of the epidermis of the nectary cells was devoid of cuticular striae. A smooth surface of the cuticle among Pomoideae representatives was also observed



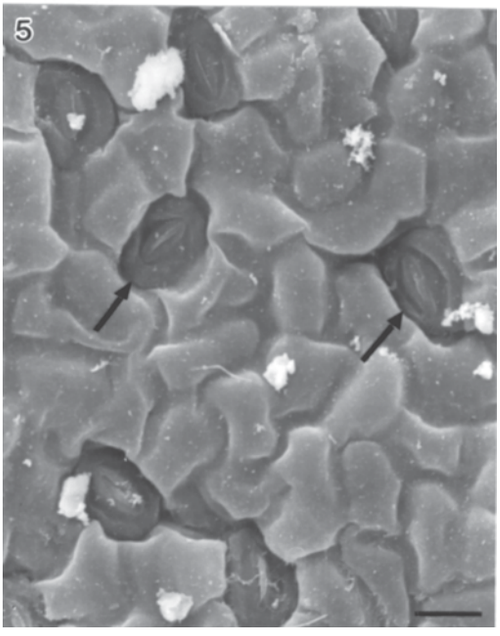
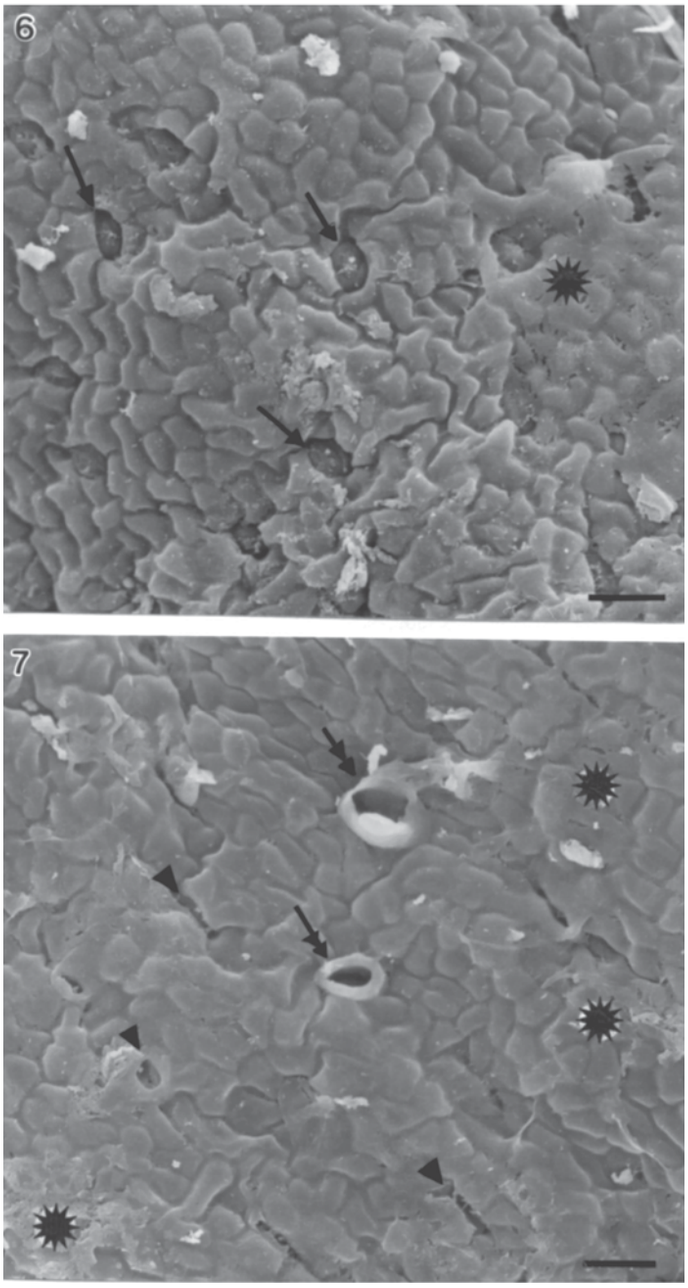




Fig. 1. *Sorbus aucuparia* flower with the marked location of the nectary (N), bar = 3 mm.

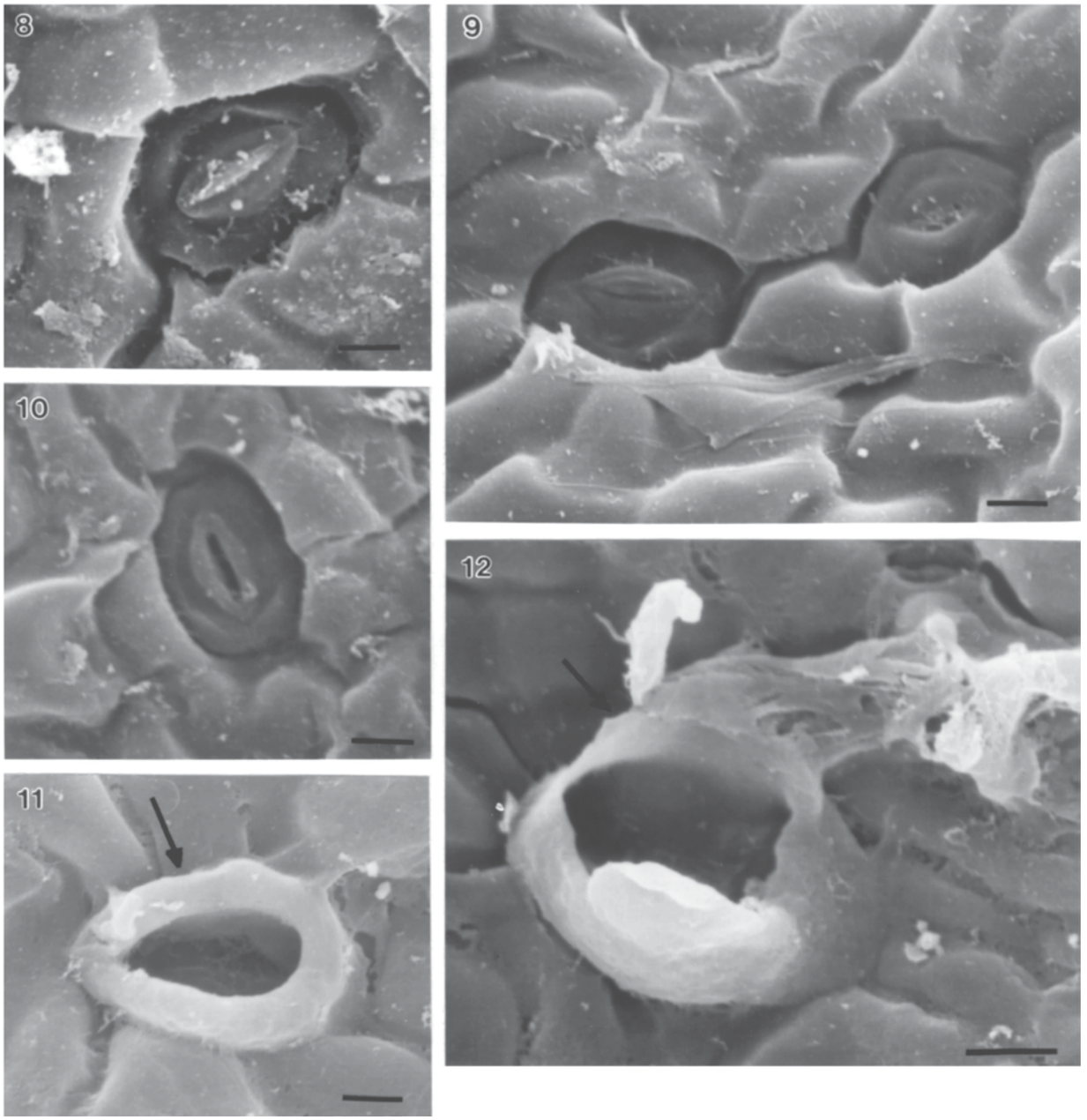
Fig. 2. Fragment of the *S. aucuparia* flower with the nectary (N), bar = 1 mm.

Fig. 3. Smooth surface of epidermal cells of the nectary (N) and cells of the region located above the nectary with visible cuticular striae (arrow), bar = = 20 µm.

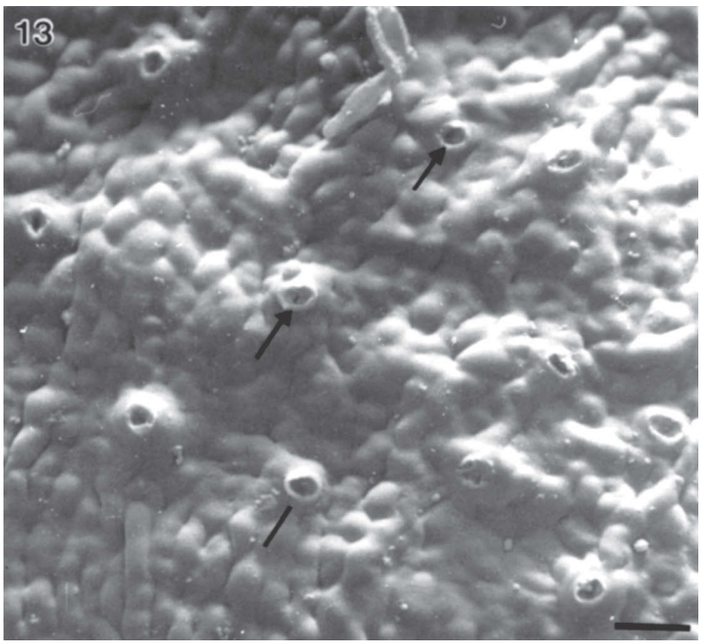
Figs 4, 5. Fragments of the surface of the nectary epidermis (stage I) with numerous closed stomata (arrows), bar = 20 µm (4), bar = 10 µm (5).

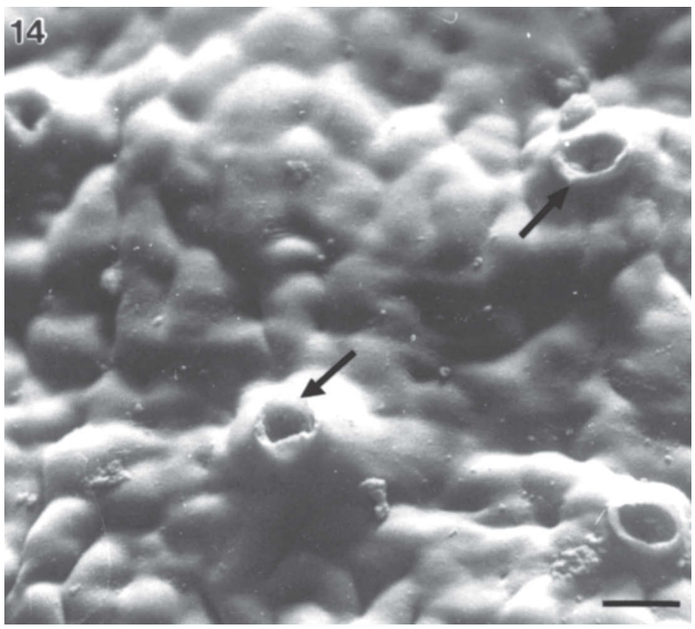



Figs 6, 7. Fragments of the nectary surface (stage II) with numerous unprotected stomata (arrows). Visible are also pores covered by dried nectar (arrowhead) and surrounded with rings formed from cuticular epithelium (double arrow). Patches of dried secretion are marked with asterisks, bars = 20 μm.




Figs 8-12. Stomata of the nectary epidermis at stage I (fig. 8, 9) and stage II (fig. 10-12). 11, 12 – visible strongly developed cuticular epithelium around the pores (arrows), bars = 2,5 μm.




Figs 13, 14. Surface of the epidermis covering the lower part of the receptacle with numerous stomata occurring on protrusions and protected by the cuticle (arrows), bar = 20 μm (13), bar = 10 μm (14).

in *Pyrus communis* and *Sorbus intermedia* (Konarska et al. 2005; Weryszko-Chmielewska and Konarska, 2006). But nectaries in other species were characterised by the presence of striated cuticle, and the size of striae significantly varied (Tóth et al., 2000; Weryszko-Chmielewska et al. 2003a; Weryszko-Chmielewska et al., 2004; Chwil et al. 2006; Konarska, 2006). The occurrence of striated cuticle on the surface of the nectary additionally protects against the drying of nectar and also favours its even distribution, as well as it reflects excessive ultraviolet radiation (Juniper and Cox, 1973; Juniper and Jeffree, 1983; Orosz-Kovács et al. 1990; 1991; Hejnowicz, 2002). The smooth cuticle of the nectary in rowan could be the reason for the formation of concentrations of dried secretion on the surface of the gland's cells as well as around the stomata. Besides, rowan nectar belongs to the type in which fructose and glucose are dominant sugars (Percival, 1961), and a high content of monosaccharides, in particular glucose, could additionally favour the crystallization of nectar. Such dependence is reported by Lipiński (1982). Crystallized nectar was also observed by Konarska et al. (2005) around the stomata in the nectary of *Pyrus communis* whose nectar is also characterised by a high content of monosaccharides (Maurizio and Grafl, 1969).

In the rowan flowers, typical modified stomata occurred which did not open until the stage of stamen maturation. Such type of stomata is characteristic for nectaries of most Pomoideae representatives (Weryszko-Chmielewska et al., 2004; Konarska, 2006; Weryszko-Chmielewska and Konarska, 2006; Konarska, 2007). In the rowan flowers, they were located below the level of epidermal cells, likewise in *Crataegus, Pyrus, Cydonia* and *Chaenomeles* (Weryszko-Chmielewska et al. 1997; Weryszko-Chmielewska et al. 2003; Konarska et al., 2005; Chwil et al., 2006), whereas in other representatives (*Malus* and *Cotoneaster*), they occurred at the level of epidermal cells (Weryszko-Chmielewska et al., 2004; Konarska, 2006; Konarska, 2007). The differences in the structure of the nectary found in the study, relating the increased degree of undulation of its surface and the opening of stomata at the studied flower development stages, were also observed in *Sorbus intermedia* by Weryszko-Chmielewska and Konarska (2006).

The stomata situated on the surface of the nectary differed in their location, compared to the stomata of the receptacle, what is probably associated with the function performed by these structures. The pores located in the lower part of the receptacle take part only in the process of transpiration and gas exchange. The location of the stomata on large protrusions of the epidermis could result from the absence of the need to protect these structures against excessive solar radiation which had impeded access to this part of the flower. But the nectary's pores which performed the secretory function were situated in small hollows and they were additionally covered with thick hairs protecting them against insolation and nectar against drying. The protection of some stomata of the nectary with a cuticular membrane, comparable to that observed around the pores of the receptacle, evidences a certain similarity in the construction of these structures. But the absence of these specific cuticular rings at the pre-secretion stage may suggest that their appearance at the secretion stage is related to a change in the activity of the gland as well as its aging.

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## Charakterystyka powierzchni epidermy nektarników kwiatowych oraz dna kwiatowego jarzębu pospolitego (*Sorbus aucuparia* L.)

Streszczenie

Strukturę powierzchni receptakularnych nektarników kwiatowych w dwu fazach kwitnienia oraz strukturę zewnętrznej powierzchni dna kwiatowego *Sorbus aucuparia* badano w skaningowym mikroskopie elektronowym. Zaobserwowano zmiany w rozwoju nabłonka kutykularnego epidermy nektarnika oraz różnice w stopniu rozwarcia aparatów szparkowych. W czasie rozwoju kwiatów stwierdzono wzrost pofałdowania powierzchni gruczołu. Liczne aparaty szaprkowe usytuowane były nieznacznie poniżej poziomu komórek skórki nektarnika. W stadium pylenia obserwowano otwarte szparki lub otoczone nabłonkiem kutykularnym, a także osłonięte zaschnięta wydzieliną. Zaschnięty nektar w postaci płatów był widoczny także na powierzchni gruczołu. Aparaty szparkowe zewnętrznej powierzchni dna kwiatowego zlokalizowane były na wzniesieniach i otoczone nabłonkiem kutykularnym.