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THE ECOLOGICAL FEATURES OF FLOWERS AND INFLORESCENCES OF TWO SPECIES OF THE GENUS *Petasites* Miller (ASTERACEAE)

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Abstract

The structural features of flowers and inflorescences of *Petasites hybridus* and *P. albus* were compared. Only individuals producing flower heads with male flowers and few female flowers were found in the studied populations. Light microscopy (LM) and scanning electron microscopy (SEM) were used for examination.

The present study shows that the stems of the above-mentioned species differed in height and number of flower heads, but the number of flowers per head was similar. Larger flowers were found on the stems of *P. albus*. The following features has been found to play an important role in pollination ecology: the strongly contrasting colours of the floral parts; on the petals, the occurrence of several types of cells which can increase the attractiveness of the flowers by refracting sunlight in a different way; production of odorous oils by the petal cells; production of significant amounts of pollen offered to insects by the well-developed pollen presenters; the development of nectaries and nectar production by the male flowers as well as the development of colour attractants by the corolla, anthers, and bracts.

Key words: *Petasites hybridus, P. albus*, inflorescences, flowers, micromorphology, pollen presenters, pollen, bracts, floral attractants

INTRODUCTION

Petasites hybridus (L.) G., M. et Sch. and *P. albus* (L.) Gaertn. are native to Europe and north-western Asia (Gibbons and Brough, 1995; Schaffner, 1996). *P. hybridus* is found more frequently in Poland and it inhabits primarily the southern and north-western parts of our country (Zając and Zając, 2001). Plants of both species grow along stream banks and in moist meadows, forming large clusters (Rutkowski, 1996).

The above-mentioned species are included in bee plants (Bornus, 1989; Lipiński, 2010). Due to their flowering period (III-V), they can provide a source of early spring pollen and nectar to insects which visit their flowers in large numbers under favourable conditions. Many papers show that plant material obtained from their leaves and underground parts (rhizomes, roots) has been used in herbalism and medicine since ancient times (Podhajska and Rivola, 1992; Schaffner, 1996; Siegenhaler and Neuenschwander, 1996; Wildi et al. 1998). However, Smith and Culvenor (1981) as well as Sadowska (2004) note that *P. hybridus* contains pyrrolizidine alkaloids with potential carcinogenic properties. In some countries *P. hybridus* has been completely withdrawn from medical use, while in other countries it is allowed for internal use on the condition that there is a low alkaloid content in the herbal preparation (Sadowska, 2004).

The above-mentioned *Petasites* species are perennials with a thick horizontally branched rhizome. They produce inflorescence stems before the leaves develop. These species belong to plants that produce separately shoots bearing female flowers, 20-45 cm in height, as well as shoots bearing male flowers and a small number of female flowers, reaching a height of 15-25 cm. These shoots are covered with numerous scaly leaves. The disk flowers are borne in small flower heads clustered in panicle-like racemes. Very large, crenate, heart-shaped leaves, with a width of up to 60 cm, are covered in the lower part with hairs forming a tomentum. The fruit is an achene with pappus (Szafer et al. 1986; Podhajska and Rivola, 1992).

Since sparse information on the structure of *Petasites* flowers was found in the literature, the aim of

the present study was to compare the structure of the flower heads and the micromorphology of flowers and leaves accompanying the inflorescences of two species: *Petasites hybridus* and *Petasites albus*, taking into account their adaptations important in pollination ecology.

MATERIALS AND METHODS

Inflorescences of *Petasites hybridus* (L.) Gaertn, Meyer et Scherb and *Petasites albus* (L.) Gaertn. were collected in March and April 2011 and 2012. The plant material came from the Botanical Garden of the Maria Curie-Skłodowska University in Lublin.

The height of 20 inflorescence stems was measured at full bloom. The diameter and height of flower heads and of their particular parts were measured and photographed under a stereoscopic microscope equipped with a NIKON COOLPIX 4500 camera. The number of flower heads on ten inflorescence stems, number of flowers per head for the capitula from different levels of the inflorescence, flower head diameter and height, flower length and involucral bract length were all determined. In each case, 10 calculations or measurements were made. Additionally, hand-cut sections were prepared from fresh leaves growing on the inflorescence stem and from the involucral bracts and they were mounted in 50% glycerol solution. The slides were observed and photographed under a Nikon Eclipse 400 light microscope. The pollen presenters located near the stigma of the pistil and hairs on the leaves were also analysed. 50 pollen grains of each species were viewed and measured.

The inflorescence segments were fixed in 4% glutaraldehyde solution in 0.1 M phosphate buffer with a pH of 7 and at a temperature of 4ºC for 12 hours. Next, the plant material was washed in the same buffer four times at 20-minute intervals and subsequently it was fixed in 1% osmium tetroxide for 1 hour. The leaf segments were dehydrated in alcohol series with the following concentrations: 30, 50, 70, 90, and 95%, and immersed twice in absolute alcohol. After dehydration, the plant material was critical-point dried. The specimens were coated with gold and analysed using a TESCAN VEGA II LMU scanning electron microscope.

RESULTS

Petasites hybridus

In the observed plant population, we did not find any individuals that had only female flowers on their inflorescences. The height of the stem with an inflorescence bearing male flowers and few female flowers was on average 15.5 cm. The flowers in the flower heads as well as the involucral bracts and leaves on the inflorescence stem were pink coloured (Figs. 1 A,C, E,F,H; 4B,C). The number of heads per inflorescence in individual plants varied greatly (44-91), with its average value of 59. The average flower head diameter was 6.6 mm, while the flower head height 13.8 mm.

The number of involucral bracts was 12-14. They showed a darker pink colour in their marginal area. They were arranged in two rows (Fig. 4B). Their average length was 7.7 mm. These leaves were glabrous and no glandular trichomes were observed on their surface, either.

A comparison of the number of flowers per head for the flower heads located in the lower, middle and upper parts of the inflorescence shows that the highest number of flowers per head was in the lower area of this organ. From the bottom upwards, on average the number of flowers was 33, 31, and 27, respectively. The majority of flowers in the capitula examined were intensely coloured male disk flowers with a non-functional ovary. The average flower length was 8 mm. The average bud length before flower opening was 6.5 mm. In the circumferential part of the flower head, there were few small white-coloured female flowers with an average length of 4.8 mm (Figs 1C,H; 2B).

The 5-toothed corolla in the male flowers was clearly coloured only in its upper part, but the edges of the lobes were brighter (Fig. 1 E,F,H). In the epidermis of the corolla lobes, elongated cells could be observed (Fig. 2C) whose outer walls slightly subsided during flowering, probably as a result of turgor loss, forming a characteristic reticulate "sculpture" on the surface of the lobes (Fig. 2A). The lobes edges were reinforced by rows of thick-walled epidermal cells (Fig. 2E,F). The petals emitted a delicate scent that probably came from the papillae located on the teeth margins (Fig. 2D).

The intensely pink fused stamen heads were also a part of the floral attractant (Fig. 1F). The anthers produced white pollen grains that were transferred to the highest part of the flower by the papillae of the pollen presenters located in the upper part of a slightly expanded style (Figs 1F,I; 3A,B,I). The length of the presenters was 1.1-1.3 mm. The papillae varied in length and they were cylindrical or conical (Fig. 3A,B,C,D). Numerous pollen grains were observed on the surface of the papillae by LM and SEM (Fig. 3D,I-,J,K). No presence of ovules was found in the ovary of the male flowers, whereas at the base of the style there was a nectary, ca. 250 μm in height, which was characterized by an intense yellow colour.

The abundantly produced pollen was collected by bees in the form of whitish pollen loads. The average size of *P. hybridus* pollen grains was 26.2 μm. These grains should be classified as medium-sized. They were distinguished by the presence of 2.5-3.5 μm long spines (Fig. 3 E,F,G,H). Numerous tryphine droplets were observed on the surface of the pollen grains.

The female flowers had a reduced whitish corolla and a calyx composed of numerous hairs (Figs 1H; 2B). The style terminated in a bipartite stigma on which no papillae were observed, unlike in the male flowers. Well-formed ovules were observed in the ovaries of these flowers.

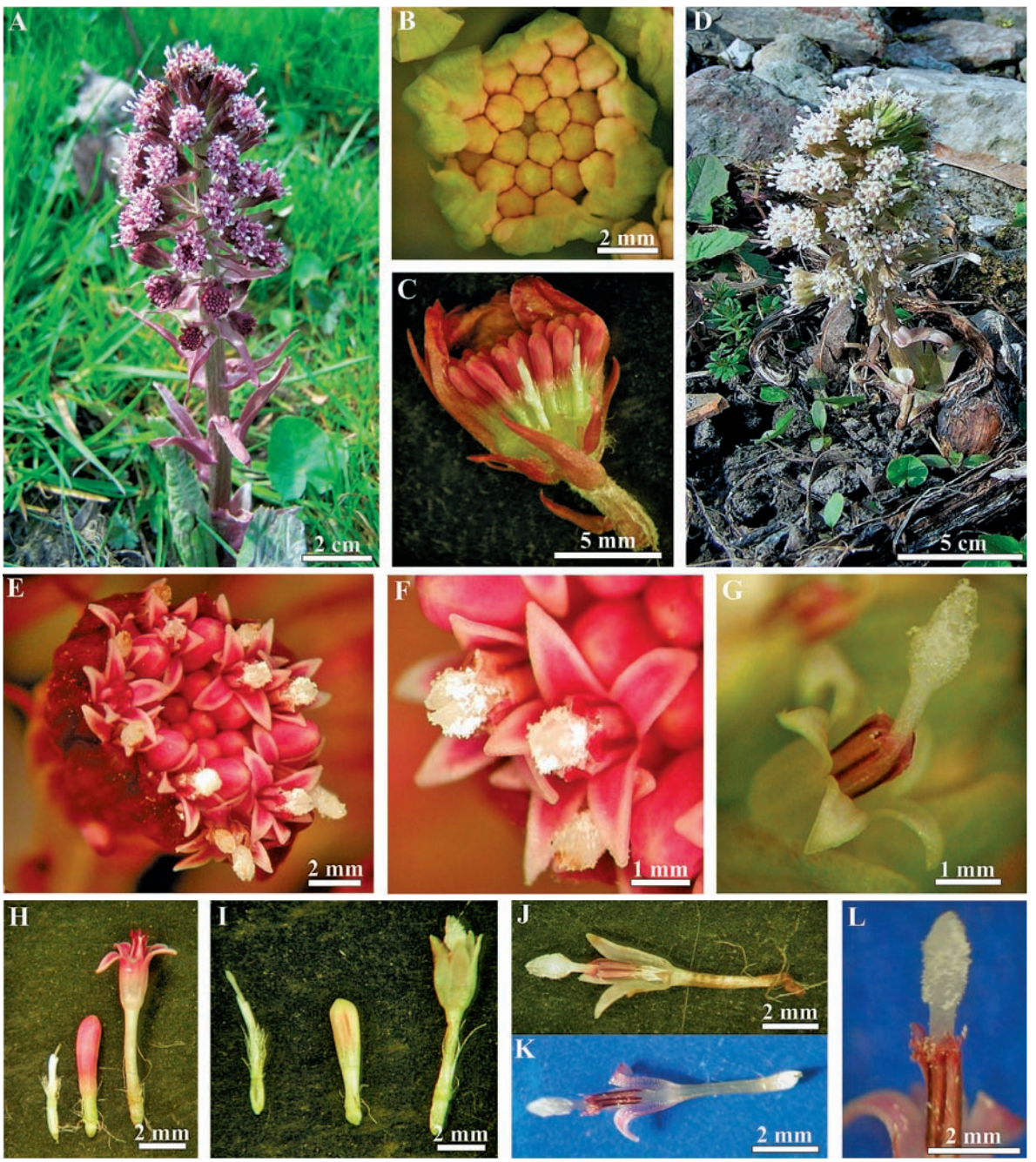

Fig. 1. Inflorescences and flowers of *Petasites hybridus* and *P. albus*.
A – *P. hybridus* stem bearing flower heads with male flowers and few female flowers.
B – *P. albus* flower head with flowers in bud.
C – *P. hybridus* flower head with male flowers (pink coloured) and two female flowers (white coloured).
D – Flowering stem of *P. albus*.
E, F – Male flowers in *P. hybridus* flower heads with visible white pollen on the pollen presenters.
G – Male flower of *P. albus* with brown and claret anthers and a white pollen presenter.
H – From the left: female flower, bud and male flower of *P. hybridus*.
I – From the left: female flower, bud and male flower of *P. albus*.
J, K – Fully developed male flowers: J – *P. albus*, K – *P. hybridus*.
L – Intensely coloured anthers and a whitish pollen presenter of *P. hybridus*.

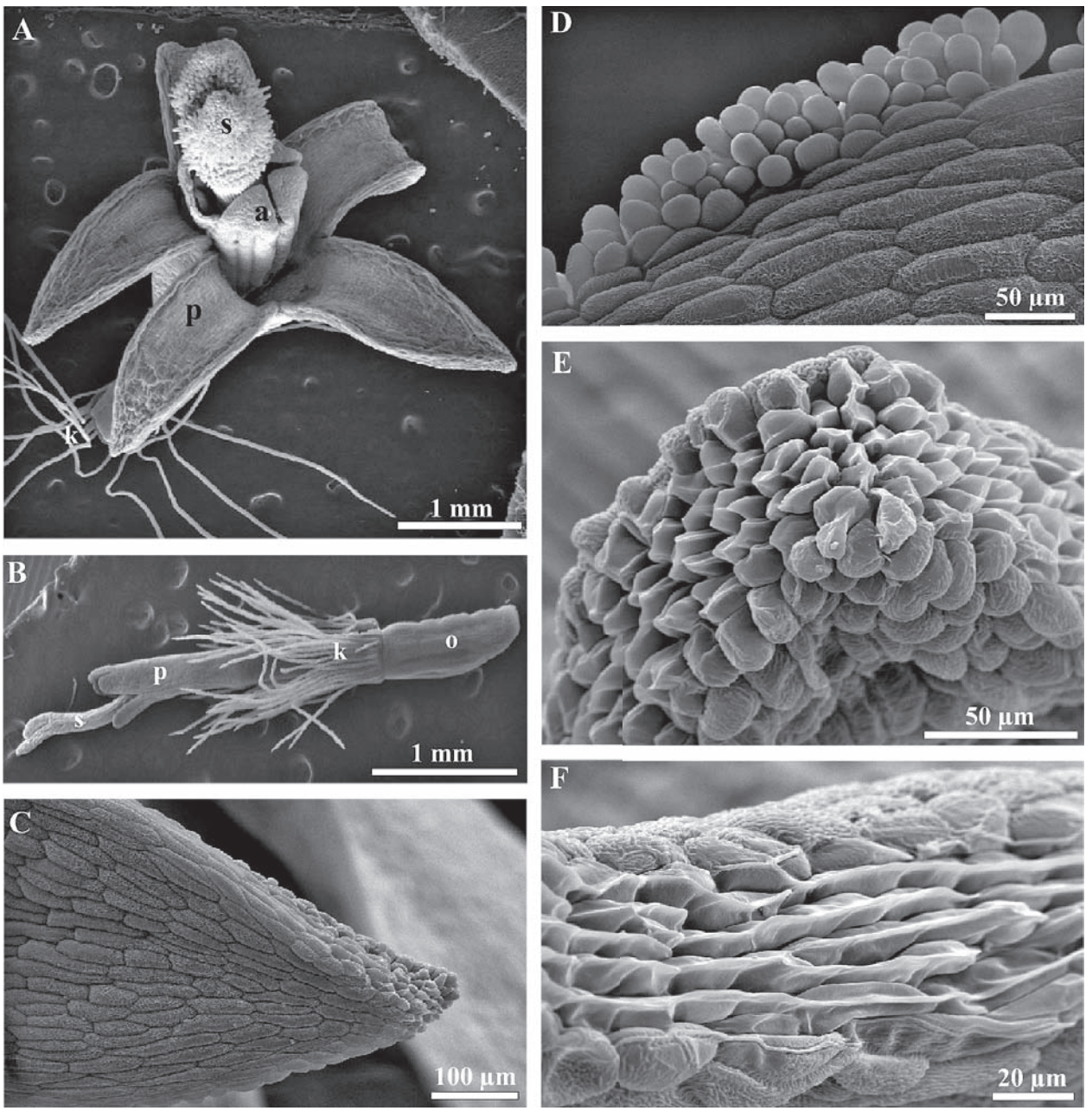

Fig. 2. Flowers and perianth segments of *P. hybridus* (SEM).

A – Male flower with a 5-toothed corolla (p), a calyx in the form of hairs (k), stamens (a), and a brush-like pollen presenter (s).

B – Female flower with a reduced corolla (p), numerous hairs of the calyx (k) which will form the pappus of the achene, an inferior ovary (o), and a style longer than the corolla (s).

C, D, E, F – Parts of the corolla tooth with epidermal cells of different structure:

C – flattened cells on the surface of the tooth.

D – papillae on the edge of the corolla tooth.

E, F – cells with thickened walls from the tip of the tooth.

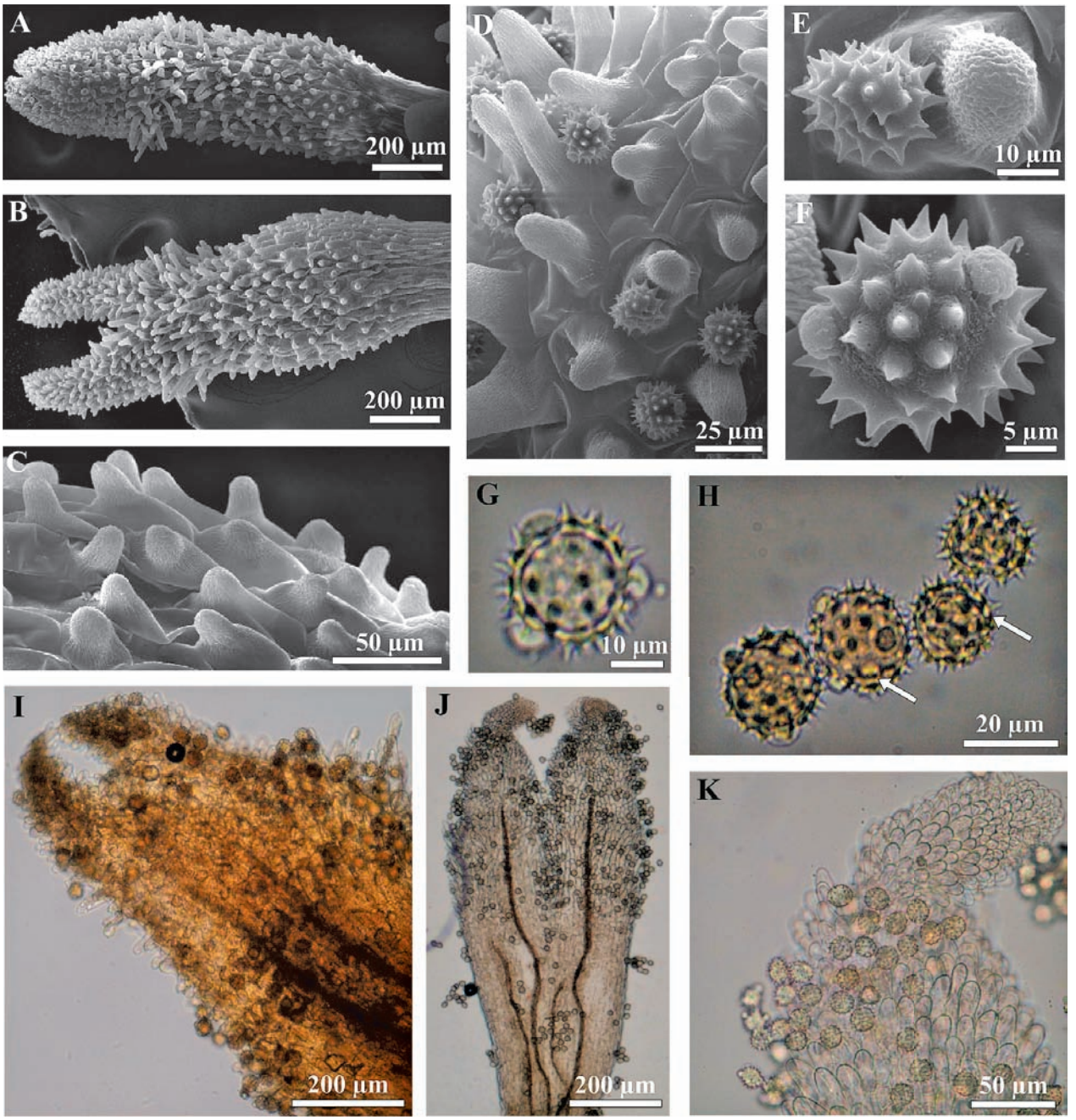

Fig. 3. Pollen presenters and pollen of *P. hybridus* and *P. albus*.

A, B – Pollen presenters from a younger and older flower of *P. hybridus* (SEM).

C, D – Parts of the presenters of *P. hybridus* with visible papillae of different length and pollen grains (D) (SEM).

E – Echinate pollen grain of *P. hybridus* and the top view of the papillae surface (SEM).

F – Pollen grain of *P. hybridus* in polar view (SEM).

G – Pollen grain of *P. albus* with cytoplasmic projections near the pores.

H – Pollen grains of *P. hybridus* with visible tryphine droplets (arrows).

I, J, K – Pollen presenters with pollen grains. I – *P. hybridus*; J, K – *P. albus* (LM).

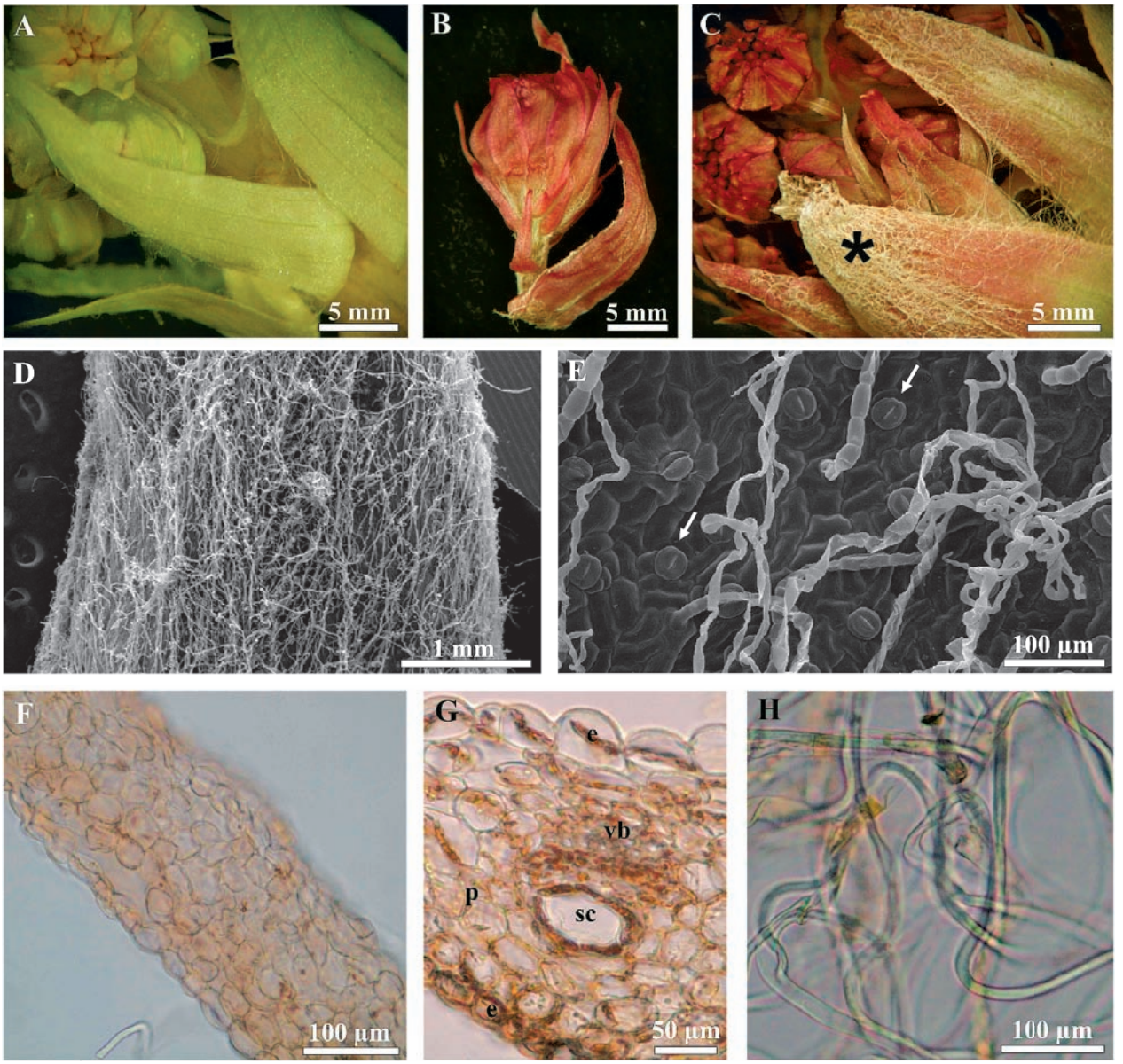

Fig. 4. Leaves on inflorescence stems of *P. albus* and *P. hybridus*.
A, B, C – Involucral bracts and scaly stem leaves: A – *P. albus*; B, C – *P. hybridus*. Visible are woolly hairs at the apical part of the leaf (C) (*) (LM).
D – Part of a scaly stem leaf of *P. hybridus* with tangled hairs (SEM).
E – Stomata (arrows) and multicellular hairs on the leaf surface of *P. hybridus* (SEM).
F – Cross section of an involucral bract of *P. albus* (LM).
G – Cross-sectional portion of an inflorescence stem of *P. albus* with the visible secretory duct (sc), different-sized epidermal cells (e), parenchyma (p) and a vascular bundle (vb) (LM).
H – Tangled hairs from the surface of a scaly leaf of *P. hybridus* (LM).

The scaly leaves on the inflorescence stem varied in terms of their size and colour. Their upper parts were dark pink and covered with long and tangled white-coloured hairs (Fig. 4C,D,H), These trichomes were multicellular. Numerous stomata were found in the epidermis of these leaves (Fig. 4E). In leaf cross-sections, the chlorenchyma was observed, undifferentiated into palisade and spongy parenchyma, as well as the secretory ducts found in the vicinity of the vascular bundles.

Petasites albus

Likewise in *Petasites hybridus*, small flowers were borne in flower heads forming racemes at the apex of the stem (Fig. 1B,D). Depending on the location of the inflorescence stem (from the bottom upwards),

30, 29 and 26 flowers were found on average in the capitulum. The observed inflorescence stems reached an average height of 13.5 cm. Flower head diameter and height are given in Table 1.

The female flowers, growing on the margin of the flower head, have small dimensions (average length – 4.9 mm). The perianth is composed of a narrow reduced corolla and a calyx in the form of pappus (Fig. 1I). The pistil has a long style terminated in a two-parted stigma (Fig. 1I).

The male flowers have a whitish 5-lobed corolla fused into a tube in the lower part and five stamens with brown and claret coloured heads. Ovules did not develop in the ovary of the male flowers. At the base of the style, there was a yellow nectary with an average height of 300 μm. In mature flowers, the upper part of the pistil forms a pollen presenter. Initially, the pollen presenter is compact, while in older flowers it is dichotomously branched (Fig. 1G,I,J). On the surface of the presenter, there are numerous densely distributed papillae of different length which are expanded at the base and rounded at the tip (Fig. 3J,K). During its elongation, the pistil presses through the anthers fused into a tube and sweeps out the pollen from the tube. Pollen grains are similar to grains found in common butterbur, but they have slightly larger dimensions (their average size is 29.6 μm) (Fig. 3G).

Around the flower heads, there were 8-13 greenish blunt-ended involucral bracts that reached an average length of 7.6 mm. No glandular trichomes were found on their surface and only long non-glandular trichomes occur at their basal part.

On the inflorescence stem, there are bright green scaly leaves which, unlike this type of leaves in common butterbur, have much fewer non-glandular trichomes on the surface (Fig. 4A). In the leaf cross-section, the epidermis can be seen with the abaxial cells larger than the adaxial ones. Underneath the epidermis, there are undifferentiated parenchymal cells of similar size containing chloroplasts. The secretory ducts can be found near the vascular bundles (Fig. 4 F,G).

DISCUSSION

In the observed populations of *P. hybridus* and *P. albus*, no plants with inflorescences producing only female flowers were found. The studied plants have been growing in the Botanical Garden for 5 years and no individuals producing achenes have been recorded over this time.

It was shown in the above-mentioned *Petasites* species that the inflorescence stems with male flowers in their capitula and few female flowers differed in height and number of flower heads. In the case of *P. albus*, these shoots were lower on average by 2 cm and they bore fewer flower heads than the shoots of *P. hybridus.* However, the flower heads of *P. albus* were slightly larger and had larger sized flowers. The flowers and bracts of *P. hybridus* were pink coloured, whereas the bracts of *P. albus* were bright green and the flowers produced a white corolla as well as brown and claret coloured anthers.

In spite of the differences in the size of flower heads and flowers in the *Petasites* species under comparison, they were found to have a similar number of flowers in their capitula, in particular in the middle and upper part of the stem. In *P. hybridus*, the flower heads located in the lower part of the stem had several flowers more. In both *Petasites* species, small flowers were borne in flower heads with a dimension of 6-7 mm in which the elements producing colour contrasts were important parts of the attractant. They were clearly visible between the pink perianth and the white pollen presenter in the case of *P. hybridus*, while in the flowers of *P. albus* between the white presenter and the brown and claret anthers.

The average length of involucral bracts of the flower head bearing two types of flowers was similar for both *Petasites* species (7.6 and 7.7 mm). Szafer et al. (1986) report a similar length of these structures in *P. hybridus* (7-8 mm).

The structure of the corolla of *Petasites* flowers shows that the rows of densely packed papillae growing on the edges of the perianth teeth were probably responsible for scent emission. Similar papillae have been recorded on the sepals in many other plant species (Vogel, 1990; Teixeira et al. 2004) as well as on the stamen filaments and connectives (Vogel and Hadacek, 2004; Weryszko-Chmielewska et al. 2007).

The pollen presenters responsible for secondary pollen presentation in flowers make it easier for insects to reach the pollen. In plants from the family Asteraceae, the presenters have different forms (Ladd and Donaldson, 1993; Erban and Leins, 1998; Weryszko-Chmielewska et al. 1999). One of them is a brush-like presenter covered with papillae on its entire surface. Such a type of presenter occurred in the male flowers of *Petasites*. This presenter, ca. 1.2 mm long, was located in the expanded apical part of the style. Its highest segment was divided into two parts. No presence of the pollen presenter was found in the female flowers of both species of this genus. On the other hand, the presenter in the male flowers of *Sylphium* was very long (7-9 mm) and unbranched (Weryszko-Chmielewska et al. 1999). Its surface was covered with multicellular trichomes with sharp-pointed ends at the tip. In turn, the epidermis of the pollen presenter of *Taraxacum officinale* produced unicellular hairs in which chromoplasts were observed

(Weryszko-Chmielewska and Chwil, 2006). Similarly as in *Petasites*, the surface of the pollen presenter in the bisexual flowers of *Chamomilla recutita* was covered with papillae whose cytoplasm was intensely stained after treatment with toluidine blue (Sulborska, 2011).

Pollen grains of *Petasites* were marked by the presence of conical spines and they represent the Aster type (Moore et al. 1991). According to Zander (1935), the average size of *P. hybridus* pollen grains is 25 µm. Beug (2004) reports that the size of *Petasites albus* pollen grains ranges 35.1-45.7 µm, with its average value of 39.7 µm, whereas *P. hybridus* pollen grains are smaller and they are in the range of 25.5-35.5 µm, with their average value of 31.2 µm. Our study shows that the plants belonging to the two *Petasites* species from the populations growing in the Botanical Garden in Lublin produced much smaller pollen grains than the grains observed by Beug (2004). The dimensions of these grains were similar to the values reported for *P. hybridus* by Zander (1935).

The features of *Petasites* flowers which are important in pollination ecology should include the following:

- The development of floral parts with strongly contrasting colours, which is one of the colour attractants;
- In the petals, the occurrence of several types of cells which can refract sunlight in a different way and lure insects;
- In the corolla lobes, the presence of papillae which probably produce odorous oils;
- The production of significant amounts of pollen from which bees form whitish pollen loads;
- The presence of a yellow nectary producing nectar in the male flowers;
- The occurrence of coloured bracts that support the floral attractant in the flower heads.

Table 1.
Characteristics of flowers and inflorescences of *Petasites hybridus* and *P. albus*

Trait			Species	
			Petasites hybridus	*Petasites albus*
Number of flowers per head	apical part	range	19-46	21-30
		mean	**27.2**	**26.2**
	middle part	range	28-34	22-37
		mean	**30.9**	**29,2**
	lower part	range	29-37	25-37
		mean	**33.5**	**30.4**
Flower head diameter [mm]		range	5.1–8.1	5.1–9.5
		mean	**6.6**	**7.2**
Flower head height [mm]		range	11.2-16.7	11.1-18.9
		mean	**13.8**	**14.6**
Male flower bud length [mm]		range	5.0-7.6	5.0-6.3
		mean	**6.5**	**5.7**
Male flower length [mm]		range	6.2-9.7	7.7-11.2
		mean	**8.3**	**9.3**
Female flower length [mm]		range	3.6-6.4	4.4-5.6
		mean	**4.8**	**4.9**
Pollen grain size [µm]		range	19.1-28.6	27.3-32.2
		mean	**26.2**	**29.6**

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Cechy ekologiczne kwiatów i kwiatostanów dwóch gatunków z rodzaju *Petasites* Miller (Asteraceae)

Streszczenie

Porównywano cechy budowy kwiatostanów i kwiatów *Petasites hybridus* i *P. albus.* W badanych populacjach znaleziono tylko osobniki wytwarzające koszyczki z kwiatami męskimi i nielicznymi żeńskimi. Do badań wykorzystano mikroskopię świetlną (LM) i skaningową elektronową (SEM).

Z badań wynika, że pędy wymienionych gatunków różniły się wysokością i liczbą koszyczków, ale liczba kwiatów w koszyczkach była zbliżona. Większe kwiaty znaleziono na pędach *P. albus*. Do cech odgrywających znaczną rolę w ekologii zapylania zaliczono: silnie skontrastowane barwy elementów kwiatowych; występowanie na płatkach kilku typów komórek, które mogą zwiększać atrakcyjność kwiatów przez załamywanie w różny sposób promieni świetlnych; wytwarzanie olejków zapachowych przez komórki płatków; produkcję znacznych ilości pyłku oferowanego owadom przez dobrze rozwinięte prezentery pyłkowe; wytwarzanie nektarników i nektaru przez kwiaty męskie oraz utworzenie barwnych atraktantów sygnalizacyjnych przez koronę, pylniki i liście przykwiatowe.