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LEAF EPIDERMIS TRAITS AS TOOLS TO IDENTIFY *SOLIDAGO* L. TAXA IN POLAND

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We used via light and scanning electron microscopy to study the leaf epidermis of five *Solidago* taxa from southwestern Poland. Light microscopy was employed to describe the epidermal surface, including stomatal types, the shape of epidermal cell walls, stomatal density, the distribution of stomata between the abaxial and adaxial epidermis, and stomatal guard cell length. From these observations we calculated the stomatal index (SI) and stomatal ratio (SR) as the basis for defining the type of leaf. From LM of transverse sections of leaf we described mesophyll structure, the presence of secretory canals, adaxial and abaxial epidermis thickness, and leaf thickness. We examined cuticular ornamentation, trichome features and epicuticular secretions by SEM. As determined by discriminatory analysis, the most important traits distinguishing these taxa were the stomatal index of the adaxial epidermis, leaf thickness, features of the walls of epidermal cells, and the presence and features of trichomes. On the basis of observations and measurements we created a key for distinguishing *Solidago* taxa.

Key words: *Solidago*, leaves, anatomy, micromorphology, stomata, trichomes.

INTRODUCTION

The genus *Solidago* L. comprises about 130 species, most of which are native to North America (Beaudry and Chabot, 1959; McNeil, 1976). This genus is one of the most complex genera of higher plants (Fernald, 1950), and its variability has further increased due to hybridization, introgression and ecological factors (Beaudry and Chabot, 1959; Beaudry, 1963). Five representatives of the genus *Solidago* are found in Central Europe. Only one species (*S. virgaurea* L.) is native to Europe. The other four are of American origin: *S. gigantea* Aiton, *S. canadensis* L., *S. altissima* L. [*S. canadensis* var. *scabra* (Muhl.) Torr. & Gray] and *S. graminifolia* (L.) Elliott (McNeil, 1976). Three of the introduced taxa (*S. gigantea*, *S. canadensis*, *S. altissima*) are expansive and morphologically resemble each other. Their taxonomic status in Europe has been discussed elsewhere (Beaudry and Chabot, 1959; Rostański, 1971; Guzikowa and Maycock, 1986; Małecka, 1988; Musiał, 1989; Weber, 1997; Weber and Schmid, 1998). The two species with a hairy stem and leaves are particularly difficult to differentiate: *S. canadensis* and *S. altissima* (Rutkowski, 2006; Rothmaler, 2007). Numerous studies have described two varieties of *S. canadensis* from Europe: var. *canadensis* and var. *scabra* (Rostański, 1971; McNeil, 1976; Wagenitz, 1979; Guzikowa and Maycock, 1986). It has been reported that var. *canadensis* is rare in Poland, whereas var. *scabra* is common (Rostański, 1971), and that plants of var. *scabra* found in Poland differ morphologically from plants of *S. canadensis* var. *scabra* (Muhl.) Torr. et Gray found in Canada (Guzikowa and Maycock, 1986). According to Semple and Cook (2006), in the North American flora, two varieties of *S. canadensis* are recognized: var. *canadensis* (with mid to proximal stems, glabrous or sparsely hairy) and var. *hargeri* (with mid to proximal stems, moderately hairy); they considered *Solidago altissima* L. to be *S. canadensis* var. *scabra*. Here we treat the disputed species as *Solidago canadensis* L. and *S. altissima* L.

Two varieties are found in North American *S. gigantea*: *S. gigantea* ssp. *gigantea* and *S. gigantea* ssp. *serotina*. In Europe, smooth goldenrod is a more uniform species (Weber and Schmid, 1998), and the second variety is hardly ever found in Poland (Rutkowski, 2006). McNeill (1976),

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however, stated that the naturalized plants in Europe are mostly referable to ssp. *serotina*, although ssp. *gigantea*, with leaves pubescent on the veins beneath, may also occur.

The chromosomal base number in *Solidago* taxa is x=9 (Semple and Cook, 2006). In most *Solidago* taxa the diploid chromosome level (2n=18) is observed. Diploid and tetraploid (2n=36) populations have been noted in only two taxa, *S. gigantea* and *S. altissima*. Among the chromosome counts, several cases of aneuploid cytotypes have been detected: 2n=34 in *S. altissima* and 2n=30, 2n=32 and 2n=38 in *S. gigantea* (Szymura, 2004). On the other hand, the American representatives of *S. altissima* are hexaploid (2n=54) (Melville and Morton, 1982).

Traditionally, plant taxonomy is based mostly on morphological characteristics. In recent years, taxonomic data from other disciplines have also been used to better understand various taxa. According to Carlquist (1961), the leaves of plants provide a variety of anatomical features that can be employed as taxonomic characters. Several authors (Metcalfe and Chalk, 1950; Dilcher, 1974; Ellis, 1979; Stace, 1980; Inamdar et al., 1986; Stace, 1989) have illustrated the use of leaf infrastructure for making taxonomic deductions. Epidermal and stomatal characters are widely employed as taxonomic evidence in several taxa (Delgen, 1980; Stace, 1980; Inamdar and Patel, 1986; Stace, 1989; Olowokudejo, 1990; Inamdar et al., 1991; Ogundipe and Adegbite, 1991; Olowokudejo, 1993; Sasikala and Narayanan, 1998). These characteristics, which probably are taxonomically valuable, have not yet been investigated in *Solidago* taxa.

In this study we (1) describe the micromorphological traits of the epidermis, trichomes and stomata of *Solidago* taxa occurring in Poland, (2) determine traits of the leaf epidermis and mesophyll that are taxonomically significant in taxa of the genus *Solidago*, and (3) create a key to separate taxa of the genus *Solidago* on the basis of micromorphological characteristics.

MATERIAL AND METHODS

Plant material was collected from natural populations of *Solidago* taxa growing in southwestern Poland. Ten individuals were examined per taxon from each of ten sites, except for *S. graminifolia*, for which only five sites were analyzed because of its rare occurrence in Lower Silesia. Often several taxa were growing at the same site, so the 45 populations analyzed originated from 30 localities.

Leaves from the middle part of the stem of mature living and herbarium plants (flowering or fruiting) were used for micromorphological observations. All measurements involved 100 replicates for each 10 individuals of the respective taxon (1000 measurements per taxon).

LIGHT MICROSCOPY OF EPIDERMAL SURFACE

Fragments from the middle part of herbarium leaves were used. Epidermal peelings were removed, cleaned in 7% sodium hydroxide and stained with aqueous ruthenium red. Slides thus prepared were used to observe stomatal types (type of stomata described following Stace, 1989), features of epidermal cells, stomata distribution, type of leaf (following Stace, 1989), length of stomatal guard cells and stomatal density (number of stomata per 1 mm^2 of epidermis).

The stomatal index (SI) was calculated as follows:

SI = [number of stomata/(number of stomata + number of epidermal cells)] × 100.

The stomatal index, unlike stomatal density, is independent of epidermal cell size.

The stomatal ratio (SR) was helpful in defining the type of leaf. It is the ratio of the number of stomata on the abaxial epidermis to the number of stomata on the adaxial epidermis. If SR>1 the leaves are classified as amphistomatic, if 0.1<SR<1 as hypoamphistomatic, and if SR<0.1 as hypostomatic.

TRANSVERSE SECTION OF LEAVES

Living samples fixed in 50% FAA and preserved in paraffin were used. Transverse sections were made with a microtome, double-stained with safranin and permanent green, and mounted in euparal. Slides thus made were used to describe transverse leaf sections, measure leaf epidermal thickness, and derive the epidermal thickness index (ETI), calculated as the ratio of abaxial epidermis thickness to adaxial epidermis thickness.

SCANNING ELECTRON MICROSCOPY

Five herbarium leaves of individual taxa were examined for the following: abaxial and adaxial epidermis surface, marginal part of leaf, cells over the main leaf vein, the presence and features of glandular hairs, and sculpture of wax. Completely dried samples were coated with pure gold, and the epidermis was observed and photographed by SEM. The nomenclature of stomata and wax characteristics follows Dilcher (1974) and Barthlott et al. (1998). Micrographs of the epidermal surface of *Solidago graminifolia* are not presented due to their poor quality.

STATISTICAL METHODS

The Kołmogorov-Smirnov test was used to test the normality of the distributions of quantitatively

TABLE 1. Average values and standard deviation (SD) of traits of adaxial (AD) and abaxial (AB) leaf epidermis of *Solidago* taxa

Trait	Taxon	*S. canadensis*	*S. altissima*	*S. gigantea*	*S. graminifolia*	*S. virgaurea*
Length of stomatal guard cells (µm)	AD	–	–	20.30 (2.59)	27.29 (1.89)	30.90 (2.21)
	AB	20.54 (3.28)	21.93 (2.75)	26.73 (2.95)	28.84 (2.72)	29.17 (4.77)
Stomatal density (N/mm²)	AD	0.50 (3.96)	5.63 (13.53)	18.39 (20.26)	190.29 (32.99)	13.24 (18.54)
	AB	299.68 (64.17)	301.87 (74.89)	212.71 (43.87)	125.76 (30.84)	96.58 (20.68)
SI	AD	0.10 (0.36)	0.87 (1.17)	0.93 (1.78)	10.66 (2.06)	0.78 (0.89)
	AB	12.98 (2.37)	11.93 (2.50)	13.06 (3.86)	9.32 (2.98)	7.61 (2.16)
SR		0.002	0.019	0.086	1.513	0.137
Leaf thickness (µm)		177.10 (12.44)	207.83 (12.94)	308.26 (10.71)	262.32 (19.45)	192.10 (31.12)
Leaf epidermis thickness (µm)	AD	19.56 (3.07)	21.61 (2.84)	31.40 (4.21)	18.31 (3.07)	22.06 (3.98)
	AB	16.15 (2.62)	15.58 (2.62)	23.65 (4.78)	20.13 (3.87)	17.06 (2.73)
ETI		1.2	1.4	1.3	0.9	1.3

SI – stomatal index; SR – stomatal ratio; ETI – epidermal thickness index.

expressed features. The significance of differences between taxa was tested by ANOVA with the LSD post hoc test. Pearson correlation coefficients were calculated to examine the relationships between individual features. Discriminant analysis was used to determine the taxonomic value of quantitative features of the epidermis.

RESULTS

LIGHT MICROSCOPY OF EPIDERMAL SURFACE

Anomotetracytic stomata were the type most frequent in *Solidago* taxa; they occurred in the epidermis of all investigated taxa. The anisocytic type occurred in the epidermis of *S. canadensis*, *S. gigantea* and *S. virgaurea*, the anomocytic type was seen in *S. altissima* and *S. graminifolia*, and the hemiparacytic type in *S. canadensis*.

The shape of the epidermal cell walls was straight in the adaxial epidermis of *S. canadensis* and in both epidermises of *S. gigantea* leaves, and V-sinous in the abaxial epidermis of *S. canadensis* and in both epidermises of *S. altissima* and *S. virgaurea* leaves. On the other hand, in both the abaxial and adaxial epidermises of *S. graminifolia* leaves the epidermal cell walls were slightly curved.

The stomatal guard cells were longest in *S. virgaurea* and shortest in *S. gigantea* leaves (Tab. 1). Stomatal guard cell length differed significantly between taxa. Because only a few stomata were present on the adaxial epidermis of *Solidago canadensis* and *S. altissima*, it was not possible to describe them in those taxa.

The number of stomata per 1 mm^2 of leaf (stomatal density) was highest in the abaxial epidermis of *S. altissima* and *S. canadensis* leaves (Tab. 1). The number of stomata per 1 mm^2 was lowest in the adaxial epidermis of those same two taxa. Stomatal density on the adaxial and abaxial epidermis differed significantly between each individual taxon except for *Solidago canadensis* and *Solidago altissima*. The stomatal index (SI) of the abaxial epidermis did not differ significantly between *Solidago canadensis*, *S. gigantea* and *S. altissima*, but was significantly lower in *S. graminifolia* and *S. virgaurea*. The SI of the adaxial epidermis was significantly higher in *Solidago graminifolia* leaves, differentiating it from the other species.

TRANSVERSE LEAF SECTIONS

The epidermis of all taxa was a single layer of cells. The mesophyll structure of the European native *S. virgaurea* differed from that of the introduced

taxa. The *Solidago* taxa of American origin had bifacial leaf structure; the palisade cells occurred in two layers: upper (near adaxial epidermis), composed of two rows, and lower, with one row of palisade cells. Spongy cells formed a clearly differentiated thin layer between the palisade layers (Fig. 1a,b,c,e). The *S. virgaurea* leaves were monofacial; the palisade cells occurred in two rows in the upper part of the leaf blade, while the spongy cells were located in the lower part (Fig. 1f).

Secretion (resin) canals were present in the leaves of all observed taxa except *S. canadensis*. They were often situated above the vascular bundles (e.g., *S. gigantea*, Fig. 1d). The outer stomatal ledge was thickened on both sides of the leaf in all observed taxa (Fig. 1a,b,e,f).

Leaf thickness as well as leaf epidermis thickness differed significantly between all studied taxa (Tab. 1). The adaxial leaf epidermis was thicker than the abaxial epidermis (ETI>1) in all majority investigated taxa except *Solidago graminifolia* (ETI=0.9). Adaxial and abaxial leaf epidermis thickness correlated positively in all investigated taxa, but there were no correlations between epidermis thickness and leaf thickness.

SCANNING ELECTRON MICROSCOPY

The general appearance of the stomatal complex, type of cuticular ornamentation, trichome features and epicuticular secretions (waxes) are presented in Figure 2 for the abaxial and Figure 3 for the adaxial epidermis. Striped cuticular ornamentation was present on the abaxial surface of the epidermis in all described taxa (Fig. 2b,d,f,g,h). The stripes were fainter on the adaxial epidermal surface (Fig. 3b,d). In *S. virgaurea* and *S. gigantea*, the adaxial epidermis was smooth, and only sparse stripes were present on the subsidiary stomata cells (Fig. 3f,h). Wax was present on the abaxial side of leaf in the form of fine flakes (*S. canadensis*, *S. gigantea*, Fig. 2a,b,e,f) or small particles (*S. altissima*, *S. virgaurea*, Fig. 2c,d,g,h). On the adaxial epidermis, wax was present in the form of fine particles (Fig. 3 a–f) or absent in the case of *S. virgaurea* (Fig. 3g,h). Trichomes were found in all investigated taxa. They varied in form, size, distribution and abundance. Two types of multicellular hairs were observed: short flabelliform hairs of 3 cells, length 100–150 μm (Figs. 2a,c,g; 3a,c,g); and long hairs of 5 or more cells, length 250–500 μm, occurring on the leaf blade (Figs. 2c, 3c) or leaf margins (Fig. 2e). In *S. canadensis*, short hairs occurred very sparsely on both sides of the leaf (Figs. 2a, 3a) and a few long hairs were observed on the main veins on the adaxial side of leaf and on the leaf margins. Hairs of both types were found on the abaxial and adaxial surfaces of the epidermis in *S. altissima*, where the long hairs were found mainly on the veins and leaf margins. The hairs on the adaxial epidermis were sparser than on the abaxial surface. In *S. gigantea* only a few small hairs were found on the abaxial leaf blade, and long hairs occurred on the leaf margins (Fig. 2e). On *S. virgaurea* and *S. graminifolia* leaves, the small flabelliform hairs were observed on the adaxial and abaxial epidermis near the main veins (Figs. 2g, 3g), and leaf margins were covered with long hairs. Few glandular hairs were observed in all taxa.

DISCRIMINATORY ANALYSIS

The three axes of discriminant analysis explained 99% of all the variation described by five variables (Fig. 4). Axis 1 clearly separated *S. graminifolia* from the other taxa. It was related to "stomatal index of the adaxial epidermis" and described 81% of the variation. Axis 2 separated *S. gigantea* from the other taxa, and was related to "leaf thickness". Axis 3 emphasized differences between *S. virgaurea* and *S. canadensis* s.l., and was related to "stomata number on the adaxial leaf epidermis" and "stomatal index of the adaxial epidermis".

DISCUSSION

Here we showed that micromorphological traits of leaves and the leaf epidermis are taxonomically useful for discriminating *Solidago* taxa. They clearly distinguished the five we examined. The shape of anticlinal walls of epidermal cells has been used successfully in taxonomical studies of the Asteraceae family in the genera *Vernonia* (Isawumi, 1994) and *Aspilia* (Ogudipe and Adegbite, 1991). In this study, two *Solidago* taxa difficult to distinguish, *S. canadensis* and *S. altissima*, were differentiated by the shape of the epidermal anticlinal cell walls.

Other important taxonomical traits were the number of stomata in the abaxial and adaxial epidermis. This was associated with the type of leaf. In taxa with hypostomatic or hypoamphistomatic leaves (*S. canadensis*, *S. altissima*, *S. gigantea*, *S. virgaurea*), stomata were more numerous on the adaxial than abaxial surface, whereas in *S. graminifolia*, a taxon with amphistomatic leaves, it was the reverse. These differences were reflected in the discriminatory analysis: *S. graminifolia* was separated from the other taxa along Axis 1 (Fig. 4). Generally, the abaxial epidermis differed between taxa more than the adaxial leaf epidermis did, and thus was more useful for distinguishing them.

SEM observations showed that the presence of different types of trichomes on the leaf epidermis is a useful character for distinguishing *Solidago canadensis*, *S. altissima* and *S. gigantea* leaves. Other work has shown the taxonomical value of tri-

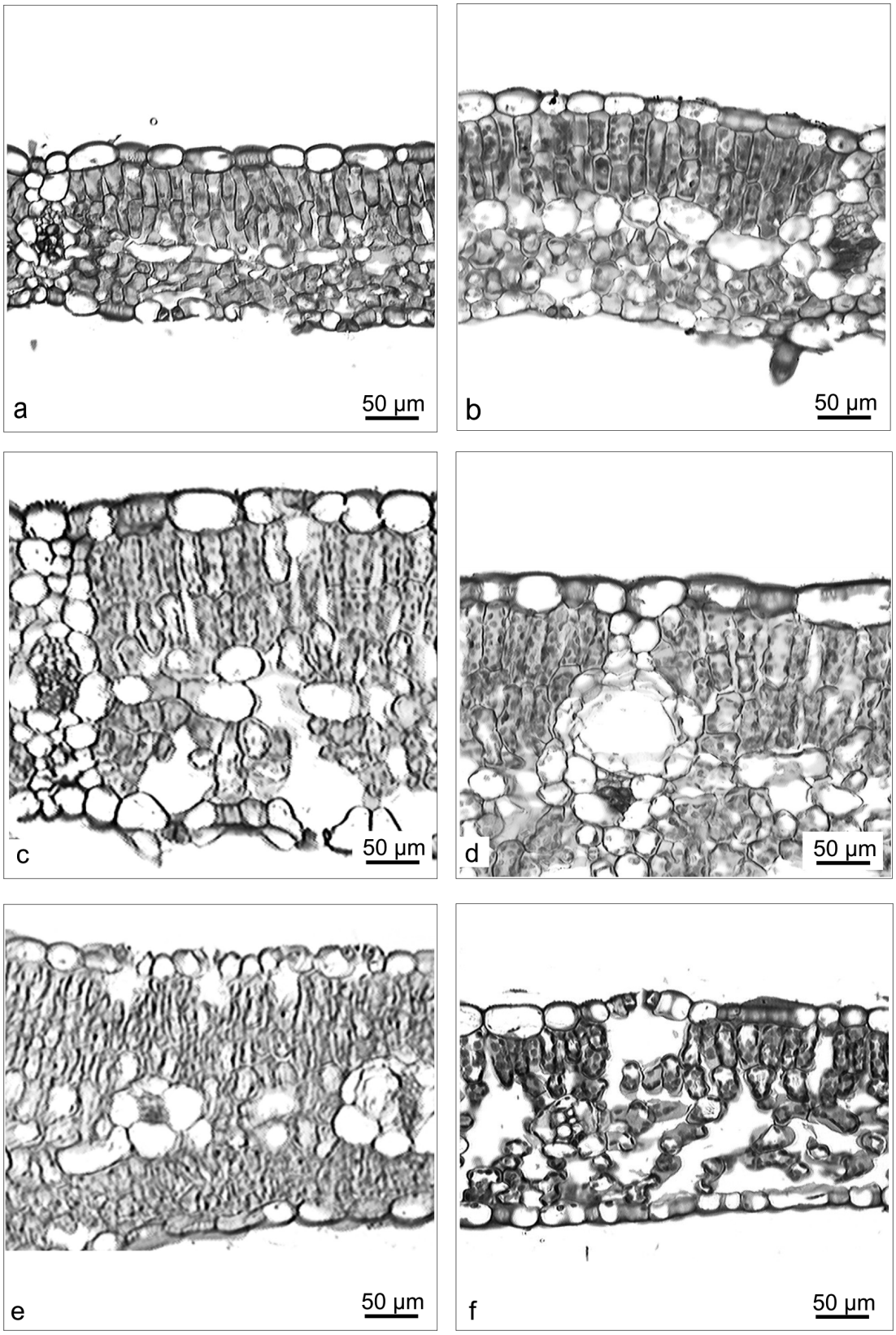

Fig. 1. Transverse leaf sections of *Solidago* taxa. (**a**) *S. canadensis*, (**b**) *S. altissima*, (**c, d**) *S. gigantea*, (**e**) *S. graminifolia*, (**f**) *S. virgaurea*.

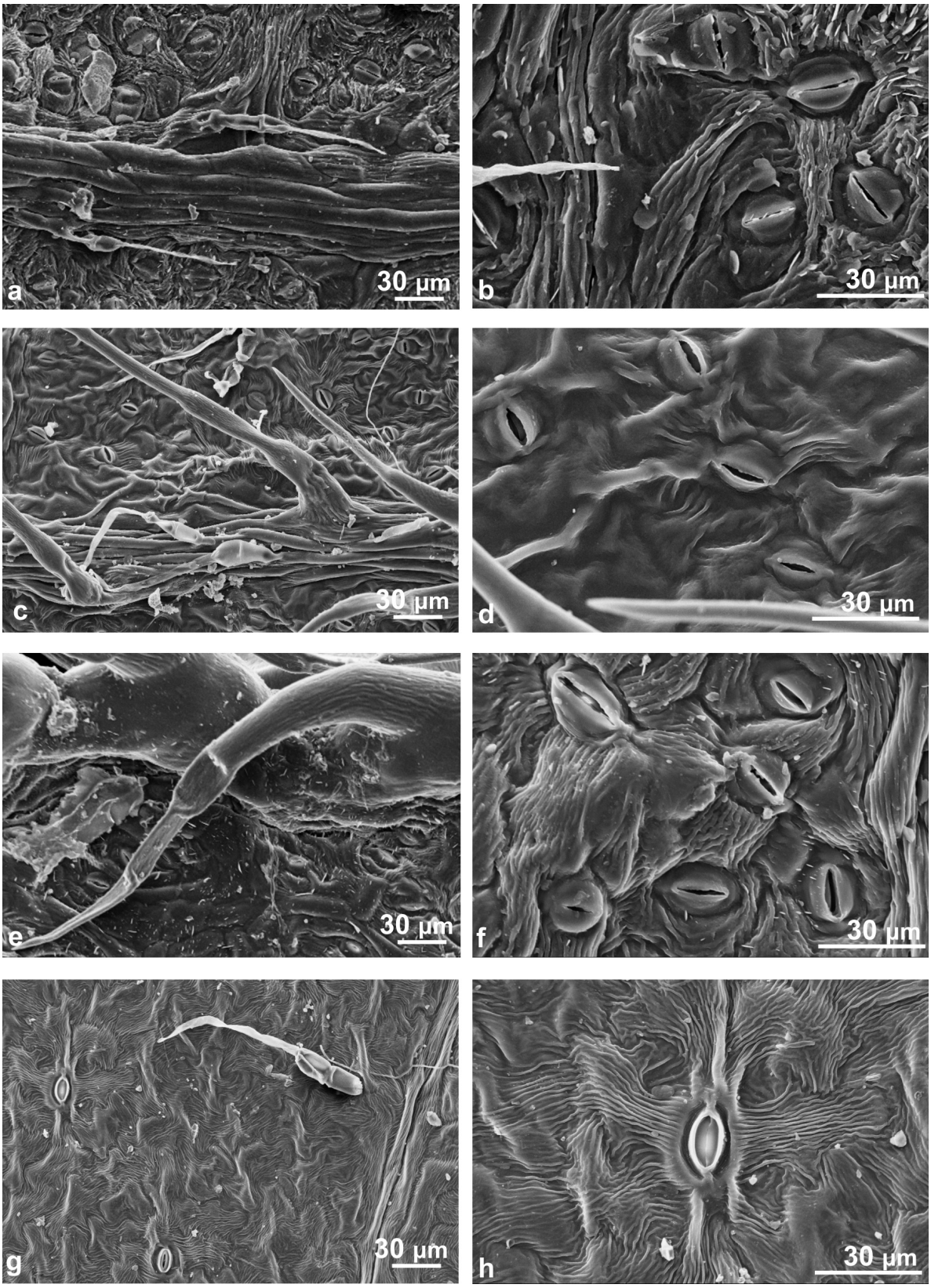

Fig. 2. SEM of abaxial epidermal surface of leaf of *Solidago* taxa. (**a, b**) *S. canadensis*, (**c, d**) *S. altissima*, (**e, f**) *S. gigantea*, (**g, h**) *S. virgaurea*. Right and left columns differ in magnification.

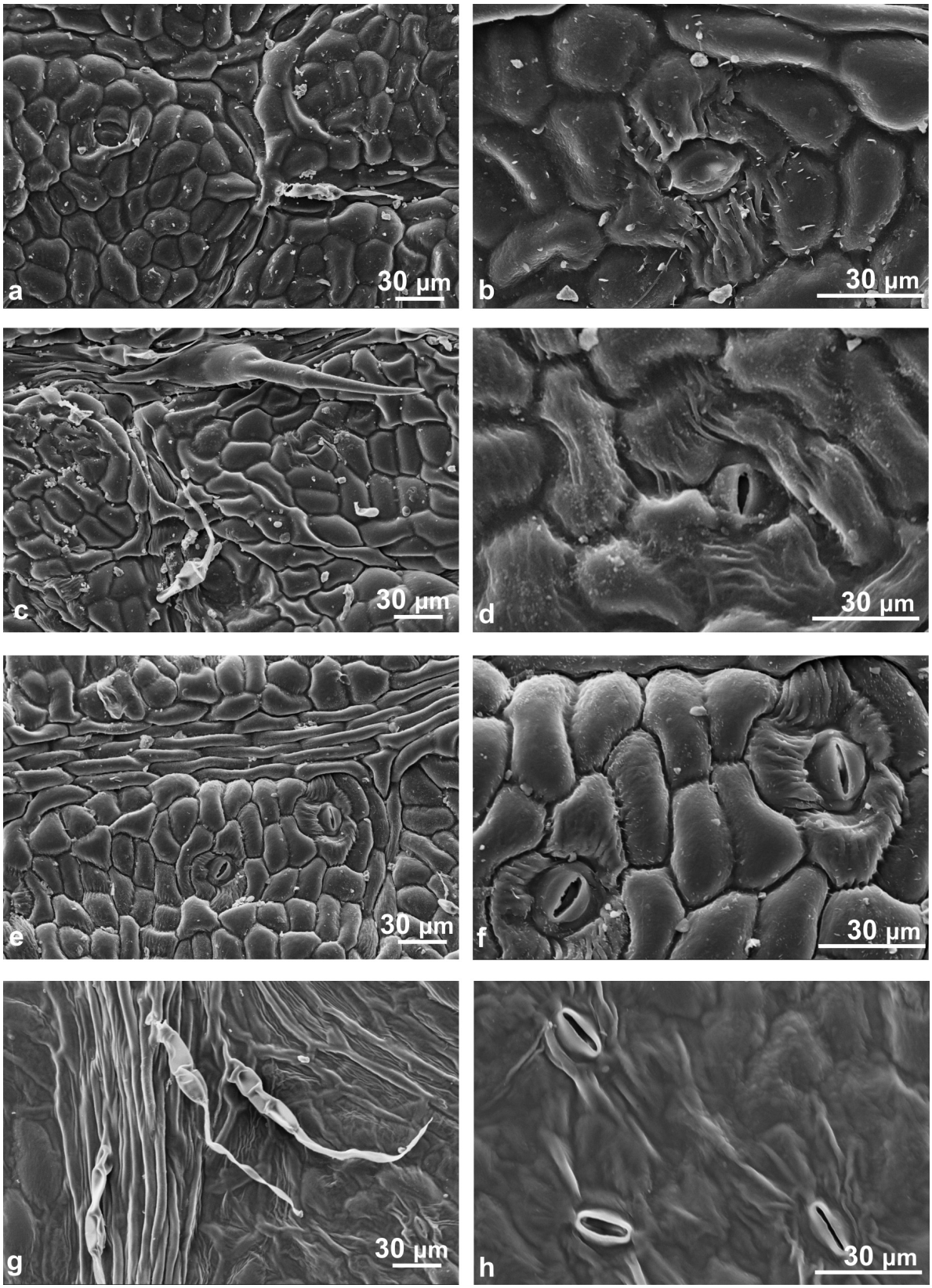

Fig. 3. SEM of adaxial epidermal surface of the leaf of *Solidago* taxa. (**a, b**) *S. canadensis*, (**c, d**) *S. altissima*, (**e, f**) *S. gigantea*, (**g, h**) *S. virgaurea*. Right and left columns differ in magnification.

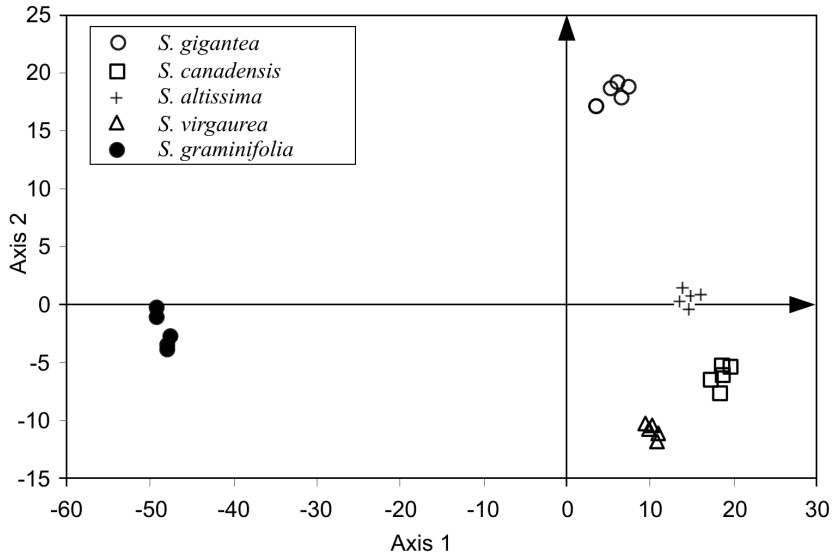

Fig. 4. Results of discriminant analysis of taxa of the genus *Solidago*.

chome characteristics and trichome distribution in genera of the Asteraceae family (Sasikaka and Narayanan, 1998) and other families (Andrzejewska-Golec and Świętosławski, 1992; Isawumi, 1994; Länger et al., 1995).

Examination of transverse leaf sections enabled us to distinguish two groups by mesophyll structure: the native European taxon *S. virgaurea* with monofacial leaves, and the introduced taxa with bifacial leaves. Generally, variability of leaf thickness and epidermis thickness was lower within than between taxa. This was especially useful in distinguishing *S. gigantea* from the other taxa along Axis 2 in discriminatory analysis.

We showed that the goldenrods occuring in Europe that belong to the *S. canadensis* complex (var. *canadensis* and var. *scabra*) can be clearly separated into two species: *S. canadensis* with straight adaxial epidermal cell walls and small, flabelliform trichomes on both sides of the leaves and with a few long hairs on the vein of the abaxial leaf epidermis; and *S. altissima* with sinuous adaxial epidermal cell walls and with both sorts of trichomes, small flabelliform and large multicellular, found on both sides of the leaves. *S. gigantea* occurring in Lower Silesia belongs to ssp. *gigantea*, differentiated by the nearly complete lack of hairs on the leaf blades.

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APPENDIX. Key to epidermal features of the studied *Solidago* taxa:

1.	Amphistomatic leaves	*Solidago graminifolia* (L.) Elliott.
1*.	Hypostomatic or hypoamphistomatic leaves	2.
2.	Trichomes on abaxial epidermis absent (except leaf margins). Leaf thickness >300 μm.	*S. gigantea* Aiton
2*.	Trichomes on adaxial epidermis present. Leaf thickness <300 μm	3.
3.	Length of stomatal guard cells on adaxial epidermis ~20 μm. Chloroplasts absent in abaxial epidermal cells	4.
3*.	Length of stomatal guard cells on adaxial and abaxial epidermis ~30 μm. Chloroplasts present in abaxial epidermal cells. Adaxial epidermal cell walls sinuous. Only small flabelliform trichomes present on abaxial leaf epidermis	*S. virgaurea* L.
4.	Adaxial epidermal cell walls straight. Only small flabelliform trichomes present on abaxial leaf epidermis	*S. canadensis* L.
4*.	Adaxial epidermal cell walls sinuous. Both types of trichomes (small flabelliform, large multicellular) present on abaxial leaf epidermis	*S. altissima* L.