

Taxonomic significance of pollen morphology in *Succisa* and *Succisella*

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Abstract. Pollen morphology of representatives of the genera *Succisa* and *Succisella* in the flora of Ukraine was studied using light and scanning electron microscopy. Pollen grains in both taxa were tricolpate, prolate, rarely oblate-spheroidal or spheroidal; large-sized. Their outline in polar view was subcircular, rarely trilobate, in equatorial view elliptical or rarely circular. Colpi short, of variable width, margins irregular with distinct, narrow margo, and blunt or acute ends. Exine sculpture was echinate-microechinate. The revealed characteristics of pollen grains are taxonomically significant at the generic and specific levels, and they can be used in pollen analysis. Palynomorphological data are consistent with the results of recent molecular phylogenetic studies. Data on pollen morphology also confirm taxonomic circumscription of Succiseae V. Mayer & Ehrend. Pollen grains in Succiseae are characterized by a tricolpate aperture type, which was probably ancestral in Dipsacaceae s. str.

Key words: pollen grains, morphology, sculpture, diagnostic characters, taxonomy, Ukraine

1. Introduction

Earlier, *Succisa* Haller and *Succisella* G. Beck were usually placed in the family Dipsacaceae Juss. (Bobrov 1957; Kotov 1961; Takhtajan 1987, 1997, 2009). According to the latest versions of the Angiosperm Phylogeny Group (APG III 2009; APG IV 2016) system, they are included in an extended family Caprifoliaceae s. l. (also with Diervillaceae Pyck, Morinaceae Raf., Valerianaceae Batsch, etc.). Molecular phylogenetic studies Dipsacaceae in the strict sense, and of some related families, were conducted by several groups of researchers (Donoghue *et al.* 1992; Caputo & Cozzolino 1994; Bell *et al.* 2001; Bremer *et al.* 2001; Zhang *et al.* 2003; Caputo *et al.* 2004; Bell & Donoghue 2005; Avino *et al.* 2009; Carlson *et al.* 2009, etc.). Earlier researchers subdivided Dipsacaceae mainly into three tribes: Knautieae Janchen, Dipsaceae Rehb., and Scabioseae DC. *Succisa* and *Succisella* were usually assigned to Scabioseae, together with *Scabiosa* L. (Bobrov 1957; Kotov 1961, etc.). According to results of molecular phylogenetic studies, *Succisa* and *Succisella* are sister taxa in the ITS and combined analyses, and only in cpDNA analyses, *Succisella* was resolved as

a weakly supported sister group to *Pseudoscabiosa* Devesa (Avino *et al.* 2009; Carlson *et al.* 2009; Jacobs *et al.* 2011; Mayer 2016). According to new morphological and molecular phylogenetic studies, *Succisa* and *Succisella* are included in Succiseae V. Mayer & Ehrend., subfam. Dipsacoideae (Mayer & Ehrendorfer 2013; Mayer 2016).

The genus *Succisa*, in its current narrow circumscription, includes three species: two with small relict ranges (*S. pinnatifida* Longe in the Iberian Peninsula and *S. trichotocephala* Baksay endemic to W Africa) and one rather widespread species, *S. pratensis*, naturally occurring in Europe, W Siberia, and N Africa (Bobrov 1957; Mabberley 1997; Mayer 2016). The genus *Succisella* contains five currently accepted species. Three of them (*S. carvalhoana* (Mariz) Baksay, *S. microcephala* (Willk.) G. Beck, and *S. andreae-molinae* Pajarón & Escudero) are endemic to the Iberian Peninsula (Amich *et al.* 2004). *Succisella petteri* (Kerner & Murb.) G. Beck is endemic to the Dinara Planina (Bosnia and Croatia) and *S. inflexa* (Kluk) G. Beck is distributed in southern and eastern parts of Europe, from Italy to Baltic states in the north and the Caucasus in the south. In other regions, *S. inflexa* is considered to be

alien and naturalized (Amich *et al.* 2004; Mabberley 1997; Mayer 2016). Two species, *Succisa pratensis* and *Succisella inflexa*, are native members the flora of Ukraine and adjacent countries (Bobrov 1957; Kotov 1961; Mosyakin & Fedoronchuk 1999).

Pollen grains of *Succisa pratensis* were earlier described using light microscopy (Erdtman 1952; Vinokurova 1959; Moore & Webb 1983). The PalDat electronic database contains information on the pollen morphology of *S. pratensis* under scanning electron microscopy (Halbritter & Svojtka 2016). Pollen grains of *S. pratensis* were also studied using both light and scanning electron microscopy (Clarke & Jones 1981). The morphological peculiarities of pollen grains of Iberian taxa *Succisella microcephala*, *S. andreae-molinae*, and *S. carvalhoana* were also investigated using both light and scanning electron microscopy (Amich *et al.* 2004).

Our main objective was to perform a more detailed palynomorphological investigation of Ukrainian species *Succisa pratensis* and *Succisella inflexa*, to provide assessment of the taxonomic significance of pollen morphology of *Succisa* and *Succisella* based on both published and original data, and to explore possibilities of its uses in taxonomy.

2. Materials and methods

Pollen grains of *Succisa* and *Succisella* were sampled in the National Herbarium of Ukraine (KW – herbarium of the M. G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv, Ukraine). Data on the studied specimens are cited exactly according to the label information, in English translation.

The methods used in the present study are essentially the same as those we used earlier (see Mosyakin & Tsymbalyuk 2015a, 2015b, 2017). Pollen morphology was studied using both light microscopy and scanning electron microscopy. For light microscopy studies (LM,

Biolar, $\times 700$), the pollen was acetolyzed following Erdtman (1952). For size determinations, 20 measurements were taken along the polar and equatorial axes for each species. Permanent preparations of pollen grains of *Succisa* and *Succisella* are deposited in the Palynothecca at the National Herbarium of Ukraine (KW). For scanning electron microscopy (SEM, JSM-6060LA), pollen grains were treated with 96%-ethanol, then the samples were sputter-coated with gold and investigated at the Center of Electron Microscopy of the M.G. Kholodny Institute of Botany. The micrographs were minimally edited with Adobe Photoshop 6.0 to enhance images.

Terminology used in descriptions of pollen grains mainly follows the glossary by Punt *et al.* (2007), with some necessary minor adjustments (Tsymbalyuk *et al.* 2018, 2019). Original and published data on quantitative pollen characters representatives of *Succiseae* are summarized in Table 1.

3. Results

3.1. General description of pollen grains of Succiseae

Pollen grains in monads, radially symmetrical, isopolar, tricolpate, prolate, rarely spheroidal or oblate-spheroidal, in polar view subcircular, rarely trilobate, in equatorial view elliptical, rarely circular. Polar axis P=66.5-98.4 μm , equatorial axis E=65.2-98.4 μm . Colpi short, of variable width, 0.7-5.3 μm wide, 26.6-37.2 μm long, margin irregular with distinct, narrow margo, 0.7-2.0 μm wide, with blunt or acute ends, colpus membrane smooth or granulate, often ruptured during acetolysis. Exine 6.6-10.6 μm thick, unevenly thickened, rarely on apocolpia thicker. Columellae distinct, short, occasionally longer in apocolpium. Exine sculpture echinate-microechinate. Echinae conical with straight sides and acute apex, 0.9-1.5 μm high, 1.0-1.3 μm wide at base. Microechinae small, more numerous than echinae, 0.2-0.3 μm high, 0.3-0.4 μm wide at base. Exine surface

Table 1. Morphometric comparison of pollen grains

Taxon	Polar axis, P (μm)	Equatorial axis, E (μm)	Colpi length (μm)	Colpi width (μm)	Margo (μm)	Exine (μm)
<i>Succisa pratensis</i> (Clarke & Jones 1981)	68(77)-84(95)	69(75)-79(98)	26-32	3-7	1.5-2.5	8-11
<i>Succisa pratensis</i> (original data)	73.1-98.4	66.5-98.4	27.9-37.2	2.0-5.3	1.3-2.0	6.6-10.6
<i>Succisella inflexa</i> (original data)	66.5-79.8	65.2-79.8	26.6-29.3	0.7-4.0	0.7-1.6	6.6-9.3
<i>Succisella carvalhoana</i> (Amich <i>et al.</i> 2004)	63.60 \pm 3.52	65.71 \pm 2.71	ld	ld	ld	ld
<i>Succisella microcephala</i> (Amich <i>et al.</i> 2004)	64.83 \pm 2.98	66.93 \pm 2.65	ld	ld	ld	ld
<i>Succisella andreae-molinae</i> (Amich <i>et al.</i> 2004)	64.11 \pm 3.10	66.27 \pm 2.89	ld	ld	ld	ld

Explanation: ld – lack of data

between echinae and microechinae rugulate or rugulate-perforate. Colpus membrane with irregular granules and short echinae.

3.2. Descriptions of pollen grains

Genus *Succisa* Haller

Succisa pratensis Moench. (Fig. 1a-c; Fig. 2a-d)

L M. Pollen grains tricolpate, prolate, rarely spheroidal, often with slightly undulating margin, in polar view subcircular, rarely trilobate, in equatorial view elliptical, rarely circular. $P=73.1-98.4\ \mu\text{m}$, $E=66.5-98.4\ \mu\text{m}$. Colpi short, $2.0-5.3\ \mu\text{m}$ wide, $27.9-37.2\ \mu\text{m}$ long, margin irregular with distinct, narrow margo, $1.3-2.0\ \mu\text{m}$ wide, with blunt or acute ends, colpus membrane smooth or granulate, often ruptured during acetolysis. Exine $6.6-10.6\ \mu\text{m}$ thick, unevenly thickened, rarely on apocolpia thicker. Tectum 3-4 times thinner than infratectum. Columellae distinct, short, of variable thickness, often

fused into groups, branched above, arranged more or less regularly, rarely on apocolpia longer. Endexine unevenly thickened. Echinae indistinct on the surface, distinct on the edges, sparsely distributed. Columellae distinct, circular, elongated or angular, at the base in LO analysis, densely distributed.

S E M. Exine sculpture echinate-microechinate. Echinae conical with straight sides and acute apex, $1.3-1.5\ \mu\text{m}$ high, $1.2-1.3\ \mu\text{m}$ wide at base. Microechinae small, more numerous than echinae, $0.2-0.3\ \mu\text{m}$ high, $0.3-0.4\ \mu\text{m}$ wide at base. Exine surface between echinae and microechinae rugulate-perforate. Colpus membrane with irregular granules and short echinae.

Specimens investigated: 1. Ukraine, Zhytomyr Region. Volodarsk-Volynsky District. St. Turchanka, pasture in the birch-alder forest. 30.07.1949. A. Zapyatova (KW). 2. Ukraine, near Vinnitsa [Vinnytsya], wet meadow north of the railway in the direction of

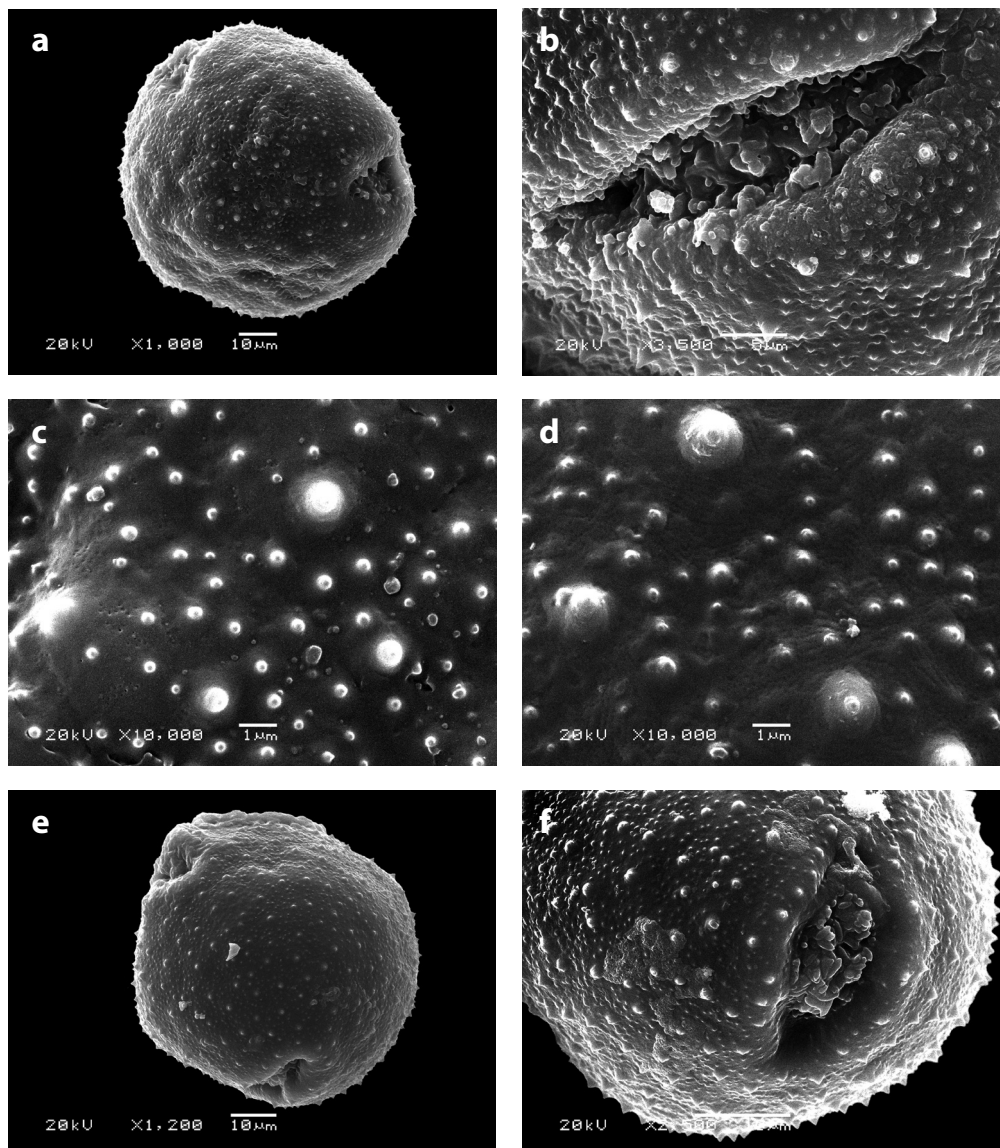


Fig. 1. Pollen grains of *Succisa pratensis* and *Succisella inflexa* (SEM)

Explanations: a-c – *S. pratensis*, d-f – *S. inflexa*, a, e – polar view, b, f – colpi membranes with irregular granules and short echinae, c, d – exine sculpture

Sosenke (Kalinovka). 24.VIII 1927. K.S. Yankovsky (KW). 3. Ukraine, Chernihiv Region, Lyubech District, Lyubech village, floodplain of the Dnipro [Dnieper] River. 28.VII 1952. D. Afanasyev (KW).

Genus *Succisella* G. Beck
Succisella inflexa (Kluk) G. Beck
 (Fig. 1d-f; Fig. 2e-h)

L.M. Pollen grains tricolpate, prolate, rarely oblate-spheroidal or spheroidal, in polar view subcircular, rarely trilobate, in equatorial view elliptical, rarely circular. P=66.5-79.8 μm , E=65.2-79.8 μm . Colpi short, 0.7-4.0 μm wide, 26.6-29.3 μm long, margin irregular with distinct, narrow margo, 0.7-1.6 μm wide, with acute or sometimes blunt ends, colpus membrane smooth and granulate, often ruptured during acetolysis. Exine 6.6-9.3 μm thick, unevenly thickened. Tectum 4 times thinner than infratectum. Columellae distinct, short, arranged more or less regularly. Endexine unevenly thickened. Echinae indistinct on the surface and at the edges, very sparsely distributed. Columellae distinct, circular, elongated and angular at the base in LO analysis, densely distributed.

S.E.M. Exine sculpture echinate-microechinate. Echinae conical with straight sides and acute apex, 0.9-1.1 μm high, 1.0-1.2 μm wide at base. Microechinae small, more numerous than echinae, 0.2 μm high, 0.3 μm wide at base. Exine surface between echinae and microechinae rugulate. Colpus membrane with irregular granules and short echinae.

Specimens investigated: 1. Ukraine, Volyn' Region, Kovel District, v.[village] Ugli, floodplain of the Stohod [Stokhid] River, peat meadows. 3. VIII 2007. T.L. Andriyenko. 083618 (KW). 2. Ukraine, Lviv Region, Kamenka-Buz'ka District, northwestern outskirts of Tishitsa village, right bank of the Western Bug River, wet meadow. 20.07.1999. O.T. Kuzynarin. 056940 (KW). 3. Belarus, Kamenyuki village, Kamenetsk District, Brest Region. July 26, 1972. O. Dubovik (KW).

4. Discussion

In general, our data are in good agreement with the results of previous studies (Clarke & Jones 1981; Amich *et al.* 2004). In particular, Amich *et al.* (2004) provided the following information about pollen grains of *Succisella*: "The pollen of the Iberian Peninsula species of *Succisella* (...) is tricolpate (...). No differences were seen between the studied taxa. (...) In all cases, the pollen is oblate-spheroid, almost spheroid, (Figs 13-15) with a weakly striated exine (Figs 19-21), covered in small, sparse spines, the largest of which are 0.8-1 mm in *S. microcephala* and *S. andreae-molinae*, and the smallest 0.2-0.3 mm in *S. carvalhoana* (Figs 16-18). These palynological characteristics reveal the primitive nature of the genus within the Dipsacaceae" (Amich *et al.* 2004, p. 355).

Pollen grains of *Succisella inflexa* are similar to those of the Iberian *Succisella* in their pollen type, size,

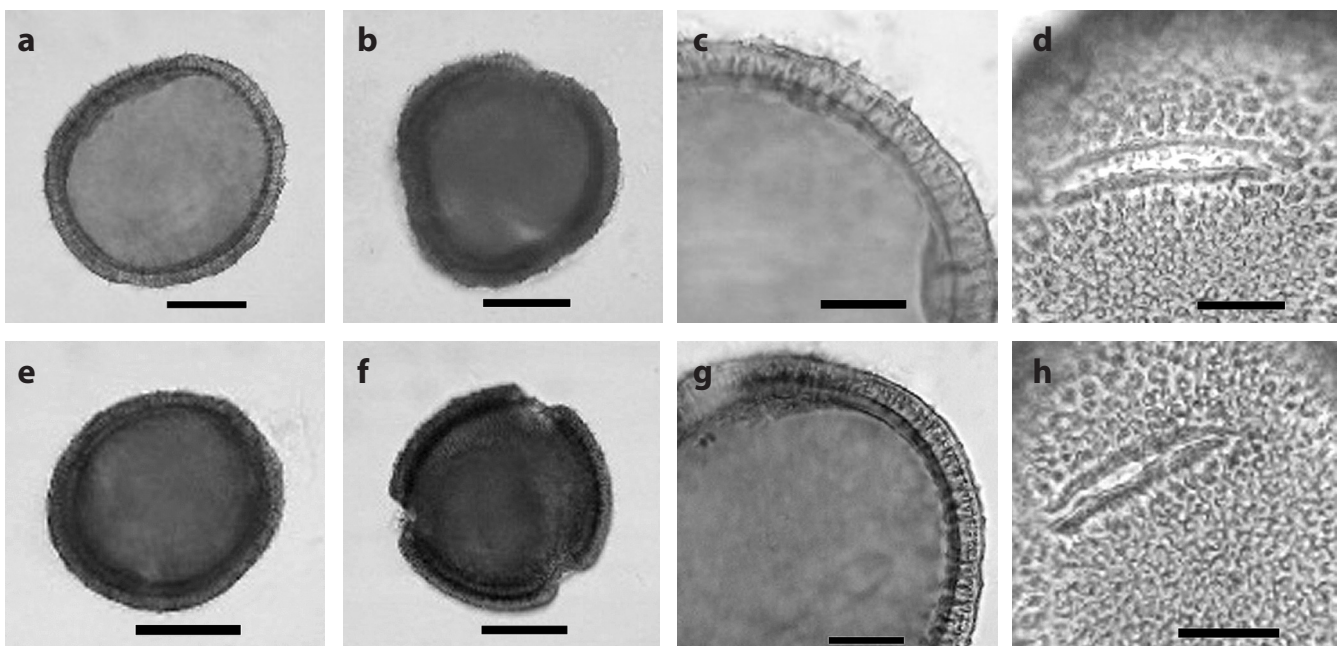


Fig. 2. Pollen grains of *Succisa pratensis* and *Succisella inflexa* (LM)

Explanations: a-d – *S. pratensis*, e-h – *S. inflexa*, a, e – equatorial view ($\times 400$), b, f – polar view ($\times 400$), c, g – exine ($\times 700$), d, h – colpi ($\times 700$); scale bars: a-h – 10 μm

and exine sculpture. Unfortunately, the illustrations and characters reported by Amich *et al.* (2004) are insufficient for a more detailed comparative analysis.

Analysis of our original palynomorphological data and literature records demonstrated that pollen grains of *Succisa* and *Succisella* representatives are characterized by the tricolpate type of apertures with echinate-microechinate sculpture (see also Clarke & Jones 1981; Amich *et al.* 2004; Mayer & Ehrendorfer 2013, and compare to original data reported here); however, they differ in their size, colpi structure, and exine structure and sculpture. Pollen grains of *Succisa* are larger in their size, with wider and longer colpi, wider margo, and thicker exine, as compared to pollen of *Succisella*. The exine sculpture in both taxa is echinate-microechinate, but in pollen grains of *Succisa* echinae are larger than those in *Succisella* (Clarke & Jones 1981; Amich *et al.* 2004, and original data). The species-specific features mentioned above are mainly visible under a light microscope (see LM descriptions above) and, therefore, LM can be used in performing pollen analysis.

Thus, available palynomorphological data are well consistent with molecular phylogenetic evidence (Avino *et al.* 2009; Carlson *et al.* 2009). Data on pollen morphology also confirm the taxonomic circumscription of Succiseae as outlined by Mayer (2016). Pollen grains in Succiseae are characterized by a tricolpate aperture type (see details above). In contrast, representatives of *Knautia* L., *Dipsacus* L., and *Cephalaria* Schrad. ex Roem. & Schult. usually have a triporate aperture type (Clarke & Jones 1981; Tsymbalyuk *et al.* 2018, 2019, and references therein). Palynological evidence, thus,

supports the phylogenetic hypothesis (Caputo *et al.* 2004; Carlson *et al.* 2009) that the 'Knautieae' group is more closely related to *Dipsacus* and *Cephalaria* than to *Succisa* and *Succisella*. The palynomorphological characters in Succiseae can be probably viewed as ancestral, or, at least, close to ancestral, or primary for those registered in other members of Dipsacaceae *sensu stricto*.

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