

Pollen morphology of Ukrainian species of the genus *Pedicularis* L. (Orobanchaceae Vent.)

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Abstract: Pollen grains of 10 species of *Pedicularis* occurring in Ukraine were investigated using light and scanning electron microscopy. Palynological data on 6 species are reported for the first time. General pollen morphology of the genus *Pedicularis* is presented. Three types of apertures (2-syncolpate, 3-colpate, and 3-syncolpate) and seven subtypes of sculpture (3-syncolpate pilate, 3-syncolpate microscabrate-tubeculate, 2-syncolpate microscabrate, 2-syncolpate microscabrate-tubeculate, 2-syncolpate microscabrate-tubeculate-perforate, 2-syncolpate microfoveolate, and 2-syncolpate microscabrate-perforate) are identified. The subgenus *Pedicularis* is heterogeneous in its types of apertures and sculpture of the surface, which indicates the need of further taxonomic revision of the group.

Key words: pollen morphology, taxonomy, *Pedicularis*, Orobanchaceae, Ukraine

1. Introduction

The genus *Pedicularis* L. (Orobanchaceae Vent., formerly placed in Scrophulariaceae Juss.), represented by hemiparasitic herbaceous plants, is one of the most taxonomically complicated groups of angiosperms. It includes about 600 (or up to 800, according to Wang *et al.* 2003) species distributed mainly in the extratropical zone of the Northern Hemisphere, from the Arctic to the Himalayas, with just a few species occurring in the Southern Hemisphere, in the Andes of South America (from Colombia to Ecuador) (Ivanina 1981; Wang *et al.* 2003; Fischer 2004).

Many researchers (Steven 1823; Maximowicz 1888; Limpricht 1924; Li 1948, 1949; Tsoong 1955, 1956; Vvedenskiy 1955; Ivanina & Popova 1998) contributed to taxonomy and developed different systems of *Pedicularis*. These systems were based, among others, on such characters as phyllotaxy and corolla morphology. Some systems or taxonomic infrageneric classifications were limited in their scope, covering only selected taxa belonging to specific taxonomic groups or occurring within certain geographical areas. Because of that, various versions of taxonomic schemes for the genus varied considerably. Some authors used informal categories, such as “grex”, “subgrex”, which are

not institutionalized by the International Code of Botanical Nomenclature (McNeill *et al.* 2006).

New methods of phylogenetic taxonomy have already challenged the circumscription and reliability of some previously recognized phylogenetic entities. Because of that, further investigations, especially those involving molecular phylogenetic and micromorphological methods and covering many taxa from all regions of the total range of the genus and belonging to various infrageneric groups, are highly desirable. Ree (2005) carried out molecular phylogenetic analysis of *Pedicularis*, but this investigation included at that stage only 2 species of those occurring in Ukraine. In the flora of Ukraine, *Pedicularis* is represented by 10 species belonging to 2 subgenera and 5 sections (Ivanina 1981; Ivanina & Popova 1998; Mosyakin & Fedoronchuk 1999).

Pollen morphology of some species of *Pedicularis* was studied by many authors. The aim of their investigations was mainly to reveal relationships between taxa, usually at high taxonomic levels, or to provide data for comparative pollen and spore analysis. Pollen grains of *P. sceptrum-carolinum* L., *P. oederi* Vahl. (Erdtman 1952), *P. sylvatica* L. (Moore & Webb 1983) and *P. labradorica* Wirsing (Aleshina 1978) were described using light microscopy. Belkina (1972) studied pollen

grains of 20 species of *Pedicularis* from Yakutia (Russian Federation) using light microscopy. She distinguished 3 types and 4 subtypes of pollen grains in these species. The criteria were the quantity and nature of colpi, presence or absence of pseudoleptoma, and size of the pollen grains. Inceoğlu (1982) studied pollen grains of 21 species of the family Scrophulariaceae s. l. in the flora of Turkey using light, scanning and transmission electron microscopy. In this study, the genus *Pedicularis* was represented by 2 species. Belyaeva (1986) studied pollen morphology of 36 species of *Pedicularis* occurring in Southern Siberia (Russian Federation). As a result, pollen grains were divided into 4 types: *Sceptrum*, *Sudeticae*, *Amoenae-Abrotanifoliae* and *Longiflorae*. These types are distinguished by the quantity and nature of colpi, and the size of pollen grains. Minkin & Eshbaugh (1989) studied pollen grains of 57 species of the families Scrophulariaceae s. l. and Orobanchaceae using light and scanning electron microscopy. The only one species of *Pedicularis* was studied (*P. canadensis*). Pollen grains of this species have atypical sculpture of the exine. This type of pollen grains occurs also in *Bellardia trixago* All., *Dasistoma macrophylla* (Nutt.) Raf., *Epifagus virginiana* (L.) W.P.C. Barton, *Melampyrum pratense* L., *Scoparia montevicensis* R.E.Fr., and *Sopubia trifida* Buch.-Ham. ex D. Don. Popova *et al.* (2005) studied pollen grains of 4 species of *Pedicularis* subgen. *Sceptrum* using light and scanning electron microscopy. Unfortunately, the author had not enough samples and therefore was unable to come to specific conclusions about possible relationships between taxa. The most important investigation of pollen grains of 32 Chinese species of *Pedicularis*, using both light and scanning electron microscopy, was carried out by Wang *et al.* (2003). The authors distinguished 3 aperture types of pollen grains and 7 subtypes of the surface sculpture. In 2009, Wang *et al.* studied pollen morphology in relation to floral and pollination syndromes in *Pedicularis*. That investigation included 23 species from North America, Japan, and China. The authors provided general descriptions of pollen grains of *Pedicularis* and segregated 2 pollen types. In this study, taxa occurring in Ukraine were represented by only 3 species (Wang *et al.* 2009).

Thus, published results of previous palynomorphological investigations reported little information concerning peculiarities of pollen grains of *Pedicularis* species of the Ukrainian flora. Of 10 species of *Pedicularis* currently known in Ukraine, brief data concerning pollen grains exist just for 4 species (*P. sceptrum-carolinum*, *P. oederi*, *P. verticillata* L., and *P. palustris* L.). Six species have never been studied palynologically.

Our main objective was to perform a palynomorphological investigation of the Ukrainian species of *Pedicularis*, to provide assessment of the taxonomic

significance of pollen morphology, and to explore possibilities and applicability of its uses in taxonomy.

2. Material and methods

Pollen from 10 species (16 samples) belonging to 3 subgenera and 5 sections of *Pedicularis* was sampled in the herbarium of the M. G. Kholodny Institute of Botany of the National Academy of Sciences of Ukraine (KW, National Herbarium of Ukraine). Pollen morphology was studied using light and scanning electron microscopy. The pollen was acetolysed following Erdtman (1952) for preparation for light microscopy (Biolar). For scanning electron microscopy (JSM-6060LA), pollen grains were treated with 96%-ethanol, then these samples were sputter coated with gold.

Terminology used in this article follows Punt *et al.* (1994), Kupriyanova & Aleshina (1972) and Tokarev (2002), with some necessary adjustments. Taxonomy of the genus *Pedicularis* is given following Ivanina (Ivanina 1981; Ivanina & Popova 1998).

3. Results

The pollen characters of all species examined are summarized based on observations from light microscopy (Table 1).

3.1. General pollen morphology in the genus *Pedicularis*

Pollen grains radially symmetrical, isopolar; spheroidal, oblate spheroidal or prolate in shape; small to medium-sized, polar axis length 11.9-39.9 µm, equatorial diameter 11.9-33.2 µm. Outline in polar view trilobate, slightly trilobate, bilobate, slightly bilobate, or circular. Outline in equatorial view elliptical or circular. Apertures tricolpate, trisyncolpate, or bisyncolpate. Colpi long, usually wide, margins indistinct or distinct, irregular; colpus membrane with scabrate or scabrate-tuberculate surface, or colpi narrow, smooth and sunken. Exine extremely thin, nearly homogeneous in thickness (0.3-2.4 µm).

Detailed studies of the surface sculpture under a scanning electron microscope (visible only at high magnifications ca. 20 000 x in SEM) enabled us to distinguish six subtypes: microscabrate, microscabrate-perforate, microscabrate-tuberculate, microscabrate-tuberculate-perforate, microfoveolate, and micropilate. On the basis of light microscopy observations of pollen aperture types, we distinguish three pollen types.

3.2. Descriptions of pollen types and subtypes

Type I. Pollen grains tricolpate, P (25.3-37.2 µm), E (27.9-33.2 µm), oblate spheroidal, prolate or spheroidal. Outline in polar view trilobate or slightly trilobate.

Table 1. Pollen parameters in the Ukrainian species of the genus *Pedicularis*

| Taxon | Polar length (P, μm) | Equatorial diam. (E, μm) | P/E, ratio | Width of colpi (μm) | Exine thickness (μm) | Shape | Apertures |
|--|-------------------------------------|---|---------------|-------------------------------------|--------------------------------------|----------|--------------|
| <i>P. oederi</i> Vahl | (17.9) 15.9-21.3 | (20.8) 19.9-21.3 | 0.86 | 2.1-2.7 | 0.3-0.7 | OS, P | 3-syncolpate |
| <i>P. exaltata</i> Besser | (16.8) 14.6-18.6 | (16.1) 14.6-17.3 | 1.04 | 2.0-2.4 (2.7) | 0.3-0.4 | P, OS, S | 2-syncolpate |
| <i>P. hacquetii</i> Graf | (16.3) 14.6-18.6 | (15.4) 13.3-17.3 (18.6) | 1.06 | 2.0-2.4 (2.7) | 0.3 | P, OS, S | 2-syncolpate |
| <i>P. kaufmannii</i> Pinzger | (19.0) 15.9-21.3 (22.6) | (16.5) (11.9) 13.3- 19.9 | 1.15 | 2.0-4.0 | 0.4-1.1 | P, OS, S | 2-syncolpate |
| <i>P. sibthorpii</i> Boiss. | (18.8) 15.9-21.3 | (15.2) 11.9-18.6 | 1.23 | 2.0-2.4 (2.7) | 0.7-1.1 (1,3) | P, S | 2-syncolpate |
| <i>P. sylvatica</i> L. | (34.5) 29.3-39.9 | (17.2) 13.3-22.6 | 2.01 | 2.4-7.9 | 0.3-1.3 | P | 2-syncolpate |
| <i>P. dasystachys</i> Schrenk | (20.2) 17.3-22.6 (23.9) | (16.5) 13.3-18.6 (19.9) | 1.23 | 2.0-2.4 | 0.7-1.1 (1,3) | P, S, OS | 2-syncolpate |
| <i>P. palustris</i> L. | (23.0) 19.9-26.6 | (18.3) 14.6-21.3 | 1.26 | 2.7-4.0 | 0.3-1.1 | P, S | 2-syncolpate |
| <i>P. sceptrum-</i> <i>carolinum</i> L. | (30.7) 25.3-37.2 | (30.8) 27.9-33.2 | 0.99 | 2.4-5.3 | 1.3-2.4 | OS, P, S | 3-colpate |
| <i>P. verticillata</i> L. | (14.5) 11.9-18.6 | (16.6) 13.3-18.6 | 0.87 | 1.3-2.4 | 0.4-0.7 | OS, P | 3-syncolpate |

Explanations: P – prolate, S – spheroidal, OS – oblate-spheroidal

Outline in equatorial view elliptical or circular. Sculpture microscabrate-perforate. Colpi long, margins indistinct, irregular and with acute ends. Colpus membrane with scabrate surface (*P. sceptrum-carolinum*) (Fig. 1/1-4; Fig. 2/1-3).

Type II. Pollen grains trisyncolpate, P (11.9-21.3 μm), E (13.3-21.3 μm), oblate spheroidal or prolate. Outline in polar view trilobate or slightly trilobate. Outline in equatorial view elliptical. Surface sculpture microscabrate-tuberculate or micropilate. Colpi long, extending to fuse at the poles, margins indistinct, irregular. Colpus membrane with scabrate-tuberculate surface (*P. oederi*, *P. verticillata*).

Subtype IIa. P (11.9-18.6 μm); E (13.3-18.6) μm . Outline in polar view trilobate or slightly trilobate. Surface sculpture micropilate. Colpi long, extending to fuse at the poles, margins indistinct, irregular. (*P. verticillata*) (Fig. 1/5-8; Fig. 2/4-6).

Subtype IIb. P (15.9-21.3 μm), E (19.9-21.3 μm). Outline in polar view trilobate. Surface sculpture microscabrate-tuberculate. Colpi long, extending to fuse at the poles, margins irregular. (*P. oederi*) (Fig. 1/9-12; Fig. 2/7-9).

Type III. Pollen grains bisyncolpate, P (14.6-39.9 μm), E (11.9-22.6 μm), oblate spheroidal, prolate or spheroidal. Outline in polar view bilobate, slightly bilobate or circular. Outline in equatorial view elliptical or circular. Surface sculpture microscabrate, microscabrate-perforate, microscabrate-tuberculate, microscabrate-tuberculate-perforate, or microfoveolate. Colpi long, extending to fuse at the poles, margins indistinct or distinct, irregular, sometimes sunken. Colpus membrane with scabrate-tuberculate or scabrate surface (*P. exaltata* Besser, *P. hacquetii* Graf, *P. kaufmannii* Pinzger, *P. sibthorpii* Boiss., *P. sylvatica*, *P. dasystachys* Schrenk, and *P. palustris* L.).

Subtype IIIa. P (14.6-18.6 μm), E (14.6-17.3 μm). Outline in polar view bilobate. Outline in equatorial view elliptical. Surface sculpture microscabrate. Colpi long, extending to fuse at the poles, margins indistinct. Colpus membrane with scabrate surface (*P. exaltata*) (Fig. 1/13-16; Fig. 2/10-12).

Subtype IIIb. P (14.6-39.9 μm), E (11.9-22.6 μm). Outline in polar view bilobate, slightly bilobate, or circular. Outline in equatorial view elliptical or circular. Surface sculpture microscabrate-tuberculate. Colpi long, extending to fuse at the poles, margins indistinct or distinct, irregular. Colpus membrane with scabrate-tuberculate or scabrate surface (*P. hacquetii* (Fig. 1/17-20; Fig. 3/1, 2), *P. sibthorpii* (Fig. 1/21-24; Fig. 3/4, 5), and *P. sylvatica* (Fig. 1/25-28; Fig. 3/3-6)).

Comments: Pollen grains of *P. sylvatica* are largest in size, among the studied taxa with the widest colpi, and are only elliptical in shape.

Subtype IIIc. P (15.9-21.3 (22.6) μm), E ((11.9) 13.3-19.9 μm), prolate, oblate spheroidal or spheroidal. Outline in polar view bilobate. Outline in equatorial view elliptical or circular. Sculpture microscabrate-tuberculate-perforate. Colpi long, extending to fuse at the poles, margins indistinct, irregular. Colpus membrane with scabrate-tuberculate (*P. kaufmannii*) (Fig. 1/29-32; Fig. 3/7, 8).

Subtype IIId. P (17.3-22.6 (23.9) μm), E (13.3-18.6 (19.9) μm), prolate, spheroidal or oblate spheroidal. Surface sculpture microfoveolate. Colpi long, extending to fuse at the poles, sunken, margins indistinct (*P. dasystachys*) (Fig. 1/33-36; Fig. 3/9, 10).

Subtype IIIe. P (19.9-26.6 μm), E (14.6-21.3 μm), prolate or spheroidal. Surface sculpture microscabrate-perforate. Colpi long, extending to fuse at the poles, sunken, margins distinct, irregular (*P. palustris*) (Fig. 1/37-40; Fig. 3/11, 12).



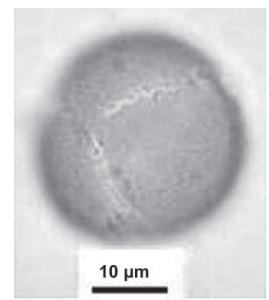
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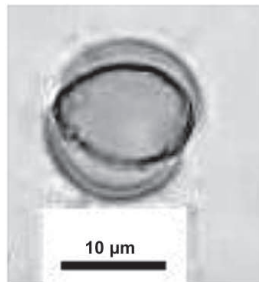
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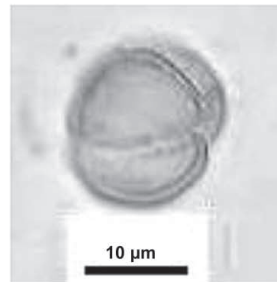
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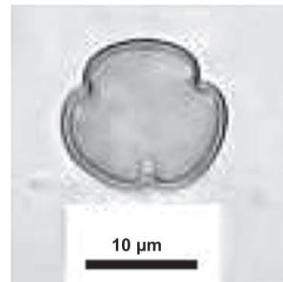
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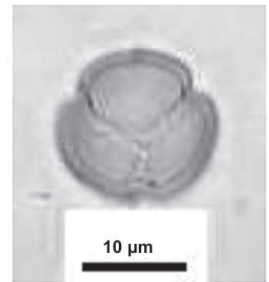
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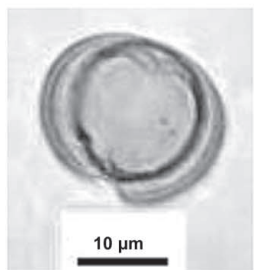
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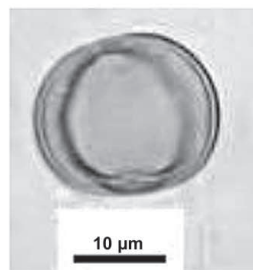
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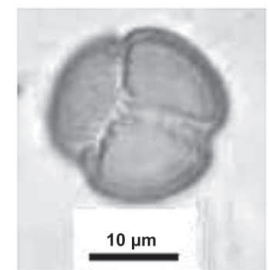
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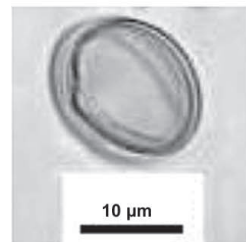
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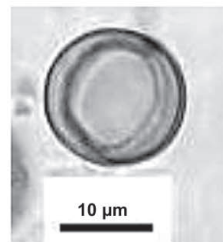
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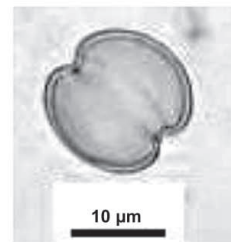
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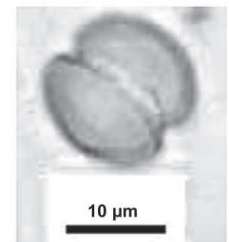
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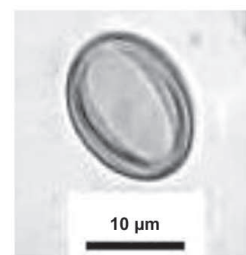
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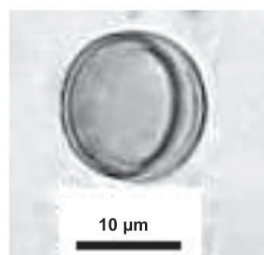
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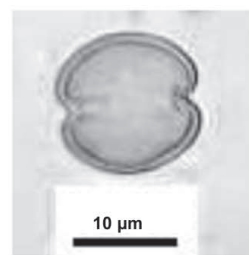
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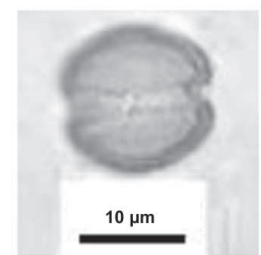
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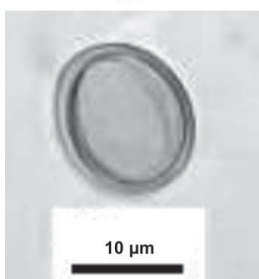
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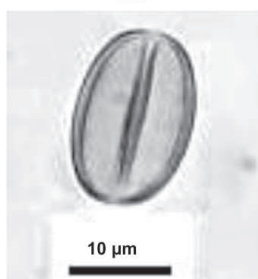
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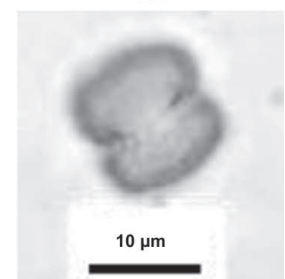
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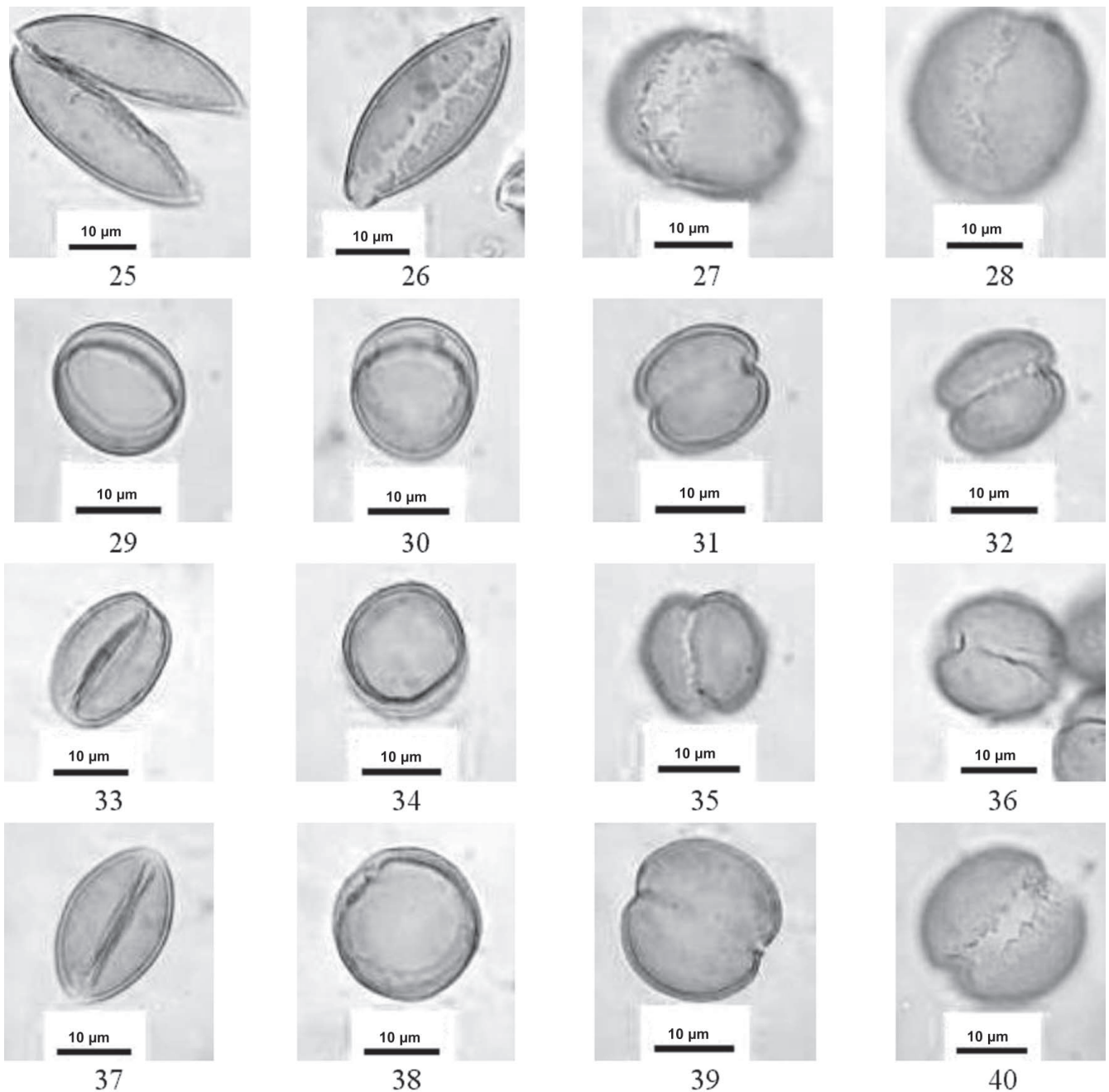


Fig. 1. Pollen grains of *Pedicularis* (LM)

Explanations: 1-4 – *P. sceptrum-carolinum*, 5-8 – *P. verticillata*, 9-12 – *P. oederi*, 13-16 – *P. exaltata*, 17-20 – *P. hacquetii*, 21-24 – *P. sibthorpii*, 25-28 – *P. sylvatica*, 29-32 – *P. kaufmannii*, 33-36 – *P. dasystachys*, 37-40 – *P. palustris*

4. Discussion

The investigated species belong to 3 subgenera and 5 sections, following Ivanina (Ivanina 1981; Ivanina & Popova 1998). Species of the subgenus *Sceptrum* Bunge (*P. sceptrum-carolinum*) differ in general morphology of their pollen grains. Pollen grains of *P. sceptrum-carolinum* belong to type I with the 3-colpate type of aperture and microscabrate-perforate sculpture. These distinctive features confirm placement of *P. sceptrum-carolinum* in a separate subgenus and section, which is also palynologically distinct from other representatives of the genus.

Pollen grains of taxa belonging to subgen. *Verticillatae* (Benth.) Ivanina sect. *Verticillatae* Benth. (*P. verticillata*) (Ivanina 1981; Ivanina & Popova 1998) belong to type II, subtype IIa, with the 3-syncolpate type of aperture and micropilate sculpture. Consequently, palynological data confirm that *P. verticillata* differs from other studied taxa and deserves placement into a separate subgenus and section.

Our investigation has demonstrated that the subgenus *Pedicularis* is heterogeneous by its types of aperture and sculpture of surface. Pollen grains of the section *Edentulae* Benth. belong to different types and subtypes. Pollen grains of *P. oederi* were classified as type II,

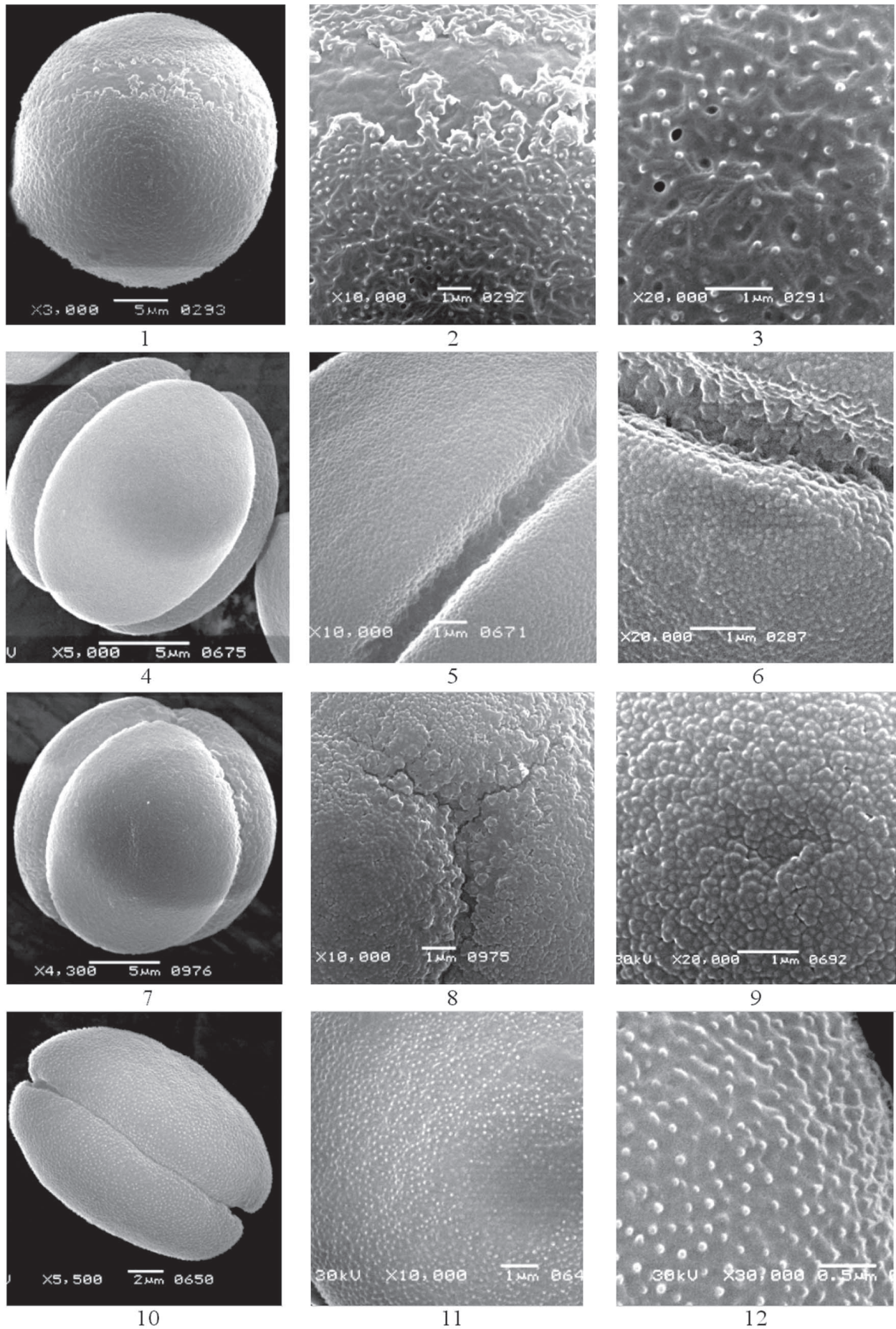


Fig. 2. Pollen grains of *Pedicularis* (SEM)

Explanations: 1-3 – *P. sceptrum-carolinum*, 4-6 – *P. verticillata*, 7-9 – *P. oederi*, 10-12 – *P. exaltata*; 1, 4, 7, 10 – equatorial view, sculpture; 2, 3 – microscabrate-perforate; 5, 6 – micropilate; 8, 9 – microscabrate-tuberculate; 11, 12 – microscabrate

Table 2. Correspondence of palynomorphological peculiarities with the system of the genus *Pedicularis* accepted by Ivanina (1981)

| Taxon | Pollen type and subtype | Apertures | Exine sculpturing |
|---|-------------------------|---------------|------------------------------------|
| Subgen. <i>Pedicularis</i> | | | |
| Sect. <i>Edentulae</i> Benth. | | | |
| <i>Pedicularis oederi</i> Vahl | IIb | 3-syncolpate | microscabrate-tubeculate |
| <i>P. exaltata</i> Besser | IIIa | 2- syncolpate | microscabrate |
| <i>P. hacquetii</i> Graf | IIIb | 2- syncolpate | microscabrate-tubeculate |
| Sect. <i>Pedicularis</i> | | | |
| <i>P. kaufmannii</i> Pinzg. | IIIc | 2- syncolpate | microscabrate-tubeculate-perforate |
| <i>P. sibthorpii</i> Boiss. | IIIb | 2- syncolpate | microscabrate-tubeculate |
| <i>P. dasystachys</i> Schrenk | IIIId | 2- syncolpate | microfoveolate |
| <i>P. sylvatica</i> L. | IIIb | 2- syncolpate | microscabrate-tubeculate |
| Sect. <i>Pharyngoton</i> Bunge | | | |
| <i>P. palustris</i> L. | IIIi | 2- syncolpate | microscabrate-perforate |
| Subgen. <i>Sceptrum</i> Bunge | | | |
| Sect. <i>Sceptrum</i> | | | |
| <i>P. sceptrum-carolinum</i> L. | I | 3-colpate | microscabrate-perforate |
| Subgen. <i>Verticillatae</i> (Benth.) Ivanina | | | |
| Sect. <i>Verticillatae</i> Benth. | | | |
| <i>P. verticillata</i> L. | IIa | 3-syncolpate | micropilate |

subtype IIb, with 3-syncolpate type of aperture and microscabrate-tubeculate sculpture. *Pedicularis oederi* is similar to *P. verticillata* in the type of apertures, but these species are different in the sculpture of surface. The characters of pollen grains of *P. oederi* differ obviously from those other taxa of subgen. *Pedicularis*. Others species of this subgenus have 2-syncolpate pollen grains and belong to type III. These species differ from each other in the surface sculpture. Pollen grains of *P. exaltata* (sect. *Edentulae*) are defined by their microscabrate sculpture of surface and belong to subtype IIIa. Pollen grains of *P. hacquetii* (sect. *Edentulae*), *P. sibthorpii* and *P. sylvatica* (sect. *Pedicularis*) have microscabrate-tuberculate sculpture and belong to subtype IIIb. This subtype includes species from different sections; among them, pollen grains of *P. sylvatica* are distinguished by their largest size, the widest colpi, and are only elliptical in shape. Two species, *P. hacquetii* (sect. *Edentulae*) and *P. sibthorpii* (sect. *Pedicularis*), are similar in their palynological characters. Pollen grains of others species of sect. *Pedicularis* differ in features of their sculpture. Pollen grains of *P. kaufmannii* have the microscabrate-tuberculate-perforate sculpture and belong to subtype IIIc. Pollen grains of

P. dasystachys, with their microfoveolate sculpture, belong to subtype IIIId. Pollen grains of *P. palustris* have microscabrate-perforate sculpture and belong to subtype IIIe. It is in agreement with placement of this species in sect. *Pharyngoton* Bunge.

Thus, our data do not correspond completely to the system by Ivanina (Ivanina 1981; Ivanina & Popova 1998), especially regarding subgen. *Pedicularis* (Table 2). The results of our investigation emphasize the need of a new taxonomic revision in this subgenus, and probably some modification of its infrageneric system at the level of sections and below.

Acknowledgements. The authors express their gratitude to the staff of the herbarium of the M. G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine (KW, National Herbarium of Ukraine; Head Curator Dr. Nataliya M. Shyian) for cooperation and assistance in extracting pollen samples from herbarium specimens. Kind help and cooperation of the Center of Electron Microscopy (Head of CEM Dr. Dmytro O. Klymchuk) of the M. G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, is greatly appreciated. The authors are grateful to an anonymous reviewer for his/her detailed review of the manuscript, valuable comments and suggestions.

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Appendix. List of pollen material studied

Pedicularis oederi Vahl: Poland, Tatra National Park, 13.08.1999. Ya. P. Didukh (KW); *P. exaltata* Besser: In montibus Cremen[ecensis]. Besser (KW); *P. hacquetii* Graf: Chernivtsi Region, Storozhinets District, environs of village Spas'ka, Dzyurkach tract, meadow. 05.06.04. A. [I.] Tokaryuk (KW); *P. kaufmannii* Pinzg.: 1. Luhansk Region, Streletskyi Step Reserve, 25.05.1956. D. [K.] Zerov, O. [M.] Dubovik, N. Glagoleva (KW), 2. Starobjel'sk [Starobel'sk]. Streletska virgin steppe, watershed between ravines. [place name illegible] and Cherepahova, square 7, 26.05.1927. I. Zoz, E. Lavrenko (KW); *P. sibthorpii* Boiss.: Crimea, Mnogorechye, Bakhchisaray District, pine forest. 06.06.1980. [Ya. P.] Didukh, [L. P.] Vakarenko (2 samples) (KW); *P. dasystachys* Schrenk: Luhansk Region, Milove District, Streletska Step Reserve. 06.05.1955. Sarycheva (KW); *P. sylvatica* L.: 1. Lviv Region, Turka District, valley of Gusnivka River, downstream of village Gusyna, tract Ratsyky, on dry parts of bog 18.05.1986. O. Kris, I. Vaynagiy (KW), 2. Volhynian Region, Kamin'-Kashirskyi District, v. Polytsi, tract Vul'os, pasture on wet soil. 19.05.1985. Shevchik (KW); *P. palustris* L.: Male Polissia, Nenkovitske bog. 19.07.1950. A. Bachurina (KW); *P. sceptrum-carolinum* L.: 1. Supiy bog, near v. Svydovets, Nizhyn District, island in the bog. 20.07.1928. D. [K.] Zerov et K. Zerov (KW), 2. Volhynian Region, Kamin'-Kashirskyi District, sedge-hypnum parts of Berezyna bog, south of village Pnivne. 01.08.1949. [E.M.] Bradis (KW), 3. Environs of c. Vinnitsa, wet places north of railway in direction to Sosenska (Kalinovka) (KW), 4. Male Polissia, Zurnovske bog. 01.08.1950. A. Bachurina; *P. verticillata* L.: 1. Transcarpathian Region, Rakhiv District, Bila Tisa [White Tysza] forestry, stone slope of m. Pip Ivan, alt. 1800-1900 m a.s.l. 03.07.1947. D. Dobrochaeva [D. M. Dobroczaeva] (KW); 2. Transcarpathian Region, Rakhiv District, m. Petros. 06.07.1981. S. M. Ziman, A. V. Chernyavskiy, A. D. Ermolenko, A. V. Shumilova (KW).

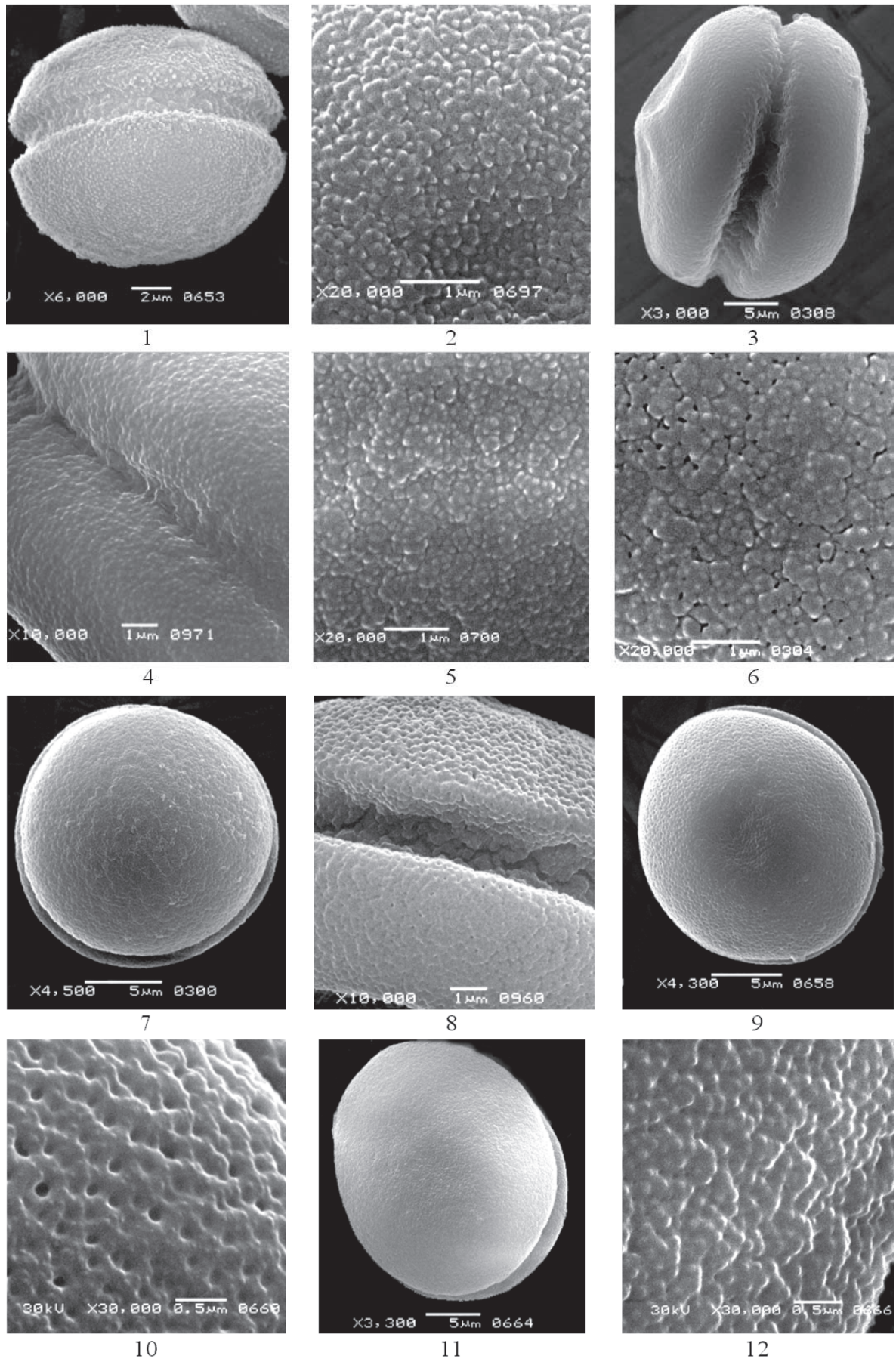


Fig. 3. Pollen grains of *Pedicularis* (SEM)

Explanations: 1, 2 – *P. hacquetii*, 3-6 – *P. sylvatica*, 4, 5 – *P. sibthorpii*, 7, 8 – *P. kaufmannii*, 9, 10 – *P. dasystachys*, 11, 12 – *P. palustris*; 1, 3 – polar view; 7, 9, 11 – equatorial view; sculpture: 2, 4-6 – microscabrate-tubeculate, 8 – microscabrate-tubeculate-perforate, 10 – microfoveolate, 12 – microscabrate-perforate