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RESEARCH ARTICLE

Seed morphology of species of *Spergula* and *Spergularia* (*Caryophyllaceae*) occurring in Ukraine and its taxonomic significance

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Abstract. The micro- and macromorphological characteristics of seeds of species of the genera *Spergula* and *Spergularia* in the flora of Ukraine were studied in order to identify new diagnostic characters useful for solving taxonomic issues. The ultrastructure of the seed surface was studied using a scanning electron microscope. Seeds of some species of these genera are similar in appearance (especially with a wide wing — *Spergula morisonii* and *Spergularia marina*), which can be one of the confirmations of the close taxonomic affinity of these genera. The results of our study showed that the ultrastructure patterns of the surface of seeds of *Spergula* and *Spergularia* species differ among themselves within these genera but for some species can be used as diagnostic characters for their identification. The data obtained confirm the results of our previous research on the taxonomic status of some representatives of the studied taxa (Fedoronchuk, 2023). In particular, taking into account the similarity of seed ultrastructure and other characteristics that have been proposed previously, we consider *Spergula vulgaris* a synonym of *Spergula arvensis* subsp. *arvensis*, *S. vernalis* — a synonym of *S. morisonii*, *Spergularia media* — a synonym of *Spergularia marina*, and *Spergularia salina* — a synonym of *Spergularia marina*. Differences in the surface ultrastructure of *Spergula sativa* and *Spergula arvensis* subsp. *arvensis*, which is consistent with our understanding of the taxon (Fedoronchuk, 2023) as *Spergula arvensis* subsp. *sativa*, as well as between *Spergula maxima* and *Spergula arvensis* subsp. *arvensis*, accordingly we propose — *Spergula arvensis* subsp. *maxima*. Compiled descriptions of the surface ultrastructure of seeds of *Spergula* and *Spergularia* species collected in the territory of Ukraine can be used as a model for assessing the possible variability of the morphological characters of these species in other regions of the world.

Keywords: macromorphology, micromorphology, Scanning electron microscope (SEM), seed, taxonomy, ultrastructure

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Introduction

The genus *Spergula* L. includes about 10 species (POWO, 2024), occurring mainly in Europe and Western Asia; some species were introduced and naturalised in other continents and parts of the world. In the flora of Ukraine, five taxa are reported: *Spergula arvensis* L. (with four subspecies — subsp. *arvensis*, subsp. *linicola* (Boreau) Janch., subsp. *maxima* (Weihe) O. Schwarz, subsp. *sativa*) and *S. morisonii* Boreau.

The genus *Spergularia* (Pers.) J. Presl & C. Presl contains about 60 species, the native and introduced ranges of which are much wider (spread in warm, subtropical and partly tropical countries of both hemispheres). In the flora of Ukraine there are about four species (*Spergularia marina* (L.) Besser, *S. media* (L.) C. Presl., *S. rubra* (L.) J. Presl, and *S. syvaschica* Tzvelev). Some species of these genera are weeds of agricultural crops. Based on the results of morphological studies (López Gonzalez, 2010), it was proposed to include *Spergularia* in the genus *Spergula*, but molecular data (Kool, 2012) confirmed the monophyly of both genera.

Both genera exhibit similar morphological characteristics, including the presence of membranous stipules, which are otherwise rare within the family *Caryophyllaceae* Juss.; because of that the genera have been assigned to a separate tribe, *Sperguleae* Dumort. These are annual or perennial, low-growing herbaceous plants with narrowly linear, more or less fleshy opposite leaves with membranous stipules, in the axils of which there are mostly shortened shoots with rather long leaves, which creates the impression of the presence of bundle leaves (*Spergula*); or such shortened the shoots are few, they are much shorter or even absent, and the leaves do not form the impression of bundles, and the membranous stipules are quite large (*Spergularia*).

Furthermore, the two genera exhibit differences in their generative features. The ovary in *Spergula* is composed of five stylodia, and the capsule opens by five spreading to somewhat recurved valves. In contrast, the ovary of *Spergularia* is composed of three stylodia and the capsule opens by three spreading valves with recurved tips.

Until now, there was no unequivocal answer regarding the species composition and nomenclature of the species of these genera in the flora of Ukraine. A different number of species of the genus *Spergula* was previously indicated for Ukraine: six — *S. linicola* Boreau, *S. maxima* Weihe, *S. pentandra* L., *S. sativa* Boenn., *S. vernalis* Willd., *S. vulgaris* Boenn. (Klokov, 1952); four — *S. arvensis* L., *S. maxima*, *S. morisonii* Boreau, *S. pentandra* (Prokudin, 1987); or five — *S. arvensis*, *S. linicola*, *S. maxima*, *S. morisonii*, *S. pentandra* (Mosyakin, Fedoronchuk, 1999).

However, subsequent research (Tsvelev, 2000) revealed that the species *S. pentandra* had been erroneously identified as *S. morisonii*. It differs from *S. morisonii* in having a smaller number of stamens in the flower (five instead of seven to ten) and the absence of papillae at the base of the seed border. The species name *Spergula vernalis* Willd. is considered to be a nomen superfluum (a superfluous name), and thus an illegitimate name (IPNI, 2024). According to Art.52.1. "A name, unless conserved (Art. 14), protected (Art. F.2), or sanctioned (Art. F.3), is illegitimate and is to be rejected if it was nomenclaturally superfluous when published, i.e. if the taxon to which it was applied, as circumscribed by its author, definitely included the type (as qualified in Art. 52.2) of a name that ought to have been adopted, or of which the epithet ought to have been adopted, under the rules (but see Art. 52.4 and F.8.1)" (Turland et al., 2018). Thus, the name *Spergula vernalis* Willd. is a synonym of *Spergula pentandra*, and for Ukraine the species was also listed erroneously.

The synonym of *Spergula arvensis* is the name *S. vulgaris* Boenn. (POWO, 2024; WFO, 2024).

The species of the genus *Spergularia*, which were previously reported for Ukraine, have undergone nomenclatural changes. *Spergularia marginata* (DC.) Kitt. (Klokov, 1952) is now considered a synonym of *S. media* (L.) C. Presl, and *Spergularia campestris* (L.) Asch. (Klokov, 1952) is treated as a synonym of *S. rubra* (L.) J. Presl & C. Presl. A synonym of *Spergularia marina* (L.) Besser (*Arenaria rubra* L. var. *marina* L. (1753)) is *S. salina* J. Presl & C. Presl (1819). However, some authors (Kurtto, 2001; Rabeler, Hartman, 2005) erroneously consider *S. marina* a synonym of *S. salina*, which contradicts the rule of priority (Fedoronchuk, 2023). In accordance with the most recent nomenclatural data (POWO, 2024), *Spergularia salina* is synonimized with *Spergularia marina*.

In order to ascertain additional features that may be useful in clarifying the taxonomic status of the species, we conducted carpological studies of both well-defined and controversial species that are represented in the flora of Ukraine. As demonstrated

by our own research and that of other authors, carpological features are a valuable tool for species identification and taxonomy within the family *Caryophyllaceae* (Crow, 1978, 1979; Fawzi et al., 2010; Martyniuk et al., 2015a, 2015b, 2015c, 2018; Abdel-Maksoud, Fawzi, 2016; Atazadeh et al., 2017).

A number of scientific publications present information on the macro- and micromorphological features of fruits and seeds of some representatives of *Spergula* and *Spergularia* (Klokov, 1952; Salisbury, 1958; Ratter, 1986; Wagner, 1986; Telenius, Torstensson, 1989, 1991, 1999; Adams et al., 2008; Memon et al., 2010). However, the available data is incomplete and requires further clarification. Furthermore, the study only concerns a limited number of species from Ukraine. The objective of the presented study is to analyse the differences in the macro- and micromorphological features (based on scanning electron microscopy — SEM) of the seed surface of species of *Spergula* and *Spergularia* from Ukraine. The aim is to provide data that will be useful for solving taxonomic problems.

Materials and Methods

Seeds of representatives of the genera *Spergula* (5 species) and *Spergularia* (4 species) were studied, of which 23 herbarium specimens were collected in the territory of Ukraine and are deposited in the National Herbarium of Ukraine — the Herbarium of M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine (KW). At least 30 seeds from each herbarium specimen were studied.

The micromorphological characteristics of the seeds were studied using a light microscope (MBF-9) and a scanning electron microscope (SEM, JSM-6060 LA). The samples were sputter-coated with a thin layer of gold (4 nm) in accordance with the standard method. The descriptions of the fruits and seeds were carried out using the terminology that has been established in a number of previous works, including those by Gvinianidze and Fedotova (1991) and Ziman et al. (2011). In particular, attention was paid to the primary, secondary and tertiary structure, in accordance with the recommendations provided by Barthlott (1981).

Examined specimens

Names of taxa are given according to the original labels; the names that we accepted are indicated in square brackets.

Spergula

1. *Spergula arvensis* L. [*Spergula arvensis* L. subsp. *arvensis*]: *Spergula arvensis* L. Khmelnytskyi Region, Shepetivsky District, pine forest between Konotop and Malyovanka, forest road. 08.07.2020. Leg., Det. V.P. Kolomiychuk. No. 151575.
2. *Spergula arvensis* L. [*Spergula arvensis* L. subsp. *arvensis*]: *Spergula arvensis* Kyiv Region, Pereyaslav-Khmelnytsky District, behind the village Divychky, on the felling in a pine forest. 31.05.2015. Leg., Det. D.A. Davydov. No. 124013.
3. *Spergula arvensis* L. [*Spergula arvensis* L. subsp. *arvensis*]: *Spergula arvensis* L. Poltava Region, Novosanzhariv District, Sobkivka village, on the sands of the pine terrace of the Vorskla River. 21.06.2009. Leg., Det. D.A. Davydov. No. 098859.
4. *Spergula arvensis* L. [*Spergula arvensis* L. subsp. *arvensis*]: *Spergula vulgaris* Boenn. Rivne Region, Dubnovsky District, Maidan village, oak-hornbeam forest. 19.06.1986. Leg., Det. A.V. Shumylova. No. 096111.
5. *Spergula maxima* Weihe [*Spergula arvensis* L. subsp. *maxima* (Weihe) O.Schwarz]: *Spergula maxima* Weihe. Near the farm Zalessye, Oster District, Chernigov Province. In the forest, near the field. 04(17).07.1904. Leg., Det. I.F. Selezhinsky. No. 031764.
6. *Spergula maxima* Weihe [*Spergula arvensis* L. subsp. *maxima* (Weihe) O. Schwarz]: *Spergula arvensis* L. Neighborhood of Kyiv. 19.06.1908. Leg., Det. F. Satsiperov. No. 031762; notae criticae: *Spergula maxima* Weihe (M. Klokov, 1955).
7. *Spergula morisonii* Boreau.: Kherson Region, Tsyuryupinsky District, (Oleshkivskyi) NPP "Oleshkivsky sands" dunes. 27.04.2013. Leg., Det. V.P.Kolomiychuk. No. 147649.
8. *Spergula morisonii* Boreau.: Zhytomyr Region, Malyn District, Malynske DLH, Malynske Forestry, quarter 14. On open sands, a lot. 12.05.2017. Leg., Det. O. Orlov. No. 131018.
9. *Spergula morisonii* Boreau.: Zhytomyr Region, Ovrutskyi District, Tosoryn Forestry, in pine forest A1, on a dune, swamp. 15.05.2011. Leg., O.O. Orlov. 09.02.2012. Det. M.M. Fedoronchuk.
10. *Spergula morisonii* Boreau.: Cherkasy Region, Kaniv District, approx. with. Leplivo, Kaniv Nature Reserve, district islands area, sandy arena of the left bank of the Dnipro River. 19.05.2016. Leg., Det. V.P. Kolomiychuk. No. 129421.

11. *Spergula morisonii* Boreau.: *Spergula vernalis* Willd. Kharkiv Region, Merefa, tract, on the sands 06.16.1966. Leg., Det. M. Klokov. No. 031695; notae criticae: *Spergula vulgaris* Boenn. (Det. O. Dubovyk, 19.11.1968); notae criticae: *Spergula morisonii* Boreau (Det. M.M. Fedoronchuk, 11.02.2022).
12. *Spergula morisonii* Boreau.: *Spergula vernalis* Willd. Rivne Region, Ostrozhsky District, Novomalinsky Forestry, Batkovtsy village, Bushchanskoe Bog. 18.06.1985. Leg., Det. A. Shumylova. No. 096378; notae criticae: *Spergula morisonii* Boreau (Det. M. Fedoronchuk, 14.02.2024).
13. *Spergula sativa* Boenn. [*Spergula arvensis* subsp. *sativa* (Boenn.) Ćelak.]: *Spergula vulgaris* Boenn. Rivne Region, Berezino, MAPO. Roadside. 22.06.1978. Leg., Det. V.V. Protopopova. No. 031761; notae criticae: *Spergula sativa* Boenn. (Det. M. Fedoronchuk).

***Spergularia*:**

1. *Spergularia marina* (L.) Besser.: *Spergularia salina* J. Presl & C. Presl. Poltava Region, Kremenchuk District, behind the Kyyashky village, on salt flats. 21.08.2015. Leg., Det. D.A. Davydov, T.P. Dzyuba. No. 129710.
2. *Spergularia marina* (L.) Besser.: Dniester estuary, Karagolskie plavni [wetlands]. August 2000. Leg., Det. E.Yu. Bondarenko No. 118580.
3. *Spergularia marina* (L.) Besser.: Meotida Reserve, Donetsk Region, near the sea, on the sand. 05.29.2002. Leg., Det. I.V. Kovtun. No. 041959.
4. *Spergularia marina* (L.) Besser.: *Spergularia salina* J. Presl & C. Presl. Zaporizhzhia Region, Yakymivsky District, near village Bogatyr, the bank of the Molochny Estuary, opposite the NPB of the Romashka MDPU, on salt marsh soils. 30.05.2013. Leg., Det. V.P. Kolomiychuk. No. 00110115; notae criticae: *S. marina* (L.) Besser. Det. M. Fedoronchuk, 14.02.2024.
5. *Spergularia marina* (L.) Besser.: *Spergularia salina* J. Presl & C. Presl. Kremenchuk, saline meadow, between the 2nd and 3rd terraces of the Dnipro [Dnieper] valley. 23.07.1921. Leg., Det. E. Lavrenko. No. 029484.
6. *Spergularia media* (L.) C. Presl.: Kherson Region, Skadovsk District, Dzharylgach Island, district Pindyky, salt flats, common. 10.07.2014. Leg., Det. V.P. Kolomiychuk. No. 00112437.
7. *Spergularia media* (L.) C. Presl.: Poltava Region, Semenivskyi District, Okrlytsi village. Obolon, on the shore of the lake Solone. 23.08.2003. Leg. H.A. Chorna, S.V. Gapon. Det. H.A. Chorna. No. 039201.
8. *Spergularia media* (L.) C. Presl.: *Spergularia marginata* (DC.) Kitt. Crimea, eastern outskirts of Evpatoria. Along the coast. 10.11.1974. Leg., Det. A. Kuzmichev, A. Krasnova.
9. *Spergularia rubra* (L.) J. Presl & C. Presl.: Herbarium I.F. Selezhansky, Litky ["Letkovo"] Forestry, Chernigov Province. Oster District. 06.22.1904. No. 032457.
10. *Spergularia rubra* (L.) J. Presl & C. Presl.: Rivne Region, Dubno District, Ozeryany railway station, near the platform No.1. 07.05.2012. Leg. V.I. Goncharenko. 03.19.2014. Det. M.M. Fedoronchuk. No. 00110926.

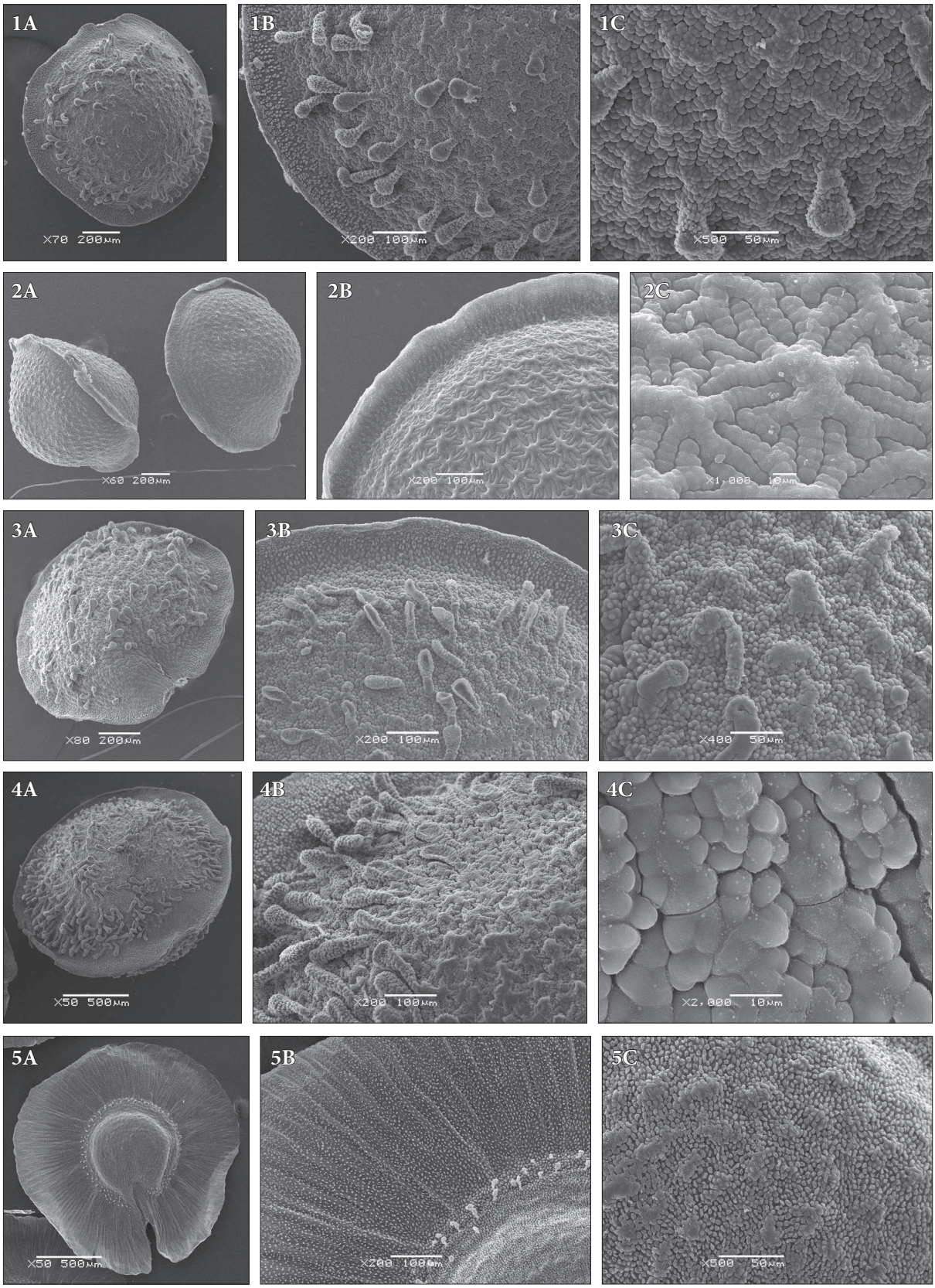
Results and Discussion

The morphological features of seeds of species of *Spergula*

Spergula arvensis L. (Fig. 1, 1A–C).

Seeds lenticular, slightly laterally compressed, round to oval in outline, up to 1.0–1.5 mm in diameter, with a narrow (up to 100 μm) light-coloured wing (margin) on the edge, with a slight notch opposite the seed scar. Hilum in the depression, barely visible. Seed surface (outside the rim) somewhat uneven, covered in places with short, tan or white, club-shaped papillae, up to 90 μm high, which, like the rim, are densely covered with small papillae-shaped formations. On the papillae they are slightly elongated, up to 5 μm long, on the periclinal walls they are rounded, up to 10 μm, often in a one or three row arrangement. Edge also densely covered with papillose formations, irregular in shape, 5 to 10 μm. Surface finely tuberculated, slightly tuberous, tubercles with stellate base, due to the presence of tortuous anticlinal walls of the testa cells. Contours of the anticlinal walls indistinct, stellate base almost indistinct. Periclinal walls convex, their middle part being more convex compared to the "rays", which gives the surface certain unevenness. Microstructure of the surface with lamellar deposits of wax, which are particularly abundant in the area of the seed scar. Matte, light black, reddish brown.

We also studied the seeds of *S. vulgaris*, samples of which, identified as "*Spergula vulgaris*", are deposited in the Herbarium (KW). This species, like the following *S. sativa*, has a dubious taxonomic status and is not recognised in modern treatments and online


1A
X70 200µm
1B
X200 100µm
1C
X500 50µm
2A
X60 200µm
2B
X200 100µm
2C
X1,000 10µm
3A
X80 200µm
3B
X200 100µm
3C
X400 50µm
4A
X50 500µm
4B
X200 100µm
4C
X2,000 10µm
5A
X50 500µm
5B
X200 100µm
5C
X500 50µm

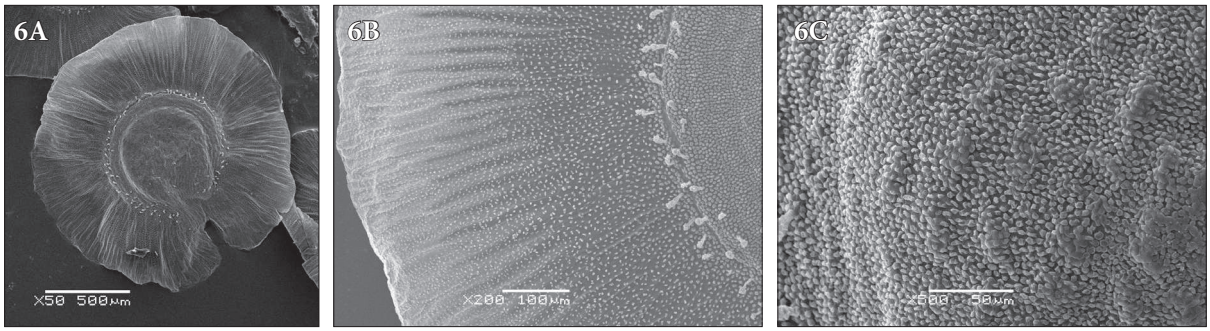


Fig. 1. Seeds of *Spergula* (SEM). A: general view; B, C: surface fragments. 1 — *Spergula arvensis* [*Spergula arvensis* subsp. *arvensis*] (Sample No. 151575); 2 — *Spergula sativa* [*Spergula arvensis* subsp. *sativa*] (Sample No. 031761); 3 — *Spergula vulgaris* [*Spergula arvensis* subsp. *arvensis*] (Sample No. 096111); 4 — *Spergula maxima* [*Spergula arvensis* L. subsp. *maxima*] (Sample No 031764"); 5 — *Spergula morisonii* (Sample No. 147649); 6 — *Spergula vernalis* [*Spergula morisonii*] (Sample No 096378)

resources (WFO, 2024; POWO, 2024 and others). It was also interesting to check whether there were any differences at the microcarpological level between representatives of these taxa (*S. arvensis* and *S. vulgaris*). Our examination of the seeds showed similarities between *S. vulgaris* (Fig. 1, 3A–C) and *S. arvensis* (Fig. 1, 1A–C), confirming the interpretation of this taxon as a synonym of *Spergula arvensis* L. subsp. *arvensis* (Fedoronchuk, 2023).

Spergula sativa Boenn. (Fig. 1, 2A–C).

Seeds similar in shape, size and general ultrastructural characteristics to the previous species. However, there are some differences in the ultrastructural features of the surface. Unlike *S. arvensis*, the surface of seeds of *S. sativa* has clear anticlinal cell walls, distinct tubercles, and a darker colour due to the absence of light brown club-shaped papillae. No wax deposits were found on the seed surface. Based on the results of our previous studies, we consider *S. sativa* to be a subspecies of *Spergula arvensis* L. subsp. *sativa* (Boenn.) Čelak. (Fedoronchuk, 2023).

Spergula maxima Weihe (Fig. 1, 4A–C).

Seed lenticular, slightly laterally compressed, round to oval in outline, up to 1.5–1.8(2.2) mm in diameter, with a narrow (up to 160 μm) pale border (wing on the margin), with a small notch opposite the seed scar. Hilum barely visible. Contours of the anticlinal walls clear, sinuous; periclinal walls slightly convex, giving the surface a fine tuberculate appearance; tubercles with a stellate base. Seed surface (up to the margin) densely covered with light brown club-shaped papillae, up to 100 μm high, which, like the periclinal walls of the testa cells, are densely covered with rounded papillae-shaped cuticular formations, up to 10 μm. Border also densely covered with papillose formations of irregular shape, from 5 to 10 μm. Wax layer in the form of lamellar formations. Matte, black, reddish brown.

As compared to *Spergula arvensis*, the seeds of *Spergula maxima* have a wider wing and a denser arrangement of club-shaped papillae; in other characteristics they are similar. It also differs from *Spergula arvensis* by its taller stems, longer leaves and capsules. We propose to consider *Spergula maxima* as a synonym of *Spergula arvensis* L. subsp. *maxima* (Weihe) O. Schwarz (Fedoronchuk, 2023). This subspecies is also recognized by other authors (Prockow et al., 2011).

Spergula morisonii Boreau (Fig. 1, 5A–C).

Seeds flattened on the sides, almost spherical in outline, with a submarginal furrow closer to the margin, up to 1.7 mm in diameter (together with the margin); margin in the form of a wing-like, pale, broad (400–460 μm), thin membranous growth (border) on the margin, almost transparent, ribbed in radial direction, with almost entire (not torn) smooth edge, with a notch opposite the seed scar. Hilum in the hollow, hardly noticeable. Club-like papillae, up to 30 μm high, arranged in two or three rows around the seed (closer to the wing). Seed surface almost smooth or slightly uneven due to the slight convexity and concavity of the outer periclinal walls of the testa cells. Contours of the anticlinal walls indistinct. Papillae and seed surface densely covered with smaller papillose formations, varying in shape and size. On the margin these are smaller (up to 5 μm) and evenly spaced, outside the margin on the surface of the seeds they are in the form of shapeless clusters, slightly raised above the surface, which is also covered with small papillae (up to 8 μm), evenly spaced between these papillose

formations. There are no wax formations. Matte, black.

We also examined the characteristics of the seeds in the plant samples identified as *Spergula vernalis*. According to the results of our studies of macro- and micromorphological characteristics of seeds of *Spergula vernalis* (Fig. 1, 6A–C), no differences were found between them and seeds of *Spergula morisonii*. This is one of the confirmations of the taxonomically correct status of *Spergula vernalis* as a synonym of *Spergula morisonii*, as suggested by one of the co-authors of our publication (Fedoronchuk, 2023) and recognised in modern online databases (IPNI, 2024; WFO, 2024).

The morphological features of seeds of species of *Spergularia*

Some members of the genus are characterised by the phenomenon of heterospermy — seeds are formed within a capsule both with a wide membranous wing on the periphery (located in the lower part of the capsule) and practically without it (located in the upper part of the capsule).

Spergularia media (L.) C. Presl (Fig. 2, 1A–C).

Seeds flattened on the sides, almost round in outline, somewhat asymmetrical, with submarginal furrow, 0,6–1,2 mm in diameter, together with a wide (up to 340–400 μm) membranous wing around the perimeter (border), which has a notch opposite the seed scar and an uneven contour (wing-margin denticulate), or rarely wingless. Hilum in the hollow hardly noticeable. Wing surface radially ribbed. Seed surface smooth or slightly uneven due to the slight convexity and concavity of some of outer periclinal walls of testa cells. Contours of the anticlinal cell walls clear. Anticlinal walls deeply curved, thickened and slightly raised. Secondary microstructure of seeds papillose, with densely arranged spherical formations (up to 2 μm in height) on the seed itself; on the wing, the papillae are of different shape, mostly elongated, not exceeding 4 μm in length, loosely, chaotically arranged, only around the perimeter of the seed, on ½ of its width. There is no wax coating. Matte, brown to dark brown, lightcolored wing.

Wingless seeds were absent in the studied herbarium specimens.

Spergularia marina (L.) Besser (Fig. 2, 2A–C).

Herbarium specimens of this species had both seeds with a broad membranous wing on the periphery or, rarely, wingless. Seeds with a wing are flattened on the sides, almost spherical in outline, broadly pear-shaped (without a border) with a submarginal furrow, 1,2–1,4 mm in diameter (together with the wing), wing wide (350–400 μm) membranous, which has a notch opposite the seed scar and an uneven contour (wing margin denticulate) of the edge. Hilum in the depression barely visible. Wing surface radially ribbed. Seed surface almost smooth or slightly uneven due to the slight convexity and concavity of some of outer periclinal walls of testa cells. Contours of anticlinal walls clear.

Anticlinal walls deeply convoluted, thickened and slightly elevated. Secondary microstructure of seeds papillose, with densely arranged spherical formations (up to 2 μm in height) on the seed itself; on the wing the papillae are of different shape, mostly elongated, not exceeding 4 μm in length, loosely, chaotically arranged, only around the seed, on ½ of its width. There is no wax coating observed. Matte, brown to dark brown, lightcolored wing.

Wingless seeds asymmetrical, laterally compressed, broadly ovoid in outline, slightly smaller than winged seeds, up to 0.7 mm long, 0.5 mm wide, with a submarginal furrow around the circumference. Hilum in the depression barely visible, rootlet clearly protruding. Seed surface almost smooth or slightly uneven due to the slight convexity and concavity of some of the outer periclinal walls of the testa cells. Microstructure of the surface is the same as that of the bordered seeds, differing only in the presence of large warty formations (up to 15 μm in diameter) along the border of the seed, which, like all other surface cells, are externally covered with small (up to 2 μm in diameter) rounded papillae. No wax coating was observed. Matte, light brown to reddish brown, wing distinctly paler than testa.

Spergularia media and *S. marina* from the flora of Ukraine showed their similarity in macro- and micromorphological characteristics. In order to avoid possible mistakes in identification of herbarium specimens from which we selected material for our research, we carefully checked them; all seed samples from different collection sites had the same structure and other morphological characteristics. In photographs (SEM) of the surface microstructure of seeds of the Australian specimens of *S. marina* and *S. media* (Adams et al., 2008), we also found no differences in seed shape, surface ornamentation and other micromorphological features. Sterk (1969), comparing Feekes (1936) and Sterk (1966), noted that *S. media* was in fact a synonym

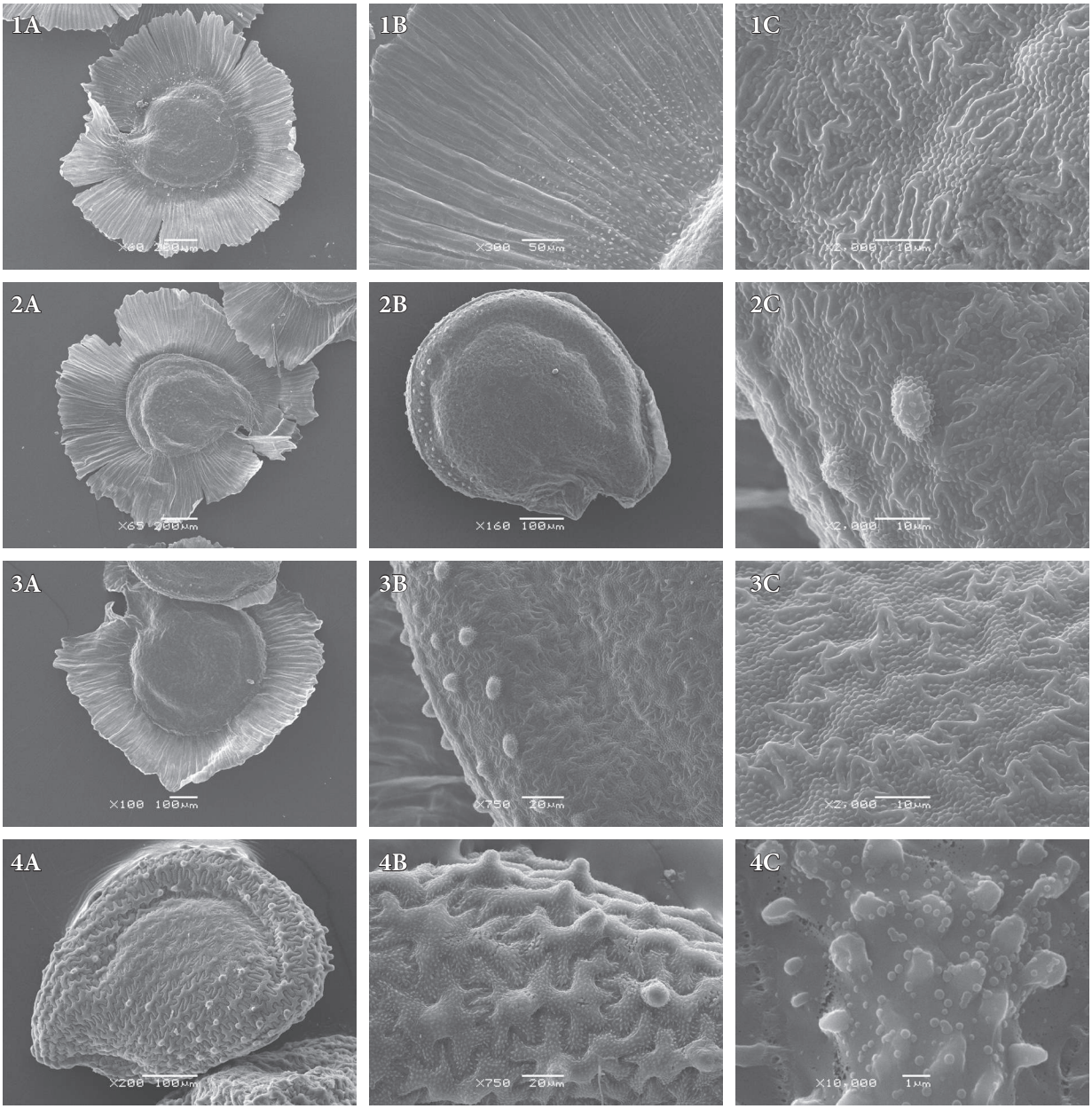


Fig. 2. Seeds of *Spergularia* (SEM). A: general view; B, C: surface fragments. 1 — *S. media* (Sample No. 039201); 2 — *S. marina* (Sample No. 118580); 3 — *S. salina* [*S. marina*] (Sample No. 00110115); 4 — *S. rubra* (Sample No. 00110926)

of *S. marina*. However, after a subsequent detailed study of *S. media* and *S. marina* in the Netherlands, he concluded that the taxa *S. media* and *S. marina* are morphologically, karyogenetically and also ecologically distinct. Sterk (1969) also pointed out the considerable variability and the presence of smooth and tuberculate seeds, which may be winged or wingless in both species.

Spergularia salina J. Presl & C. Presl (Fig. 2, 3A–C).

We have also studied the ultrastructure of the seed surface of *Spergularia salina*. In all carpological characteristics, *S. salina* is similar to *S. marina*, so we provide only SEM images of the seeds without their description. The absence of macro- and micromorphological differences is an

additional confirmation that they are in fact the same species, *S. marina* (Dobignard, Chatelain, 2011; Chang et al., 2021) and *S. salina* is a synonym, according to the priority of the species-rank name (see Principle III and Art. 11 of the *ICN*: Turland et al., 2018).

Spergularia rubra (L.) J. Presl & C. Presl (Fig. 2, 4A–C).

Seeds flattened at sides, ovate-triangular, broadly pyriform to semicircular in outline, wingless 0,4–0,6 mm long, with a submarginal furrow and a furrow only on the dorsal side. Hilum in the depression barely visible, radicle clearly protruding. Seed surface almost smooth or slightly uneven due to the slight convexity and concavity of some outer periclinal walls of testa cells. Contours of the anticlinal walls clear. Anticlinal walls concave, deeply curved on the dorsal and lateral surfaces of seed. Periclinal walls of the testa cells with a slight uniform elevation in the centre, giving the surface an uneven appearance. Some cells with large (up to 10 μm) warty papillae on the surface of periclinal walls, in their central part. These in turn are covered with smaller papillae, as is the entire surface of the periclinal walls. At higher magnification (×10,000), dotted papillose formations are visible between the papillae of the periclinal cell walls. There is no waxy coating. Matte, gray-brown, brown to black.

The results of our studies on the shape and ultrastructure of the seed surface of species of the genera *Spergula* and *Sperularia* mainly confirmed the current literature data on their taxonomy and nomenclature. In particular, we found no significant differences in the morphology of the seeds of *Spergula arvensis* and *Spergula vulgaris*, which is an additional argument for considering *Spergula vulgaris* as a synonym of *Spergula arvensis.* No differences were found in morphology of seeds of *Spergula morisonii* and *Spergula vernalis*, which is another evidence to interpret *Spergula vernalis* as a synonym of *Spergula morisonii.* At the same time, the observed differences in seed morphology between *Spergula sativa* and *Spergula arvensis* do not support the view that *Spergula sativa* is a synonym of *Spergula arvensis*. In contrast to *Spergula arvensis*, the surface of seeds of *Spergula sativa* has clear anticlinal cell walls, distinct tubercles and a darker colour due to the absence of light brown club-shaped papillae. No waxy deposits were found on the seed surface.

No differences in the morphology of the seed samples of *Spergularia salina* and *Spergularia marina* were found, which is also evidence for considering *Spergularia salina* as a synonym of *Spergularia marina*.

Thus, as a result of the study of macro- and micromorphological features of the seeds of representatives of the genera *Spergula* and *Spergularia* occurring in Ukraine, their detailed morphological characteristics were compiled. The seeds of some species of these genera are similar in appearance (especially with the broad-winged *Spergula morisonii* and *Spergularia marina*), which confirms the taxonomic relationship of the genera. However, at the generic level, some differences were found between them (characteristics of the wing margin and ultrastructural tests). The remaining species of these genera examined differed significantly in both seed shape and ultrastructure. The revealed macro- and micromorphological differences confirm the literature data (Kool, 2012; Fedoronchuk, 2023; etc.) regarding the lack of reasonable arguments in favor of combining these genera into one genus. These two genera are also recognized in modern taxonomic databases (IPNI, 2024; POWO, 2024; WFO, 2024). At the species level, within each genus, some species differ from each other in a number of macro- and microstructural characters. Based on the identified carpological characters, we consider *Spergula sativa* and *S. maxima* to be subspecies of *S. arvensis (S. arvensis* ssp. *sativa* and *S. arvensis* ssp. *maxima)* as suggested, based on morphological and geographical analysis, by one co-author of our present publication (Fedoronchuk, 2023). However, in modern databases or species lists they are presented as synonyms of *S. arvensis* (POWO, 2024; WFO, 2024).

In our opinion, all the observations on the ultrastructure of the seeds of *Spergula* and *Spergularia* provide knowledge on the diversity of this group, as a result of which the characteristics of the seeds may be useful in the identification of this particular species. The obtained research results may be important for further taxonomic studies of representatives of these genera.

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ETHICS DECLARATION

The authors declare no conflict of interest.

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Морфологія насінин видів *Spergula* і *Spergularia* (*Caryophyllaceae*) флори України та її систематичне значення

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Реферат. Досліджено мікро- та макроморфологічні характеристики насінин видів родів *Spergula* та *Spergularia* флори України з метою виявлення нових діагностичних ознак для вирішення таксономічних питань. Ультраструктуру поверхні насінин вивчали за допомогою сканувального електронного мікроскопа. Насінини деяких видів цих родів схожі за зовнішнім виглядом (особливо ті, що мають широке крило, наприклад *Spergula morisonii* і *Spergularia marina*). Це може бути одним з підтверджень таксономічної спорідненості цих родів. Результати показали, що ультраструктури поверхні насінин відрізняються всередині досліджених родів і для деяких видів можуть бути використані як допоміжні діагностичні ознаки для їхньої ідентифікації. Отримані дані підтверджують результати наших попередніх досліджень щодо таксономічного статусу представників досліджених таксонів. Зокрема, враховуючи подібність ультраструктури насінин та інші характеристики, які були запропоновані раніше, вважаємо *Spergula vulgaris* синонімом *Spergula arvensis* subsp. *arvensis*, *S. vernalis* — синонімом *S. morisonii*, *Spergularia media* — синонімом *Spergularia marina*, *Spergularia salina* — синонімом *Spergularia marina*. Виявлені відмінності в ультраструктурі поверхні насінин *Spergula sativa* та *Spergula arvensis* subsp. *arvensis* узгоджуються з нашим розумінням єдиного таксону як *Spergula arvensis* subsp. *sativa*. Відповідно, зважаючи на відмінності між *Spergula maxima* та *Spergula arvensis* subsp. *arvensis*, ми пропонуємо приймати назву *Spergula arvensis* subsp. *maxima*. Складені описи ультраструктури поверхні насінин видів *Spergula* та *Spergularia*, зібраних з території України, можуть бути корисними для оцінки можливої мінливості ознак цих видів з інших регіонів світу.

Ключові слова: мікроморфологія, скануючий електронний мікроскоп (СЕМ), ультраструктура, насінини, таксономія