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Spatio-temporal differentiation of distribution patterns of *Salicornia perennans*, *Halimione verrucifera*, and *Suaeda cf. prostrata* (*Chenopodiaceae*) in the plain part of Ukraine during the Allerød–Holocene

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Abstract. The article provides paleofloristic evidence for the history of formation of modern halophytic vegetation in the plain part of Ukraine. Pollen grains of representatives of selected taxa of the family *Chenopodiaceae*, which belong to the ecological group of halophytes, are important components of palynological characteristics of the Pleistocene–

Holocene deposits. Results of species-level identifications of halophyte fossil pollen provide a solid basis for the reconstruction of distribution patterns of plant communities on saline soils in space and time. Our analysis of paleofloristic data included both the original results of species-level identifications of pollen grains of *Chenopodiaceae* and the relevant literature data. The objective of the present research was to analyze and generalize the results of paleofloristic studies that provide evidence on the participation of three characteristic species (*Salicornia perennans*, *Halimione verrucifera*, and *Suaeda cf. prostrata*) in the palynofloras of the Allerød–Holocene deposits of the Right-Bank and Left-Bank parts of the Forest, Forest-Steppe, and Steppe physiographic and vegetation zones of Ukraine. The selected model species at present predominantly occur on wet solonchaks within the present-day Steppe Zone of Ukraine. Only occasionally they occur in the southern parts of the Left-Bank area of the Forest-Steppe Zone. It is worth noting that *S. perennans*, *H. verrucifera* and *S. cf. prostrata* can be also considered as indicators of changes of soil conditions in the past. To increase the reliability of specific-level identifications of fossil pollen of these model taxa, additional palynomorphological studies using both light microscopy and scanning electronic microscopy were performed. The generalized results of paleofloristic studies (fossil palynofloras in deposits of 12 sections) allowed tracing the spatiotemporal differentiation of distribution patterns of *S. perennans*, *H. verrucifera*, and *S. cf. prostrata* in the plain part of Ukraine during the Allerød–Holocene. We first reconstructed both a history of the dynamic ranges (areas of distribution/occurrence) of each of these three indicator species of halophytic vegetation and paleofloristic evidence of distribution of saline soils (in particular, wet salt meadows, salt marshes) in the plain part of Ukraine in space and time for the considered period. It is worth emphasizing that, as compared to the Right-Bank area, paleofloristic materials presently available demonstrate that the processes of soil salinization were more common in the territory of the Left Bank of the Forest and Forest-Steppe zones of Ukraine during the Late (Younger) Dryas. This trend is also quite clearly traced in the Holocene. *Salicornia perennans*, *H. verrucifera*, and *Suaeda cf. prostrata* most often participated in the formation of plant communities common in saline soils during the Early (PB, BO) and Middle (SB) Holocene in the Left-Bank area of the Forest-Steppe Zone. Due to the results of palynomorphological studies, additional qualitative and quantitative diagnostic characters have been identified and summarized; these characters can be used in the future for species-level identification of pollen grains of *S. perennans*, *H. verrucifera*, and *S. cf. prostrata* in the spore-pollen analysis of deposits of the Quaternary of Northern Eurasia.

Key words: paleofloristics, palynoflora, halophytes, Allerød–Holocene, pollen grains, morphology, spore-pollen analysis, Ukraine

Просторово-часова диференціація поширення *Salicornia perennans*, *Halimione verrucifera* та *Suaeda cf. prostrata* (*Chenopodiaceae*) на рівнинній частині України впродовж алереду–голоцену

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Анотація. В статті розглядається питання палеофлористичного обґрунтування історії формування сучасної галофітної рослинності на рівнинній частині України. Пилкові зерна представників родини *Chenopodiaceae* Vent., які відносяться до екологічної групи галофітів, є однією з вагомих складових палінологічних характеристик відкладів плейстоцену–голоцену. Результати видової ідентифікації викопного пилку галофітів створюють надійну основу для реконструкції поширення рослинних угруповань на засоленних ґрунтах в просторі та часі. До аналітичної обробки палеофлористичних матеріалів видового рівня були залучені як отримані нами результати видової ідентифікації пилкових зерен *Chenopodiaceae*, так і літературні дані. Метою статті були аналіз та узагальнення результатів палеофлористичних досліджень, які свідчать про участь трьох модельних видів (*Salicornia perennans*, *Halimione verrucifera* та *Suaeda* cf. *prostrata*) в палінофлорах відкладів алереду–голоцену Правобережної та Лівобережної частин Лісової, Лісостепової та Степової зон України. Зазначимо, що обрані нами модельні види, сьогодні поширені переважно на мокрих солончаках на території Степової зони. Зрідка вони трапляються на півдні Лівобережжя Лісостепової зони. Варто наголосити, що *S. perennans*, *H. verrucifera* та *S. cf. prostrata* можна також розглядати і як індикатори змін ґрунтових умов в минулому. Для підвищення ступеня обґрунтованості видових визначень викопного пилку цих модельних таксонів було проведено їхнє паліноморфологічне дослідження з використанням як світлової, так і електронної сканувальної мікроскопії. Отримані та узагальнені результати палеофлористичних досліджень (викопні палінофлори відкладів 12 розрізів) дозволили простежити просторово-часову диференціацію поширення *S. perennans*, *H. verrucifera* та *S. cf. prostrata* на рівнинній Україні впродовж алереду–голоцену. Нами вперше було реконструйовано як історію поширення кожного з цих індикаторних видів галофітної рослинності, так і наведено палеофлористичне обґрунтування поширення засоленних ґрунтів (мокрі солончаки) на рівнинній Україні в просторі та часі. Важливо наголосити, що порівняно з Правобережжям наявні на цей час палеофлористичні матеріали свідчать про більше поширення процесів засолення ґрунтів на території Лівобережжя Лісової та Лісостепової зон України впродовж пізнього дріасу. Ця тенденція досить чітко простежується і в голоцені. *S. perennans*, *H. verrucifera* та *S. cf. prostrata* найчастіше брали участь у формуванні рослинних угруповань, поширених на засоленних ґрунтах впродовж раннього (PB, BO) та в середньому (SB) голоцені на території Лівобережжя Лісостепової зони. За результатами паліноморфологічних досліджень були встановлені та узагальнені діагностичні ознаки якісного та кількісного рівнів, які перспективно використовувати для видової ідентифікації викопних пилкових зерен *S. perennans*, *H. verrucifera* та *S. cf. prostrata* в практиці спорово-пилкового аналізу відкладів квартеру Північної Євразії.

Ключові слова: палеофлористика, палінофлора, галофіти, алереду–голоцен, пилкові зерна, морфологія, спорово-пилковий аналіз, Україна

Introduction. In Ukraine, the main stages of studies of modern halophilous vegetation and complicated issues of its classification were comprehensively considered in the pioneering work by G.I. Bilyk (1963). Subsequently, integrated studies of this azonal type of vegetation allowed obtaining new data, developing modern approaches for their interpretation, and producing an updated syntaxonomic scheme for communities of the halophyton in Ukraine (Dubyna, Dziuba, Neuhäuslova, Solomakha, Tyshchenko, Shelyag-Sosonko, 2007). Results of analyses of the taxonomic composition of the halophyte flora of Ukraine demonstrated that most of halophilous species occurring here belong to the family *Chenopodiaceae* Vent. These species play a significant role in the formation of the ecological group of halophytes that are common in the territory of modern Steppe and Forest-Steppe zones of Ukraine (Bilyk, 1963).

In modern palynology of the Pleistocene and Holocene deposits of Ukraine, many problems of paleobotanical and paleoecological reconstructions can be solved by increasing the number of more reliable species-level identification of components of fossil palynofloras (Bezusko, Mosyakin, Bezusko, 2011; Mosyakin, Bezusko, Tsybalyuk, 2017; Andrieieva, 2011; Gerasimenko, Korzun, Ridush, 2014; Sirenko, 2017; Bezusko, Tsybalyuk, Mosyakin, 2018). In this context, identifications of fossil pollen grains of representatives of *Chenopodiaceae* provide significant components for such reconstructions

(Monoszon, 1985; Pashkevich, 1987; Grichuk, 1989; Bolikhovskaya, 1995; Komar, 2000; Yelovicheva, 2001; Velichko, Zelikson, 2001; Bezusko, Mosyakin, Tsybalyuk, 2003, 2006; Bezusko, Mosyakin, Bezusko, 2011; Andieieva, 2010, 2011; Korniets, Komar, 2001). Such more accurate identifications are also important for solving many problems of the present-day indicative paleofloristics (Monoszon, 1973a). The successful development of paleofloristic studies was facilitated by the results of a thorough palynomorphological study of taxa of *Chenopodiaceae* conducted by M.H. Monoszon (1973b). At the present stage of palynological studies of the Pleistocene and Holocene deposits in Ukraine, we used for our species-level identification of pollen grains of *Chenopodiaceae* both a traditional identification key proposed by M.H. Monoszon (1973b) and new palynomorphological approaches that resulted from research by Z.M. Tsybalyuk (Tsybalyuk, 2005; Tsybalyuk, Mosyakin, Bezusko, 2005) focused on pollen morphology of *Chenopodiaceae* of Ukraine using light and scanning electron microscopy.

It can be argued that a high degree of reliability of paleobotanical and paleoecological reconstructions is achieved with comprehensive application of paleopalynological and palynomorphological (actuopalynological) data, and that has been taken into account when formulating the purpose of the present article.

The objective of our present research was to

analyze the lists of species of *Chenopodiaceae* in the palynofloras of the Allerød–Holocene sediments of the plain part of Ukraine and to determine the participation of the three model species: *Salicornia perennans* Willd., *Halimione verrucifera* (M. Bieb.) Aellen, and the species complex of *Suaeda* cf. *prostrata* – *S.* cf. *salsa* (L.) Pall.; these taxa belong to the ecological group of typical halophytes (occurring mainly in wet salt marshes, solonets and solonchak types). Another objective was to reconstruct their distribution in space and time and, using the example of these model taxa, to present the results of palynomorphological studies as revealing the patterns of formation of the present-day halophytic vegetation within the territory of Ukraine.

In the modern flora of Ukraine, *Salicornia perennans* Willd. (= *S. prostrata* Pall., nom. illeg.; *S. herbacea* auct. non L., *S. europaea* auct. non L., p.p.) occurs in the Steppe, southeastern Left Bank areas of the Forest–Steppe zones, and in steppe and maritime habitats of Crimea. The range of *S. perennans* covers areas of continental and coastal saline habitats (Opredelitel vysshikh rastenyi Ukrainy, 1987; Monoszon, 1973a). *Salicornia perennans* has a root system in the surface layers of wet to moist highly saline soils. The species is part of plant communities of wet saline soils and is an indicator of strongly mineralized chloride salinization of groundwater. The plant communities of *S. perennans* belong to the true solonchak succulent-herbaceous vegetation (Bilyk, 1963). Taxonomy and nomenclature of the species is accepted here following N.N. Tzvelev (1993, 1996a) and H. Freitag (2011). In earlier Ukrainian and East European publications [Iljin, 1936, 1952, and references therein] the names *S. prostrata*, *S. herbacea* (auct. non L., p.p.), and *S. europaea* (auct. non L., p.p.) were commonly used (mainly misapplied) to our species.

Halimione verrucifera (M. Bieb.) Aellen (= *Atriplex verrucifera* M. Bieb.) occurs along the shores of the Black Sea and the Sea of Azov on wet saline soils (solonets and solonchak). Occasionally isolated exclaves of the species occur on the Left Bank of the Forest–Steppe zone (Bilyk, 1963; Opredelitel vysshikh rastenyi Ukrainy, 1987). Communities of *H. verrucifera* belong to the true solonchak semi-shrub (subshrub) vegetation (Bilyk, 1963).

Two related species of *Suaeda* sect. *Brezia* (Moq.) Volkens (= sect. *Heterosperma* Iljin), *Suaeda prostrata* Pall. and *S. salsa* (L.) Pall., are distributed in Ukraine in the south of the Forest–Steppe Zone (occasionally), in the Steppe Zone, and in Crimea on wet solonchaks (Bilyk, 1963; Opredelitel vysshikh

rastenyi Ukrainy, 1987). Nomenclature of these and some other taxa of *Suaeda* was rather confused (see Iljin 1936, 1952; Tzvelev, 1996b); here we accept the taxonomic and nomenclatural scheme proposed by H. Freitag and M. Lomonosova (2006). Since the pollen grains of these taxa are similar (probably somewhat larger in tetraploid *S. salsa*) and these two species were often not distinguished (or misidentified) in the past, we use here for fossil pollen the conventional identification "*Suaeda* cf. *prostrata*". The present-day communities with participation of *S. prostrata* and *S. salsa* belong mainly to the true solonchak succulent-herbaceous vegetation (Bilyk, 1963).

Materials and methods. In order to achieve the objectives of our research, the two main blocks of studies were performed. The basic method during paleofloristic studies was spore-pollen analysis of the species composition of *Chenopodiaceae* in the palynofloras of the Allerød–Holocene deposits of sections in the plain part of Ukraine. Fossil pollen grains of the three model taxa of halophytic vegetation (*Salicornia perennans*, *Halimione verrucifera* and *Suaeda* cf. *prostrata*) were identified. We used both original species-level identifications of paleofloristic material, based on our identification approach for *Chenopodiaceae* (Bezusko, Mosyakin, Bezusko, 2011), and available data from literature (Andrieieva, 2010, 2011; Korniets, Komar, 2001). The main attention was paid to the presence/absence of pollen of the model taxa in the fossil palynofloras, which served as the base for further reconstruction of their distribution patterns in space and time.

The palynomorphological part of this study was aimed at increasing the level of reliability of species-level identifications of fossil pollen of *Salicornia perennans*, *Halimione verrucifera*, and *Suaeda* cf. *prostrata*. Pollen grains were sampled in the National Herbarium of Ukraine (KW, herbarium of the M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine). For light microscopy (CM, Biolar) the material was treated according to the generally accepted acetolysis method (Erdtman, 1952). For studies of pollen under a scanning electron microscope (CEM, JSM-6060 LA), the material was fixed in 96% ethanol and sputter-coated with gold using the standard methods (Tsybalyuk, Mosyakin, 2013). Morphology of pollen grains was described using the commonly used terminology (Kupriyanova, Aleshina, 1972; Punt, Hoen, Blackmore, Nilsson, Le Thomas, 2007), with minor adjustments.

Results and their analysis. Spatiotemporal distribution patterns of *Salicornia perennans*, *Halimione verrucifera*, and *Suaeda* cf. *prostrata* in

the plain part of Ukraine were revealed according to the results of processing of the lists of species of *Chenopodiaceae* in the palynofloras of the Allerød–Holocene deposits of 12 sections: Doroshiv (Lviv Region), Ikva–I (Ternopil Region), Kukarins'ke (Chernihiv Region), Roman'kovo (Sumy Region), Komarivka (Kharkiv Region), Chugmak (Cherkasy Region), Orzhytsya and Perevod (Poltava Region), Kardashins'ke–II (Kherson Region), Kam'yana Mohyla and Chapayivka (Zaporizhzhya Region), and Razdol'ne (Donetsk Region).

Data on the presence/absence of pollen grains of the model taxa in Allerød–Holocene palynofloras provide new amended information on the composition and distribution of representatives of halophytic vegetation of Ukraine in space and time. It should be noted that the selected model species are now distributed mainly on wet saline soils within the territory of the present-day Steppe Zone of Ukraine. Occasionally they (or some of them) occur in the southern part of the Left bank of the Forest–Steppe Zone. It is worth noting that *S. perennans*, *H. verrucifera* and *S. cf. prostrata* can also be considered as indicators of changes in soil conditions in the past.

The obtained paleofloristic material provides the basis for reconstructions of the history of possible range changes of *H. verrucifera*, *S. perennans*, and *S. cf. prostrata* in the territory of the Forest, Forest–Steppe, and Steppe zones of Ukraine in the Allerød–Holocene (Table).

The results of our analysis of the species composition of *Chenopodiaceae* in fossil palynofloras of the last climatic rhythm of the Late Glacial indicate the participation of the three model species (*Halimione verrucifera*, *Salicornia perennans*, *Suaeda cf. prostrata*) in the halophytic vegetation of the studied area.

Palynofloras of deposits: SA – Subatlantic, SB – Subboreal, AT – Atlantic, BO – Boreal, PB – Preboreal times of the Holocene; DR–3 – Late (Younger) Dryas, AL – Allerød; «+» – presence of pollen grains in fossil palynofloras; «–» – absence of pollen grains in fossil palynofloras.

It has been demonstrated that *S. perennans* during the Allerød participated in the formation of halophytic vegetation in the territory of the Right Bank of the present-day Forest Zone area of Ukraine (sections Doroshiv and Ikva–I). During the same time interval both *S. perennans* and *S. cf. prostrata* were found in the Left-Bank area of the present-day Forest Zone (Kukarins'ke section).

During the Late (Younger) Dryas, *S. perennans* (sections Doroshiv and Ikva–I), *H. verrucifera*

(sections Doroshiv and Ikva–I), and *S. cf. prostrata* (section Ikva–I) were components of halophytic vegetation on the Right Bank of the present-day Forest Zone. On the Left Bank of the Forest Zone, halophytic plant communities were formed with participation by *S. perennans* (sections Kukarins'ke and Roman'kovo), *H. verrucifera* (Roman'kovo section), and *S. cf. prostrata* (Kukarins'ke section). It should be noted, however, that there is no information available about the presence of fossil pollen grains of *S. perennans*, *H. verrucifera* and *S. cf. prostrata* in the Right Bank area of the Forest–Steppe Zone during the Allerød and Late Dryas. In the Late Dryas, *S. perennans* (Orzhytsya and Chugmak sections), *H. verrucifera* (Orzhytsya section), and *S. cf. prostrata* (Chugmak section) participated in the formation of halophytic plant communities on the Left Bank of the Forest–Steppe Zone.

The results of our analysis of the species composition of *Chenopodiaceae* in fossil palynofloras of the Holocene deposits on the plain part of Ukraine indicate the presence of *S. perennans*, *H. verrucifera*, and *S. cf. prostrata* in the territory of the plain part of Ukraine, including some continental habitats. However, there is no information yet available about occurrence of halophilic communities with participation of *S. perennans* in the territory of the Right Bank of the Forest Zone in the Holocene, but *H. verrucifera* participated in the formation of halophytic vegetation in the Right Bank area of the present-day Forest Zone in the Preboreal times (sections Doroshiv and Ikva–I), while *S. cf. prostrata* was registered there at the Boreal times of the Holocene (Ikva–I section). Plant communities with *S. perennans* occurred on the Left Bank of the modern Forest Zone in the Preboreal and Subboreal times (Roman'kovo section). However, it looks like *H. verrucifera* was present among components of halophilic vegetation in that area during the Preboreal, Boreal, and Subboreal times of the Holocene (Roman'kovo section). That probably indicates that this species had a much larger range at least in the Early Holocene, as compared to its present-day range.

It should be emphasized that there is no information available on the occurrence of halophytic communities with participation of *S. perennans*, *H. verrucifera*, and *S. cf. prostrata* in the territory of the Right-Bank part of the Forest–Steppe Zone in the Holocene. The results of our analysis of palynofloras of the Holocene deposits on the Left-Bank area of the Forest–Steppe Zone indicate some participation of *S. perennans* in plant communities on saline soils in the Preboreal (Orzhytsya section), Boreal

Table. Spatiotemporal patterns of distribution of the model species of halophytes in the plain part of Ukraine in the Allerød–Holocene

Taxon	Palynofloras of deposits of the Allerød–Holocene						
	SA	SB	AT	BO	PB	DR-3	AL
Forest Zone, Right Bank area							
<i>Salicornia perennans</i> (= <i>S. prostrata</i>)	–	–	–	–	–	+	+
<i>Halimione verrucifera</i> (= <i>Atriplex verrucifera</i>)	–	–	+	+	+	+	–
<i>Suaeda</i> cf. <i>prostrata</i>	–	–	–	+	+	+	–
Forest Zone, Left Bank area							
<i>Salicornia perennans</i> (= <i>S. prostrata</i>)	–	+	–	–	+	+	+
<i>Halimione verrucifera</i> (= <i>Atriplex verrucifera</i>)	–	+	–	+	+	+	–
<i>Suaeda</i> cf. <i>prostrata</i>	–	–	–	–	–	–	+
Forest-Steppe Zone, Right Bank area							
<i>Salicornia perennans</i> (= <i>S. prostrata</i>)	–	–	–	–	–	–	–
<i>Halimione verrucifera</i> (= <i>Atriplex verrucifera</i>)	–	–	–	–	–	–	–
<i>Suaeda</i> cf. <i>prostrata</i>	–	–	–	–	–	–	–
Forest-Steppe Zone, Left Bank area							
<i>Salicornia perennans</i> (= <i>S. prostrata</i>)	–	+	–	+	+	+	–
<i>Halimione verrucifera</i> (= <i>Atriplex verrucifera</i>)	–	+	–	+	+	+	–
<i>Suaeda</i> cf. <i>prostrata</i>	–	–	–	+	–	+	–
Steppe Zone, Right Bank area							
<i>Salicornia perennans</i> (= <i>S. prostrata</i>)	–	–	–	–	–	–	–
<i>Halimione verrucifera</i> (= <i>Atriplex verrucifera</i>)	–	–	–	–	–	–	–
<i>Suaeda</i> cf. <i>prostrata</i>	–	–	–	–	–	–	–
Steppe Zone, Left Bank area							
<i>Salicornia perennans</i> (= <i>S. prostrata</i>)	+	–	–	–	–	–	–
<i>Halimione verrucifera</i> (= <i>Atriplex verrucifera</i>)	–	–	–	–	–	–	–
<i>Suaeda</i> cf. <i>prostrata</i>	+	–	+	–	–	–	–

Palynofloras of deposits: SA – Subatlantic, SB – Subboreal, AT – Atlantic, BO – Boreal, PB – Preboreal times of the Holocene; DR-3 – Late (Younger) Dryas, AL – Allerød; "+" – presence of pollen grains in fossil palynofloras; "-" – absence of pollen grains in fossil palynofloras.

(sections Komarivka and Perevod), and Subboreal (sections Orzhytsya, Komarivka, and Perevod) times of the Holocene. Paleofloristic material confirms the Holocene distribution of *H. verrucifera* in the studied area in the Preboreal (Orzhytsya section) and Boreal and Subboreal (sections Orzhytsya and Perevod) times. *Suaeda* cf. *prostrata* was present in this area (section Chugmak) during the Boreal time of the Holocene.

The participation of *Salicornia perennans* and *Suaeda* cf. *prostrata* in the formation of halophytic vegetation of the Steppe Zone is confirmed only for its Left Bank part. We confirmed the occurrence of *S. perennans* during the Subatlantic times (section Kardashins'ke–II) and that of *S. cf. prostrata* in the Atlantic (sections Kam'yana Mohyla, Razdol'ne,

and Chapayivka) and Subatlantic (Razdol'ne section) times of the Holocene.

Pollen grains of *S. perennans*, *H. verrucifera* and *S. cf. prostrata* are also representatives of halophytic *Chenopodiaceae* present in the subfossil spore-pollen spectra of the Steppe Zone of Ukraine. We can thus conclude that pollen grains of these three species form the dominant complex in the subfossil (or almost recent) spore-pollen spectra of the Artemisia–grass (Artemisia + Poaceae) steppes of the present-day Steppe Zone of Ukraine (areas with halophytic vegetation) (Bezusko, Mosyakin, Bezusko, 2011).

The obtained and generalized results of paleofloristic studies allowed to trace the spatiotemporal differentiation of distribution patterns of *S. perennans*, *H. verrucifera* and *S. cf. prostrata* in the plain part

of Ukraine during the Holocene. The reconstructed history of distribution of each of these indicator species of halophytic vegetation indicates the spread of saline soils (wet salt meadows) in the plain part of Ukraine in space and time. It is important to emphasize that paleofloristic materials available indicate more frequent salinity processes in the territory of the Left Bank of the Forest and Forest–Steppe zones of Ukraine during the Late Dryas, as compared to the Right Bank area. This trend is also quite clearly observed in the Holocene. *Salicornia perennans*, *Halimione verrucifera* and *Suaeda* cf. *prostrata* most often participated in the formation of plant communities in saline soils during the Early (Preboreal, Boreal) and Middle (Subboreal) Holocene on the Left Bank of the Forest–Steppe zone. The history of distribution of *S. perennans*, *H. verrucifera* and *S. cf. prostrata* reconstructed here for the plain part of Ukraine during the Holocene is in agreement with palaeopalynological data on the presence of saline soils on the Left Bank of the Forest–Steppe Zone reported by other researchers (Artiushenko, 1970; Korniets, Komar, 2001; Bezusko, Mosyakin, Bezusko, 2011).

Species-level identifications of fossil pollen grains of *Chenopodiaceae* are largely based on palynomorphological studies of representative modern material (Tsybalyuk, Mosyakin, Bezusko, 2005; Bezusko, Mosyakin, Tsybalyuk, 2003, 2006; Bezusko, Bezusko, Mosyakin, Tsybalyuk, 2007; Bezusko, Mosyakin, Bezusko, 2011). In the following part of our research, the main focus is on the palynomorphological study of the three indicator species of halophytes.

***Halimione verrucifera* (M. Bieb.) Aellen** (Figure, 1–4).

LM. Pollen grains pantoporate, spheroidal, in outline circular, slightly undulate on edges. Diameter of pollen grains 18.6–22.6 μm . Number of pores 40–62, pore diameter 2.0–2.7 μm , pores with distinct or indistinct margins; border thin, mainly distinct, and rarely indistinct. Sculptural elements of the pore membrane centrally located or occupying most of the surface. Distance between adjacent pores 1.3–2.4 μm , between the centers of pores – 3.3–5.0 μm . Exine 2.4–2.7 μm thick. Columellae indistinct or distinct, long, arranged regularly. Endexine thin, regularly thickened. Exine texture indistinct, medium-punctate.

SEM. Sculpture spinulate. Spinules small, elongated, with acute apex, located with average density. Pore membrane with sparse spinules. Spinules 6–12, different in size, occasionally with merging bases, arranged unevenly.

Specimens investigated: 1. Crimea, Kerch

Peninsula, Cape Kazantip, sands. 18.VIII 1976. O. Dubovik (KW). 2. Mariupol District, Berdyansk, solonets. 26.VIII 1929. M. Kotov (KW).

***Salicornia perennans* Willd.** (Figure, 5–8).

LM. Pollen grains pantoporate, spheroidal, rarely oval, in outline almost circular, slightly undulate or undulate on edges. Diameter of pollen grains 22.6–29.3 μm . Number of pores 36–62, pore diameter 2.4–4.0 μm , pores with distinct or indistinct margins; border thin, mainly distinct, and rarely indistinct. Sculptural elements of pore membrane centrally located or occupying most of the surface. Distance between adjacent pores 2.0–2.7 μm , between the centers of pores – 4.4–7.3 μm . Exine 1.6–2.7 μm thick. Columellae indistinct. Endexine thin, irregularly thickened. Exine texture indistinct, small-punctate (barely visible).

SEM. Sculpture spinulate. Spinules minute, rounded, with blunt apex, located sparsely and more or less evenly. Pore membrane with sparse spinules. Spinules 3–10, different in size, arranged unevenly.

Specimen investigated: On solonets places in the floodplain of the Donets, near Verhne [? illegible], Lisichansky District [now within Lysychansk town], Voroshilovgrad [now Luhansk] Region. 10.VIII 1939. F. Hryn' (KW).

***Suaeda prostrata* Pall.** (Figure, 9–12)

LM. Pollen grains pantoporate, spheroidal, in outline almost circular, slightly undulate on edges. Diameter of pollen grains 22.6–25.3 μm . Number of pores 54–64, pore diameter 1.3–2.0 μm ; border thin, distinct. Sculptural elements of pore membrane centrally located. Distance between adjacent pores 2.0–2.4 μm , between the centers of pores – 3.3–4.0 μm . Exine 2.0–2.7 μm thick. Columellae indistinct. Endexine thin, regularly thickened. Exine texture distinct, small-punctate.

SEM. Sculpture spinulate. Spinules minute, rounded, with acute apex, located rarely and evenly. Pore membrane with sparse spinules. Spinules 5–7, different in size, arranged unevenly.

Specimen investigated: Kherson Region, Genichesk District, near Sivash st. [station?], solonchak. 31.VIII 1971. N. Loskot (KW).

For each of the three model species, descriptions and photomicrographs of pollen grains are presented. The additional morphological characters can be used in the practice of paleopalynological research, which may significantly increase the degree of reliability of species-level identifications of fossil pollen grains.

Conclusions. For the first time, three model taxa belonging to the ecological group of halophytes (*Salicornia perennans*, *Halimione verrucifera*, and

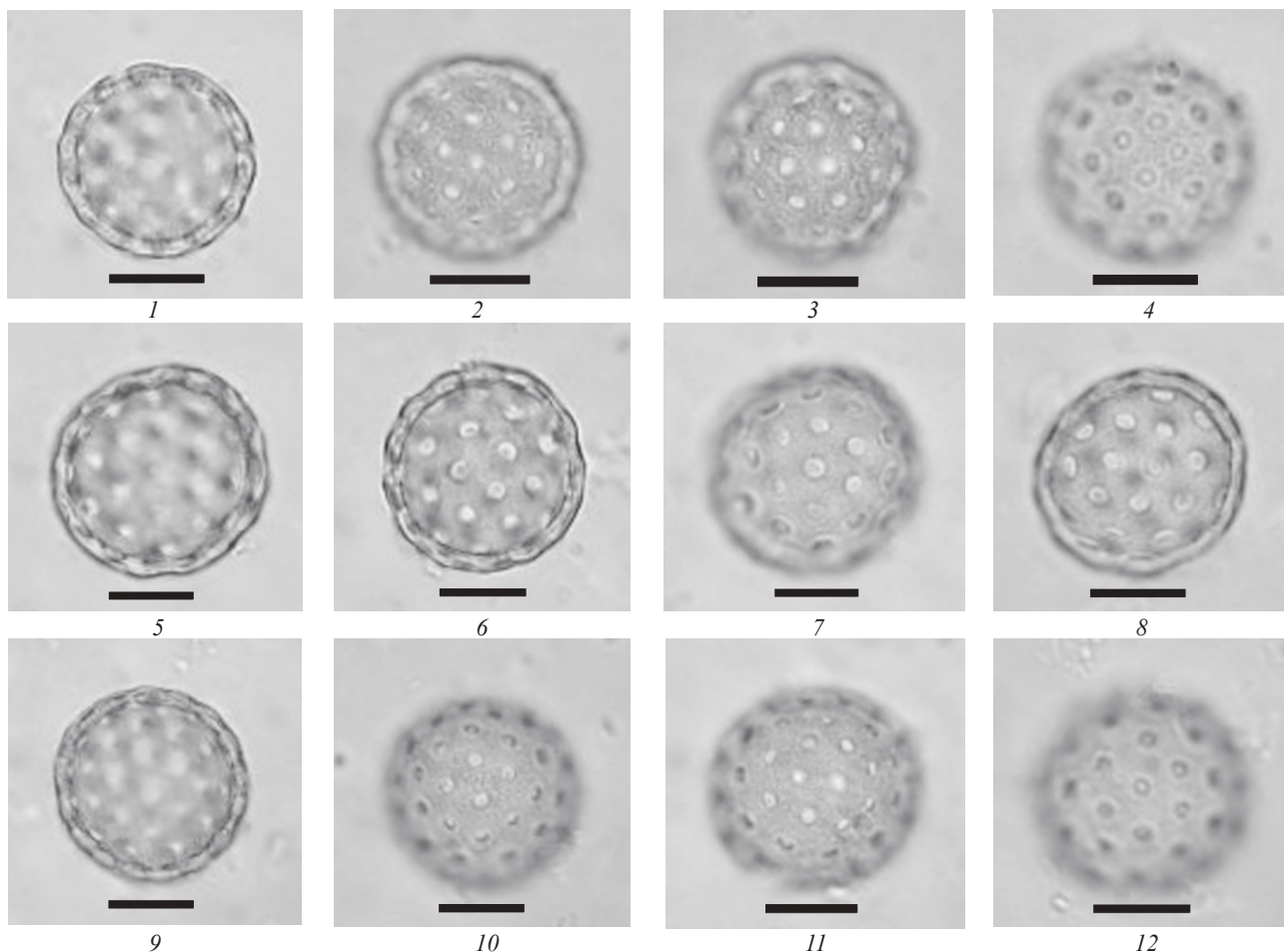


Figure. Pollen grains of the studied species (light microscopy): 1–4 – *Halimione verrucifera*; 5–8 – *Salicornia perennans*; 9–12 – *Suaeda prostrata*. Scale bars: 1–12 – 10 μm

Suaeda cf. prostrata) have been identified in the fossil palynofloras of the Allerød–Holocene deposits in the plain part of Ukraine (Forest, Forest–Steppe, and Steppe zones). Based on case studies of these species, we reconstructed the spatiotemporal differentiation of their distribution in the composition of halophytic vegetation in the plain part of Ukraine during the Allerød–Holocene. Paleofloristic evidence of the presence of saline soils (mainly wet solonchaks) in the plain part of Ukraine during the Allerød–Holocene is provided. It has been demonstrated that the studied paleofloristic material shows somewhat wider distribution of soil salinity processes in the territory of the Left Bank of the present-day Forest and Forest–Steppe zones of Ukraine during the Late Dryas. The obtained and summarized results of paleofloristic studies indicate that the same trend is also quite clearly traced in the Holocene. *Salicornia perennans*, *Halimione verrucifera*, and *Suaeda cf. prostrata* most often participated in the formation of plant communities widespread in saline soils during the Early (Preboreal, Boreal) and Middle (Subboreal) Holocene on the Left Bank of the present-day Forest–Steppe Zone. The qualitative and quantitative

diagnostic characters are promising for species identification of fossil pollen grains of *Salicornia perennans*, *Halimione verrucifera*, and *Suaeda cf. prostrata* for spore-pollen analysis of deposits of the Quaternary.

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