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RESEARCH PAPER

CLASSIFICATION OF OPEN HABITATS IN THE PALAEARCTIC

Syntaxonomy of steppe depression vegetation of Ukraine

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Abstract

Aims: To revise the syntaxonomy of the vegetation of steppe depressions (*pody*), in particular (1) to identify the associations and to reveal their environmental, structural and compositional peculiarities; (2) to assign the associations to higher syntaxa; and (3) to correct nomenclatural aspects according to the ICPN.

Study area: Steppe zone of Ukraine, Left-Bank of the Lower Dnieper basin.

Methods: 641 relevés were included in the final analysis in the PCOrd program integrated into Juice software. Two expert systems (EVC and EUNIS-ESy) were used to assign relevés to vegetation classes and to EUNIS units.

Results: The analysis resulted in nine clusters, which were interpreted as *Festuco-Brometea* (two units), *Molinio-Arrhenatheretea* (three units), *Isoëto-Nanojuncetea* (three units) and one derivate community of the *Festuco-Puccinellietea*. Detailed characteristics of the species composition, structure, distribution, and environmental conditions are provided for each unit. According to the DCA ordination, the leading factors of the syntaxa differentiation are soil moisture and fluctuating water level.

Conclusions: We could clarify the placement of steppe depression vegetation in the system of syntaxonomic units of Europe. The previously described syntaxa of the rank of alliance (*Myosuro-Beckmannion eruciformis*), suballiance (*Galio ruthenici-Caricenion praecocis*), and six associations are validated. Two associations and two subassociations are described as a new to science.

Taxonomic references: Euro+Med PlantBase (https://www.emplantbase.org), except Mosyakin and Fedoronchuk (1999) for *Phlomis scythica* Klokov & Des.-Shost. and *Tulipa scythica* Klokov & Zoz.

Syntaxonomic references: Mucina et al. (2016) for syntaxa from alliance to class level; Dubyna et al. (2019) for associations.

Abbreviations: DCA = Detrended Correspondence Analysis; DES = Didukh Ecological Scales; EUNIS = European Nature Information System; EVC = EuroVegChecklist; GIVD = Global Index of Vegetation-Plot Databases; ICPN = International Code of Phytosociological Nomenclature.

Keywords

Althaeion officinalis, Bern Convention, Didukh ecological scales, EUNIS, expert system, grasslands, *Myosuro-Beckmannion eruciformis*, steppe depressions, syntaxonomy, wetlands

Introduction

Steppe depressions (*pody* in Ukrainian) are large closed depressions, up to 16,000 ha in area, elliptical or round in shape with gentle slopes and flat bottoms, periodically flooded by meltwater and characterized by Planosol soils and peculiar ephemeral mesic to wet grassland phytocenoses. These depressions accumulate natural runoff in poorly drained steppe plains within the periglacial area of the Quaternary glaciation. In Ukraine, the largest depressions are concentrated on the Left Bank of the Lower Dnieper (Kherson and Zaporizhia administrative oblasts), while sporadic, smaller depressions and steppe "saucers" occur on the Right Bank of the Dnieper (Kherson, Mykolaiv, rarely Odessa oblasts). In the Russian Federation, similar depressions are common in the Lower Don River and Lower Volga River regions (Molodykh 1982; Evdokimova and Bykovskaya 1985; Marinich et al. 1985; Shapoval 2007; Zakharov 2018).

Following the flooding of depressions, over the entire area of the shallow basin, there is an "explosive" formation of ephemeral hydrophilic cenoses. They exist for a short period, being rapidly replaced by xeromorphic flora and finally become steppic when the depression dries. The average duration of the period between severe floods is, according to various estimates, from 7 to 12 years (Shapoval and Zvegintsov 2010). During periods of flooding and subsequent drying, distinctive alternating phytocenoses with wide ecological amplitude are observed, which consist of plants that withstand drought well and «explosively» increase in number during floods, i.e. are adapted to significant fluctuations in water levels. During short-term floods, the vegetation of depressions is characterized by high values of aboveground phytomass. For example, after the floods of 2003, the average values on the hayfields of the «Black Valley» depression was 12892 ± 518.0 kg/ha in the dry state. However, these values decline rapidly during periods of drought. Also, their productivity decreases due to overgrazing. In particular, in the post-flood period, the value of aboveground phytomass of the adjacent intensively grazed «Sugakli» depression was only 912 ± 239.2 kg/ha, which is significantly less than similar values of hayfields with better moderate grazing management. In general, the stocks of aboveground phytomass in the studied *pody* under different landuse regimes vary in a wide range from 588 to 14788 kg/ha in the dry state (Shapoval 2004). During the latter, the dominant species become low, sparse, some hydrophytes disappear from the phytocenosis, enduring a prolonged drought in a latent state (seeds formed under a favorable moisture regime, or underground perennial organs such as caudex, rhizomes, etc.).

Vegetation types of depressions are separated in time and space, as actual phytocenoses are scattered territorially (some are confined to the deepest, wettest areas of a depression bottom, others tend to its dry periphery), and they are delimited in time (open water surface overgrown with wetland vegetation, which is later replaced by mesic and semi-dry grasslands). At the same time, the boundaries between these phytocenoses are often blurred, and the spatial transitions among them are very gradual.

The problem of the origin of the depressions still has no unambiguous solution; many issues remain problematic and debatable. During the long history of studying the loess cover of the lowland steppes of the Southern Ukraine, many hypotheses and theories of the origin of steppe *pody* have been put forward. They were considered as remnants of the ancient hydrographic network (Krokos 1927; Lichkov 1927; Zamoriy 1934; Sambur et al. 1956; Mulika 1961; Bulavin 1972) or relict elements of the periglacial area of the Quaternary glaciation (Dokuchaev 1892; Dostovalov 1952; Velichko 1965; Molodykh 1982). According to the results of the recent studies of the morphology and genesis of the large depression relief of the Eastern Azov Sea region (Zakharov 2018) it is established that the existing *pody* lie in the thickness of loess sediments and do not affect the underlying sediments of sea and river terraces, therefore, they are of aeolian origin and are large deflationary basins, which was assumed earlier (Tutkovskiy 1910; Levengaupt 1932). However, it seems most probable that these geomorphological structures represent a polygenetic group, and their development is caused by a complex of subsidence-suffusion, fluvial and aeolian transformations.

Unfortunately, in Ukraine most of the steppe depressions are plowed, and the surviving remnants are exploited, mainly as hayfields and pastures without compliance with rational management standards, including nature conservation. The only steppe depression that has a national conservation status is the Great Chapelsky *pid*, as part of the natural core of the Biosphere Reserve «Askania-Nova» (2,376 hectares). Steppe depressions are the sole localities of local and regional endemics in the region of the Left Bank of the Lower Dnieper (*Elytrigia repens* subsp. *pseudocaesia*, *Phlomis scythica*, *Tulipa scythica*).

The syntaxonomy of these unique complexes is still poorly known and needs to be thoroughly revised. The first attempt to develop a classification of the steppe depression vegetation was made by a team led by Solomakha (Solomakha et al. 2005) in the study of coenotic affinity of *Allium regelianum* and *Ferula orientalis*. It was proposed to include such communities in a new alliance *Carici praecocis-Elytrigion pseudocaesiae* of the new order *Carici praecocis-Elytrigietalia pseudocaesiae*, which was assigned to the class *Festuco-Limonietea* (= *Festuco-Puccinellietea*). In this case, the dataset used for the analysis was only 34 relevés, selected by the criterion of the presence of two target species. The following year, a study on the syntaxonomy of the steppe depression vegetation based on 367 relevés was published (Shapoval 2006). In this article, the author proposed another syntaxonomic solution: the wettest communities are classified within the class *Isoëto-Nanojuncetea*, order *Nanocyperetalia* and two alliances – *Eleocharition ovatae* and newly described *Myosuro-Beckmannion eruciformis*. Mesic communities of depressions were included in the class *Molinio-Arrhenatheretea*, order *Molinietalia* and a new alliance *Lythro virgati-Elytrigion pseudocaesiae*. Xero-mesic communities, common in small, shallow depressions, were included in the class *Festuco-Brometea*, order *Festucetalia valesiacae*, alliances *Amygdalion nanae* and *Festucion valesiacae*. However, given the distinctiveness of the depression vegetation, it was proposed to distinguish two suballiances – *Cerastio ucrainici-Festucenion valesiacae* and *Galio ruthenici-Caricenion praecocis* within the alliance *Festucion valesiacae*. All the associations described by Shapoval (2006) were new to science. To date, the latter work remains the most complete overview of the vegetation and syntaxonomic interpretation of the phytocenotic diversity of steppe depressions of the Left Bank of Ukraine. However, the status of many syntaxa remains controversial. Thus, from the above new syntaxa of alliance rank, only the *Myosuro-Beckmannion eruciformis* is accepted in Mucina et al. (2016). Also, Mucina et al. (2016) mention the order «*Myosuro-Beckmannietalia eruciformis* Shapoval 2006 (2b, 5)» as synonymous of the *Nanocyperetalia*. However, the *Myosuro-Beckmannion eruciformis* with the single association *Myosuro-Beckmannietum eruciformis* from the beginning was assigned to the classical order *Nanocyperetalia*, and the order *Myosuro-Beckmannietalia eruciformis* was not described by Shapoval (2006) and is not mentioned in any other sources, except in Mucina et al. (2016); therefore it should obviously be considered as a phantom name. Finally, the order *Carici praecocis-Elytrigietalia pseudocaesiae* is considered by Mucina et al. (2016) as a syntaxonomic synonym of the *Galietalia veri*, and the alliances *Carici praecocis-Elytrigion pseudocaesiae* and *Lythro virgati-Elytrigion pseudocaesiae* are considered as synonyms of the *Agrostion vinealis*. The latter decision seems insufficiently justified because the alliance *Agrostion vinealis* is described from the forest zone of Ukraine with completely different climatic conditions (Sypailova et al. 1985), and practically none of its diagnostic species, except the widespread *Poa angustifolia* and *Carex praecox*, have been found in the steppe depression communities.

Adding to syntaxonomic incertainty, in the recently published Prodromus of Vegetation of Ukraine (Dubyna et al. 2019) the order *Carici praecocis-Elytrigietalia pseudocaesiae* as well as alliances *Carici praecocis-Elytrigion pseudocaesiae* and *Poo angustifoliae-Ferulion orientalis* are accepted, but are considered within the class *Festuco-Puccinellietea*; also, alliance *Lythro virgati-Elytrigion pseudocaesiae* is considered as a synonym for alliance *Carici praecocis-Elytrigion pseudocaesiae*, and alliance *Myosuro-Beckmannion eruciformis* assigned as synonyms of the alliance *Beckmannion eruciformis* of the class *Festuco-Puccinellietea*. All the associations described in Solomakha et al. (2005) and Shapoval (2006) are also mentioned in the Prodromus, some as accepted names, some as synonyms. In particular, the association *Carici praecocis-Elytrigietum pseudocaesiae* is assigned as synonym of the *Pycreo flavescenti-Arabidopsietum toxophyllae*, *Herniario glabrae-Poetum angustifoliae* as synonym of the *Achilleo micranthoidis-Poetum angustifoliae*, as well as *Potentillo orientalis-Caricetum melanostachyae* and *Euphorbio virgati-Caricetum melanostachyae* as synonyms of the *Galio ruthenici-Caricetum praecocis*. The Prodrome also states that all syntaxa described in the two mentioned publications (Solomakha et al. 2005; Shapoval 2006) are invalid because their typification does not meet the requirements of art. 5 ICPN (Weber et al. 2000; Theurillat et al. 2021), i.e., the Latin word '*typus*' ('*holotypus*', '*lectotypus*', '*neotypus*') was not used *expressis verbis* for the designation of the type of a syntaxon name, although the nomenclature type itself was designated.

The above review has shown that many questions remain unresolved in the syntaxonomy of the steppe depression vegetation. And the biggest, quite objective problem of syntaxonomic analysis of *pody* vegetation is the availability of representative data because the object of study is quite ephemeral. The precondition for its occurrence is a flood. Due to the exceptional rarity of this phenomenon, it is possible to observe and describe the *pody* phytocenoses in very limited periods of time, and the interval between the favorable seasons for the mentioned ephemeral vegetation can be decades. Only after the major flooding in 2010 was sufficiently representative data for the current analysis available for collection.

Given this, our aim was to revise the syntaxonomy of the steppe depressions (*pody*) vegetation, in particular (1) to identify the associations and to reveal their environmental, structural and compositional peculiarities; (2) to assign the associations to higher syntaxa; and (3) to correct nomenclatural aspects according to the ICPN.

Study area

In accordance with the modern administrative-territorial structure of Ukraine, the studied *pody* are located within Kakhovka and Henichesk districts of Kherson oblast and Melitopol district of Zaporizhia oblast. Great Chapelskyi *pid*, as well as Staryi *pid* and a number of small depressions within "Southern" site are components of the natural core of the Askania-Nova Biosphere Reserve (Figure 1, Table 1). The altitudinal range of the studied pody is from 10 m (Novotroitsky and Syvasky) to 45 m (Garbuzy).

In accordance with the Worldwide Bioclimatic Classification System the study area is located on the border of Temperate xeric steppic and Mediterranean pluviseasonal continental steppic variants, Supra-submediterranean and Supramediterranean variants within the Dobrujo-Crimean subregion of the Eurosiberian biogeographic region (Rivas-Martínez et al. 2004). The climate is characterized as aride, steppe, cold (Beck et al. 2018).

According to the agro-meteorological station Askania-Nova, the average annual temperature is 11.3°C. The average annual precipitation is 400 mm. Most precipitation (37% of the annual amount) falls in the summer in a form of showers and short-term rains. During the period of moisture accumulation (November-March) the amount of precipitation does not exceed 100 mm. Evaporation is 900–1000 mm, and in the summer months it exceeds precipitation by 5–7 times (Figure 2).

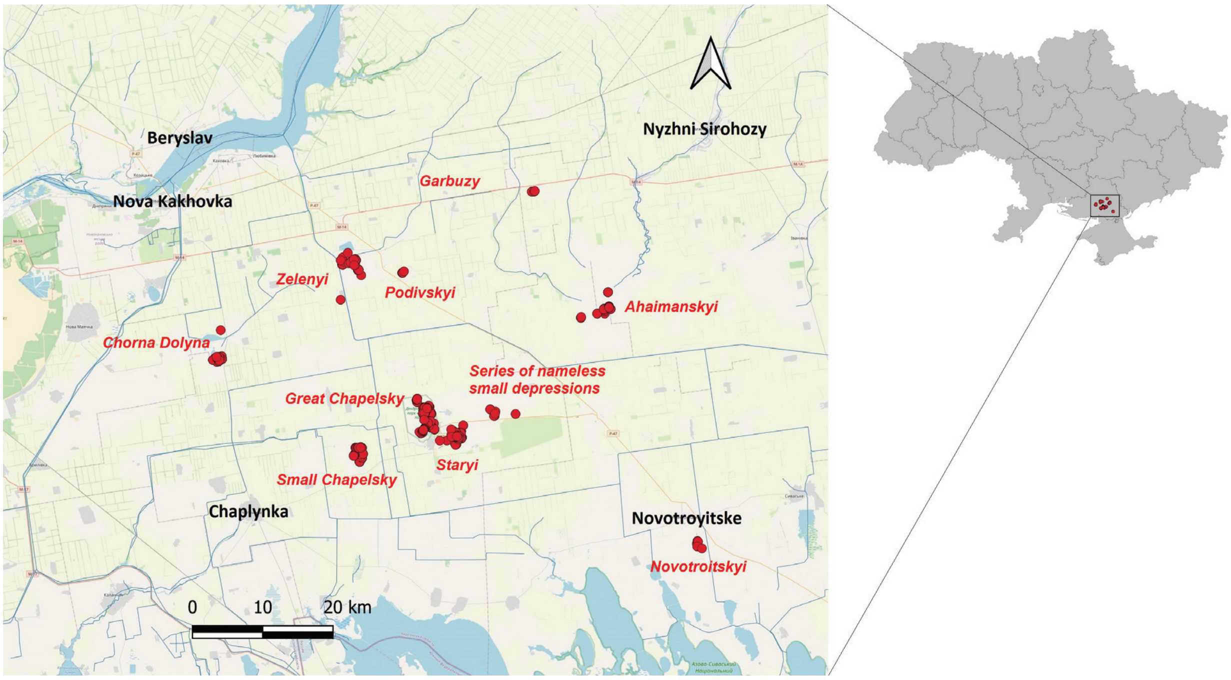

Figure 1. Locations of the vegetation plots (red dots) used for the analysis (region of the Left Bank of the Lower Dnieper).

Table 1. Characteristics of the studied steppe depressions (*pody*).

Name	Coordinates of the conditional central point	Administrative location	Preserved area (pristine land and perennial fallows), hectares	Size (bottom and slopes forming a closed «bowl» of the depression), km	Protection
Great Chapelsky	46.484630° 33.850533°	near Askania Nova, Kakhovka district, Kherson oblast	2376	4,5×6	natural core of the Askania-Nova Biosphere Reserve
Staryi	46.456985° 33.918434°	near Askania Nova, Kakhovka district, Kherson oblast	140	0.3×0.5	natural core of the Askania-Nova Biosphere Reserve
Series of nameless small depressions	46.465470° 34.007211°	near Askania Nova, Kakhovka district, Kherson oblast	up to 300 (in total)	–	natural core of the Askania-Nova Biosphere Reserve
Small Chapelsky	46.427852° 33.731158°	outskirts of Khrestivka and Dolynske villages, Kakhovka district, Kherson oblast	1022	5,5×6,5	Emerald site UA0000372
Barnashivsky	46.547296° 33.977308°	near the Maryanivka village, Kakhovka district, Kherson oblast	738	2.5×4	Emerald site UA0000367
Chorna Dolyna (Black Valley)	46.554197° 33.474011°	near the Chorna Dolyna village, Kakhovka district, Kherson oblast	494	3×6	Emerald site UA0000368
Zeleny (Green)	46.670855° 33.717165°	outskirts of Zeleny *pid* and Zelena Rubanivka villages, Kakhovka district, Kherson oblast	1580	5,5×8	Emerald site UA0000370
Podivsky	46.664349° 33.825659°	near Podivka village, Kakhovka district, Kherson oblast	258	1.5×2.4	–
Garbuzy	46.768667° 34.053785°	near Stepne village, Henichesk district, Kherson oblast	152	1.2×1.7	Emerald site UA0000383
Ahaimansky	46.670501° 34.193323°	near Ahaimany village, Henichesk district, Kherson oblast	4849	10×16	Emerald site UA0000366
Koianly	46.690165° 34.482390°	near Shotivka village, Henichesk district, Kherson oblast	148	5,5×11	–
Domuzlynsky	46.603908° 34.728707°	near Zeleny Hai village, Henichesk district, Kherson oblast and Trudove village с. Трудове, Melitopol district, Zaporizhzhia oblast	4743	9×13	Emerald site UA0000369
Novotroitsky	46.319373° 34.360386°	near Novotroitse urban village, Henichesk district, Kherson oblast	97	3.5×4	–
Syvasky	46.349037° 34.529281°	Near Syvaske village Henichesk district, Kherson oblast	1549	6×8,5	Emerald site UA0000371

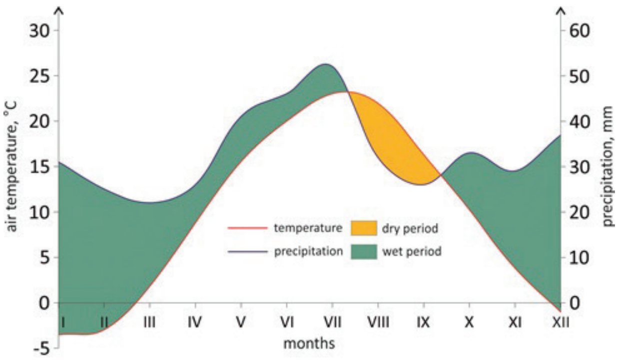

Figure 2. Climate diagram of the Askania Nova region.

Depressions in lowland steppes are represented by two structural and genetic forms – steppe saucers and *pody*. Steppe saucers are small, with depth up to 0.5 m and diameter 2–150 (up to 600) m. Their density is 30–120 saucers per 1 km^2, depending on erosional dissection and inclination of the terrain. Almost all of them are plowed today. Depressions with a depth of 3–5 (sometimes 10–15) m and a total area of more than 1 ha (up to 16,000 ha), with erosive slopes, catchment basins and flat bottoms represent the second group of depressions – *pody*. In the interfluve of the Dnieper and Molochna rivers, small depressions with a diameter of up to 1000 m and a depth of about 0.5–3 m are common. Most of depressions are plowed due to their easy accessibility; pristine vegetation is preserved only in the small depressions within the territory of the Biosphere Reserve «Askania-Nova». Other interfluve *pody* have significant size (see Table 1). The depths of these depressions (relative elevations of watersheds above the bottoms) vary from 1.5–2 m (Small Chapelsky) to 10–15 m (Agaymansky, Great Chapelsky, Sivashsky, Domuzlynsky). The slopes and periphery of the bottoms of these large depressions are plowed, with the exception of the Great Chapelsky. Some depressions (Sugakli, Mustapa, Oleksandrivsky, Rubanovsky, Timoshivsky, etc.) are completely plowed.

In general, *pody* is a key typological unit of macro- and mesorelief forms of the Steppe zone, and expresses the geomorphological, hydrographic, edaphic, and biotic identity of the whole catchment. The actual concept of steppe depressions (*pody*) means a complex formation, which includes the following elements: a bottom (perfectly flat surface delineated by the lowest closed horizontal), the slopes, which form a closed depression bowl (its sides) and, finally, the estuaries of a ravine catchment, cut into the general slopes (Shapoval and Zvegintsov 2010) (Figure 3). Only a few depressions have a circle shape, the rest are more or less ellipsoidal, elongated from north to south. The average inclination of slopes is about 2°. The slopes of southern and eastern exposures are steeper (up to 4–6°) and have more pronounced excess of a depression edge over its bottom. This kind of asymmetry of *pody* is due to the general tendency of lowering the relief in the direction to the Black Sea. In large depressions, slopes are complicated by catchment hollows, and temporary watercourses have produced erosive leaks where these depressions occur in floodplains. The width of such catchment hollows is 500–1000 m, and the length is 7–9 km. Deeper ravines can reach more than 60 km in length (Chekmenchi ravine, which flows into the Ahaimansky *pid*). In places of transition from a hollow to a bottom, the soil deposits brought by water are formed. These are peculiar deltas that are clearly identified by the steppe nature of vegetation. The slopes of some depressions (Ahaimansky and Sivashsky *pody*) are terraced. Sometimes there are several bottoms within the large depression, due to generalization of a series of smaller depressions.

The most common and typical soils of the studied region are Luvic Planosol or gleyosolod in the traditional Ukraininan soil classification (Polupan et al. 2005). Their formation is determined by periodic stagnation of melt and rainwater, processes of gleying and sweetening (hydrolysis). This soil type is well diagnosed by numerous iron-manganese nodules. In general, soil varieties in the *pody* are localized by strips with concentrically closed contours. The width of the strips is determined by an exposure of the slope, a depth of depression, an intensity and nature of moistening, and so on (Anon 1984).

There are two seasonal types of depression flooding: winter-spring, caused by melting snow during thaw, and extremely rare summer-autumn – caused by heavy rains (Drohobych and Polishchuk 2003). A key role in winter-spring floods is played by the snow factor, which accumulates and retains water reserves until the melting period. In addition, heavy rainfall in the previous moisture accumulation period, deep freezing of the soil and the formation of a “frost lock” that prevents infiltration of water; crust and rapid warming are also the key to severe flooding. According to the analysis of well-known dates of flooding in 19–21 centuries, the average duration of the period between severe floods is 7–12 years (Shapoval and Zvegintsov 2010). Occasionally flooding is observed for two or three years in a row, much more often with intervals of 15–17 years or more. In the past, the flooding of the depressions of the Black Sea steppe was much larger (Shalyt 1930) and therefore on old maps they were marked as lakes.

Currently, due to the over-regulation of the catchment area, with much plowing and crossing by various communications (water supply canals, highways, etc.), the frequency and duration of floods have decreased significantly, causing xerophytization of these habitats. Modern heavy floods begin in February and last until the beginning of June (the last small puddles in the depths of the bottom may last until the end of July). The area of flooding can reach 3–4 thousand hectares with the water depth up to 20–40 cm in the center of the depression.

Polygenetics, different sizes, differentiation of microrelief and soil cover of depressions together with sporadic hydrogenic fluctuations, historical and current management determine the nature and dynamics of their vegetation. In fact, it is a unique dynamic complex of hydro-, meso- and xeromorphic communities, which, of course, complicates its study.

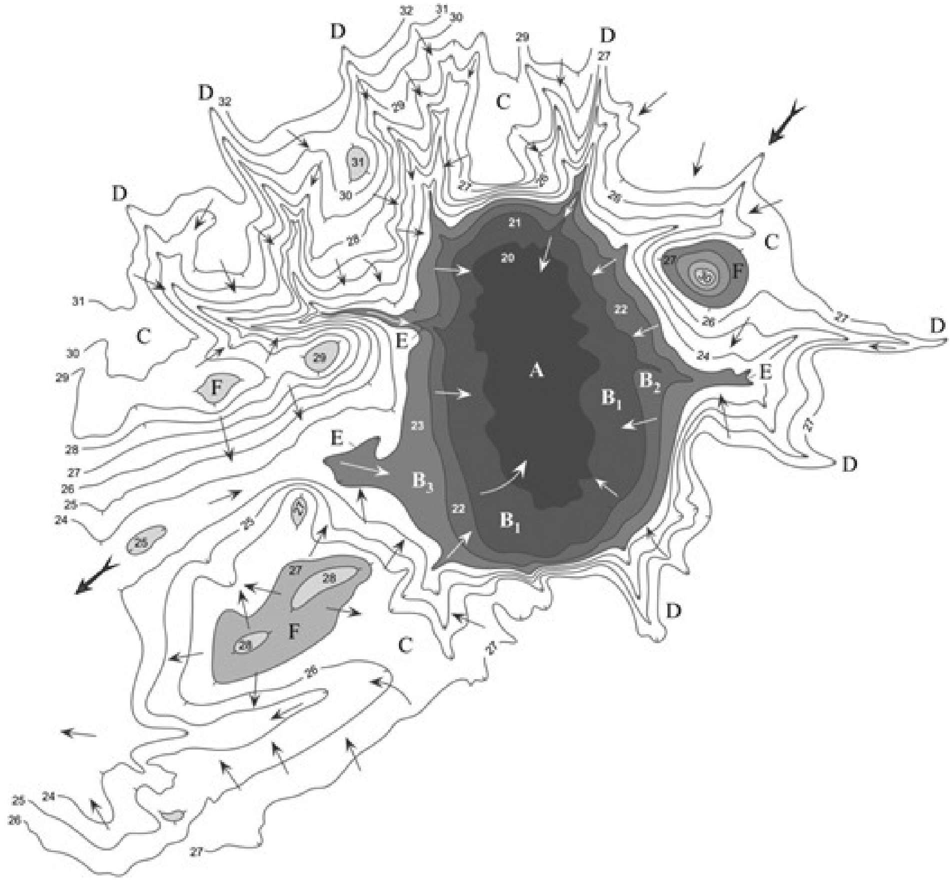

Figure 3. Relief of the hydrographic network of the basin of the Great Chapelsky *pid*, fragment (Shapoval and Zvegintsov 2010). A: bottom, B1–B3: closed slopes of depression, B: general slopes with indented watershed hollows (D), C: ravine estuaries, F: plakor (slightly convex or almost flat elevated area); 20–32: altitudes; arrows indicate direction of the runoff (bold arrows: general regional runoff).

Methods

The materials for the study were 1897 vegetation plots made by V.V. Shapoval, O.P. Goffman, N.Y. Drohobych, N.A. Dotsenko, N.S. Shestakova, A.A. Kuzemko and I.I. Moysienko in the depressions of the Steppe zone of Ukraine in the period from 1967 to 2019. Plots are stored in the Turboveg format (Hennekens and Schaminée 2001) as a part of the Ukrainian Grassland Database (Kuzemko 2012), registered as EU-UA-0001 in GIVD (https://www.givd.info/ID/EU-UA-001). These vegetation plots covered most of the large steppe depressions within the Kherson region (see Figure 1). The relevés were made according to the standard method of the Braun-Blanquet school on plots from 9 and 16 m^2 (relevés of small spots of hydrophilic vegetation in 2010 and some relevés of 2019) to 100 m^2 (the rest of relevés). Different plot sizes are due to the specifics of spatial differentiation of *pody* vegetation. "Small" plots (9–16 m^2) are mostly timed to small microrelief forms (saucer depths, road tracks, trampled cattle tracks, shores of the arches, etc.) with different moisture conditions and small sizes of vegetation contours. All "large" plots have a standard area of 100 m^2 and characterize relatively homogeneous vegetation. The vast majority of the relevés did not include cryptogam species, which are very poorly represented in steppe depressions and mostly have no diagnostic value. For historical relevés, georeferences were determined by the original characteristics of their location in the quarter network of the natural core of the Askania-Nova Biosphere Reserve, corrals of the Great Chapelsky *pid* or other landmarks – position in relief, adjacency with settlements or economic objects. The new relevés were georeferenced with GPS-navigators Lowrance iFinder and Garmin eTrex 20X, coordinate system WGS-84. A graphical summary of the catena of depression vegetation was completed in the form of an idealized transect, which was constructed based on the results of generalized analysis of vegetation plots and visualization of the results of ordination and territorial differentiation of syntaxa. Images of typical plants were obtained by scanning herbarium specimens of plants collected directly in steppe depressions.

Since the aim of our work was the syntaxonomic analysis of mesic and wet communities of steppe depressions, we deliberately removed from the analysis all vegetation plots of typical steppes, which according to a preliminary phytoindication assessment received an average score 7 or less on the moisture scale based on the DES (Didukh 2011). We also removed from the analysis vegetation plots with cover of shrub layer more than 15%. All taxa identified to the genus level were removed from the species list. The resulting dataset of 641 vegetation plots containing 261 species was analyzed in the Juice software (Tichý 2002). We tested several variants of cluster analysis (both divisive and agglomerative), but the best results in terms of separation and sharpness of vegetation units were obtained with the agglomerative cluster analysis in PCOrd (McCune and Mefford 2006) with the following parameters: square root transformation of species data, Relative Sørensen index as distance measure, flexible Beta -0.25 as group linkage method. Phytoindication assessment of syntaxa was performed using DES for flora of Ukraine (Didukh 2011) in the Juice program. In one case, we rearranged the plots manually between units 7 and 8, for a clearer separation of the two subassociations, moving all plots with presence of *Damasonium alisma* to a cluster where this species had a much greater frequency. Diagnostic taxa for vegetation units were determined based on their fidelity values calculated with phi coefficient (Chytrý et al. 2002) with Fisher's exact test at $p > 0.001$ and standardisation of relevé groups to equal size. The threshold value of the phi coefficient for diagnostic species for syntaxa of all ranks was 0.3. For the assignment of communities to syntaxonomical classes and to EUNIS units we used two expert systems: EVC, which allows with a fairly high degree of reliability to determine the affiliation of vegetation plots to vegetation classes and is based on a recent review of the European vegetation (Mucina et al. 2016) and EUNIS-ESy (Chytrý et al. 2020). Both expert systems were used in the Juice program environment.

Results

Description of vegetation units

As a result of the classification, we obtained nine units (Table 1, Suppl. materials 1, 2). Below we provide characteristics of their distribution, environmental conditions, structure and composition.

***Cluster 1 "Ferulo euxinae-Caricetum praecocis»* (Table 2, column 1)**

Distribution. Small shallow depressions of the natural core of the Askania-Nova Biosphere Reserve.

Environmental conditions. Communities characterized by clear signs of succession with accumulation of a thick litter. The territory is kept in a completely protected regime ('absolut zapovednost"). Here, the ecosystem is not grazed by wild ungulates which contributes to growth of vegetative-mobile mesophytic species and impoverishment of phytodiversity. Soils are meadow-chestnut gleyed sweetened and gley-sweet Planosol. These small depressions are almost not flooded, although they usually have better moisture conditions compared to the adjacent steppe. Sometimes during snowy winters, there may be short-term puddles on the bottoms in February-March, but heavy floods are not observed and the water completely disappears before the period of active vegetation.

Structure and composition. Total cover varies in a wide range – from 19 to 100%, an average of 75,3%, litter – from 5 to 70%. In general, phytocenoses are quite dynamic and are characterized by various combinations of mesomorphic rhizome species and rotations of their coenotic positions depending on different changes in the environment. Dominant species are *Bromopsis inermis*, *Elytrigia repens*, *Carex praecox*, *Poa angustifolia*, rarely *Bromopsis riparia* (Figure 4). *Elytrigia repens* subsp. *pseudocaesia*, *Alopecurus pratensis* and *Carex melanostachya*, which are the most mesophytic components, occur sporadically. Turf-forming xeromorphic species (*Stipa capillata* and *Agropyron cristatum* subsp. *pectinatum*) are rare. The herb layer has clear vertical differentiation. The first layer is formed by tall forbs (*Ferula euxina*, *Peucedanum ruthenicum*, *Asparagus officinalis*) and grasses – *Bromopsis inermis* and *Elytrigia repens*, sporadically *Stipa capillata*, *Rumex crispus*, *Sisymbrium altissimum*. In the second layer, *Carex praecox* and *Poa angustifolia* dominate, *Falcaria vulgaris*, *Galium ruthenicum*, *Vicia villosa* are common. The third layer is formed by *Viola kitaibeliana*, *Lamium amplexicaule* var. *orientale*, *Cruciata pedemontana*, *Veronica arvensis*. Some synanthropic plants are present in the floristic composition, even among the characteristic species of the syntaxon, due to sporadic zoogenic soil disturbances – anthills (*Lasius*) or vole's colonies (*Microtus*), which are optimal stations for weeds. *Sisymbrium altissimum* and *Salsola tragus* spread in bulk after fires; *Falcaria vulgaris*, *Eryngium campestre*, *Atriplex oblongifolia*, *Lactuca serriola* are also common.

Figure 4. Phytocenoses of the association *Ferulo euxinae-Caricetum praecocis* at the bottom of the «Old» depression (natural core of the Askania-Nova Biosphere Reserve, «Southern» massif, quarter №44) with the aspect of *Bromopsis inermis*, 16.06.2005.

Table 2. Synoptic table of the steppe depression vegetation. Taxa percentage frequency (constancy) and modified fidelity index (phi coefficient × 100) superscripted are shown. Species within units are arranged in descending order of fidelity index; the table shows only diagnostic species; diagnostic species with percentage frequency values more than 30% and constant species with percentage frequency more than 30% are indicated in bold.

Group No.	1	2	3	4	5	6	7	8	9
No. of releves	**140**	**85**	**32**	**122**	**52**	**54**	**95**	**44**	**18**
Bromopsis inermis	**82^{71}**	7	31	1	.	.	.	.	.
Viola kitaibeliana	**52^{55}**	25^{21}	.	.	.	.	.	.	.
Vicia villosa	**74^{53}**	**48^{28}**	12	11	10	2	.	.	.
Elytrigia repens	24^{40}	1	.	5	.	.	.	.	.
Lamium amplexicaule var. *orientale*	17^{39}	.	.	.	.	.	.	.	.
Phlomis herba-venti subsp. *pungens*	**34^{38}**	27^{29}	.	.	.	.	.	.	.
Salsola tragus	16^{35}	.	.	.	2	.	.	.	.
Dianthus guttatus	19	**65^{53}**	.	**30^{17}**	.	.	.	5	.
Thesium arvense	.	20^{42}	.	1	.	.	.	.	.
Carex melanostachya	9	**74^{42}**	**31**	29	15	9	20	20	6
Linaria biebersteinii	15	**47^{41}**	3	**31^{23}**	.	2	.	.	.
Seseli tortuosum	10	27^{38}	.	4	.	.	.	.	.
Eryngium planum	12	**35^{36}**	3	16	.	.	3	2	.
Euphorbia seguieriana	2	16^{34}	.	1	.	.	.	.	.
Tragopogon dasyrhynchus	7	19^{32}	.	2	.	.	.	.	.
Allium flavum subsp. *tauricum*	8	18^{30}	.	3	.	.	.	.	.
Veronica arvensis	19^{5}	9	**94^{79}**	10	.	.	.	.	.
Artemisia austriaca	2	8	**88^{76}**	26^{13}	.	.	.	.	.
Cerastium pumilum	2	10	**75^{74}**	8	.	.	.	.	.
Carex spicata	.	1	**56^{72}**	.	.	.	.	.	.
Trifolium retusum	.	1	**81^{70}**	7	.	33^{20}	.	.	.
Poa bulbosa	.	1	**66^{67}**	20^{12}	.	.	.	.	.
Festuca valesiaca	.	6	**56^{57}**	21^{15}	.	.	.	.	.
Lepidium draba	5	3	**50^{57}**	10^{3}	.	.	.	.	.
Vicia lathyroides	.	15^{10}	**50^{56}**	4	.	.	.	.	.
Capsella bursa-pastoris	6	.	**41^{52}**	7	.	.	.	.	.
Taraxacum sect. *Taraxacum*	7	7	**62^{50}**	21^{8}	19	4	1	2	.
Medicago minima	.	.	28^{47}	.	4	.	.	.	.
Crepis ramosissima	9	17	**62^{45}**	**36^{20}**	17	.	1	.	.
Cruciata pedemontana	17^{8}	26^{19}	**47^{43}**	.	.	.	.	.	.
Arenaria leptoclados	.	3	**41^{38}**	20^{13}	8	13	.	.	.
Trifolium arvense	4	1	25^{36}	9^{8}	.	.	.	.	.
Stellaria graminea	3	14	**38^{32}**	15^{6}	21^{13}	.	.	.	.
Allium regelianum	1	8	.	**66^{59}**	15	.	11	5	.
Herniaria glabra	.	.	.	**45^{47}**	.	28^{25}	2	.	.
Artemisia santonicum	.	3	.	**71^{47}**	**38^{17}**	**35^{14}**	14	5	6
Plantago lanceolata	.	2	25^{20}	**44^{44}**	.	2	4	2	.
Ventenata dubia	.	2	.	20^{39}	.	.	1	.	.
Lepidium ruderale	.	.	.	12^{33}	.	.	.	.	.
Potentilla argentea	1	**51^{21}**	**34**	**65^{33}**	2	7	25	**39**	.
Polycnemum arvense	.	.	.	11^{32}	.	.	.	.	.
Cyperus flavescens	.	3	.	8	**58^{48}**	.	**36^{25}**	7	.
Lathyrus nissolia	.	.	6	.	**31^{48}**	.	.	.	.
Armoracia rusticana	.	.	.	.	19^{37}	.	4	.	.
Crepis sancta	2	1	.	2	19^{36}	.	.	.	.
Lathyrus tuberosus	.	.	.	3	17^{36}	.	.	.	.
Phalacrachena inuloides	.	7	19	16^{7}	**38^{32}**	.	6	10	.
Lotus angustissimus	.	1	.	**43^{23}**	12	**93^{68}**	15	.	.
Myosurus minimus	1	15	3	$28^{6.0}$	.	**98^{67}**	28^{7}	10	6
Mentha pulegium	.	.	.	.	.	39^{57}	3	.	.
Lythrum virgatum	.	5	.	**34^{5}**	17	**91^{49}**	**54^{20}**	**56^{22}**	.
Chaiturus marrubiastrum	.	.	.	2	.	**31^{43}**	13^{12}	.	.
Polygonum aviculare	.	20	9	**57^{8}**	23	**100^{40}**	**45**	**61^{12}**	**83^{28}**
Erigeron canadensis	2	.	.	10^{6}	8	**31^{39}**	.	.	.
Xanthium orientale subsp. *riparium*	.	.	.	5	.	22^{33}	9^{10}	.	.
Aegilops cylindrica	.	.	.	.	.	11^{32}	.	.	.
Lythrum borysthenicum	.	.	.	12^{12}	.	.	**31^{41}**	2	.
Elatine hungarica	.	.	.	1	12^{10}	.	24^{31}	10	.
Damasonium alisma	.	5	.	2	.	.	.	**100^{97}**	.
Elatine alsinastrum	.	5	.	11	.	.	25^{12}	**80^{69}**	.
Butomus umbellatus	.	.	.	28^{8}	**37^{16}**	.	**41^{20}**	**66^{42}**	.
Rumex crispus	9	24	9	**30**	**40^{14}**	.	**42^{15}**	**61^{30}**	.
Rorippa brachycarpa		**30**	6	**31**	**52^{15}**	**48^{12}**	**54^{16}**	**71^{29}**	.
Puccinellia distans	.	.	.	1	.	.	.	.	**67^{79}**

Group No.	1	2	3	4	5	6	7	8	9
Rumex ucranicus	.	.	.	2	.	.	.	.	**67**^{79}
Juncus gerardi	.	1	.	.	.	.	.	.	**61**^{76}
Juncus bufonius	.	.	.	9	.	.	2	.	**67**^{73}
Plantago major	.	1	.	3	.	**30**^{18}	.	.	**78**^{70}
Ranunculus sceleratus	.	.	.	.	.	.	7	5	**61**^{68}
Bolboschoenus maritimus	.	.	.	1	.	.	.	.	**50**^{68}
Veronica anagallis-aquatica	.	.	.	.	.	.	.	.	**44**^{65}
Petrosimonia triandra	.	.	.	.	.	.	.	.	**39**^{60}
Echinochloa crus-galli	.	.	.	1	.	.	.	.	**39**^{59}
Atriplex prostrata	.	.	.	.	.	.	.	.	**33**^{56}
Crypsis schoenoides	.	.	.	1	.	.	.	5	**39**^{55}
Taraxacum besarabicum	.	2	.	.	.	.	.	.	33^{53}
Setaria pumila	.	.	.	2	.	2	.	.	22^{41}
Persicaria maculosa	.	.	.	.	.	4	9^{8}	.	28^{39}
Juncus compressus	.	.	.	1	.	.	.	.	17^{38}
Xanthium spinosum	.	.	.	2	.	.	.	.	17^{36}
Plantago tenuiflora	.	2	.	12^{2}	2	.	15^{5}	22^{14}	**39**^{33}
Falcaria vulgaris	**81**^{61}	**51**^{33}	.	14	.	4	.	.	.
Galium ruthenicum	**79**^{55}	**66**^{44}	6	13	.	.	.	.	.
Carex praecox	**83**^{47}	**95**^{58}	.	29	13	.	1	2	.
Poa angustifolia	**87**^{32}	**90**^{34}	**75**^{23}	**59**	2	2	15	**56**	.
Alopecurus pratensis	8	**42**^{8}	**100**^{52}	27	.	6	18	**71**^{29}	17
Achillea micranthoides	.	3	**47**^{42}	**39**^{33}	.	4	1	.	.
Gypsophila muralis	.	10	.	**69**^{38}	10	**100**^{64}	22	.	.
Inula britannica	1	27	.	**56**^{16}	**81**^{34}	**87**^{39}	24	29	6
Eleocharis palustris	.	.	.	25	**35**	**100**^{44}	**53**^{10}	**46**^{5}	**94**^{40}
Gratiola officinalis	.	17	.	**41**^{6}	10	**80**^{36}	**63**^{23}	**83**^{38}	.
Beckmannia eruciformis	.	8	.	2	6	**76**^{35}	31	**61**^{23}	**94**^{49}
Juncus atratus	.	6	.	3	.	.	**37**^{32}	**44**^{40}	.
Pulicaria vulgaris	.	2	.	16^{3}	.	**31**^{19}	13	17	**39**^{27}

Cluster 2 «Diantho guttati-Caricetum melanostachyae» (Table 2, column 2)

Distribution. Small depressions of the natural core of the Askania-Nova Biosphere Reserve and sporadically on the slopes and dry bottom of the Great Chapelsky *pid*.

Environmental conditions. Communities are mostly localized along the bottom edge and at lower slopes (on the verge of flooding) or in local depressions, surrounded by more xerophytic phytocenoses, so they occur in depressions with preserved slopes and adjacent pristine steppe. During strong floods they give way to more hydrophytic communities; during severe droughts they are in a depressed state, lose hygromesophytic elements, and are replaced by more dry communities. The conditions of this association are perfectly suited to *Carex melanostachya*, which can resist extreme changes in moisture conditions, growing both in a dry steppe and among ephemeral shallow-water vegetation.

Structure and composition. The total cover varies in a wide range from 40 to 100%, occasionally 10–25%, on average 73%. Communities are more mesophytic than the *Ferulo-Caricetum praecocis*, which is manifested primarily in the strong phytocenotic position of the dominant *Carex melanostachya* and *Elytrigia repens* subsp. *pseudocaesia*, increase in the occurrence and total proportion of *Alopecurus pratensis*, presence of *Eryngium planum* (which tends in the Ascanian steppe to depressions with saline soils and sufficient moisture) as well as *Hypericum perforatum*, *Veronica spicata*, *V. barrelieri*, *Gagea transversalis*, *Euphorbia esula* subsp. *tommasiniana*, *Ferula euxina* and *Rumex crispus*, and sometimes a significant admixture of annual plants, confined to short-term wetlands ("saucers", puddles), namely *Gypsophila muralis*, *Cyperus flavescens*, *Myosurus minimus* and *Rorippa brachycarpa* and *Phalacrachena inuloides* as characteristic element of the mesophytic forbs of steppe depressions. Another typical mesophytic species of these communities is *Sibbaldianthe bifurca* subsp. *orientalis*, which is found in watershed hollows and depressions with semi-dry or mesic grassland vegetation. Thus, the phytocenoses of this unit show a more mesomorphic character, although they are accompanied by many xerophytic steppe elements (*Seseli tortuosum*, *Euphorbia seguierana*, *Sisymbrium polymorphum*, *Festuca valesiaca*, *F. pseudovina*, *Agropyron cristatum* subsp. *pectinatum*, *Phlomis herba-venti* subsp. *pungens*, and very rarely *Stipa capillata* and *S. ucrainica*), which generally reveals the mixed, transition nature of these communities.

Cluster 3 «Vicio lathyroidis-Alopecuretum pratensis» (Table 2, column 3)

Distribution. Peripheral part of the Great Chapelsky *pid* bottom.

Environmental conditions. The territory is grazed by wild ungulates, mostly in a state of modest overgrazing.

Structure and composition. Litter is almost absent. Sometimes, where there is considerable aboveground phytomass, strands of coarse dry biomass from common rhizome grasses can be present. Total cover of herb layer is 70–100% (average 80.3%). Phytocenoses are characterized by an absolute dominance of rhizome-turf mesophytic grass *Alopecurus pratensis* (Figure 5). Sometimes,

Figure 5. Phytocenoses of the association *Vicio lathyroidis-Alopecuretum pratensis* in the corral №6 of the Great Chapelsky *pid* (peripheral part of the bottom) after flooding, aspect of *Alopecurus pratensis* with an admixture of *Phlomis scythica*, 27.05.2010.

Poa angustifolia is codominant. Occasional species include *Elytrigia repens* subsp. *pseudocaesia*, *Bromopsis inermis*, *Carex spicata* and *Carex melanostachya*; *Festuca valesiaca* s.l. is quite common; it generally tolerates short-term flooding well and, if soaked, restores coenotic positions during the xerotic series. Forbs are represented by *Achillea micranthoides*, *Convolvulus arvensis*, *Ferula euxina*, *Phalacrachena inuloides*, *Phlomis scythica*, *Plantago lanceolata*, *Potentilla argentea* and several legumes: *Vicia lathyroides*, *V. hirsuta*, *V. tetrasperma*, *V. villosa*, *Lathyrus nissolia*, *Trifolium arvense*.

Long-term grazing regime of this community leaves an imprint on the structure of herb layer and is marked by a significant participation of *Artemisia austriaca* (the number of individuals increases markedly in dry periods with increasing grazing pressure), *Poa bulbosa*, *Capsella bursa-pastoris*, *Cardaria draba*, *Polygonum aviculare*, *Senecio vernalis*, *Lactuca serriola*, *L. tatarica*, *Lamium amplexicaule*, *Erodium cicutarium*, *Euphorbia esula* subsp. *tommasiniana*, *Taraxacum* sect. *Taraxacum* etc. However, trampling and fragmentary exposure of soil contributes to spreading of many annual plants including *Trifolium retusum*, *Arenaria leptoclados*, *Cerastium pumilum*, *Crepis ramosissima*, *Cruciata pedemontana*, *Draba verna*, *Medicago minima*, *Myosotis stricta*, *Veronica arvensis* etc. In general, these phytocenoses are characterized by low floristic richness and insignificant physiognomic variability due to an admixture of meadow forbs, and dominance of *Alopecurus pratensis*.

Cluster 4 "Herniario glabrae-Poetum angustifoliae" (Table 2, column 4)

Distribution. Slopes and dry bottoms of Zeleny, "Black Valley", Ahaimansky, Garbuzy, Small Chapelsky *pody*, nameless depressions from the outskirts of the village Podivka and the village Novotroyitske, on the slopes of the Great Chapelsky *pid*, as well as known from old relevés (1970s) from the natural core of the Biosphere Reserve «Askania-Nova» («Southern» site). Today, due to reservogenic succession (i.e. succession caused by the protected regime of the territory, with an unbalanced or incomplete structure), accompanied by the accumulation of abundant litter, these phytocenoses have disappeared from the «Southern» site and are replaced mainly by monodominant communities of *Poa angustifolia* belonging to cluster 1.

Environmental conditions. This vegetation unit includes the most common phytocenoses, distributed in dry small depressions and in concentric strips on non-flooded edges of major depressions, which are used as pastures and periodic hayfields (under favorable vegetation conditions). Communities are confined to meadow-chestnut residual saline sweetened gley heavy loam soils. At the same time, they are characterized by a relatively stable floristic composition, which in general is maintained in scattered depressions with a similar landuse regime.

Structure and composition. Total cover varies from 25 to 95%, averaging 78.4%. Dominants are *Poa angustifolia*, *Elytrigia repens* subsp. *pseudocaesia*, *Ventenata dubia*, *Artemisia santonicum* and *A. austriaca*, in some places *Festuca valesiaca*, *Alopecurus pratensis*, *Carex praecox* and *C. melanostachya*. Extremely bright and colorful aspects are formed by the large and coenotically strong contribution of forbs (Figure 6), especially *Achillea micranthoides*, *Allium regelianum*, *Dianthus guttatus*, *Ferula euxina*, *Inula britannica*, *Linaria biebersteinii*, *Lythrum virgatum*, *Phlomis scythica*, sporadically *Vicia villosa*, *Phalacrachena inuloides*, *Eryngium planum*, and *Lathyrus tuberosus*. Phytocenoses are characterized by high floristic richness and pronounced vertical structure. Due to periodic flooding and grazing, numerous bare inter-turf plots are observed, which serve as temporary habitats for a rich group of low-growing annual plants: *Herniaria glabra*, *Juncus bufonius*, *Myosurus minimus*, *Lotus angustissimus*, *Lythrum thymifolia*, *Gypsophila muralis*, *Scleranthus annuus*, *Elatine hungarica*, *Lythrum borysthenicum*, *Rorippa brachycarpa*, *Arenaria leptoclados*, etc.

The heterogeneous nature of these communities is visualized by the combination of xeromorphic plants, such as *Festuca valesiaca*, *F. pseudovina*, *Koeleria macrantha*, *Limonium sareptanum*, *Medicago romanica*, *Ventenata dubia*, *Polycnemum arvense*, *Filago arvensis*, *Seseli tortuosum* with hydrophilic species like *Butomus umbellatus*, *Elatine alsinastrum*, *Eleocharis palustris*, *E. uniglumis*, *Gratiola officinalis*, *Lythrum virgatum*, *Plantago tenuiflora*, *Pulicaria vulgaris*, *Rorippa austriaca*, occasionally *Beckmannia eruciformis*.

Finally, the condition and structure of the communities are significantly affected by grazing, which is manifested in sporadic distribution of *Ambrosia artemisiifolia*, *Artemisia austriaca*, *Cardaria draba*, *Centaurea diffusa*, *Consolida orientalis*, *Descurainia sophia*, *Eryngium campestre*, *Euphorbia esula* subsp. *tommasiniana*, *Polygonum aviculare*, *Tripleurospermum inodorum*, *Xanthium orientale* subsp. *riparium*, etc.

In general, these phytocenoses are relatively open, so in between beds of grasses, it is easy to see the whitish-dusty dried soil with iron-manganese nodules (beans) common on the surface, sometimes quite large (up to 1.5–2 cm in diameter, 20–30 pcs./m^2).

***Cluster 5 «Lathyro nissoliae-Phalacrachenetum inuloidis»* (Table 2, column 5)**

Distribution. Along the edge of Ahaimanskyi *pid* bottom, including the old fallows, which were plowed in inter-flood periods. Sporadic spots and rather large closed massifs are observed in the lower part of the catchment basins and in the northern part of the Great Chapelsky *pid* bottom.

Structure and composition. Sparse communities with a total cover of 50–90% (average 66%), with three herbal layers. The first layer is formed by tall *Elytrigia repens* subsp. *pseudocaesia* and *Rumex crispus*, sporadically *Armoracia rusticana*, *Lythrum virgatum*, *Schoenoplectus lacustris* and *Butomus umbellatus* (in the first stages of post-hydrogeneous succession). In the second layer *Phalacrachena inuloides* prevails (Figure 7), mixed with *Inula britannica*, *Artemisia santonicum*, *Pseudoarabidopsis toxophylla*, *Eleocharis palustris*, *Gratiola officinalis*, *Vicia hirsuta*. The lower layer is formed by *Cyperus flavescens*, *Lotus angustissimus*, *Polygonum aviculare*, *Gypsophila muralis*, *Rorippa brachycarpa*, *Stellaria graminea*, which are typical for bare, temporarily wet, bottom areas. In general, these bottoms are floristically poor, low-productive communities with unstable composition, depending on various disturbances, moisture regime, cover of the dominant *Phalacrachena inuloides*, etc.

Figure 6. Phytocenoses of the association *Herniario glabrae-Poetum angustifoliae*. Small Chapelsky *Pid*, peripheral part of the bottom, public pasture of cattle (near the village of Dolynsky), communities dominated by *Poa angustifolia* with *Artemisia santonica*, *Allium regelianum*, *Achillea micranthoides*, *Diantus guttatus*, *Plantago lanceolata*, 26.06.2010.

Figure 7. Phytocenoses of the association *Lathyro nissoliae-Phalacrachenetum inuloidis* on the bottom of the Ahaimansky *pid* (near the village of Podove), aspect of *Phalacrachena inuloides*, single shoots of *Rumex crispus* and *Beckmannia eruciformis* visible in the background, 6.06.2008.

***Cluster 6 «Myosuro-Beckmannietum eruciformis» (*Table 2, column 6)**

Distribution. Large depressions during heavy flooding (Ahaimansky, Domuzlynsky, Great Chapelsky, Zeleny *pody*).

Environmental conditions. These communities have a fluctuating nature. The ecological optimum is realized during severe floods and in the short post-hydrogenous period.

Structure and composition. Phytocenoses are formed by polycarpic biomorphs and hemicryptophytes, which are dominants (predominate numerically or by mass) and edificators (determine the structure and functioning of the community, form a specific environment); namely, *Beckmannia eruciformis*, *Gratiola officinalis*, *Elytrigia repens* subsp. *pseudocaesia*, *Lythrum virgatum* etc. The proportion of therophytes is 60–80%. These syntaxa are related to the previous cluster 5, but are more hydrophilic and tend to more wet habitats.

The total cover varies in the range of 65–97%, averaging 82.2%. Litter is not developed – up to 4%, sometimes 10-20%, due to soaked strands of the previous year's vegetation that floated with the flowing water. Phytocenoses are distributed sporadically in local concavities of the bottom, sometimes merging into large integral massifs, characterized by distinct layers and sparse synusia. The first layer is dominated by perennial hemicryptophytes and cryptophytes: the characteristic dominant *Beckmannia eruciformis* (cover up to 80%), *Elytrigia repens* subsp. *pseudocaesia*, *Lythrum virgatum*, *Schoenoplectus lacustris*, occasionally *Alopecurus pratensis* (Figure 8). The second layer is quite dense and closed, and it is formed mostly by rhizome vegetative-mobile species *Gratiola officinalis*, *Eleocharis palustris*, *Inula britannica*, *Mentha pulegium*, *Carex melanostachya*, *Rorippa austriaca*, *Artemisia santonicum*, as well as annuals *Chaiturus marrubiastrum*, *Pulicaria vulgaris* and *Vicia hirsuta*. The lowest layer consists of characteristic therophytes of drying habitats: *Myosurus minimus*, *Lotus angustissimus*, *Gypsophila muralis*, *Rorippa brachycarpa*, *Herniaria glabra*, sporadically *Lythrum tribracteatum*, *Trifolium retusum*, *Scleranthus annuus* and *Myosotis stricta*.

Due to combined mowing and grazing land-use in the «Black Valley» *pid*, synanthropic elements are abundant: *Aegilops cylindrica*, *Ambrosia artemisiifolia*, *Centaurea diffusa*, *Erigeron canadensis*, *Lactuca serriola*, *L. tatarica*, *Plantago major*, *Polygonum aviculare*, *Xanthium orientale* subsp. *riparium*.

Cluster 7 «Elatino-Butometum umbellati typicum» (Table 2, column 7)

Distribution. Large depressions: Great Chapelsky, Ahaimanskyi, Zeleny, "Black Valley" *pody*.

Environmental conditions. Hydrophilous coenoses formed during heavy flooding. Concentrated in local concavities and furrows, or occurs sporadically in the depression bottoms.

Structure and composition. Total cover is 35–97%, in average 78.7%. Quite diverse, mosaic communities with a wide range of dominants and codominants, and combined in different variants based on the forms of microrelief, soil disturbances, and degree of flooding: *Butomus umbellatus*, *Schoenoplectus lacustris*, *Elytrigia repens* subsp. *pseudocaesia*, *Eleocharis palustris*, *E. uniglumis*, *Cyperus flavescens*, sporadically in dry places *Inula britannica* (Figure 9). Other characteristic dominants and edificators of wet grasslands are less common and have low cover: *Alopecurus pratensis*, *Carex melanostachya*, *Beckmannia eruciformis*, *Lythrum virgatum*, *Gratiola officinalis*. The structure is generally similar to the phytocenoses described above. The fraction of tall hygromesophilic forbs is composed by *Rumex crispus*, *Pulicaria vulgaris*, *Persicaria maculata*, *Armoracia rusticana*. Low-growing annual plants are widespread in the exposed fragments of drying soil: *Rorippa brachycarpa*, *Gypsophila muralis*, *Pholiurus pannonicus*, *Myosurus minimus*, *Lythrum tribracteatum*, *Lotus angustissimus*, *Elatine alsinastrum*, as well as diagnostic species of this subassociation – *Lythrum borysthenicum*, *Juncus atratus*, *Elatine hungarica*. *Polygonum aviculare* occurs with high constancy and considerable abundance; *Plantago tenuiflora*, *Alisma plantago-aquatica*, *Allium regelianum*, *Juncus atratus*, *Ranunculus sceleratus*, *Typha angustifolia*, *Verbena supina* are sporadic.

Cluster 8 «Elatino-Butometum umbellati damasonietosum alismae» (Table 2, column 8)

Distribution. Phytocenoses of the Great Chapelsky *pid* with the presence of rare species *Damasonium alisma* (Figure 10). Outside this depression, *D. alisma* grows only near the village of Sofiyivka, Novotroitske district, Kherson oblast, in a gulley that connects the basins of the Barnashivka site and the Ahaimansky *pid*, on both sides of the former sewage sump, near the Kherson – Henichesk highway (Shapoval 2012). In other depressions, no specimen of *D. alisma* was found, despite the similar ecological and coenotic parameters and related floristic composition of these habitats.

Environmental conditions. Phytocenoses of the subassociation tend to occur in shallow water, often with open water gaps. In general, the described phytocenoses are extremely rare and exist ephemerally, with an exceptionally favorable flooding regime. In insufficiently wet seasons, such hydrophilic communities are transformed into mesic grasslands, preserving the core of dominant plants that are able to resist of moisture deficiency. But a whole complex of water demanding ephemeral species of depression disappear and are replaced by the more resistant mesophytic species.

Structure and composition. Total cover varies in the range of 65–97%, averaging 87.5%. The first herbal layer is formed by tall dominants and edificators, generally typical for bottom of depressions during periods of flooding: *Elytrigia repens* subsp. *pseudocaesia* and *Lythrum virgatum* with an admixture of *Beckmannia eruciformis*, *Alopecurus pratensis*, *Butomus umbellatus*, *Rumex crispus*, *Poa angustifolia* and *Juncus atratus*. The second layer is composed of dominants *Eleocharis palustris*, *Carex melanostachya* and *Gratiola officinalis*, with a significant proportion of *Euphorbia esula* subsp. *tommasiniana*, *Phlomis scythica* and sporadically *Inula britannica*, *Rorippa austriaca*, *Phalacrachena inuloides*.

Figure 8. Hygrophytic cenoses of the association *Myosuro-Beckmannietum eruciformis*, flooded bottom of the Zeleny *pid*, aspect of *Lythrum virgatum* with admixture of *Inula britanica*. 7.07.2010.

Figure 9. Phytocenoses of the subassociation *Elatino-Butometum umbellati typicum*, concentrated in the center of the newly dried bottom of the Ahaimansky *pid*, aspect *Butomus umbellatus*, *Schoenoplectus lacustris*, *Elytrigia repens* subsp. *pseudocaesia*, 9.06.2010.

Figure 10. Phytocenoses of the *subassociation Elatino-Butometum umbellati damasonietosum alismae* in the central part of the bottom of the Great Chapelsky *pid* during flooding, flowering individuals of *Damasonium alisma* among vegetative shoots of *Butomus umbellatus* and *Elytrigia repens* subsp. *pseudocaesia*, 17.05.2010.

Finally, as the water recedes the damp soil is covered by *Damasonium alisma*, *Rorippa brachycarpa*, *Elatine alsinastrum*, rarely *Elatine hungarica*, *Lotus angustissimus*, *Lythrum thymifolia*, *Lythrum borysthenicum*, *Myosurus minimus*, *Pholiurus pannonicus*, *Plantago tenuiflora*, *Polygonum aviculare* (due to trampling), *Potentilla argentea* (numerous seedlings and juveniles), *Gypsophila muralis*, *Cyperus flavescens*. Sometimes, under optimal moisture conditions, *Damasonium alisma* reach 40–60 cm in height and extends into to the second layer.

***Cluster 9 Derivative community «Rumex ucranicus+-Puccinellia distans»* (Table 2, column 9)**

Distribution. Great Chapelsky *pid.*

Environmental conditions. Fragmentary cenoses, confined to the trampled shores of artificial watercourses, which are flooded all year round and filled with artesian water (ditches for watering wild ungulates). Localized in a narrow strip along a watercourse. Characterized by clear signs of salinity.

Structure and composition. The total cover varies from 30 to 90%. The most common species are *Rumex ucranicus*, *Taraxacum bessarabicum*, *Plantago tenuiflora*, *Pholiurus pannonicus*, *Petrosimonia triandra*, *Myosurus minimus*, *Juncus bufonius*, and *J. compressus*. On the edge of a water pool *Veronica anagallis-aquatica*, *Ranunculus sceleratus*, *Persicaria maculata* grow. Due to significant trampling, species that spread include *Polygonum aviculare*, *Plantago major*, *Echinochloa crus-galli*, *Setaria pumila*, *Ambrosia artemisiifolia*, *Lactuca tatarica*, *Xanthium spinosum*. The most common dominants are *Beckmannia eruciformis*, *Bolboschoenus maritimus*, *Eleocharis palustris*, *Elytrigia repens* subsp. *pseudocaesia*, *Juncus gerardii*, *Pulicaria vulgaris*, *Puccinellia distans*, and sporadically *Schoenoplectus lacustris*.

Ordination and territorial differentiation of vegetation units

The DCA ordination of the identified units (Figure 11) showed that they are distributed along the first ordination axis from the driest (cluster 1) to the wettest (cluster 9). Xerophytic and mesoxerophytic units 1–3 are located in the right part of the ordination diagram and units 4–9, which are characteristic for wetter conditions, are located in the left part of the diagram. Clusters 3–5 are concentrated in the central part, which indicates their mesic nature, not only by moisture, but also by other closely correlated edaphic factors, including soil aeration, fluctuating water level, nitrogen content in soil and salt regime of the soil. Units 1 and 9 are located at the extremes of the first ordination axis, while the remaining units are separated into two rows along the second ordination axis. In the lower part of the diagram are units 3, 4 and 6, and in the upper part are units 2, 5 and 7. Probably the leading factors of differentiation along the second axis are climatic – first of all, thermal regime and light. Almost all units are well separated from each other, with the exception of units 7 and 8, which we have interpreted as subassociations of one association. Regardless of the number of vegetation plots in these units, which varies widely, the amplitude of the units is approximately the same.

Peculiarities of ecological differentiation of steppe depression syntaxa can be traced on the transect across the conditional (model) depression, which has well-preserved natural slopes and bottom and is periodically flooded (Figure 12). Xero-mesophytic and mesic communities of syntaxa 1, 2 and 4 are formed at the edges of the depression, its slopes are occupied by communities belonging to units 3 (upper part of a slope) and 5 (lower part of a slope), and communities of units 6, 7 and 8 at the bottom as well as unit 9 (the latter in the presence of a shallow artificial watercourse constantly filled with artesian water). The abrupt change of ecological values on the slopes and especially on the bottom of a depression are clearly visible. In addition to a sharp increase of moisture, there is an increase in the variability of dampness, soil aeration, soil pH and salt regime and a decrease in the carbonates content of the soil. At the same time indicators of climatic factors do not change.

Identification of vegetation units by expert systems

The classification of vegetation plots by the expert system EVC (Suppl. material 3: Fig. A) showed a predominance of plots belonging to the class *Festuco-Brometea* within units 1–2, although a significant portion of the plots also belonged to the *Molinio-Arrhenatheretea* class. In addition, the plots assigned to the class *Molinio-Arrhenatheretea* represented a significant portion in cluster 3, although the predominant portion of the plots assigned in that cluster by the expert system belonged to

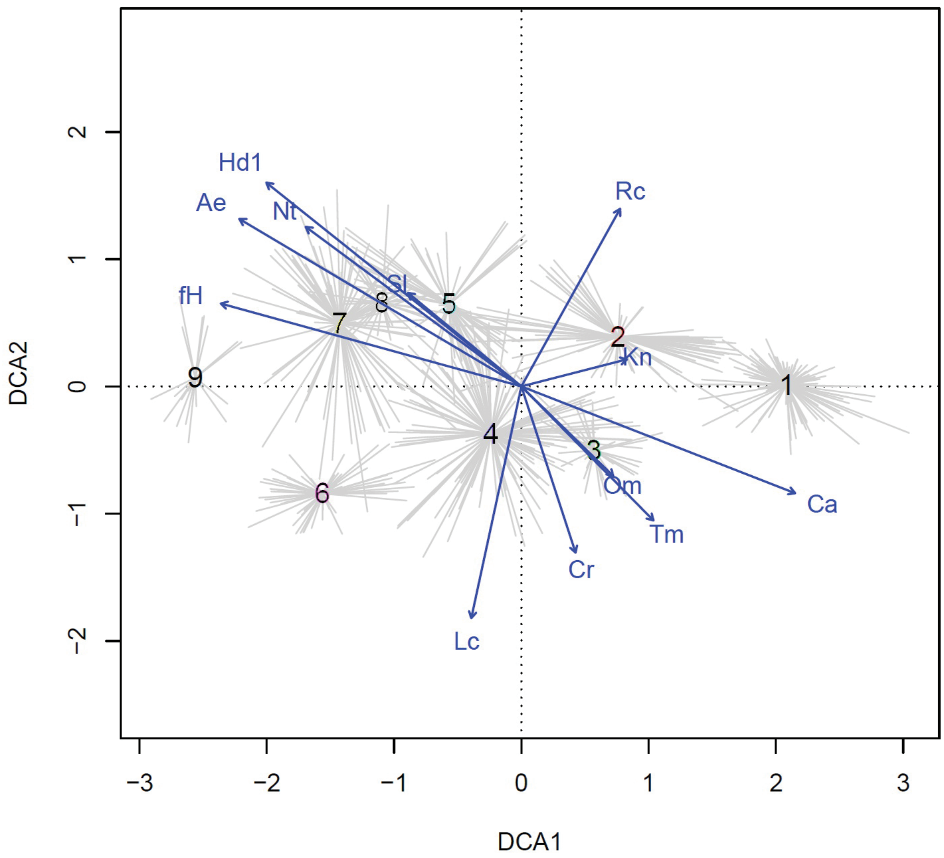

Figure 11. DCA-ordination of the resulted vegetation units. Numbers in the centroids correspond to the unit number in the text. Environmental verctors of DES: Hd – moisture, fH – variability of damping, Rc – soil acidity, Sl – salt regime of a soil, Ca – carbonate content in a soil, Nt – nitrogen content in a soil, Ae – soil aeration, Tm – thermal regime, Om – humidity of climate (ombroregime), Kn – continentality of climate, Cr – cryoregime, Lc – light. Eigenvalues: 1st axis (DCA1) 0.6533, 2nd axis (DCA2) 0.2723.

the class *Sedo-Scleranthetea*. In the clusters 4–8 there was a clear predominance of plots assigned to the class *Molinio-Arrhenatheretea*, although in cluster 7 there was also a significant portion of plots assigned to the classes *Isoëto-Nanojuncetea* and *Phragmito-Magnocaricetea*. Cluster 9 clearly shows the predominance of plots assigned by the expert system to Festuco-Puccinellietea class.

The interpretation of vegetation plots by the expert system EUNIS-ESy in units of the EUNIS habitat classification (Suppl. material 3: Fig. B) showed that most plots of unit 1 were classified as anthropogenic habitat, which can probably be explained by the large number of therophytes in xerophytic communities of the steppe depressions, which are also characteristic for xerophytic anthropogenic vegetation. Within the units 2–6 the plots assigned to grassland habitats prevailed. A significant part of those units was identified only to the first level of the hierarchy (R). Clusters 2 and 3 contained a considerable proportion of plots of dry and mesic grasslands, cluster 5 largely contained plots of wet and subhalophytic meadows, and plots in cluster 4 were distributed evenly to grassland habitats and anthropogenic habitats, and somewhat less commonly to wetlands. The latter clearly predominated in clusters 7–9. Cluster 8 also showed a high proportion of plots assigned to freshwater habitats, in particular to type C35b (periodically exposed shore with stable mesotrophic sediments with pioneer vegetation).

Discussion

Syntaxonomy

The obtained results of the vegetation classification, in particular the list of diagnostic, constant and dominant species of the syntaxa (Suppl. material 4), supported by the results of their phytoindication analysis, distribution in relief, as well as the interpretation by two expert systems, allowed us to develop an ecologically sound syntaxonomic system of the steppe depression vegetation of Ukraine. We then attempted to fit these units into the existing system of syntaxa in Europe (Mucina et al. 2016). Cluster 1 (*Ferulo euxinae-Caricetum praecocis*) occupies an intermediate position between the classes *Festuco-Brometea* and *Artemisietea vulgaris* (*Agropyretalia intermedio-repentis*). Communities of this association are characterized by a significant participation of synanthropic species. However, these species do not form clear diagnostic blocks, and

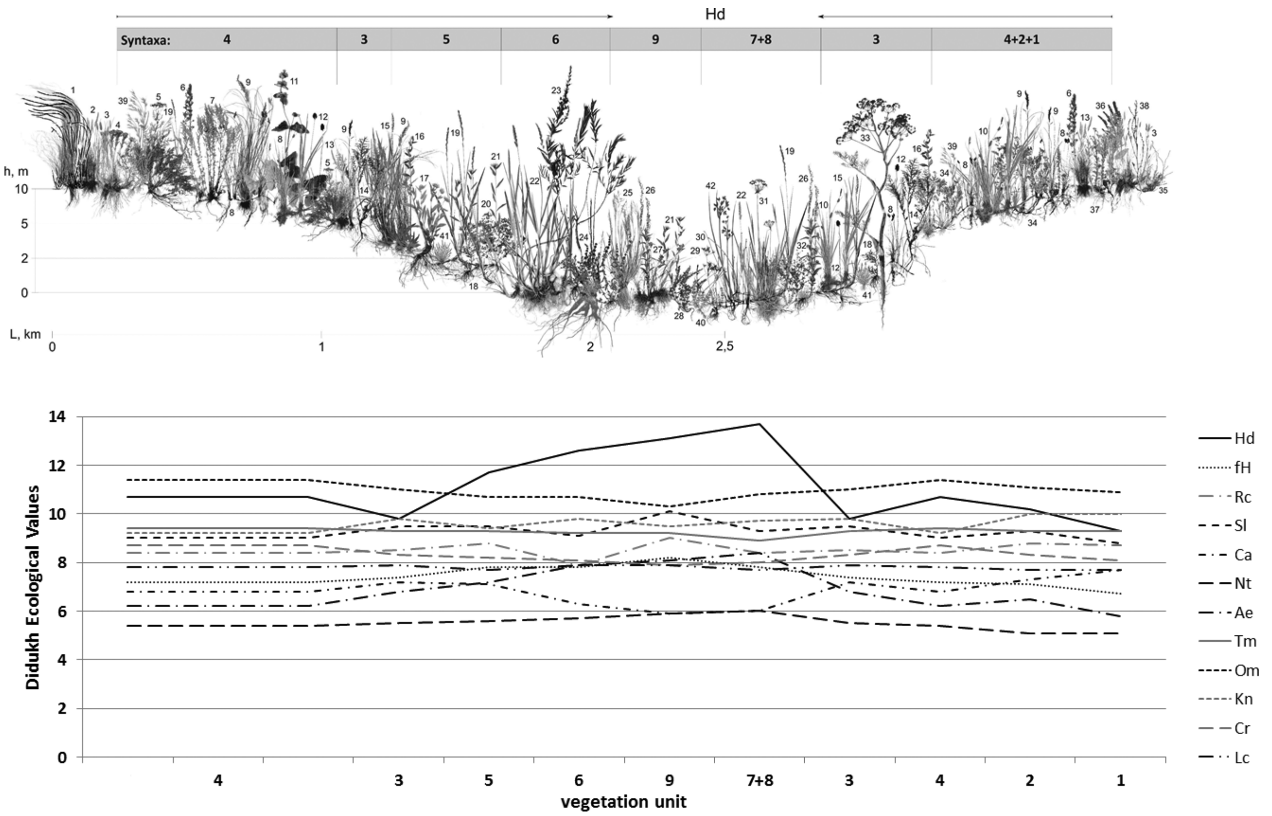

Figure 12. Ecological and coenotic profile of model steppe depressions of the Left Bank of the Lower Dnieper. The central part of the bottom is occupied by wetland communities, which change along the slopes by wet, mesic and xero-mesic phytocenoses. The transectshows the difference in absolute height between the bottom of the depression and its slope, the length and asymmetry of the «body» of the depression along the line: slope-bottom. Species: 1 – *Stipa ucrainica*, 2 – *Koeleria macrantha*, 3 – *Agropyron cristatum* subsp. *pectinatum*, 4 – *Galatella villosa*, 5 – *Achillea micranthoides*, 6 – *Atriplex oblongifolia*, 7 – *Artemisia austriaca*, 8 – *Carex praecox*, 9 – *Poa angustifolia*, 10 – *Carex melanostachya*, 11 – *Phlomis scythica*, 12 – *Allium regelianum*, 13 – *Festuca valesiaca*, 14 – *Artemisia santonicum*, 15 – *Alopecurus pratensis*, 16 – *Chaiturus marrubiastrum*, 17 – *Inula britannica*, 18 – *Rorippa brachycarpa*, 19 – *Elytrigia repens* subsp. *pseudocaesia*, 20 – *Lotus angustissimus*, 21 – *Phalacrachena inuloides*, 22 – *Beckmannia eruciformis*, 23– *Lythrum virgatum*, 24 – *Mentha pulegium*, 25 – *Puccinellia distans*, 26 – *Gratiola officinalis*, 27 – *Juncus atratus*, 28 – *Rumex ucranicus*, 29 – *Damasonium alisma*, 30 – *Eleocharis palustris*, 31 – *Butomus umbellatus*, 32 – *Pulicaria vulgaris*, 33 – *Ferula euxina*, 34 – *Sibbaldianthe bifurca* subsp. *orientalis*, 35 – *Bassia prostrata*, 36 – *Salvia nemorosa* subsp. *tesquicola*, 37 – *Tanacetum millefolium*, 38 – *Polygonum patulum*, 39 – *Ventenata dubia*, 40 – *Elatine alsinastrum*, 41 – *Myosurus minimus*, 42 – *Schoenoplectus lacustris*. For the two-letter abbreviations of environmental factors – see Figure 11.

secondly, the communities are formed naturally, not due to human activities, which does not allow them to be classified within synanthropic vegetation syntaxa e.g., to assign them to the *Agropyretalia intermedio-repentis* order. Therefore, at this stage, we assign these communities, as in the original publication (Shapoval 2006), to the class *Festuco-Brometea*, order *Festucetalia valesiacae* and alliance *Festucion valesiacae*. Whereas these comunities are somewhat different from the typical communities of the alliance, we consider them as a separate suballiance *Galio ruthenici-Caricenion praecocis*. It is quite possible that in the future this suballiance will get the rank of alliance, but so far the lack of their own character species does not allow to consider them in the rank of a separate alliance. Cluster 2 (*Diantho guttati-Caricetum melanostachyae*) can be included in the same suballiance, although this association is slightly more mesophytic according to the results of phytoindication assessment, but according to the expert systems, it contains the most plots of the *Festuco-Brometea* class and true steppe habitat type – R1B. In addition, its floristic composition is quite similar to the previous association. Earlier these coenoses were described as association *Potentillo orientalis-Caricetum melanostachyae*; however, a significant increase in the plots used in our dataset revealed the sporadic nature of *Sibbaldianthe bifurca* subsp. *orientalis* (syn. *Potentilla orientalis*) in this syntaxon. Instead, *Dianthus guttatus* has a higher diagnostic value for this association (see Table 1). These features of the floristic composition, as well as nomenclature changes in relation to *Sibbaldianthe bifurca* subsp. *orientalis*, prompted us to reject the previous invalid name and describe these communities as a new association.

Units 3–5 obviously represent mesic grasslands and their mesophytic character was shown by the results of phytoindication. According to the results of the analysis using the EVC expert system, a significant number of plots are assigned to the class *Molinio-Arrhenatheretea*, which is also confirmed by the results of the analysis using the expert system EUNIS-ESy, which assigned these plots to mesic grassland habitats. Therefore, we classify them within the *Molinio-Arrhenatheretea* class. Among the higher-ranking syntaxa recognized in EuroVegCheklist, these communities are the most similar to the order *Althaeetalia officinalis* and its alliance *Althaeion officinalis*. Although the diagnosis of the order and alliance in the original publication (Golub 1995) is not clearly defined, its definition as "Tall-herb periodically flooded meadows of the steppe and semi-desert zones of Eastern Europe" in Mucina et al. (2016) is fully consistent with the steppe depression vegetation. Thus, we synonymize the previously described alliances of the mesic vegetation of the steppe depressions, *Carici praecocis-Elytrigion pseudocaesiae*, *Poo angustifoliae-Ferulion orientale*, and *Lythro virgati-Elytrigion pseudocaesiae*, as was done in a previous publication (Shapoval 2006), and consider them within the *Althaeion officinalis* alliance.

The wettest associations of depression bottoms (clusters 6–8) showed some inconsistency in their interpretation by expert systems – on the one hand, the EVC expert system assigned most of their plots to the *Molinio-Arrhenatheretea* class, and on the other hand the EUNIS-ESy expert system interpreted most of their plots as C (Surface waters) and Qb (Wetlands) groups. But this inconsistency is quite understandable given the ephemeral and complex nature of these habitats and irregularity of flooding. In view of this, we propose that the nature of these communities best fits the class *Isoëto-Nanojuncetea*, defined as "Pioneer ephemeral dwarf-cyperaceous vegetation in periodically freshwater flooded habitats of Eurasia" in Mucina et al. (2016). We include these units (two associations and one additional subassociation) to an alliance of steppe depression vegetation, which is currently accepted in the EVC – *Myosuro-Beckmannion eruciformis* – within the order *Nanocyperetalia*. The floristic composition of these communities is quite unique and differs significantly from other alliances of this order, such as the *Verbenion supinae* alliance, which includes pioneer ephemeral communities in the nemoral zone in habitats flooded with fresh water without signs of salinity or sweetening. Moreover, the fluctuating nature of ephemeral communities of *pody* hardly makes it possible to consider them as pioneer.

Cluster 9, according to the list of diagnostic species and the analysis using expert systems, can be assigned to the class *Festuco-Puccinellietea*. This is the only community that has a pronounced halophytic character, which distinguishes it from all other analyzed units. This difference, both floristic and ecological, might explain the erroneous attribution of the steppe depression vegetation in general to the halophytic type. This unit should probably be attributed to the order *Scorzonero-Juncetalia gerardi*. However, the transitional nature of the communities as well as the source of the chloride salinity does not currently allow them to be attributed to any of the existing alliances.

The obtained results once again showed that the vegetation of steppe depressions (*pody*) is indeed rather complex, but not «mosaic», because it was not possible to isolate phytocenoses of annual (ephemeral) plants characteristic for the class *Isoëto-Nanojuncetea*, and separate them spatially or in time from grassland or wetland communities of perennial plants. Even in the plots of small size in small depressions and bottom depressions with the longest duration of flooding, both ephemeral annual and perennial species were present. Of course, the increase in the plot size slightly changed the proportions of individual and total cover, but in no way affected the homogeneity and integrity of the studied plant communities. It can be assumed that with sufficiently long floods and increasing depth of a water body, some mesophytic or xeromesophytic plants, which are common in dry, non-flooded depressions, would disappear from the communities. Then we would probably get localized occurrences of ephemeral annual vegetation, confined to drying puddles. But irregular and short-term flooding of depressions (every 7–10 yrs, sometimes 20 yrs, lasting only 2–3 months), as well as the shallowness of temporary standing water (about 30–40 cm deep at the peak of the flood and then becoming shallow, 5–10cm) do not adversely affect perennial mesophytic species. It is worth noting that the closed bottoms of the depressions in the natural intact state is a perfectly flat surface, so the edaphic conditions, moisture regime and other abiotic parameters are almost identical throughout a flooded bottom. Thus, when the depressions are flooded and then begin to dry in the same season, peculiar combinations of ephemeral annual aquatic plants and perennial grassland and wetland plants are observed. These plants grow in different layers, but within the same phytocenosis. Such an original complex of hydrophytic vegetation ("ephemeretum") is indivisible either territorially or chronologically.

When interpreting the obtained units, we tried to compare them with the units described in the very first work on the *pody* vegetation (Solomakha et al. 2005). However, we did not succeed, since the diagnostic species of those associations were in most cases not concentrated in one cluster but distributed among different units in the dataset. We believe that the reason for this is that these units were identified using insufficiently representative data. With the increase in the number of vegetation plots from 34 to 367 (Shapoval 2006), and in the present work to 641, the blocks of diagnostic species have been dissolved. Therefore, we can say that, although they are somewhat similar to our associations, we cannot synonymize them. For example, we can assume that the association *Achilleo micranthoides-Poetum angustifoliae* is close to *Herniario glabrae-Poetum angustifoliae*; however, from the three species that are listed as diagnostic for *Achilleo micranthoidis-Poetum angustifoliae*, *Achillea micranthoides* has a fairly high fidelity in our clusters 3 and 4, *Poa angustifolia* in clusters 1 and 2, and *Potentilla argentea* in clusters 2 and 4, which may indicate their diagnostic significance for syntaxa of a higher rank than the association.

Our testing of two expert systems showed that they can be used as an additional tool for interpreting the results of vegetation classification, especially for assigning associations to syntaxa of a higher hierarchical rank. However, for such complex communities, and, accordingly, complex habitat types, the use of expert systems has limitations, since their nature is such that communities can contain species of different ecological groups, different vegetation classes, and, accordingly, different discriminant or functional species groups, which often overlap. These features prevent the correct interpretation of the relevés by an expert system.

Nomenclatural notes

Taking into account that all previously described units of the steppe depression vegetation are invalid, because the nomenclature type was not indicated using *expressis verbis* the Latin words '*typus*' or '*holotypus*'(ICPN Art. 5, par.3), we validly describe the syntaxa of the steppe depression vegetation which we accepted, according to the analysis presented in this paper. When validating the previously described syntaxa, we have kept all their nomenclature types, which are also presented in this article in the Suppl. material 1, but we have slightly modified the lists of diagnostic species of these syntaxa, in accordance with the taxonomic nomenclature used in this paper and the results of calculating their fidelity on the basis of the phi coefficient (Chytrý et al. 2002).

Suballiance ***Galio ruthenici-Caricenion praecocis*** *Shapoval ex Shapoval et Kuzemko suball. nov. hoc loco*

Validated name: *Galio ruthenici-Caricenion praecocis* Shapoval 2006 nom. inval. (Art. 5).

Holotypus hoc loco: ass. *Ferulo euxinae-Caricetum praecocis* Shapoval ex Shapoval et Kuzemko hoc loco.

Diagnostic taxa: *Bromopsis inermis*, *Carex praecox*, *Convolvulus arvensis*, *Cruciata pedemontana*, *Dianthus guttatus*, *Falcaria vulgaris*, *Galium ruthenicum*, *Galium spurium*, *Phlomis herba-venti* subsp. *pungens*, *Poa angustifolia*, *Seseli tortuosum*, *Veronica spicata*, *Vicia hirsuta*, *Vicia villosa*, *Viola kitaibeliana.*

Association ***Ferulo euxinae-Caricetum praecocis*** *Shapoval ex Shapoval et Kuzemko ass. nov. hoc loco*

Validated name: *Ferulo euxinae-Caricetum praecocis* Shapoval 2006 nom. inval. (Art. 5).

Holotypus hoc loco: Shapoval (2006: table 13, relevé 12), or the same relevé in the Suppl. material 1, relevé 1010 (this paper):

V. Shapoval, 16.05.2005, 46.462707°N, 33.91405°E, plot size 9 m^2, total cover 90%, litter 70%.

Species (with cover of the Braun-Blanquet scale): *Bromopsis inermis* 3; *Carex praecox* 3; *Falcaria vulgaris* 2; *Galium ruthenicum* 2; *Ferula euxina* 2; *Poa angustifolia* 2; *Vicia hirsuta* 1; *Viola kitaibeliana* 1; *Vicia villosa* +; *Eryngium campestre* r; *Eryngium planum* r; *Limonium sareptanum* r.

Diagnostic taxa: *Bromopsis inermis*, *Carex praecox*, *Elytrigia repens*, *Falcaria vulgaris*, *Galium ruthenicum*, *Lamium amplexicaule* var. *orientale*, *Phlomis herba-venti* subsp. *pungens*, *Poa angustifolia*, *Salsola tragus*, *Vicia villosa*, *Viola kitaibeliana*

Association ***Diantho guttati-Caricetum melanostachyae*** *ass. nov. hoc loco*

Synonym: *Potentillo orientalis-Caricetum melanostachyae* Shapoval 2006 nom. inval. (Art. 5)

Holotypus hoc loco: Shapoval (2006: table 14, relevé 4), or the same relevé in the Suppl. material 1, relevé 871 (this paper):

V. Shapoval, 12.07.2004, 46.456164°N, 33.918493°E, plot size 100m^2, total cover 95%, litter 5%.

Species: *Poa angustifolia* 4; *Carex praecox* 2; *Falcaria vulgaris* 2; *Galium ruthenicum* 2; *Sibbaldianthe bifurca* subsp. *orientalis* 2; *Veronica spicata* 2; *Allium flavum* subsp. *tauricum* 1; *Artemisia austriaca* 1; *Bromopsis inermis* 1; *Carex melanostachya* 1; *Convolvulus arvensis* 1; *Dianthus guttatus* 1; *Elytrigia repens* subsp. *pseudocaesia* 1; *Phlomis herba-venti* subsp. *pungens* 1; *Vicia hirsuta* 1; *Vicia villosa* 1; *Euphorbia esula* subsp. *tommasiniana* +; *Hylotelephium maximum* +; *Eryngium campestre* r; *Lactuca serriola* r; *Lepidium perfoliatum* r; *Rumex crispus* r; *Sisymbrium altissimum* r; *Tragopogon dasyrhynchus* r.

Diagnostic taxa: *Allium flavum subsp. tauricum*, *Carex melanostachya*, *Carex praecox*, *Dianthus guttatus*, *Eryngium planum*, *Euphorbia seguieriana*, *Falcaria vulgaris*, *Galium ruthenicum*, *Linaria biebersteinii*, *Poa angustifolia*, *Seseli tortuosum*, *Thesium arvense*, *Tragopogon dasyrhynchus*

Association ***Vicio lathyroidis-Alopecuretum pratensis*** *Shapoval ex Shapoval et Kuzemko ass. nov. hoc loco*

Validated name: *Vicio lathyroidis-Alopecuretum pratensis* Shapoval 2006 nom. inval. (Art. 5)

Holotypus hoc loco: Shapoval (2006: table 12, relevé 2), or the same relevé in the Suppl. material 1, relevé 1085 (this paper):

V. Shapoval, 17.05.2005, 46.476654°N, 33.862878°E, plot size 9m^2, total cover 80%, litter 5%.

Species: *Alopecurus pratensis* 3; *Poa angustifolia* 3; *Bromopsis inermis* 2; *Festuca valesiaca* 2; *Artemisia austriaca* 1; *Cerastium pumilum* 1; *Convolvulus arvensis* 1; *Lepidium draba* 1; *Medicago minima* 1; *Poa bulbosa* 1; *Taraxacum* sect. *Taraxacum* 1; *Veronica arvensis* 1; *Vicia lathyroides* 1; *Capsella bursa-pastoris* +; *Achillea micranthoides* r; *Crepis ramosissima* r; *Plantago lanceolata* r.

Diagnostic taxa: *Achillea micranthoides*, *Alopecurus pratensis*, *Arenaria leptoclados*, *Artemisia austriaca*, *Capsella bursa-pastoris*, *Carex spicata*, *Cerastium pumilum*, *Crepis ramosissima*, *Cruciata pedemontana*, *Festuca valesiaca*, *Lepidium draba*, *Medicago minima*, *Poa bulbosa*, *Stellaria graminea*, *Taraxacum sect. Taraxacum*, *Trifolium arvense*, *Trifolium retusum*, *Veronica arvensis*, *Vicia lathyroides.*

Association ***Herniario glabrae-Poetum angustifoliae*** *Shapoval ex Shapoval et Kuzemko ass. nov. hoc loco*

Validated name: *Herniario glabrae-Poetum angustifoliae* Shapoval 2006 nom. inval. (Art. 5)

Holotypus hoc loco: Suppl. material 1, relevé 932 (this paper):

V. Shapoval, 18.07.2004, 46.437786°N, 33.740333°E, plot size 100m^2, total cover 65%, litter 1%.

Species: *Inula britannica* 3; *Artemisia santonicum* 2; *Euphorbia esula subsp. tommasiniana* 2; *Holosteum umbellatum* 2; *Lotus angustissimus* 2; *Myosurus minimus* 2; *Poa angustifolia* 2; *Polycnemum arvense* 2; *Polygonum aviculare* 2; *Potentilla argentea* 2; *Trifolium retusum* 2; *Veronica arvensis* 2; *Achillea micranthoides* 1; *Carex praecox* 1; *Elytrigia repens* subsp. *pseudocaesia* 1; *Filago arvensis* 1; *Gypsophila muralis* 1; *Herniaria glabra* 1; *Linaria biebersteinii* 1; *Allium regelianum* +; *Crepis ramosissima* r; *Erysimum repandum* r.

Diagnostic taxa: *Achillea micranthoides*, *Allium regelianum*, *Artemisia santonicum*, *Gypsophila muralis*, *Herniaria glabra*, *Lepidium ruderale*, *Plantago lanceolata*, *Polycnemum arvense*, *Potentilla argentea*, *Ventenata dubia.*

Association ***Lathyro nissoliae-Phalacrachenetum inuloidis*** *Shapoval ex Shapoval et Kuzemko ass. nov. hoc loco*

Validated name: *Lathyro nissoliae-Phalacrachenetum inuloidis* Shapoval 2006 nom. inval. (Art. 5)

Holotypus hoc loco: Shapoval (2006: table 6, relevé 9)), or the same relevé in the Suppl. material 1, relevé 805 (this paper):

V. Shapoval, 27.05.2004, 46.618698°N, 34.198073°E, plot size 100m^2, total cover 50%, litter 40%.

Species: *Elytrigia repens* subsp. *pseudocaesia* 3; *Cyperus flavescens* 2; *Inula britannica* 2; *Phalacrachena inuloides* 2; *Rorippa brachycarpa* 2; *Eleocharis palustris* 1; *Lathyrus nissolia* 1; *Stellaria graminea* 1; *Vicia hirsuta* 1; *Senecio leucanthemifolius* subsp. *vernalis* +; *Crepis sancta* r.

Diagnostic taxa: *Armoracia rusticana*, *Crepis sancta*, *Cyperus flavescens*, *Inula britannica*, *Lathyrus nissolia*, *Lathyrus tuberosus*, *Phalacrachena inuloides*

Alliance ***Myosuro minimi-Beckmannion eruciformis*** *Shapoval ex Shapoval et Kuzemko all. nov. hoc loco*

Validated name: *Myosuro-Beckmannion eruciformis* Shapoval 2006 nom. inval. (Art. 5)

Holotypus hoc loco: ass. *Myosuro-Beckmannietum eruciformis* Shapoval ex Shapoval et Kuzemko hoc loco

Diagnostic taxa: *Butomus umbellatus*, *Chaiturus marrubiastrum*, *Damasonium alisma*, *Elatine alsinastrum*, *Gratiola officinalis*, *Juncus atratus*, *Lythrum virgatum*, *Mentha pulegium*, *Myosurus minimus*, *Rorippa brachycarpa*

Association ***Myosuro minimi-Beckmannietum eruciformis*** *Shapoval ex Shapoval et Kuzemko ass. nov. hoc loco*

Validated name: *Myosuro-Beckmannietum eruciformis* Shapoval 2006 nom. inval. (Art. 5)

Holotypus hoc loco: Shapoval (2006: table 5, relevé 10), or the same relevé in the Suppl. material 1, relevé 982 (this paper):

V. Shapoval, 12.08.2004, 46.557254°N, 33.472972°E, plot size 100m^2, total cover 80%, litter 2%.

Species: *Beckmannia eruciformis* 3; *Lotus angustissimus* 3; *Eleocharis palustris* 2; *Herniaria glabra* 2; *Myosurus minimus* 2; *Polygonum aviculare* 2; *Carex melanostachya* 1; *Elytrigia repens* subsp. *pseudocaesia* 1; *Gratiola officinalis* 1; *Gypsophila muralis* 1; *Inula britannica* 1; *Lythrum virgatum* 1; *Mentha pulegium* 1; *Rorippa brachycarpa* 1; *Trifolium retusum* 1; *Ambrosia artemisiifolia* +; *Plantago major* +.

Diagnostic taxa: *Aegilops cylindrica*, *Beckmannia eruciformis*, *Chaiturus marrubiastrum*, *Eleocharis palustris*, *Erigeron canadensis*, *Gratiola officinalis*, *Gypsophila muralis*, *Inula britannica*, *Lotus angustissimus*, *Lythrum virgatum*, *Mentha pulegium*, *Myosurus minimus*, *Polygonum aviculare*, *Xanthium orientale subsp. riparium*

Association ***Elatino hungaricae-Butometum umbellati*** *ass. nov. hoc loco*

Holotypus hoc loco: Suppl. material 1, relevé 675 (this paper):

V. Shapoval, 25.06.2010, 46.433217°N, 33.7257°E, plot size 100m^2, total cover 80%, litter 0%.

Species: *Butomus umbellatus* 4; *Chaiturus marrubiastrum* 1; *Elatine hungarica* 1; *Lythrum borysthenicum* 1; *Pholiurus pannonicus* 1; *Polygonum aviculare* 1; *Pulicaria vulgaris* 1; *Gratiola officinalis* +; *Plantago tenuiflora* +; *Rorippa austriaca* +; *Rorippa brachycarpa* +.

Diagnostic taxa: *Elatine hungarica*, *Juncus atratus*, *Lythrum borysthenicum*,

Subassociation ***Elatino-Butometum umbellati damasonietosum alismae*** *subass. nov. hoc loco*

Holotypus hoc loco: Suppl. material 1, relevé 641 (this paper):

V. Shapoval, 24.06.2010, 46.487017°N, 33.8533°E, plot size 100m^2, total cover 80%, litter 0%.

Species: *Eleocharis palustris* 3; *Elytrigia repens* subsp. *pseudocaesia* 3; *Butomus umbellatus* 1; *Damasonium alisma* 1; *Elatine alsinastrum* 1; *Euphorbia esula* subsp. *tommasiniana* 1; *Juncus atratus* 1; *Rorippa brachycarpa* 1; *Gratiola officinalis* +; *Lythrum virgatum* +; *Rorippa austriaca* +; *Rumex crispus* +.

Diagnostic taxa: *Alopecurus pratensis*, *Butomus umbellatus*, *Damasonium alisma*, *Elatine alsinastrum*, *Gratiola officinalis*, *Juncus atratus*, *Rorippa brachycarpa*, *Rumex crispus.*

Thus, the classification scheme of the steppe depression vegetation of Ukraine in accordance with our results has the following form:

Cl. *Festuco-Brometea* Br.-Bl. et Tx. ex Soó 1947
Ord. *Festucetalia valesiacae* Soó 1947
All. *Festucion valesiacae* Klika 1931
Suball. *Galio ruthenici-Caricenion praecocis* Shapoval ex Shapoval et Kuzemko hoc loco
Ass. *Ferulo euxinae-Caricetum praecocis* Shapoval ex Shapoval et Kuzemko hoc loco
Ass. *Diantho guttati-Caricetum melanostachyae* Shapoval et Kuzemko hoc loco
Cl. *Molinio-Arrhenatheretea* Tx. 1937
Ord. *Althaeetalia officinalis* Golub et Mirkin in Golub 1995
All. *Althaeion officinalis* Golub et Mirkin in Golub 1995
Ass. *Vicio lathyroidis-Alopecuretum pratensis* Shapoval ex Shapoval et Kuzemko hoc loco
Ass. *Herniario glabrae-Poetum angustifoliae* Shapoval ex Shapoval et Kuzemko hoc loco
Ass. *Lathyro nissoliae-Phalacrachenetum inuloidis* Shapoval ex Shapoval et Kuzemko hoc loco
Cl. *Isoëto-Nanojuncetea* Br.-Bl. et Tx. in Br.-Bl. et al. 1952
Ord. *Nanocyperetalia* Klika 1935
All. *Myosuro-Beckmannion eruciformis* Shapoval ex Shapoval et Kuzemko hoc loco
Ass. *Myosuro-Beckmannietum eruciformis* Shapoval ex Shapoval et Kuzemko hoc loco
Ass. *Elatino-Butometum umbellati* Shapoval et Kuzemko hoc loco
Subass. *Elatino-Butometum umbellati typicum*
Subass. *Elatino-Butometum umbellati damasonietosum alismae* Shapoval et Kuzemko hoc loco
Cl. *Festuco-Puccinellietea* Soó ex Vicherek 1973
Ord. *Scorzonero-Juncetalia gerardi* Vicherek 1973
All.?
D.c. *Rumex ucranicus+Puccinellia distans*

Conservation values

We have noted 21 taxa in the depression communities that have a protected status, including nine species protected at the regional level in the Kherson oblast (Andriyenko and Peregrym 2012, Anon. 2013), six species from the Red Book of Ukraine (Didukh 2009), two species from the European Red List (Bilz et al. 2011), one species from the IUCN list (Anon. 2020) and three species having several protection statuses (Table 3). *Elytrigia repens* subsp. *pseudocaesia*, which is protected at the regional level and is found in all syntaxa of the *pody* vegetation, has the greatest frequency in the dataset. Among the species of national and international protection status, *Allium regelianum* has the highest frequency and is present in six units. In cluster 4, it has a constancy of 65.6%. This cluster, which we interpret as the association *Herniario glabrae-Poetum angustifoliae*, is characterized by the largest number of red listed species, 13 in all (see Table 3). It should also be not-

Table 3. Distribution of rare and endangered vascular plant taxa in nine units of *pody* vegetation (the cluster numbers correspond to their numbers in the text, see Section 4.1). Status of red-listed species: RBU – Red Data Book of Ukraine (Didukh 2009), RLKhO – Red List of Kherson oblast (Andriyenko and Peregrym 2012; Anon. 2013); Bern – Annex I of the Resolution 6 of Bern Convention (Anon. 2011); IUCN RL – The IUCN Red List of threatened species (Anon. 2020), Eu RL (Bilz et al. 2011); category correspond to IUCN categories. For each taxon, percentage frequency for all relevés (= Total) and per association are given.

Taxon	Status (category)	Total	Clusters								
			1	2	3	4	5	6	7	8	9
Achillea micranthoides	RLKhO	10.6		3.5	46.9	38.5		3.7	1.1		
Alisma gramineum	IUCN RL (dd)	0.3								4.7	
Allium regelianum	RBU (r), Bern, Eu RL (dd)	16.8	0.7	8.2		65.6	15.4		10.5	4.7	
Beckmannia eruciformis	Eu RL (dd)	19.3		4.7		1.6	5.8	75.9	30.5	65.1	94.4
Bellevalia speciosa	RLKhO	0.2	0.7								
Damasonium alisma	RBU (en), Eu RL (nt)	7.2		2.4		1.6				97.7	
Elatine alsinastrum	Eu RL (nt)	11.7		2.4		11.5			25.3	81.4	
Elatine hungarica	RBU (vu), RLKhO, Eu RL (dd)	5.1				0.8	11.5		24.2	7.0	
Elytrigia repens subsp. *pseudocaesia*	RLKhO	52.9	10.7	96.5	28.1	57.4	92.3	79.6	38.9	62.8	44.4
Ferula caspica	RLKhO	0.3	0.7	1.2							
Juncus sphaerocarpus	RBU (en)	2.2				5.7			7.4		
Lathyrus nissolia	RLKhO	2.8			6.3		30.8				
Lythrum thymifolia	RBU (vu)	7.3				20.5			22.1	2.3	
Peucedanum ruthenicum	RLKhO	3.3	12.1	4.7							
Phalacrachena inuloides	RLKhO	9.7		7.1	18.8	16.4	38.5		6.3	9.3	
Phlomis scythica	RBU (ne)	13.1	16.4	8.2	9.4	19.7			13.7	32.6	
Pholiurus pannonicus	RLKhO	6.1				9.8	3.8		21.1		27.8
Prunus tenella	RLKhO	0.2	0.7								
Stipa capillata	RBU (ne)	1.7	7.1	1.2							
Stipa ucrainica	RBU (ne)	0.2		1.2							
Tulipa scythica)	RBU (en)	0.6				3.3					
Total number of red listed taxa per vegetation unit		21	8	12	5	13	7	3	11	10	3

ed that the species protected at the national level, *Damasonium alisma*, has a clear coenotic confinement to cluster 8 (*Elatino-Butometum umbellati damasonietosum alismae*), in which its constancy reaches 97.7%.

Given the floristic, coenotic and habitat specificity of steppe depressions, as well as the absence of such units in the existing EUNIS hierarchy, and accordingly to Resolution 4 of the Bern Convention (Anon 1997), which makes it impossible to protect this habitat type in the Emerald Network of Ukraine, we have prepared proposals to include them into Resolution 4 (Kuzemko et al. 2017). In 2018, our proposals were adopted by the Steering Committee of the Bern Convention, and the depressions (*pody*) of the steppe zone of Ukraine were included as a complex type X36 to Resolution 4, accordingly, to the EUNIS classification (https://eunis.eea.europa.eu/habitats/8009), which requires a comprehensive study and protection of this habitat type. In 2019, we prepared proposals for the inclusion of seven new sites to the Emerald Network of Ukraine specifically for the preservation of the X36 habitat type. All these sites were officially recognized at the end of 2019 and included in the existing Emerald network. Taking into account their international conservation status, as well as the high proportion of red listed taxa, which was also confirmed by our research, the next step should be to develop effective management plans for the protection and maintenance of these communities and habitat types. The most important task is the maintenance of the optimal moisture regime, as well as the limits on land issues related to the current land reform in Ukraine; namely that it be impossible to plow them further.

Conclusions

Our analysis allowed us to propose an updated syntaxonomic system of mesic and wet grassland vegetation of the steppe depressions, which reflects their ecological and territorial differentiation, to restore a syntaxonomic status of a number of syntaxa that were considered doubtful, and to find a proper place of the steppe depression vegetation in the syntaxonomic system of the European vegetation (Mucina et al. 2016). Our study confirmed the existence of at least eight associations of the *pody* vegetation. We tried to correct nomenclatural aspects according to the current addition of the ICPN, and we have validated all syntaxa of the steppe depression vegetation of Ukraine, the existence of which has been proven by a comprehensive analysis using currently accepted methods of phytosociological research. The results of our study will contribute to further inventory of the steppe depression vegetation, organization of proper management and effective protection, which will preserve these unique habitats and provide a system of phytocenotic monitoring of their current state, structure, functional organization and dynamic trends.

Data availability

The data used in the paper are available as Supplementary material in *.xlsx format and in *.csv format.

Author contributions

V.S. formulated the idea of the paper, prepared the dataset for the analysis (85% of the relevés are his own), reviewed the literature, wrote a description of the obtained vegetation units and interpreted them at the level of associations, subassociations and alliances. A.K. planned the research, made all analyzes and interpreted the obtained units at the level of orders and classes. The authors jointly prepared the manuscript.

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References

Andriyenko TL, Peregrym MM [Eds] (2012) Ofitsiyni pereliky rehionalno ridkisnykh roslyn administratyvnykh terytoriy Ukrainy (dovidkove vydannya) [Official lists of regionally rare plants of administrative territories of Ukraine (reference edition)]. Alterpres, Kyiv, UA, 148 pp. [in Ukrainian]

Anon (1984) Geomorfologicheskaya i landshaftnaya kharakteristika territorii Biosfernogo zapovednika “Askaniya-Nova”: Otchet po dopolnitelnomu planu rabot v sootvetstvii s postanovleniem № 134 Prezidiuma AN USSR ot 17.03.1982 [Geomorphological and landscape characteristics of the territory of the Biosphere Reserve “Askania-Nova”: Report on the additional work plan in accordance with the decree No. 134 of the Presidium of the Academy of Sciences of the Ukrainian SSR dated 17.03.1982]. Department of Geography of the S.I. Subbotin Institute of Geophysics [Report no. 4470], Kiev, UA, 47 p. [In Russian]

Anon (1997) Convention on the Conservation of European Wildlife and Natural Habitats. Standing Committee. Texts Adopted by the Standing Committee of the Bern Convention on the Conservation of European Wildlife and Natural Habitats (19 September 1979): 1982-96. Council of Europe Publishing, Strasbourg, FR.

Anon (2011) Revised Annex I of Resolution 6 (1998) of the Bern Convention listing the species requiring specific habitat conservation measures (year of revision 2011). https://eunis.eea.europa.eu/references/2443/species [accessed 12 December 2020].

Anon (2013) Dodatok 1 do rishennya XXVI sesii oblasnoi rady VI sklykannya vid 13.11.2013 № 893 «Chervonyi spysok Khersonskoi oblasti. 1. Roslyny, shcho okhoronyayutsya na mistsevomu rivni v mezhakh Khersonskoi oblasti" [Annex 1 to the decision of the XXVI session of the regional Council of the VI convocation dated 13.11.2013 № 893 "Red list of the Kherson region. 1. Plants protected at the local level within the Kherson region"]. Vykonavchyi aparat Khersonskoi oblasnoi rady, Kherson, UA, 8 pp. [In Ukrainian]

Anon (2020) The IUCN Red List of Threatened Species. Version 2014.3. http://www.iucnredlist.org [accessed 15 Dec 2020].

Beck HE, Zimmermann NE, McVicar TR, Vergopolan N, Berg A, Wood EF (2018) Present and future Köppen-Geiger climate classification maps at 1-km resolution. *Scientific Data* 5: 180214. https://doi.org/10.1038/sdata.2018.214

Bilz M, Kell SP, Maxted N, Lansdown RV (2011) European Red List of Vascular Plants. Publications Office of the European Union, Luxembourg, LU, 132 pp.

Bulavin BP (1972) Genezis i litologicheskie fatsii lessa Russkoy ravniny. [Genesis and lithological facies of the Russian Plain loess]. Izdatelstvo Moskovskogo universiteta, Moscow, RU, 154 pp. [In Russian]

Chytrý M, Tichý L, Holt J, Botta-Dukát Z (2002) Determination of diagnostic species with statistical fidelity measures. Journal of Vegetation Science 13: 79–90. https://doi.org/10.1111/j.1654-1103.2002.tb02025.x

Chytrý M, Tichý L, Hennekens SM, Knollová I, Janssen JAM, Rodwell JS, Peterka T, Marcenò C, Landucci F, …, Schaminée JHJ (2020) EUNIS Habitat Classification: expert system, characteristic species combinations and distribution maps of European habitats. Applied Vegetation Science 23: 648–675. https://doi.org/10.1111/avsc.12519

Didukh YP [Ed.] (2009) Chervona knyha Ukrainy. Roslynnyi svit [Red Book of Ukraine. Plant World]. Hlobalkonsaltynh, Kyiv, UA, 900 pp. [In Ukrainian]

Didukh YP (2011) The ecological scales for the species of Ukrainian flora and their use in synphytoindication. Phytosociocentre, Kyiv, UA, 176 pp.

Dokuchaev VV (1892) Nashi stepi prezhde i teper [Our steppes before and now]. E. Evdokimov's printing house, St. Petersburg, RU, 128 pp. [In Russian]

Dostovalov BN (1952) O fizicheskikh usloviyakh obrazovaniya morozoboynykh treshchin i razvitiya treshchinnykh ldov v rykhlykh merzlykh porodakh [On the physical conditions for the formation of frost cracks and the development of fissured ice in loose frozen rocks]. Issledovanie vechnoy merzloty v Yakutskoy respublike 3: 162-194. [In Russian]

Drohobych NE, Polishchuk IK (2003) Ekotopicheskie flyuktuatsii askaniyskikh biotsenozov [Ecotopic fluctuations of the Askanian biocenoses]. In: Stepi Severnoy Evrazii. Etalonnye stepnye landshafty: problemy okhrany, ekologicheskoy restavratsii i ispolzovaniya. IPK "Gazprompechat", Orenburg, RU, 187–190. [In Russian]

Dubyna DV, Dzyuba TP, Yemel'yanova SM, Bahrikova NO, Borysova OV, Borsukevych LM, Vynokurov DS, Hapon SV, Hapon YV, ..., Yakushenko DM (2019) Prodromus Roslynnosti Ukrayiny. [Prodrome of the vegetation of Ukraine]. – Naukova Dumka, Kyiv, UA, 784 pp. [in Ukrainian]

Evdokimova TI, Bykovskaya TK (1985) Pochvy podovykh ponizheniy yuga Ukrainy [Soils of *pody* depressions in the south of Ukraine]. Izdatelstvo Moskovskogo universiteta, Moscow, RU, 96 pp. [In Russian]

Golub VB (1995) Halophytic, desert and semi-desert plant communities on the territory of the former USSR. Institute of Ecology of the Volga River Basin of RAS Publisher, Togliatti, RU, 32 pp.

Hennekens SM, Schaminée JHJ (2001) Turboveg, a comprehensive database management system for vegetation data. Journal of Vegetation Science 12: 589–591. https://doi.org/10.2307/3237010

Krokos VI (1927) Materialy do kharakterystyky chetvertynnykh pokladiv skhidnoi i pivdennoi Ukrainy [Materials for the characteristics of Quaternary deposits of eastern and southern Ukraine]. Materialy doslidzhennya gruntiv Ukrainy. Sektsiya gruntoznavstva 9: 1–325. [In Ukrainian]

Kuzemko A (2012) Ukrainian Grasslands Database. Biodiversity & Ecology 4: 430–430. https://doi.org/10.7809/b-e.00217

Kuzemko A, Vasyliuk O, Marushchak O, Kolomytsev G (2020) 730,000 hectares of grasslands are included in the Emerald Network of Ukraine. Palaearctic Grasslands 45: 89–93.

Kuzemko AA, Didukh YP, Onyshchenko VA, Kish RY, Chorney II, Moysienko II, Vynokurov DS (2017) Habitats of Ukraine offered for inclusion in Resolution 4 of the Bern Convention. In: Bardin P, Pénzesné Kónya E, Peregrym M (Eds) Save Plants for Earth's Future. Book of abstracts: 8th Planta Europa Conference (May 22-26, 2017, Kyiv, Ukraine). Palyvoda AV, Kyiv, UA, 61–61.

Levengaupt AI (1932) Pochvennyi ocherk levoberezhnogo Nizhnedneprovya [Soil survey of the left bank of the Lower Dnieper region]. Giprovod, Leningrad, RU, 108 pp. [In Russian]

Lichkov BL (1927) Ob iskopaemykh rekakh i bezottochnykh vpadinakh [About fossil rivers and drainless depressions]. Zapiski Kievskogo obshchestva estestvoispytateley 28: 49–73. [In Russian]

Marinich AM, Pashchenko VM, Shishchenko PH [Eds] (1985) Priroda Ukrainskoy SSR. Landshafty i fiziko-geograficheskoe rayonirovanie [The nature of the Ukrainian SSR. Landscapes and physical and geographical zoning]. Naukova Dumka, Kiev, UA, 224 pp. [in Russian]

McCune B, Mefford MJ (2006) PC–ORD. Multivariate Analysis of Ecological Data. Version 5. MjM Software, Gleneden Beach, Oregon, US.

Molodykh II (1982) Grunty podov i stepnykh blyudets subaeralnogo pokrova Ukrainy [Soils of *pody* and steppe saucers of the subaerial cover of Ukraine.]. Naukova Dumka, Kiev, UA, 159 pp. [in Russian]

Mosyakin SL, Fedoronchuk MM (1999) Vascular plants of Ukraine. A nomenclatural checklist. M.G. Kholodny Institute of Botany, Kyiv, UA, 345 pp.

Mulika AM (1961) Budova i pokhodzhennya podiv [Structure and origin of *pody*]. Heohrafichnyi zbirnyk 4: 14–23. [in Ukrainian]

Mucina L, Bültmann H, Dierßen K, Theurillat J-P, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, ..., Tichý L (2016) Vegetation of Europe: Hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19 (suppl. 1): 3–264. https://doi.org/10.1111/avsc.12257

Polupan MI, Solovey VB, Velychko VA (2005) Klasyfikatsiya gruntiv Ukrainy [Classification of soils of Ukraine]. Ahrarna nauka, Kyiv, UA, 300 pp. [in Ukrainian]

Rivas-Martínez S, Penas A, Díaz TE (2004) Bioclimatic and biogeographic maps of Europe. https://www.globalbioclimatics.org/form/maps.htm [accessed 22 April 2021]

Shalyt MS (1930) Velykyi Chapelskyi pid ta yoho roslynnist roku 1927-1928 [Great Chapelsky *pid* and its vegetation in 1927–1928]. Visti Derzhavnoho Stepovoho Zapovidnyka «Chapli» (k. Askaniya-Nova) 7: 165–199. [in Ukrainian]

Shapoval VV (2004) Nadzemna produktsiya fitotsenoziv depresiy Prysyvasko-Pryazovskoho nyzovynnoho stepu [Aboveground production of phytocenoses of depressions of the Prysyvasko-Pryazovsky lowland steppe]. Visti Biosfernoho zapovidnyka "Askaniya-Nova" 6: 14–20. [in Ukrainian]

Shapoval VV (2006) Do syntaksonomii roslynnosti depresiy Livoberezhzhya Nyzhnoho Dnipra. Klasy: *Isoeto-Nanojuncetea* Br.-Bl. et R. Tx. ex Westhoff et al. 1946, *Molinio-Arrhenatheretea* R. Tx. 1937 ta *Festuco-Brometea* Br.-Bl. et R. Tx. in Br.-Bl. 1949 [To the syntaxonomy of vegetation of depressions of the Left Bank of the Lower Dnieper. Classes: *Isoeto-Nanojuncetea* Br.-Bl. et R. Tx. ex Westhoff et al. 1946, *Molinio-Arrhenatheretea* R. Tx. 1937 and *Festuco-Brometea* Br.-Bl. et R. Tx. in Br.-Bl. 1949]. Visti Biosfernoho zapovidnyka "Askaniya-Nova" 8: 15–48. [in Ukrainian]

Shapoval VV (2007) Pody prychornomorskoho stepu: aktualnyi stan ta problemy okhorony [*Pody* the Black Sea region steppe: the current state of the problem of protection]. In: Shmalyey SV (Ed.) Falts-Feynivski chytannya: zbirnyk naukovykh prats. PP Vyshemyrskyi, Kherson, UA, 361–362. [in Ukrainian]

Shapoval VV (2012) Komentari do biomorfolohii ta tsenopopulyatsiynoi struktury *Damasonium alisma* Mill. (Alismataceae) u podakh prychornomorskoho stepu. [Comments on biomorfology and cenopopulation structure of *Damasonium alisma* Mill. (Alismataceae) in the Black Sea area steppe depressions]. In: Mosyakin SL (Ed.) The Plant Kingdom in the Red Data Book of Ukraine: Implementing the Global Strategy for Plant Conservation. Proceedings of II International Conference (9 –12 October 2012, Uman', Cherkasy region). Palyvoda AV, Kyiv, UA, 188–190. [in Ukrainian]

Shapoval VV, Zvehintsov SS (2010) Ekoloho-hidrolohichnyi narys pavodku 2010 r. u Velykomu Chapelskomu podi [Ecological and hydrological essay of the 2010 flood in Great Chapelsky Pid]. Visti Biosfernoho zapovidnyka "Askaniya-Nova" 12: 33–55. [in Ukrainian]

Solomakha VA, Shapoval VV, Vinichenko TS, Moysiyenko II (2005) Fitotsenotychna pryurochenist ta stan populyatsiy *Allium regelianum* A. Becker ex Iljin i *Ferula orientalis* L. u rehioni Biosfernoho zapovidnyka «Askaniya-Nova» [Phytocenotic affinity and status of populations of *Allium regelianum* A. Becker ex Iljin and *Ferula orientalis* L. in the region of the Askania-Nova Biosphere Reserve]. Chornomorskyi botanichnyi zhurnal 1: 66–81. [in Ukrainian] https://doi.org/10.14255/2308-9628/05.11/7

Sypailova LM, Mirkin BM, Shelyag-Sosonko YR, Solomakha VA (1985) Novi soyuzy *Agrostion vinealis* ta *Festucion pratensis* luchnoyi roslynnosti [New alliances *Agrostion vinealis* and *Festucion pratensis* of the meadow vegetation]. Ukrayins'kyi Botanichnyi Zhurnal 42: 13–18. [in Ukrainian]

Theurillat J-P, Willner W, Fernández-González F, Bültmann H, Čarni A, Gigante D, Mucina L, Weber H (2021) International Code of Phytosociological Nomenclature. 4th edition. Applied Vegetation Science 24: e12491. https://doi.org/10.1111/avsc.12491

Tichý L (2002) JUICE, software for vegetation classification. Journal of Vegetation Science 13: 451–453. https://doi.org/10.1111/j.1654-1103.2002.tb02069.x

Tutkovskiy PA (1910) Iskopaemye pustyni severnogo polushariya [Northern Hemisphere Desert Fossils]. Tipo-lit. t-va I.N. Kushnerev i K°, Moscow, RU, 273 pp. [in Russian]

Velichko AA (1965) Kriogennyi relef pozdnepleystotsenovoy periglyatsialnoy zony (kriolitozony) Vostochnoy Evropy [Cryogenic relief of the Late Pleistocene periglacial zone (cryolithozone) of Eastern Europe]. In: Gromov VI et al (Eds) Chetvertichnyi period i ego istoriya: sbornik nauchnykh statey. Nauka, Moscow, RU, 104–120. [In Russian]

Weber HE, Moravec J, Theurillat JP (2000) International Code of Phytosociological Nomenclature. 3rd edition. Journal of Vegetation Science 11: 739-768. https://doi.org/10.2307/3236580

Zakharov AL (2018) Krupnozapadinnyi relef Vostochnogo Priazovya: morfologiya, genezis, istoriya razvitiya [Large depression relief of the Eastern Azov region: morphology, genesis, history of development]. Candidate of geographical sciences thesis. FGBUN Institute of Geography of the Russian Academy of Sciences, Moscow, RU. [In Russian]

Zamoriy PK (1934) Kopalni pody livoberezhzhya Nyzo-Dnipryanskoho rayonu [Digging *pody* of the left bank of the Lower Dnieper district]. Chetvertynnyi period 7: 41–66. [In Ukrainian]

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Supplementary material

Supplementary material 1
Ordered relevé table of the steppe depression vegetation of Ukraine (*.xlsx)
Link: https://doi.org/10.3897/VCS/2020/62825.suppl1

Supplementary material 2
Ordered relevé table of the steppe depression vegetation of Ukraine (*.csv)
Link: https://doi.org/10.3897/VCS/2020/62825.suppl2

Supplementary material 3
Results of analyzes using expert systems EVC (A) and EUNIS-ESy (B) in units of steppe depression vegetation of Ukraine (*.pdf)
Link: https://doi.org/10.3897/VCS/2020/62825.suppl3

Supplementary material 4
Diagnostic, constant, and dominant species of the steppe depression vegetation of Ukraine (*.pdf)
Link: https://doi.org/10.3897/VCS/2020/62825.suppl4