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-Nonojuncetea (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-Caricion 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.

Syntonomic 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 Zaporizhzhia 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; Evodkinova 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 censuses. 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 Zveginetsov 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 “explosive” 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; Zamoriz 1934; Sambur et al. 1956; Mulika 1961; Bulavin 1972) or relic elements of the periglacial area of the Quaternary glaciation (Dokuchaeva 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; Levengauprt 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 regelium* and *Ferula orientalis*. It was proposed to include such communities in a new alliance *Carici praecocis-Elytrigion pseudocaesiae* of the new order *Carici praecocis-Elyrigietalia 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 Isoeto-Nanojuncetalia, order Nanocyperetalia and two alliances – Eleocharition ovatae and newly described *Myosurus-Beckmannion eruciformis*. Mesic communities of depressions were included in the class Molinio-Arrhenatheretalia, order Molinitalia and a new alliance *Lythro virgati-Elytrigion pseudocaesiae*. Xero-mesic...
communities, common in small, shallow depressions, were included in the class Festuco-Brometalia, 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 praecosis 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-Beckmannietalia 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-Beckmannietalia 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 Poa angustifolia and Carex praecox, have been found in the steppe depression communities.

Adding to syntaxonomic uncertainty, in the recently published Predromus of Vegetation of Ukraine (Dubyna et al. 2019) the order Carici praecocis-Elytrigietalia pseudocaesiae as well as alliances Carici praecocis-Elytrigion pseudocaesiae and Poo angustifolii-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-Beckmannietalia 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 Predromus, some as accepted names, some as synonyms. In particular, the association Carici praecocis-Elytrigietumpseudocaesiaeassignsasynonym of the Pycreo flavescenti-Arabidopsietum toxophyllae, Herniario glabrae-Poetum angustifolii as synonym of the Achilleo micranthoidis-Poetum angustifolii, as well as Potentillo orientalís-Caricetum melanostachyae and Euphorbioc virgati-Caricetum melanostachyae as synonyms of the Galio ruthenici-Caricetum praecocis. The Predrome 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 ICNP (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 ICNP.

**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 Chapelsky 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 Euro-Siberian 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).
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° 33.71158°                        | 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° 33.717655°                       | 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 Stepe 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                            |
| Kianly                            | 46.690165° 34.482390°                       | near Shotivka village, Henichesk district, Kherson oblast | 148                                                            | 5.5×11                                                                 | –                                               |
| Domuzlynsky                       | 46.603908° 34.728707°                       | near Zeleni Hai village, Henichesk district, Kherson oblast and Trudove village c. Tyasnie, Melitopol district, Zaporizhzhia oblast | 4743                                                          | 9×13                                                                   | Emerald site UA0000369                            |
| Novatroitsky                      | 46.319373° 34.360386°                       | near Novatroitse 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                            |
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 km², 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). 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. Drohobykh, 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](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 m² (relevés of small spots of hydrophilic vegetation in 2010 and some relevés of 2019) to 100 m² (the rest of relevés). Different plot sizes are due to the specifics of spatial differentiation of pody vegetation. “Small” plots (9–16 m²) 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 m² 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 phytoidentication 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. Phytosociological 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. pseudocasia, Alopecurus pratensis and Carex melnostachya, 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 rheneticum, 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 rhenicum, Vicia villosa are common. The third layer is formed by Viola kitaibeliana, Lamium amplexicaule var. orientale, Crucia 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 relevés | 140 | 85  | 32  | 122 | 52  | 54  | 95  | 44  | 18  |

**Viktor Shapoval & Anna Kuzemko: Syntaxonomy of steppe depressions**
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 grass communities; during severe droughts they are in a depressed state, lose hygromesophytic elements, and are replaced by more xerophytic phytocenoses, so they occur in localized along the bottom edge and at lower slopes (on saline soils and sufficient moisture) as well as Hypericum perforatum, Veronica spicata, V. barbeyeri, Gagea transversalis, Euphorbia esula subsp. tommasiniana, Ferula eucina 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 Phalacrencha inoidae 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 (Serisi 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,
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 eucina, Phalacronema 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 resutus, Arenaria leptocladus, Cerasium pumilum, Crepis ramosissima, Crucia 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 “Herniaria glabrae-Poetum angustifolii” (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, Venetanata 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 eucina, Inula britannica, Linaria biebersteinii, Lythrum virgatum, Phlomis scythica, sporadically Vicia villosa, Phalacronema 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, Elatinie hungarica, Lythrum boryschemicum, Rorippa brachycarpa, Arenaria leptocladus, etc.

The heterogeneous nature of these communities is visualized by the combination of xeromorphic plants, such as Festuca valesiaca, F. pseudovina, Koeleria macrantha, Limonium sappontanum, Medicago romanica, Venetanata dubia, Polycnemum arvense, Filago arvensis, Seseli tortuosum with hydrophilic species like Batomus umbellatus, Elatine alsinastrum, Eleocharis palustris, E. uniglumis, Gratiola officinalis, Lythrum virgatum, Plantago tenuifolia, 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 artemisifolia, 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./m²).

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

Distribution. Along the edge of Ahaimansky 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 santonica, Pseudoarabidopsis toxophylla, Eleocharis palustris, Gratiola officinalis, Vicia hirsuta. The lower layer is formed by Cyperus flavescentis, 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.

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-hydrogeneous period.

Structure and composition. Phytocenoses are formed by polycarpic biromorphs and hemicyptophytes, 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 hemicyptophytes 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 santonica, 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 trivraceatum, 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,
**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 hygroscopic forb is composed by Rumex crispus, Pulsatilla 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 trivacteatum, 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 regelium, Juncus atratus, Ranunculus sceleratus, Typha angustifolia, Verbena supina are sporadic.

**Cluster 8 «Elatino-Butometum umbellati damasonieto-sum 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, Novoortoiisk district, Kherson oblast, in a gulley that connects the basins of the Barnashivka site and the Ahaimansky pide, 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 epemherally, 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 composed 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 palastris, Carex melanostachya and Gratiola officinalis, with a significant proportion of Euphorbia esula subsp. tommasiniana, Phalomi scythica and sporadically Inula britannica, Rorippa austriaca, Phalacrrhena 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 britannica. 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 pidd 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 alismastrum, rarely Elatine hungarica, Lotus angustissimus, Lythrum thymifolia, Lythrum boryshenicum, Myosurus minimus, Pholiurus pannonicus, Plantago tenuiflora, Polygonum aviculare (due to trampling), Potentilla argentea (numerous seedlings and juveniles), Gypsophila muralis, Gysopha leafescens. Sometimes, under optimal moisture conditions, Damasonium alisma reach 40–60 cm in height and extends into the second layer.

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

Distribution. Great Chapelsky pidd.

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, Echinocloa crus-galli, Setaria pumila, Ambrosia artemisifolia, Lactuca tatarica, Xanthium spinosum. The most common dominants are Beckmannia crusgalliformis, 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-Arrhenatheretalia class. In addition, the plots assigned to the class Molinio-Arrhenatheretalia 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 vectors 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 (Ferulio eucinace-Caricetum praecocis) occupies an intermediate position between the classes Festuco-Brometea and Artemisietea vulgaris (Agropyretalia intermedia-repantis). 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 transect shows 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 – Chaeturus marrubiastrum, 17 – Inula britannica, 18 – Rorippa brachycarpa, 19 – Elytrigia repens subsp. pseudocaesia, 20 – Lotus angustissimus, 21 – Phalacrochena inuloides, 22 – Beckmannia eruciformis, 23 – Lythrum virgatum, 24 – Mentha pulegium, 25 – Puccinellia distans, 26 – Gratiola officinalis, 27 – Juncus atratus, 28 – Rumex cranicus, 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 alisinastrum, 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-repentes order. Therefore, at this stage, we assign these communities, as in the original publication (Shapoval 2006), to the class Festuco-Brometea, order Festucetalia valesiaca and alliance Festucion valesiacae. Whereas these communities are somewhat different from the typical communities of the alliance, we consider them as a separate suballiance Galio ruthenici-Caricenion praeocis. 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 Molino-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 Molino-Arrhenatheretea class. Among the higher-ranking syntaxa recognized in EuroVegChecklist, these communities are the most similar to the order Althaeo-Arctideae 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 the “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 pseudocaeasaeae, Poo angustifolii-Ferulion orientale, and Lythro virgati-Elytrigion pseudocaeasaeae, 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 Molino-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 cruciformis – 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, 5–10 cm) 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 (“ephemertum”) 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 miranthisoides-Poetum angustifolii is close to Herniario glabrae-Poetum angustifolii; however, from the three species that are listed as diagnostic for Achilleo miranthisoides-Poetum angustifolii, Achillea miranthisoides 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 (Chytry 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. *Ferula eucinae-Caricetum praecocis* Shapoval et Kuzemko hoc loco.

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

**Association Ferulo eucinae-Caricetum praecocis**

Shapoval ex Shapoval et Kuzemko ass. nov. hoc loco

Validated name: *Ferulo eucinae-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 m², total cover 90%, litter 70%.

Species (with cover of the Braun-Blanquet scale): *Bromopsis inermis* 3; *Carex praecox* 3; *Falkaria vulgaris* 2; *Galium ruthenicum* 2; *Ferula eucina* 2; *Poa angustifolia* 2; *Vi-
ya hirsuta* 1; *Viola kitaibeliana* 1; *Vicia villosa* ±; *Eryngium campestr* e 1; *Eryngium planum* 1; *Limonium sareptanum* r.

**Diagnostic taxa:** *Bromopsis inermis*, *Carex praecox*, *Elytrigia repens*, *Falkaria 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 100 m², total cover 95%, litter 5%.

Species: *Poa angustifolia* 4; *Carex praecox* 2; *Falkaria 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; *Convovulus 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. *tommisiniana* ±; *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*, *Falkaria 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 9 m², total cover 80%, litter 5%.

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

**Diagnostic taxa:** *Achillea micianthoides*, *Alopecurus pratensis*, *Arcenaria leptocolada*, *Artemisia austriaca*, *Capsella bursa-pastoris*, *Carex spicata*, *Cerastium pumilum*, *Capsella bursa-pastoris*, *Carex spicata*, *Cerastium pumilum*, *Capsella bursa-pastoris*, *Carex spicata*, *Cerastium pumilum*, *Capsella bursa-pastoris*, *Carex spicata*, *Cerastium pumilum*. 
Valuated name: *Herniaria glabrae-Phacturnetum angustifolium* Shapoval et Kuzemko ass. nov. hoc loco

Validated name: *Herniaria glabrae-Phacturnetum angustifolium* Shapoval 2006 nom. inval. (Art. 5)

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

V. Shapoval, 12.08.2004, 46.557254°N, 33.479272°E, plot size 100m², total cover 80%, litter 2%.

Species: *Elytrigia repens* subsp. *pseudoaeasia* 1; *Filago arvensis* 1; *Gypsophila muralis* 1; *Herniaria glabra* 1; *Linaria biebersteinii* 1; *Allium regelianum* +; *Crepis ramosissima* r; *Erysimum repandum* r.

Diagnostic taxa: *Achillea marnchrioides*, *Allium regelianum*, *Artemisia santonicum*, *Gypsophila muralis*, *Herniaria glabra*, *Lepidium ruderale*, *Lotus angustissimus*, *Potentilla argentea*, *Plantago lanceolata*, *Rorippa brachycarpa*.

Association *Lathyrus nissoliace-Phalacracenemum inuloidis* Shapoval ex Shapoval et Kuzemko ass. nov. hoc loco

Validated name: *Lathyrus nissoliace-Phalacracenemum inuloidis* 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 100m², total cover 65%, litter 1%.

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

Diagnostic taxa: *Achillea marnchrioides*, *Allium regelianum*, *Artemisia santonicum*, *Gypsophila muralis*, *Herniaria glabra*, *Lepidium ruderale*, *Lotus angustissimus*, *Potentilla argentea*, *Plantago lanceolata*, *Rorippa brachycarpa*.

Association *Lathyrus nissoliace-Phalacracenemum inuloidis* Shapoval ex Shapoval et Kuzemko all. nov. hoc loco

Validated name: *Lathyrus nissoliace-Phalacracenemum 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, 34.190873°E, plot size 100m², total cover 50%, litter 40%.

Species: *Elytrigia repens* subsp. *pseudoaeasia* 3; *Cyperus flavescent* 2; *Inula britannica* 2; *Phalacracena inuloides* 2; *Rorippa brachycarpa* 2; *Echechris palustris* 1; *Lathyrus nissolia* 1; *Stellaria graminea* 1; *Vicia hisruta* 1; *Senecio leucanthemifolius* subsp. *vernalis* +; *Crepis sancta* r.

Diagnostic taxa: *Armoracia rusticana*, *Crepis sancta*, *Cyperus flavescent*, *Inula britannica*, *Lathyrus nissolia*, *Lathyrus tuberosus*, *Phalacracena inuloides*.

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

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

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

V. Shapoval, 25.06.2010, 46.433217°N, 33.75275°E, plot size 100m², total cover 80%, litter 0%.

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

Diagnostic taxa: *Elatine hungarica*, *Juncus aratus*, *Lythrum borysthenicum*.

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

Validated name: *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 100m², total cover 80%, litter 0%.

Species: *Elytrigia repens* subsp. *pseudoaeasia* 3; *Butomus umbellatus* 1; *Damasosion alisma* 1; *Elatine alismastrum* 1; *Euphorbia esula* subsp. *tommasiniana* 1; *Juncus aratus* 1; *Rorippa brachycarpa* 1; *Gratiola officinalis* +; *Lythrum virgatum* +; *Rorippa austriaca* +; *Rumex crispus* +.

Diagnostic taxa: *Alopecurus pratensis*, *Butomus umbellatus*, *Damasosion alisma*, *Elatine alismastrum*, *Gratiola officinalis*, *Juncus aratus*, *Rorippa brachycarpa*, *Rumex crispus*. 

Association *Myosuro minimi-Beckmannietum eruciformis* 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, 33.479272°E, plot size 100m², total cover 80%, litter 2%.

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

Diagnostic taxa: *Aegilops cylindrica*, *Beckmannia eruciformis*, *Chaiturus marrubiastrum*, *Echechris 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

Valuated name: *Elatino hungaricae-Butometum umbellati* ass. nov. hoc loco
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 valesiaca Soó 1947  
All. Festucion valesiaca Klika 1931  
Suball. Galio rutenici-Caricion paeocis Shapoval ex Shapoval et Kuzemko hoc loco  
Ass. Ferulo eucinacae-Caricetum paeocis Shapoval ex Shapoval et Kuzemko hoc loco  
Ass. Diatanto gutti-Caricetum melanostachyae Shapoval et Kuzemko hoc loco  
Cl. Molino-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. Herniarico glabrae-Poetum angustifoliae Shapoval ex Shapoval et Kuzemko hoc loco  
Ass. Lathyro nissolae-Phalacrachenetum inuloidis Shapoval ex Shapoval et Kuzemko hoc loco  
Cl. Isoëto-Nanojuncetea Br.-Bl. et Tx. ex Soó 1947  
Ord. Althaeion officinalis Golub et Mirkin in Golub 1995  
All. Myosuro-Beckmannietum eruciformis Shapoval ex Shapoval et Kuzemko hoc loco  
Ass. Myosuro-Beckmannietum eruciformis Shapoval ex Shapoval et Kuzemko hoc loco  

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 Peregryn 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 Herniarico 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 Peregryn 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 glaucescens        | IUCN RL (dd)      | 0.3   |         |         |         |         |         |         |         |         |
| 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    |         |
| Bellavaria speciosa       | RLKhO             | 0.2   |         |         |         |         |         |         |         |         |
| Damasonium alisma         | RBU (en), Eu RL (nt) | 7.2   | 2.4     | 1.6     |         |         |         | 97.7     |         |         |
| Elatino alismiastrium     | Eu RL (nt)        | 11.7  | 2.4     | 11.5    | 25.3    | 81.4    |         |         |         |         |
| Elatino hungarica         | RBU (vu), RLKhO, Eu RL (dd) | 5.1   | 0.8     | 11.5    | 24.2    | 7.0     |         |         |         |         |
| Elytrigia repens subsp.   | RLKhO             | 52.9  | 10.7    | 96.5    | 28.1    | 57.4    | 92.3    | 79.6    | 38.9    | 62.8    | 44.4    |
| pseudocaesia              |                   |       |         |         |         |         |         |         |         |         |         |
| Ferula caspica            | RLKhO             | 0.3   | 0.7     | 1.2     |         |         |         |         |         |         |
| Juncus spharocarpus       | RBU (en)          | 2.2   |         | 5.7     |         |         |         |         |         |         |
| Lathyrus nissolia         | RLKhO             | 2.8   | 6.3     |         | 30.8    |         |         |         |         |         |
| Lythrum thymifolia        | RBU (vu)          | 7.3   |         |         | 20.5    | 22.1    | 2.3     |         |         |         |
| Poedanum ruthenicum       | RLKhO             | 3.3   | 12.1    | 4.7     |         |         |         |         |         |         |
| Phalacrochenia inuloides  | RLKhO             | 9.7   | 7.1     | 18.8    | 16.4    | 38.5    | 6.3     | 9.3     |         |         |
| Phalnium scythica          | RBU (ne)          | 13.1  | 16.4    | 8.2     | 9.4     | 19.7    | 13.7    | 32.6    |         |         |
| Phalnirus 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, *Damaso-
ium alisma*, has a clear coenotic confinement to cluster 8
(*Elatinо-Butometum umbellatі 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 Resolu-
tion 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 in-
clude them into Resolution 4 (Kuzemko et al. 2017). In
2018, our proposals were adopted by the Steering Com-
mittee 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/hab-
itats/8009](https://eunis.eea.europa.eu/habitats/8009)), which requires a comprehensive study and
protection of this habitat type. In 2019, we prepared pro-
posals 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 conser-
vation 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 syntaxo-
nomic 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 fur-
ther inventory of the steppe depression vegetation, organi-
ization 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 vegeta-
tion 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.

**Acknowledgements**

The authors are grateful to Orysia Goffman for the data
provided, to Ivan Moisiyenko for his help with field study
in 2019 and information provided about previously un-
known depression in the “Harbuzy” site, to Dariia Shyri-
eva for the preparation of the map in Figure 1 as well as
to Milan Chytrý for encouraging revising of the existing
syntaxonomy of the steppe depression vegetation. The
study was partially supported by the National Research
Foundation of Ukraine (project no. 2020.01/0140).

**References**

Andriyenko TL, Peregrym MM [Eds] (2012) Ofitsiyni perdikly rekho-
no ridkisnykh roslyn administratyvnykh terytoriy Ukrainy (dovidk-
ove vydannya) [Official lists of regionally rare plants of administra-
tive territories of Ukraine (reference edition)]. Altermes, Kyiv, UA,
148 pp. [in Ukrainian]

Anon (1984) Geomorfologicheskaya i landshaftnaya kharakteristika
territoriiz Biosfernoogo zapovednika “Askaniya-Nova”: Otchet po do-
polnitelnomu planu rabot v sootvetstvii s postanovleniem № 134
Prezidiuma AN USSR ot 17.03.1982 [Geomorphological and land-
scape characteristics of the territory of the Biosphere Reserve "Aska-
nia-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 Stand-
ing Committee of the Bern Convention on the Conservation of Eu-
ropean 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 Con-
vention listing the species requiring specific habitat conservation
measures (year of revision 2011). [https://eunis.eea.europa.eu/ref-
erences/2443/species](https://eunis.eea.europa.eu/references/2443/species) [accessed 12 December 2020].
Anon (2013) Dodatok 1 do rishennya XXVI sessii oblasnoi rady VI sklykannya vid 13.11.2013 № 893 «Chervonyi spysok Khersonskoi oblasti. 1. Roslyn, shcho okhoronyayutsya na mizstevomu rivni v mezhhkh 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”]. Vyzvanychiy apparat Kheronskoi 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, Masted 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 fakty 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, Hoff 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, Knolová I, Janssen JAM, Rodwell JS, Peterka T, Marcenó C, Landucci F, ... Schaminée JH (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]. Hlobalkonsultynh, 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 presto i teper [Our steppes before and now]. E. Chytrý M, Tichý L, Hennekens SM, Schaminée [HJ] (2001) Turboveg, a comprehensive database management system for vegetation data. *Journal of Vegetation Science* 12: 589–591. https://doi.org/10.2307/32327010

Kroko VI (1927) Materialy do karakterystyky chvertvetynnykh poklad-iv skhidnoi i pivdennoi Ukrainy [Materials for the characteristics of Quaternary deposits of eastern and southern Ukraine]. Materialy doslidzhennya gruvitn Ukrainy. Sektsiya gruntoznawstva 9: 1–325. [In Ukrainian]

Kuzemko A (2012) Ukrainian Grasslands Database. Biodiversity & Ecology 4: 430–430. https://doi.org/10.7809/b-e.00017

Kuzemko A, Vasyliuk O, Marushchak O, Kolomytsev G (2020) 730,000 hectares of grasslands are included in the Emerald Network of Ukraine. Palaeartic 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, Pén- esné Kónya E, Peregrym M (Eds) Save Plants for Earth’s Future. Book of abstracts: 8th Planta Europa Conference (May 22–26, 2017, Kyiv, Ukraine). Palynova AV, Kyiv, UA, 61–61.

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

Lichkov BL (1927) Ob iskopayemых rekakh i bezototicnyh vpadinakh [About fossil rivers and drained depressions]. Zapiski Kievskogo obschestva estestvoispytateley 28: 49–73. [In Russian]

Marinich AM, Paschchenko VM, Shishchenko PH [Eds] (1985) Priroda Ukrainskoy SSR. LANDSHAFTy i fiziko-geografichesko 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. MJ&M Software, Gleneden Beach, Oregon, US.

Molodých II (1982) Grunty podov i stepnych blyudets subaerialnego pokrova Ukrainy [Soils of podol and steppe sources of the subaerial cover of Ukraine]. Naukova Dumka, Kiev, UA, 159 pp. [In Russian]

Mossykin 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]. Heorafichnyi zbirnyk 4: 14–23. [In Ukrainian]

Mucina I, Búltmann H, Dierßen K, Theurillat J-P, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, ... Tichý L (2016) Vegetation Europe: Hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19 (suppl. 1): 3–64. https://doi.org/10.1111/avsc.12257

Polupan MI, Solovey VB, Velychko VA (2005) Klasyifikatsiya gruvitn Ukrainy [Classification of soils of Ukraine]. Ahrarnaya 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/graphical.htm [accessed 22 April 2021]

Shalyl MS (1930) Velykyi Chapelskiy 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) Nadzenna produktsiya fitotsenoz depresii Prys- vyasko-Priazovskogo nyozvyvodnogo stepu [Aboveground production of phytozones of depressions of the Prysvyasko-Priazovskiy lowland steppe]. Visti Biosfernoho zapovidnyka "Askaniya-Nova" 6: 14–20. [In Ukrainian]
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

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