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https://doi.org/10.26565/2410-7360-2022-56-01
UDC 561+581.9:551.735.2(477.6)

Received 8 December 2021
Accepted 13 January 2022

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Late Pennsylvanian vegetation changes in the Donets Basin: syndynamic aspect

ABSTRACT

The purpose of the article. The article is devoted to the study of one from forms of syndynamics in Late Pennsylvanian time, namely phytocoenogenesis. The study of the phytocoenogenesis of ancient plant communities, i.e., the formation of new types of palaeophytocoenoses, is based on the research of vegetation diversity that is reflected in the ecological-floristic classification of the Late Pennsylvanian phytocoenoses of the Donets Basin by the Brown-Blanquet method.

Material and research methods. The phytocoenogenetic researches consisted of the analysis of the changes of the species and syntaxonomic composition of vegetation cover throughout the Late Pennsylvanian. The peculiarities and main factors of phytocoenogenesis have been identified on the palaeosyntaxa in rank of the orders of the following vegetation types: wetland forests and woodlands of coastal lowlands, wetland forests and woodlands of deltaic plains, seasonally dry woodlands of river valleys and lagoon coasts. The palaeophytocoenotic data are based on the plant fossil assemblages from lacustrine, lacustrine-swamp, lacustrine-deltaic, floodplain-lacustrine, floodplain and lacustrine-lagoon deposits in more than 17 localities and 11 boreholes located within the Bakhmutska and Kalmius-Toretska troughs.

Research results. Based on the analysis of the phytocoenogenetic processes (progressive and regressive development of plant communities) and the manifestations of phytocoenogenesis (formation of new communities and loss of old communities) in the development of the Late Pennsylvanian vegetation, three models of the formation of new communities and one model of the loss of communities from vegetation cover have been proposed. Each of the models reveals the relationship between the phytocoenogenetic processes and environmental changes. The evolution-progression model reflects the progressive development of palaeophytocoenoses that is expressed by the appearance of evolutionary new coenopopulations in the conditions of the expansion of landscape types (expanding biotopes). The migration-progression model conforms to the progressive development of palaeophytocoenoses as a result of the migration of plants from decreasing landscape types to expanding ones (expanding biotopes). The substitution-regression model is consistent with the regressive development of palaeophytocoenoses along with structure simplification and dominant substitution of plant communities due to the contraction of certain landscape types (decreasing biotopes). The elision-regression model of the loss of communities reflects the regressive development of palaeophytocoenoses that is expressed by the decrease in the number of coenopopulations and the number of individuals in remaining coenopopulations in the conditions of the contraction of some landscape types (decreasing biotopes).

The scientific novelty. For the first time, the Late Pennsylvanian vegetation dynamics (syndynamic) have been studied. The proposed three models of the formation of new communities and one model of the loss of communities reveal the main directions in evolution of palaeophytocoenoses and give the first ideas about phytocoenogenesis in late Palaeozoic times.

Keywords*: vegetation cover, phytocoenogenesis, Late Pennsylvanian, Donets Basin.*

In cites: Boyarina N. I. (2022). Late Carboniferous vegetation cover changes in the Donets Basin: syndynamic aspect. Visnyk of V. N. Karazin Kharkiv National University, series "Geology. Geography. Ecology", (56), 8-23. https://doi.org/10.26565/2410-7360-2022-56-01

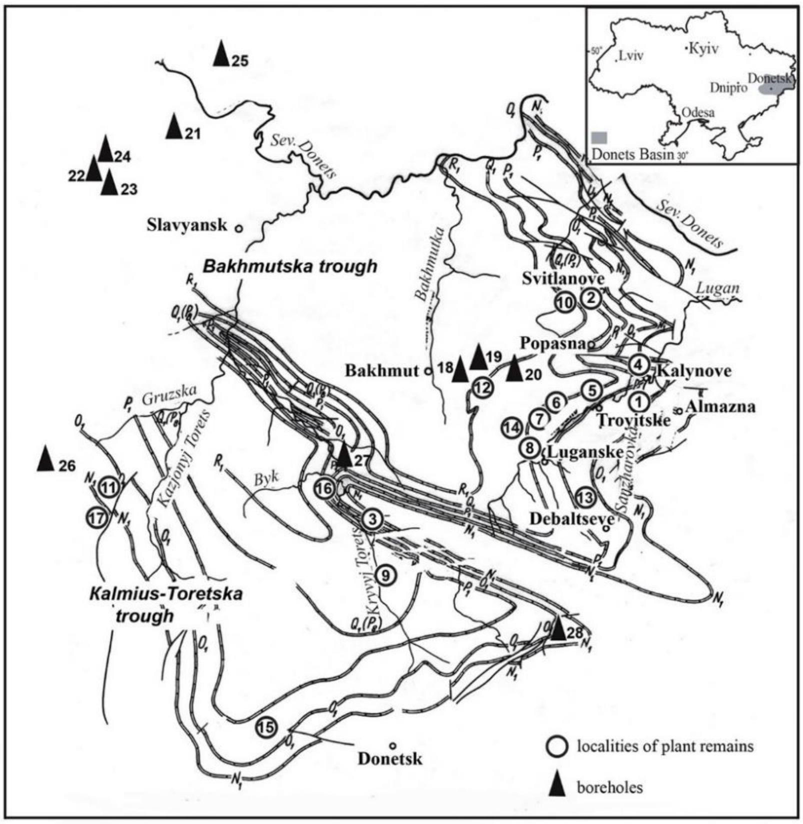
Introduction. The vegetation research of the geological past is based on the study of plant fossil remains along with the facial features of plant-bearing deposits and the subsequent reconstructions of palaeophytocoenoses. The Carboniferous and early Permian plant communities in varying degrees of detail have been reconstructed by W. Gothan&O. Gimm, F. Němejc, A.M. Krishtafovich, M.D. Zalessky, G.P. Radchenko, A. Cridland&J. Morris, M. Barthel, A. Scott, A.K. Shchegolev, O.P. Fisunenko, M.V. Oshurkova, Iwaniw E., Falcon-Lang H.J., N.I. Boyarina, S.V. Naugolnykh, I.A. Ignatiev, etc.

The present study focuses on the Late Pennsylvanian vegetation dynamics (syndynamics), including the issues of the evolution of ancient plant communities, i.e., phytocoenogenesis. The phytocoenogenetic researches involve, at the outset, the identification of the floristic composition, ecological-coenotic structure and habitats of palaeophytocoenoses for successive long-time intervals, then the analysis of changing vegetation diversity reflected in the classification of phytocoenoses [22-24].

The detailed studies of the plant fossil assemblages of the Donetsk Basin from the complete strata of the upper Carboniferous deposits have been conducted by A.K. Shchegolev [27-29] and N.I.

Boyarina [6-8, 35]. The current study of vegetation dynamics is based on these published data as well as the reconstructions and classification of the late Carboniferous (Late Pennsylvanian) plant communities of the Donetsk Basin performed by the author in recent years that have been partly published [9, 10]. The detailed description of the late Carboniferous plant communities and its classification are the subject of a forthcoming publication. This paper represents the review of transformations of plant palaecommunities and the first ideas about phytocoenogenesis in the late Carboniferous.

Geological setting and material. The Donets Basin located in eastern Ukraine is the part of the Dnieper-Donets intracratonic rift basin (Fig. 1). In the Carboniferous the territory of the Donets Basin was periodically covered by shallow epicontinental seas, resulting in the formation of the powerful strata of mixed carbonate-siliciclastic sediments. The upper Carboniferous deposits, which are consisted of the alternating fluvio-deltaic and nearshore-marine facies, was divided into suites (= formations) based of limestone marker beds and correspond to three regional stages, namely Toretskian, Kalynovian, Myronivskian [20].



1 – Kartanash, **2** – Svitlanove, **3** – Chernyshove, **4** – Kalynove, **5** – Troyitske, **6** – Krasnuj Pahar, **7** – Myronivske, **8** – Luganske, **9** – Novgorodske, **10** – Kamyshevaha, **11** – quarry Kalynove, **12** – Klynove, **13** – gully near the Volchanivka village, **14** – gully near the Roty railway station, **15** – gully Memryk near the Galytsynivka village, **16** – gully Kravetska near the Ivanopilje village, **17** – quarry near the Keramik village, **18** – borehole 4377, **19** – borehole 4385, **20** – borehole 4395, **21** – borehole 4453, **22** – borehole 743, **23** – borehole 741, **24** – borehole 181, **25** – borehole 811, **26** – borehole 239, **27** – borehole 232, **28** – borehole A-3

Fig. 1. Scheme of research region with the structure plan of suite limestones (from the fund materials of PGO "Donbas geology" 1985) and the position of the localities of plant remains

The research of the Late Pennsylvanian vegetation cover was conducted on the basis of plant fossils from the Toretskian and Kalynovian deposits that were studied by A.K. Shchegolev [27-29] and from the upper Kalynovian and Myronivskian deposits studied by the author of this paper [6-8, 35]. The data about the Kasimovian (Toretskian) and Gzhelian (Kalynovian and Myronivskian) plant communities are based of the plant fossil assemblages from lacustrine, lacustrine-swamp, lacustrine-deltaic, floodplain-lacustrine, floodplain and lacustrine-lagoon deposits in more than 17 localities and 11 boreholes that located within the Bakhmutska and Kalmius-Toretska troughs (Fig. 1).

Analysis of main research and publications. The study of the Late Pennsylvanian vegetation is carried out in accordance with the views about the development of phytocoenoses in vegetation science, using the terminology, which is applied for the research of today's vegetation dynamics [1, 11-15, 24, 26, 31, 33, 39, 45]. In vegetation dynamics (syndynamics) two basic forms have been described. The various types of irreversible cyclic changes in plant communities, which resulted to the formation of already existing combinations of species, are referred as successions [13, 22-25, 45]. In contrast to successions, the evolution of phytocoenoses, as the second form of syndynamics, leads to the formation of the completely new combinations of altered flora in response to changing environmental conditions [11-12, 18-19, 22-24, 39, 44, 45]. In the evolution of phytocoenoses, florogenesis (historical process of flora formation) and phytocoenogenesis (formation of new phytocoenoses) are distinguished. The phytocoenogenesis (or phylocoenogenesis, according to V.N. Sukachev [23-24]), as the sequential evolution of plant communities over a long geological time leading to the appearance of new types of phytocoenoses (associations, formations, vegetation types), occurs in parallel with the evolution of species constituting phytocoenoses and is traced in the change of vegetation syntaxonomic units [11, 23-24, 32-33]. Several ways of the commission or basic acts of phytocoenogenesis are differentiated: speciogenesis – gradual transformation of one community into another due to the evolutionary change of species that make up its composition, especially dominants and subdominants; esogenesis – transformation of communities by the changes of species role, in particular, when one dominant is changed by another; transgenesis – transformation of some phytocoenoses into others by invasion (embedding of niche) or elision (disappearance of niche); substitution – transformation of communities by the replacement of ecological niches due to competitive exclusion of species [12, 21]. Such phytocoenogenetic processes have been best studied for the Quaternary period of the Earth's history [14, 24].

The research of the Pennsylvanian vegetation is predominantly undertaken at the biome level [34, 36-38]. In the Pennsylvanian vegetation of the Euramerican tropical region, two tropical biomes have been identified, namely wetland and seasonally dry. Throughout Late Pennsylvanian time in the conditions of gradually increasing aridization and seasonality, the periodic changes in distribution of wetland forests and seasonally dry woodlands as well as the change of the role of major plant groups (lycopods, ferns, pteridosperms, horsetails, cordites, and conifers) in the composition of biomes have been recognized. The spread and dominance of individual biomes are correlated with the global sea-level and climate changes that are associated with the glacial-interglacial intervals of the Late Palaeozoic Ice Age [38, 40-43].

Research methods. The study of vegetation dynamics (phytocoenogenetic processes) throughout the Late Pennsylvanian consists of the analysis of the changes of the floristic composition of plant communities and the syntaxonomic composition of the Kasimovian and Gzhelian vegetation of the Donets Basin. The syntaxonomic composition of vegetation cover was identified based on the conducted ecological-floristic classification of the Kasimovian and Gzhelian plant communities by the Braun-Blanquet method [9, 10].

The object of the study of phytocoenogenetic processes is the florocoenotic complex that includes the sum of similar species in ecological-coenotic strategy and variability dynamics [14, 15, 30, 31]. Three groups of species are distinguished in modern florocoenotic complexes: 1 – relict species of preceding flora, 2 – ancient core of modern flora, 3 – autochthonous products of species transformation [15]. Based on the analysis of florocoenotic complexes, four phytocoenogenetic manifestations can be identified: (1) progressive development (increase in the number of coenopopulations, increase in species abundance, strong transformation of external environments into phytocoenotic ones, mesophytization of communities); (2) regressive development (decrease in the number of coenopopulations, decrease in species abundance, weak transformation of external environments into phytocoenotic ones, xerophytization or hygrophytization of communities); (3) a loss of phytocoenoses from vegetation cover; (4) an appearance of new types of phytocoenoses [14, 15].

Taking into consideration the possibilities of the use of plant fossils in palaeophytocoenogenetic researches, the study of syndynamics concentrated on the identification of the role of individual species in florocoenotic complexes (ancient elements of flora and new species) and the foregoing directions in the development of the late Carboniferous phytocoenoses. For the definition of species abundances as the important indicator of phytocoenogenetic processes, the quantity of plant remains in fossil assemblages and the number of locations were taken into account.

Research results and discussions

Phytocoenogenetic analysis of the Late Pennsylvanian vegetation cover of the Donetsk Basin. The study of phytocoenogenetic processes is based on the analysis of the florocoenotic complexes that include the diagnostic species of the palaeosyntaxa of the Late Pennsylvanian vegetation in the Donetsk Basin. It should be emphasized that the diagnostic species of syntaxa are considered as the indicators of environmental conditions in the Braun-Blanquet classification system and reflect the ecological-coenotic feature of phytocoenoses [18]. The peculiarities and main factors of phytocoenogenesis are identified on the basis of the palaeosyntaxa in rank of the orders of the following vegetation types: wetland forests (WFl) and woodlands (WWl) of coastal lowlands, wetland forests (WFp) and woodlands (WWp) of deltaic plains, seasonally dry woodlands of river valleys (SWv) and lagoon coasts (SWc). The changes of vegetation cover of different landscapes associated with changing tectonic processes and environmental conditions are considered for four time intervals, which correspond to the upper Carboniferous regional stratigraphic subdivisions (Fig. 2).

The Toretskian vegetation cover developed under the conditions of ascending tectonic movements in the beginning of Toretskian time and the predominance of descending movements in the next bigger part of this period [3-5]. The descending movements were accompanied by extensive transgressions as well as the spread of swampy territories with rich wetland vegetation [27].

The Toretskian vegetation was represented by the plant communities of three orders (Fig. 2). The florocoenotic complex of the wetland forest communities of coastal lowlands of the order *Neuroptero ovata-Crenulopteretalia lamuriana* Boyarina ms. (WFl-1) is characterised by the appearance of numerous new coenopopulations (19 form-species, including the endemic species of *Sphenopteris rossica* Zalessky) and the increase in abundance of individual species (Fig. 3). According to species abundance (rich plant fossil assemblages), the calamitaleans with stems of *Calamites suckowii* Brongniart and with foliage of *Annularia sphenophylloides* (Zenker) Gutbier, *A. stellata* Schlotheim ex Wood, *Asterophyllites equisetiformis* (Sternberg) Brongniart, the ferns with foliage of *Crenulopteris lamuriana* (Heer) Wittry et al., *P. arborescens* (Schlotheim) Brongniart, *P. hemitelioides* Brongniart, *Nemejcopteris feminaeformis* (Schlotheim) Barthel, *Sphenopteris rossica* and the pteridosperms with foliage of *Neuropteris ovata* Hoffmann played a major role in wetland forests. These changes indicate the progressive development of wetland forest communities within coastal lowlands. The analysis of the florocoenotic complex of the wetland forest communities of deltaic plains of the order *Subsigillario-Acithecetalia polymorpha* Boyarina ms. (WFp-1) testifies to the progressive development too, which was manifested in the appearance of more than 10 new coenopopulations (Fig. 4). These coenopopulations are mainly presented by the subsigillarian lycopsids, such as *Subsigillaria biangula* (Weiss) Shchegolev, *S. brardii* (Brongniart) Weiss emend. Shchegolev, *S. halensis* (Weiss) Shchegolev, *S. sulcata* (Ščurovskij) Shchegolev, *S. weisii* Shchegolev, *Syringodendron angustum* Shchegolev, *S. brardi* Shchegolev. The composition of the seasonally dry woodland communities of river valleys of the order *Cordaito principalis-Odontopteretalia subcrenulata* Boyarina ms. (SWv-1) was replenished by a few new coenopopulations at the beginning and end of Toretskian time (Fig. 5). It should be noted that the data about the vegetation of river habitats are not sufficient, because the fossil assemblages from floodplain deposits are only composed of rare allochthonous plant remains and these fluvial sediments are presented less than lacustrine-deltaic strata in the Toretskian section. The exception is the numerous conifer remains that were found at the base of the Toretskian. These walchian conifers belonged to the woodland conifer-communities, which grew within river valley slopes and plakor areas, and are not considered here in phytocoenogenetic aspect. It follows from the above that the progressive development of the plant communities of coastal lowlands and deltaic plains took place in middle and late Toretskian times, during which the lowland areas with a humid climate were widespread.

The Kalynovian vegetation cover developed under the conditions of tectonic regime changes, namely: the short period of descending movements by the longer period of the predominance of ascending ones. The latter period was characterized by the extensive distribution of river networks in a context of the tectonic activation of demolition areas [5].

The Kalynovian vegetation was represented by the new types of wetland forest communities of coastal lowlands (WFl-2) and deltaic plains (WFp-2), as well as seasonally dry woodland communities of river valleys (SWv-1) of the same order as in Toretskian time (Fig. 2). The florocoenotic complex of the wetland forests of coastal lowlands of the new order *Calamito suckowii-Pecopteretalia densifolia* Boyarina ms. (WFl-2) includes the new coenopopulations, which were represented by the ferns with foliage of *Pecopteris densifolia* (Goeppert) Weiss, *P. platonii* Grand'Eury, *P. oreopteridia* Brongniart. In general, this complex is characterised by the increased species abundance of the ferns with foliage of *Pecopteris densifolia, P. arborescens, P. bredovii* Germar, *P. unita* Brongniart, *Nemejcopteris feminaeformis* (Fig. 3). Consequently, the formation of new plant communities of coastal lowlands was the result of their progressive development. The wetland forest communities of the new order *Subsigillario-Odontopteretalia schlotheimii* Boyarina ms. (WFp-2) within deltaic plains were also formed due to the progressive development as evidenced by the appearance of up to 10 new coenopopulations, including the endemic species: *Subsigillaria simplex* Shchegolev, *S. donetciana* Shchegolev, *Pecopteris mironovana* Zalessky and Tschirkova (Fig. 4). The communities of deltaic plains were replenished by both new species (pteridosperms and ferns) and some species of the ferns that grew within coastal lowlands in Toretskian time. The particularity of the plant fossil assemblages from deltaic deposits of the Kalynovian is the more common plant remains of the hygro-mesophytic pteridosperms with foliage of *Neuropteris crassinervis* Shchegolev ms. and *Odontopteris schlotheimii* Brongniart in comparison with the rare remains of subsigillarian lycopsids. The increasing role of hygro-mesophytic pteridosperms may testify about the mesophytization of deltaic plain communities that is another indication of the progressive development of these communities. The florocoenotic complex of the seasonally dry communities of river valleys (SWv-1) shows the increased number of coenopopulations from the end of Toretskian time without the change of phytocoenotic properties of species in Kalynovian time (Fig. 5). Such phytocoenotic processes demonstrate only the increased species diversity of these woodland communities in the composi-

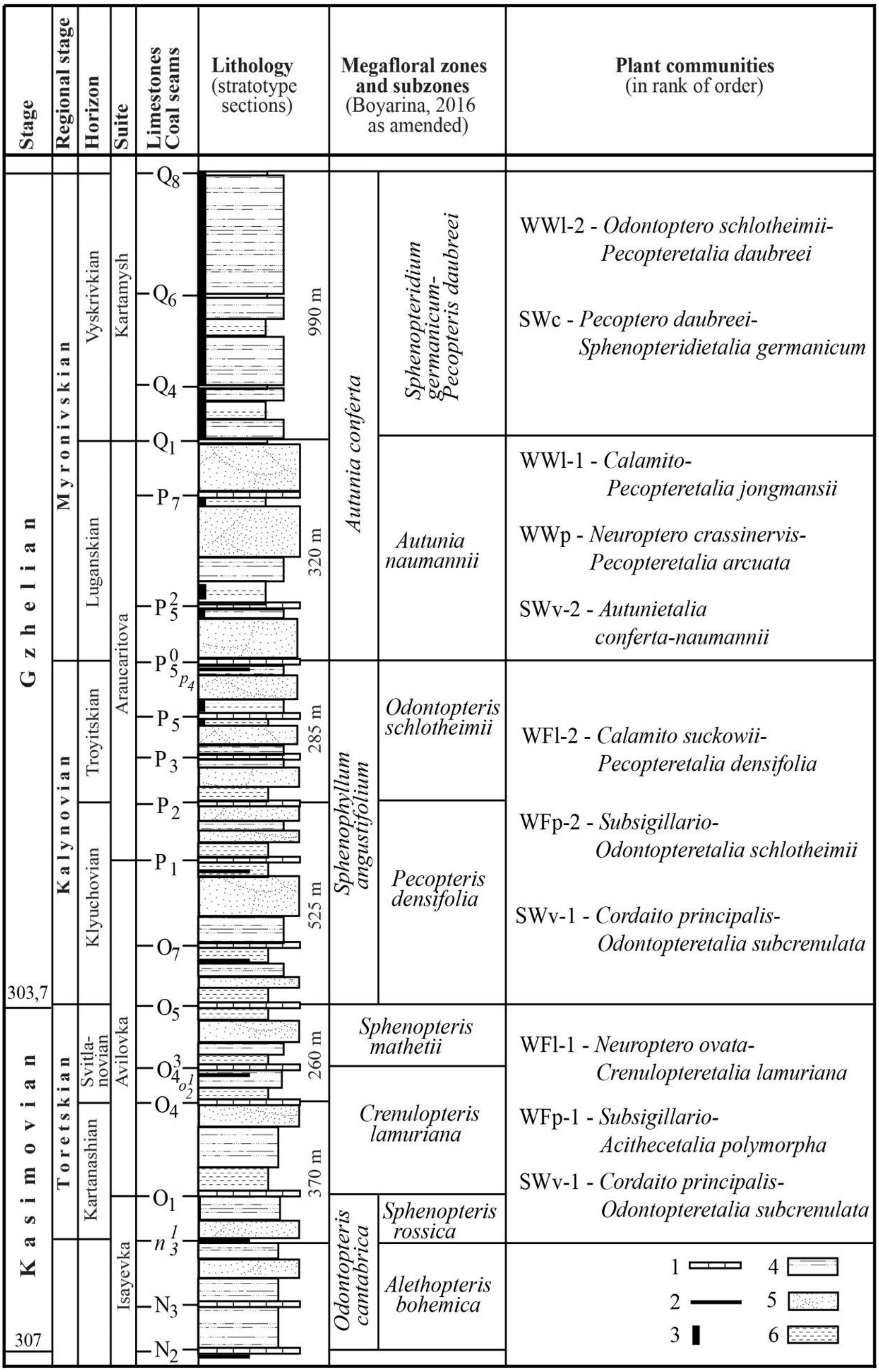


Fig. 2. The upper Carboniferous regional and megafloral subdivisions, lithostratigraphy and the late Carboniferous vegetation of the Donets Basin: 1 – limestones; 2 – coal seams; 3 – red beds; 4 – siltstones; 5 – sandstones; 6 – mudstones; WFl – wetland forests of coastal lowlands; WWl – wetland woodlands of coastal lowlands; WFp – wetland forests of deltaic plains; WWp – wetland woodlands of deltaic plains; SWv – seasonally dry woodlands of river valleys; SWc – seasonally dry woodlands of lagoon coasts

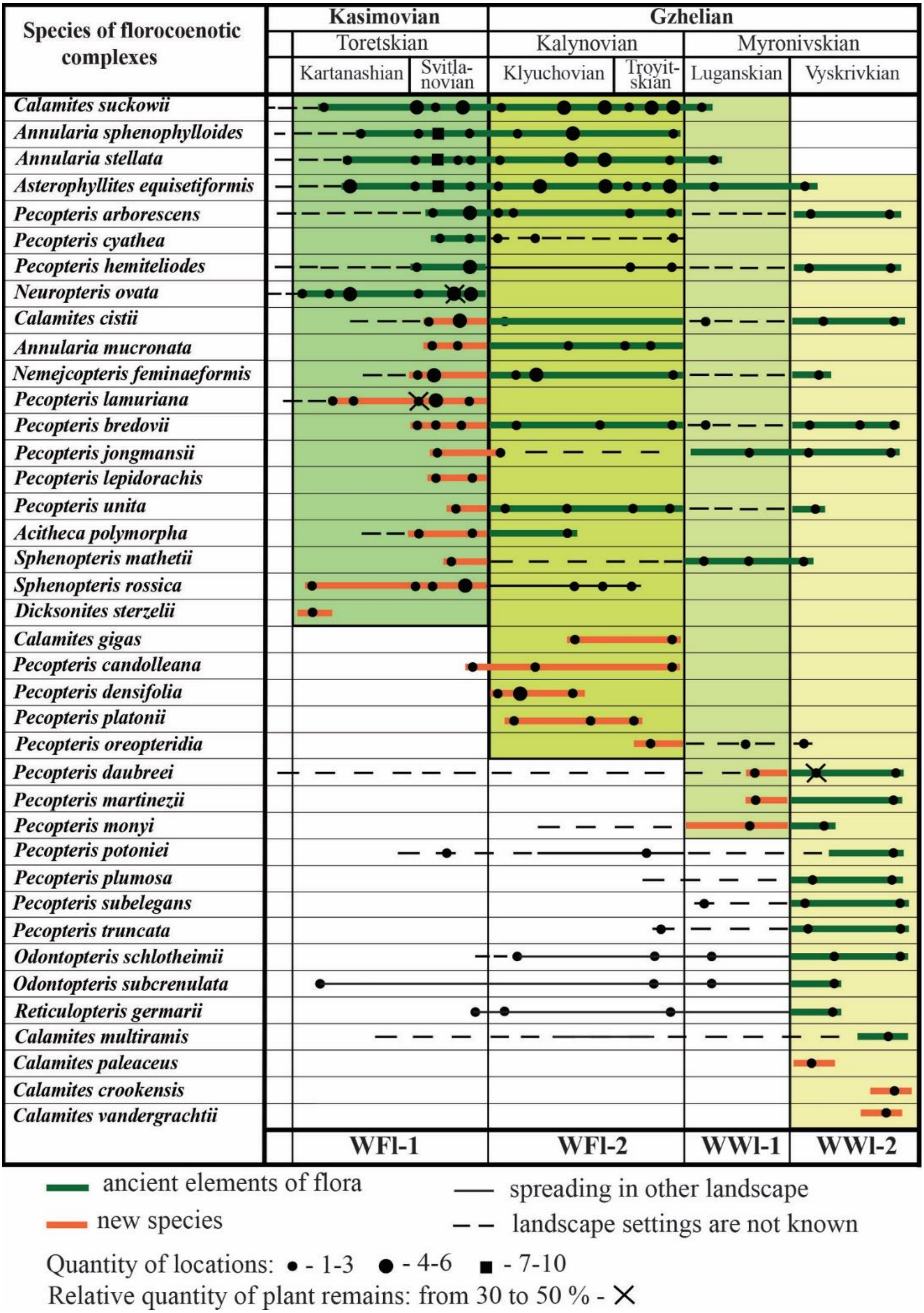


Fig. 3. Composition of the florocoenotic complexes of tropical wetland forests (WFl) and woodlands (WWl) of coastal lowlands of the Donets Basin

Fig. 4. Composition of the florocoenotic complexes of tropical wetland forests (WFp) and woodlands (WWp) of deltaic plans of the Donets Basin (legend see Fig. 3)

tion of the same order *Cordaito principalis-Odontopteretalia subcrenulata*.

The Luganskian vegetation cover evolved in the conditions of the tectonic activity of demolition areas and the gradual isolation of the Donets epicontinental sea [3-5]. The intensification of ascending movements and the growth of climate aridization since the end of Kalynovian time led to the contraction of coastal wetland territories and the most spread of river systems and interfluvial spaces. This caused the significant transformations of plant communities reflected in the vegetation composition of Luganskian time.

The Luganskian vegetation was represented by the woodland communities of three new orders (Fig. 2). The wetland woodland communities of coastal lowlands of the new order *Calamito-Pecopteretalia jongmansii* Boyarina ms. (WWl-1) were formed as a result of the considerable decline of the number of coenopopulations, as well as the decrease in species abundance of some coenopopulations, especially the calamitaleans with foliage of *Annularia stellata, Asterophyllites equisetiformis* and the ferns with foliage of *Nemejcopteris feminaeformis, P. unita*. The decrease of plant species composition is evidenced by the fact that the calamitaleans with stems of *Calamites gigas* Brongniart and foliage of *Annularia mucronata* Schenk and also the ferns with foliage of *Pecopteris densifolia, P. candolleana* Brongniart*, P. cyathea* (Schlotheim) Brongniart*, P. platonii, Sphenopteris rossica* are unknown since early Luganskian time in the Donets Basin (Fig. 3). The ancient core of the florocoenotic complex of these woodland communities consisted of the species that were previously part of the wetland forest communities of coastal lowlands. But in doing so, the main role in these communities became to belong to the ferns, which had small pinnules (*Pecopteris arborescens, P. jongmansii* Wagner*, P. martinezii* Stockmans & Willière*, P. monyi* Zeiller) as well as the pinnules with fine hairs on its surface, as could be seen from the point indentations on fossil materials (*Pecopteris daubreei*

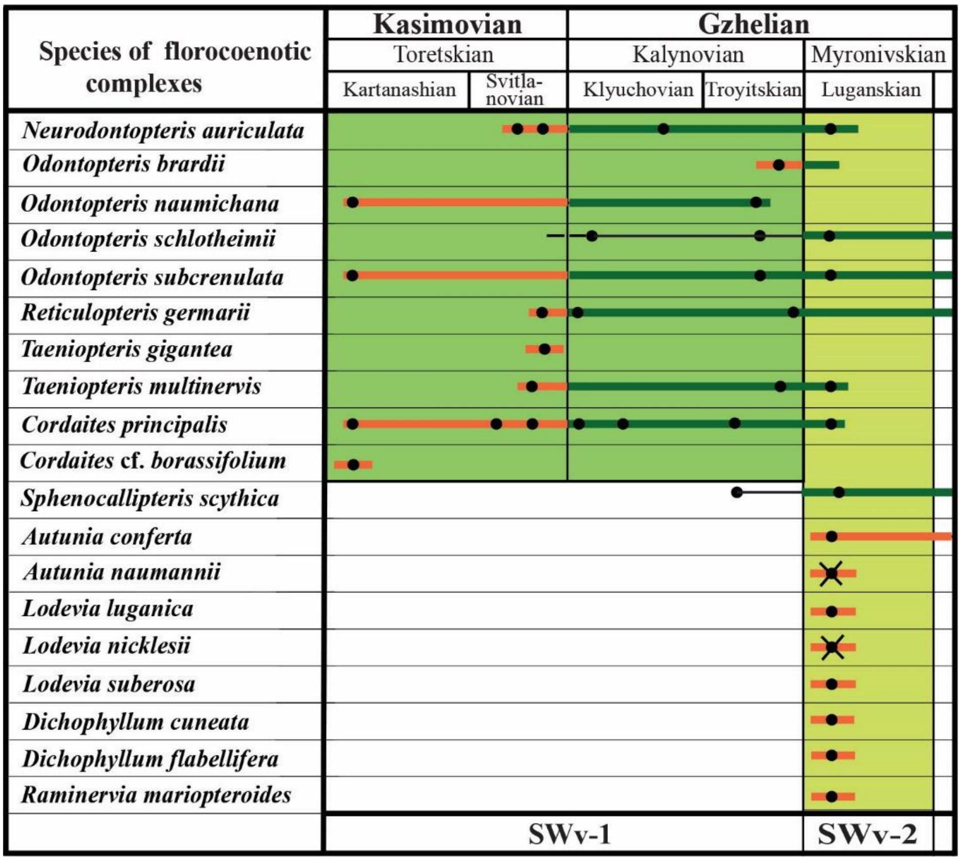


Fig. 5. Composition of the florocoenotic complexes of tropical seasonally dry woodlands of river valleys (SWv) of the Donets Basin (legend see Fig. 3)

Zeiller). Such morphological characteristics of foliage are usually considered as xeromorphic [16] and may point to the moderate xerophytization of communities. The decreases in the number of coenopopulations and species abundances together with the xerophytization of lowland palaeophytocoenoses testify to its regressive development in Luganskian time. The communities of wetland woodlands within deltaic plains of the new order *Neuroptero crassinervis-Pecopteretalia arcuata* Boyarina ms. (WWp) included the ferns of one new species (*Pecopteris arcuata* Halle) as well as some pteridosperms and calamites that were formerly associated with the wetland forests of deltaic plains (Fig. 4). The pteridosperms *Neuropteris crassinervis* and the ferns *Pecopteris arcuata* were distinguished by increased species abundances. Whereas, the subsigillarian lycopsids and practically all ferns, which grew within deltaic plains in Kalynovian time, were absent in these communities. The considered features of the florocoenotic complexes of wetland woodland communities of coastal lowlands and deltaic plains identify the regressive development of communities that resulted in the loss of wetland forests and the formation of wetland woodlands.

At the same time as the transformation of forests into woodlands within coastal lowlands and deltaic plains, the plant communities of river valleys underwent progressive development. It was manifested by the appearance of 10 new coenopopulations that included mainly peltasperm pteridosperms (Fig. 4). The pteridosperms *Autunia naumannii* and *Lodevia nicklesii* of them were characterized by high species abundances. These seasonally dry shrub and woodland communities of the new order *Autunietalia conferta-naumannii* Boyarina ms. (SWv-2) occupied widespread river landscapes in Luganskian time.

The Vyskrivkian vegetation cover was formed at the time of growing climate aridization and tectonic activation of demolition areas that were expanded into the Ukrainian crystalline shield, where the formation of red weathering crusts was going on. The weathering products were mainly transported by temporary or seasonal rivers and streams, resulting to the accumulation of thick red-colored deposits. According to the facies analysis of the Vyskrivkian strata, the predominant landscape types were the plain spaces with lacustrine-lagoon water bodies [2, 4].

The vegetation of Vyskrivkian time was represented by the wetland woodland communities of coastal lowlands of the new order *Odontoptero schlotheimii-Pecopteretalia daubreei* Boyarina ms. (WWl-2) and seasonally dry woodland communities of lagoon coasts of the new order *Pecoptero daubreei-Sphenopteridietalia germanicum* Boyarina ms. (SWc). The former communities consisted of the plants that were part of the woodland communities of coastal lowlands and deltaic plains in Luganskian time (Fig. 3). The formation of these coastal lowland communities was most likely the result of both the expansion of population ranges and the migration of plants from deltaic plains to coastal lowlands. These processes were caused by the contraction of river landscapes and apparently the smoothing out of ecological-coenotic differences in the palaeophytocoenoses of these two landscape types against the background of increasing climate aridization. The change of ecological conditions led to the spread of the mesophytic pteridosperms, such as *Odontopteris subrenulata* (Rost) Zeiller and *Reticulopteris germarii* (Giebel) Gothan, within coastal lowlands, where the ferns *Pecopteris daubreei* continued to dominate. It can be interpreted as the mesophytization process of coastal lowland communities. It follows that the considered specificities of communities, namely the increase of coenopopulations and the mesophytization of communities, may testify in favor of the formation of new woodland communities of coastal lowlands due to their progressive development, but without the evolutionary changes of flora and with maintaining low species abundances.

The seasonally dry woodland communities of lagoon coasts (SWc) were also composed of the plants of two groups. The plants of the first group (*Pecopteris daubreei, P. arborescens, P. biotii* Brongniart*, P. jongmansii*) were widespread in Luganskian and continued to grow in Vyskrivkian times within coastal lowlands (Fig. 3). The second plant group (*Pecopteris subelegans* (Potonié) Doubinger*, Sphenopteridium germanicum* (Weiss) Kerp et DiMichele) was associated with the seasonally dry woodlands of river valleys in Luganskian time. Consequently, the formation of lagoon coast communities could also be the result of plant migrations along with the expansion of some population ranges.

The discussed features of dynamics in the palaeophytocoenoses of wetland forests and woodlands of coastal lowlands and deltaic plains, as well as seasonally dry woodlands of river valleys and lagoon coasts in Kasimovian and Gzhelian times are displayed in the scheme of phytocoenogenesis (Fig. 6) that has been drawn up on the basis of the considered florocoenotic complexes.

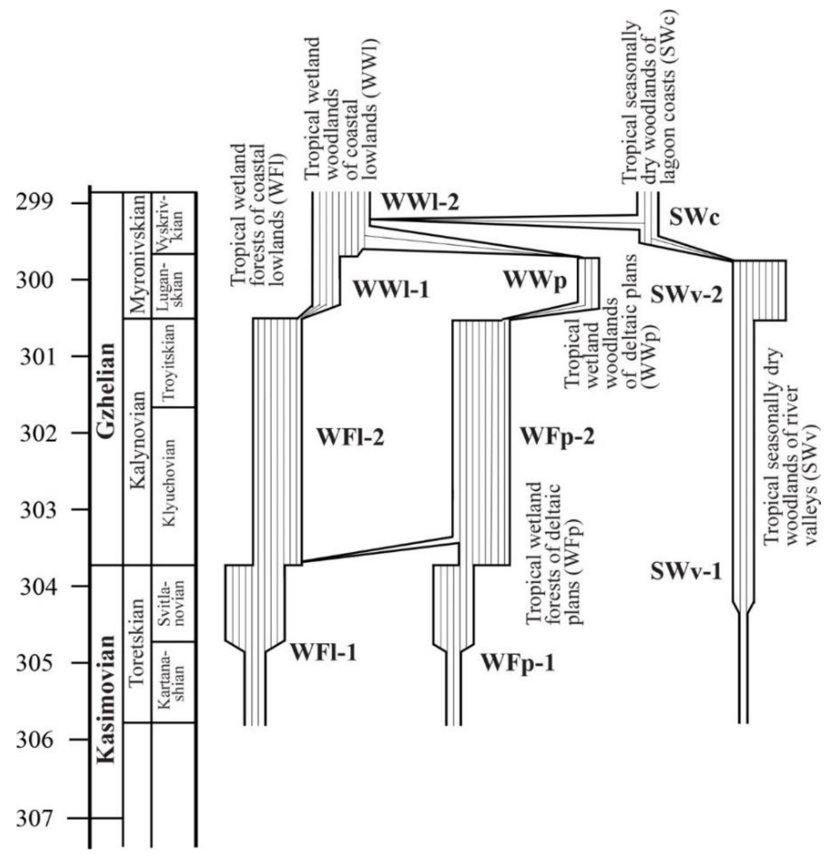


Fig. 6. The scheme of phytocoenogenesis of the Late Pennsylvanian vegetation cover in the Donets Basin

Models of phytocoenogenesis. According to the modern concepts in vegetation science, the evolution of plant communities leading to the formation of new types of phytocoenoses (phytocoenogenesis) occurs in conformity with the transformations of ecological niches and coenotic systems that were caused by the changes of abiotic factors [12, 18]. Following these views, the relationships between the development of the Late Pennsylvanian phytocoenoses and changing landscape conditions are analyzed. In the evolution of palaeophytocoenoses, we distinguish *phytocoeno-*

genetic processes (progressive or regressive development of communities), which are caused by the changes of landscape conditions, and *manifestations of phytocoenogenesis* (formation of new communities and loss of old communities) that were generated by these phytocoenogenetic processes. The features of such transformations of palaeophytocoenoses in response to changing conditions are shown in Table 1.

As can be seen from this table, three models of the formation of new types of communities and one model of the loss of communities from vegetation cover can be identified in Gzhelian time. During Kasimovian time, the progressive development of plant communities (WLl-1, WFp-1, SWv-1) has been only determined (Fig. 6).

Each of the phytocoenogenetic models reveals the certain phytocoenogenetic processes and factors of transformations of communities. Thus, the formation of one group of the new communities (WFl-2, WFp-2, SWv-2), which are characterized by the

Table 1

Dependence of phytocoenogenetic processes and manifestations on the changes of ecological-landscape conditions of the Donets Basin in the Late Pennsylvanian

Landscape changes	Age	Phytocoenogenetic processes	Manifestation of phytocoenogenesis
Vegetation of coastal lowlands			
Expansion of coastal lowlands with humid climate	Early Kalynovian	Progressive development (appearance of new coenopopulations and increase in species abundance)	Formation of new wetland forest communities (WFl-2)
Contraction of coastal lowlands with humid climate	Early Luganskian	Regressive development (decrease in the number of coenopopulations and species abundance)	Loss of wetland forest communities (WFl-2)
		Regressive development and substitution of dominants	Formation of new wetland woodland communities (WWl-1)
Expansion of coastal lowlands and contraction of deltaic plains in the conditions of increasing aridization	Vyskrivkian	Progressive development (increase in the number coenopopulations due to the migration of plants from other landscapes)	Formation of new wetland woodland communities (WWl-2)
Vegetation of deltaic plains			
Expansion of deltaic plains with humid climate	Early Kalynovian	Progressive development (appearance of new coenopopulations)	Formation of new wetland forest communities (WFp-2)
Contraction of deltaic plains with humid climate	Early Luganskian	Regressive development (decrease in the number of coenopopulations and species abundance)	Loss of wetland forest communities (WFp-2)
		Regressive development and substitution of dominants	Formation of new wetland woodland communities (WWp)
Contraction of deltaic plains with humid climate	Early Vyskrivkian	Regressive development (decrease in the number of coenopopulations)	Loss of wetland woodland communities (WWp)
Vegetation of river valleys			
Expansion of river valleys with seasonally dry climatic conditions	Luganskian	Progressive development (appearance of new coenopopulations and increase in species abundance)	Formation of new seasonally dry woodland communities (SWv-2)
Contraction of river valleys with seasonally dry climatic conditions	Early Vyskrivkian	Regressive development (decrease in the number of coenopopulations and species abundance)	Loss of seasonally dry woodland communities (SWv-2)
Vegetation of lagoon coasts			
Expansion of lacustrine-lagoon plains and contraction of alluvial plains in the conditions of increasing aridization	Vyskrivkian	Progressive development (increase in the number coenopopulations due to the migration of plants from other landscapes)	Formation of new seasonally dry woodland communities (SWc)

appearance of new coenopopulations and increased species abundance (*evolution, progressive development*), refers to *an evolution-progression model*. The development of these communities took place within expanding certain landscape types (biotope expansion) and accompanied by the increasing differentiation of ecological niches.

The formation of another group of the communities (WWl-2, SWc), which is related to the increase in the number of coenopopulations (*progressive development*) owing to the migration of plants (*migration processes*) from transformed landscapes to the ecological analogs of ecotopes within expanding landscapes (biotope expansion), belongs to *a migration-progression model*. And in doing so, the coastal lowland communities (WWl-2) were augmented by the migrants from deltaic plains, whereas the communities of lagoon coasts (SWc) were formed by the migrants from coastal lowlands and river valleys.

The next two phytocoenogenetic models are connected with the regressive development of communities caused by the contraction of certain landscape types that resulted in, for one thing, the loss of forest communities and, for the other thing, the formation of the new vegetation types, namely woodland communities (Fig. 6). The formation of the new communities (WWl-1, WWp), which is associated with the decrease in the number of coenopopulations and species abundance (*regressive development*) as well as structure simplification and dominant *substitution* in palaeophytocoenoses, relates to *a substitution-regression model*. These phytocoenogenetic processes can be explained by the reduction in ecological niches because of the contraction of landscapes (biotope contraction).

The loss of communities (WFl-2, WFp-2, WWp, SWv-2) from vegetation cover, which occurred as a result of the decrease in the number of coenopopulations and individuals in remaining coenopopulations (*elision, regressive development*), is put forward as *an elision-regression model*. The data about the disappearance of species and the decrease in species abundances obtained from the upper Gzhelian plant assemblages indicate the significant decline in density and simplified structure of vegetation cover, namely forest degradation on coastal areas in Luganskian time and woodland degradation within river landscapes in Vyskrivkian time. Such transformations of communities are attributed to the contraction of certain landscape types (biotope contraction).

Phytocoenogenetic regularities in development of the Late Pennsylvanian vegetation cover. The proposed models of phytocoenogenesis reflect the main specific features of the Late Pennsylvanian vegetation dynamics in response to environmental changes. As already mentioned, the changes of environmental conditions were the consequences of, on the one hand, the global fluctuations of sea levels and increasing climate aridization [41-43], and, on the other hand, the tectonic processes in the Donets epicontinental basin in Late Pennsylvanian times [4-5, 17]. It follows that the interaction between global sea-level (eustatic) variations and regional tectonic settings led to certain environmental changes and the changes of palaeophytocoenoses. The four models of phytocoenogenesis describe the regularities in development of the Late Pennsylvanian phytocoenoses associated with environmental changes.

The evolution-progression model of phytocoenogenesis reflects the progressive development of palaeophytocoenoses that is expressed by the appearance of evolutionary new coenopopulations in the conditions of the expansion of certain landscape types (biotopes). In early Gzhelian (Kalynovian) time, the phytocoenogenesis of wetland forest communities under this model occurred in the period of the predominance of descending movements that resulted in the expansion of coastal lowlands and deltaic plains with a humid climate. In middle Gzhelian (Luganskian) time, the phytocoenogenesis of seasonally dry woodland communities by this model took place under the conditions of predominant ascending movements that led to the expansion of river landscapes.

The migration-progression model of phytocoenogenesis conforms to the progressive development of palaeophytocoenoses as a result of the migration of plants from decreasing landscape types to expanding ones (expanding biotopes). The phytocoenogenesis of woodland communities under this model was paralleled by the shallowing of the Donets epicontinental sea and increasing climate aridization in late Gzhelian (Vyskrivkian) time. In these condition, the formation of new wetland woodland communities was due to the expansion of coastal lowlands and the contraction of deltaic plains and, also, the formation of the new seasonally dry woodland communities was due to the expansion of lacustrine-lagoon plains and the contraction of river valleys. The latter was the obvious result of the transformation of rivers into temporary rivers and streams that experienced alternating wet and dry periods.

The substitution-regression model of phytocoenogenesis is consistent with the regressive development of palaeophytocoenoses along with structure simplification and dominant substitution of plant communities due to the contraction of certain landscape types (biotopes). The phytocoenogenesis of communities by this model was caused by the transformation of wetland forest communities in woodland communities. It was a consequence of the contraction of coastal lowlands and deltaic plains with a humid climate against the background of the tectonic activity of demolition areas and gradually increasing climate aridization in middle Gzhelian (Luganskian) time.

The elision-regression model of the loss of plant communities represents the regressive development of palaeophytocoenoses in the conditions of the contraction of some landscape types (biotopes). In late Gzhelian time, the loss of wetland forest communities was caused by the contraction of coastal lowlands and deltaic plains (early Luganskian time), as well as the loss of wetland and seasonally dry woodland communities was caused by the contraction of river landscapes with deltaic plains and river valleys (early Vyskrivkian time).

In summary, it should be pointed out that three proposed models of the formation of new plant communities reflect three main directions in the evolution of palaeophytocoenoses, in which the basic pathways of phytocoenogenesis, according to B.A. Bykov [12], manifest themselves. Namely, speciogenesis and esogenesis are reflected in the evolution-progression model with evolutionarily new species and the change of dominants. Transgenesis (invasion) and esogenesis are incorporated into the migration-progression model without the evolutionary transformations of flora, but with the increased number of species and the change of phytocoenotic properties of species. Transgenesis (elision) and esogenesis are present in the substitution-regression model with the decreased number of species and dominant substitution.

Conclusions. The composition of the Late Pennsylvanian (Toretskian, Kalynovian, Luganskian and Vyskrivkian) vegetation of the Donetsk Basin reflected in the ecological-floristic classification by the Brown-Blanquet method have been used for the study one from forms of syndynamics, namely phytocoenogenesis. The study of phytocoenogenesis has been carried out on the basis of the palaeosyntaxa in rank of orders including the communities of tropical wetland forests and woodlands of coastal lowlands and deltaic plains, as well as seasonally dry woodlands of river valleys and lagoon coasts. Based on the analysis of the phytocoenogenetic processes (progressive and regressive development of plant communities) and the manifestations of phytocoenogenesis (formation of new communities and loss of old communities) in development of the Late Pennsylvanian phytocoenoses, three models of the formation of new communities and one model of the loss of communities from vegetation cove have been proposed. The models of the formation of new communities reflect the main directions in the evolution of palaeophytocoenoses and reveal the relationship between phytocoenogenetic processes and environmental changes.

Acknowledgments

This study was supported in part by the Ministry of Education and Science of Ukraine (project no. 0116U004691) and the National Academy of Sciences of Ukraine (budget program with budget classification code no. 6541230 "Support for the development of priority areas of scientific research").

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Зміни пізньопенсильванської рослинності Донецького басейну: синдинамічний аспект

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Стаття присвячена вивченню еволюції пізньопенсильванських фітоценозів Донецького басейну та дає перші уявлення про фітоценогенез в пізньому палеозої. Палеофітоценотичні дослідження викопного рослинного матеріалу із озерних, озерно-болотних, дельтових, заплавних та озерно-лагунних відкладів в більш ніж 17 місцезнаходженнях та 11 свердловинах були проведені відповідно до сучасних уявлень про розвиток рослинності. Вивчення процесів фітоценогенезу базується на аналізі флористичного різноманіття, яке відображене в еколого-флористичній класифікації пізньокам'яновугільної рослинності Донецького басейну за методом Браун-Бланке. На основі аналізу флороценотичних комплексів, що являють собою набір діагностичних видів синтаксонів рослинності в ранзі порядків, розглянуто процеси і прояви фітоценогенезу та запропоновано три моделі формування нових угруповань – еволюційно-прогресивну, міграційно-прогресивну, субституційно-регресивну та одну модель випадання угруповань з рослинного покриву – елізійно-регресивну. Эволюційно-прогресивна модель відповідає прогресивному розвитку палеофітоценозів, який проявився появою еволюційно нових ценопопуляцій у їх складі. Міграційно-прогресивна модель відображає прогресивний розвиток палеофітоценозів в результаті міграції рослин із скорочуваних до широко розповсюджених типів ландшафту. Субституційно-регресивна модель відповідає регресивному розвитку палеофітоценозів при спрощенні структури та зміні (субституції) домінантів рослинних угруповань. Елізійно-регресивна модель відображає регресивний розвиток та випадіння (елізію) палеофітоценозів із складу рослинного покриву. Для кожної із моделей фітоценогенезу виявлені закономірності формування рослинних угруповань, які розкривають зв'язок динаміки рослинного покриву та змін ландшафтно-екологічних і кліматичних умов.

***Ключові слова**: рослинний покрив, фітоценогенез, пізній пенсильваній, Донецький басейн.*

Надійшла 8 грудня 2021 р.
Прийнята 13 січня 2022 р.