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Late Pennsylvanian vegetation dynamics of the Donets Basin, Ukraine

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abstract

The dynamics of the Late Pennsylvanian vegetation cover of the Donets Basin is represented by a succession of formations of new plant communities (phytocoenogenesis) of a wetland forest and woodland biome and a seasonally dry woodland biome because of the changing landscape and climate conditions resulting from the glacio-eustatic changes during the Late Paleozoic Ice Age. The Late Pennsylvanian vegetation consisted of plant communities of wetland marattialean fern-dominated forests on coastal lowlands and wetland lycopsid-fern forests on deltaic plains in the Kasimovian as well as wetland marattialean fern-dominated forests with new dominants on coastal lowlands and wetland lycopsid-pteridosperm-calamitalean-fern forests with new dominants on deltaic plains in the early Gzhelian that were formed according to the evolutionary progressive model of phytocoenogenesis under conditions of an expansion of coastal lowlands and deltaic plains in the long-term period of a relatively stable higher sea level with frequent sea level fluctuations during the late Kasimovian–early-mid-Gzhelian interglacial interval. The subsequent transformation of wetland forests to wetland woodlands on coastal lowlands and deltaic plains according to the substitutionary regressive model of phytocoenogenesis and the formation of the new seasonally dry peltaspermalen pteridosperm-dominated woodland communities in river valleys according to the evolutionary progressive model of phytocoenogenesis took place against the background of a reduction of coastal lowlands and an expansion of river landscapes in the long-term period of a relatively stable sea level drop during the early phase of the late Gzhelian glacial interval. The new plant communities of wetland calamitalean-fern-pteridosperm woodlands on coastal lowlands and seasonally dry fern-pteridosperm woodlands on lagoon coasts in the late Gzhelian were formed according to the migration progressive model of phytocoenogenesis due to a migration of plants from reduced river landscapes to coastal lowlands and lagoon coasts in the period of the further sea level drop with low-amplitude sea level oscillations and an increased drying during the continued late Gzhelian glacial interval.

Динаміка пізньопенсильванської рослинності Донецького басейну України

Наталія Бояріна

Резюме. Динаміка пізньопенсильванського рослинного покриву Донецького басейну представлена послідовністю формувань нових рослинних угруповань (фітоценогенезів) вологого лісового та рідколісного біому та сезонно-сухого рідколісного біому внаслідок змін ландшафту та клімату, пов'язаних із гляціоевстатичними змінами упродовж пізньопалеозойського льодовикового періоду. Пізньопенсильванська рослинність складалась із рослинних угруповань вологих лісів з домінуючими маратієвими папоротями на прибережних низовинах і вологих лікопсидо-папоротевих лісів на дельтових рівнинах у касимовський час, а також вологих лісів з домінуючими маратієвими папоротями з новими домінантами на прибережних низовинах і вологих лікопсидо-птеридоспермово-каламітово-папоротевих лісів з новими домінантами на дельтових рівнинах у ранньогжельський час, які були сформовані згідно з еволюційно-прогресивною моделлю фітоценогенезу в умовах розширення прибережних низовин і дельтових рівнин у довготривалий період відносно стабільного високого рівня моря з частими флуктуаціями упродовж пізньокасимовського–ранньо-середньогжельського міжльодовикового інтервалу. Подальша трансформація вологих лісів у вологі рідколісся на прибережних низовинах і дельтових рівнинах згідно з субституційно-регресивною моделлю фітоценогенезу та формування нових сезонно-сухих рідколісних угруповань з домінуванням пельтаспермових птеридоспермів у долинах річок згідно з еволюційно-прогресивною моделлю фітоценогенезу відбувалися на тлі скорочення прибережних низовин і розширення річкових ландшафтів в довготривалий період відносно стабільного зниження рівня моря упродовж ранньої фази пізньогжельського гляціального інтервалу. Нові рослинні угруповання вологого каламітово-папоротево-птеридоспермового рідколісся на прибережних низовинах та сезонно-сухого папоротево-птеридоспермового рідколісся на узбережжях лагун у пізньогжельський час сформувалися згідно з міграційно-прогресивною моделлю фітоценогенезу внаслідок міграції рослин з річкових ландшафтів, які скорочувались, до прибережних низовин та лагунних узбереж в період подальшого падіння рівня моря з низькою амплітудою коливань та посилення осушення упродовж пізньогжельського гляціального інтервалу.

Ключові слова: зміни рослинності, фітоценогенез, гляціоевстатика, касимовський вік, гжельський вік, Донецький басейн.

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Introduction

The Pennsylvanian tropical vegetation of Euramerican Pangea was represented by wetland and seasonally dry (dryland) biomes [DiMichele & Aronson 1992; DiMichele *et al.* 2001, 2005]. In Late Pennsylvanian times, the flora of the wetland biome consisted of marattialean tree ferns and sphenopsids of peat-forming habitats [Phillips & Peppers 1984; DiMichele & Phillips 1996; Wagner 1997; Willard *et al.* 2007; Elrick *et al.* 2017] as well as pteridosperms, ferns, and calamitaleans of flood basin habitats [Scott 1977; Pfefferkorn & Thomson 1982; Gastaldo *et al.* 1995]. The flora of the seasonally dry biome was dominated by seed plants, including conifers, peltasperms with other pteridosperms, and cordaitaleans of fluvio-deltaic and elevated (upland) habitats [Cridland & Morris 1963; Havlena 1971; Broutin *et al.* 1990; Gastaldo 1996; Falcon-Lang *et al.* 2009]. The habitats of wetland and drought-tolerant plants mainly differed by soil moisture conditions that determined a particular vegetation type [Lyons & Darrah 1989; Cleal & Thomas 2005; Dimitrova *et al.* 2011; Thomas & Cleal 2017; DiMichele *et al.* 2020].

The distribution of wetland and dryland vegetation with the differing species composition of plants was due to climate and sea level oscillations that were controlled by a glacial-interglacial cyclicity [Phillips & Peppers 1984; DiMichele *et al.* 2010, 2020, 2023; Cecil *et al.* 2014; Pfefferkorn *et al.* 2017]. The wetland vegetation was predominant in the periods of humid to perhumid climate with year-round rainfalls [Falcon-Lang 2004; Cleal & Thomas 2005; Opluštil & Cleal 2007; Cleal *et al.* 2011, 2012], whereas the dryland drought-tolerant vegetation was widespread under subhumid to semi-arid climate with rainfall seasonality [Pfefferkorn 1980; Falcon-Lang 2003; DiMichele *et al.* 2008; Bashforth *et al.* 2016]. The climatic and wetland-dryland vegetation dynamics were recognised within individual glacial-interglacial cycles (single glacial-interglacial cycle, 10^5 yr) [Cecil 2013; Cecil *et al.* 2014; DiMichele 2014]. In this case, the wet periods of glacial-interglacial cycles with wetland-dominated floras corresponded to the early phases of transgression from middle to late sea level lowstand at times of maximum glacial ice, while dryland floras predominated from late sea level high-stand to early and middle sea level lowstand at interglacial-glacial transition [Cecil *et al.* 2003; Horton *et al.* 2010; Montañez & Poulsen 2013; DiMichele 2014]. In the periods of changes from interglacial to glacial parts of cycles and climatic drying, the seasonally dry vegetation of moisture-deficient habitats existed within basinal territories together with the reduced wetland vegetation of lowland habitats [DiMichele *et al.* 2006; Opluštil *et al.* 2013; Bashforth *et al.* 2014, 2021]. The complex composition of the Late Pennsylvanian flora and a growth of these plants into basinal landscapes of tropical Pangea are evidenced by both the macrofloral assemblages consisting of wetland or dryland plant fossils from different lithofacies within the same stratigraphic section and the mixed assemblages of wetland and drought-tolerant plants [Gastaldo 1996; Looy *et al.* 2014; Opluštil 2013; DiMichele 2014, 2024; Bashforth *et al.* 2021].

The intra-biomic and inter-biomic reorganisations were related to the climatic dynamics that was caused by an alternation of global glacial and interglacial intervals accompanied by atmospheric CO_2 fluctuations during the Late Paleozoic Ice Age [Heckel 2008; DiMichele *et al.* 2009, 2023; DiMichele 2014; Looy *et al.* 2014]. The Pennsylvanian was characterised by a series of discrete glacials and intervening warmer periods with ice retraction [Montañez & Poulsen 2013; Montañez 2022] that provided a determining influence on vegetation dynamics. Particularly, the disappearance of lycopsid-dominated forests in the Middle–Late Pennsylvanian transition [Pfefferkorn & Thomson 1982; DiMichele & Phillips 1996; DiMichele *et al.* 2009; Falcon-Lang *et al.* 2018] occurred during the early Kasimovian short-lived glacial interval [Richey *et al.* 2021; Montañez 2022]. The development of the Late Pennsylvanian vegetation was associated with the late Kasimovian–early-mid-Gzhelian interglacial interval [Fielding *et al.* 2008; Montañez & Poulsen 2013; Montañez 2022] and the onset of aridification across the palaeotropics [Montañez *et al.* 2007; Tabor & Poulsen 2008]. Under conditions of interglaciation and increasing aridity, the lycopsid-dominated vegetation with tree ferns and seed ferns of the Middle Pennsylvanian had initially been replaced with tree fern-dominated forests [Shchegolev 1975; Pfefferkorn & Thomson 1982; Phillips & Peppers 1984; DiMichele & Phillips 1996; Cleal 2007] and then callipterid pteridosperm-conifer-dominated vegetation in the end of the Late Pennsylvanian [Shchegolev 1965, 1975; Broutin *et al.* 1990; DiMichele *et al.* 2001, 2005, 2008; Opluštil *et al.* 2013; Cleal *et al.* 2011, 2012].

The vegetation composition and its changes during the Late Pennsylvanian have been studied in the Donets Basin [Shchegolev 1964, 1975, 1991; Boyarina 2010, 2016, 2017, 2022, 2023]. O. K. Shchogolev (A. K. Shchegolev in russian transcription) described three main vegetation types (ecofloras) of the late Carboniferous in the Donets Basin: forest vegetation of accumulative lowlands (shoreline sphenopsids, swamp sphenopsids and hygrophilous ferns, lowland ferns and pteridosperms); shrubby (pteridosperms) and forest (cordaitaleans) vegetation of territories adjacent to accumulative lowlands; conifer forest vegetation of elevated habitats. In recent years, reconstruction of plant communities and identification of plant associations within coastal lowlands, deltaic plains, floodplains, and river valley slopes were carried out on the basis of the Kasimovian and Gzhelian plant fossil assemblages that consisted of wetland or drought-tolerant plants [Boyarina 2022, 2023]. The conducted classification of plant communities reveals the syntaxonomic composition of the Late Pennsylvanian wetland and seasonally dry vegetation of the Donets Basin [Boyarina 2023]. The changes of the species composition of plant communities during the Late Pennsylvanian reflect the sequential evolution of plant communities (phytocoenogenesis) that led to the formation of the new palaeophytocoenoses in response to changing environmental conditions [Sukachev 1928, 1954; van der Maarel 1988;

Mirkin & Naumova 2012]. Based on the analysis of the changing palaeophytocoenoses during the Kasimovian and Gzhelian, three models of phytocoenogenesis were proposed that reveal the features of relationships between phytocoenogenetic processes and environmental changes [Boyarina 2022].

The present paper is devoted to the review and analysis of the vegetation cover dynamics in the Late Pennsylvanian in the context of environmental changes that gives an understanding of the nature of vegetational transformations. The review includes detailed descriptions of the vegetation with the prodromus of palaeosyntaxa for the four time intervals during the Kasimovian and Gzhelian. The main development directions of wetland and seasonally dry vegetation due to climatic and landscape changes during the Late Pennsylvanian portion of the Late Paleozoic Ice Age are considered.

Stratigraphy and Facies Settings

The Upper Pennsylvanian deposits are widespread in the western part of the Donets Basin (Fig. 1) and reaches a thickness of more than 2500 metres [Poletaev *et al.* 2011; Stratigraphy … 2013]. The Upper Pennsylvanian succession is composed of four lithostratigraphic units, i.e. suites (= formations) with the marker beds of limestone: the upper part of the Isaevska suite (benchmark level n_3^1-N_5–limestone N_5^2), the Avilovska suite (limestones O_1–O_7), the Araucaritova suite (limestones P_1–P_7), and the lower part of the Kartamyshska suite (limestone Q_1–carbonate bed Q_7). Three regional stages, namely Toretskian, Kalynovian, Myronivskian, with six horizons are corresponded to the Kasimovian and Gzhelian stages.

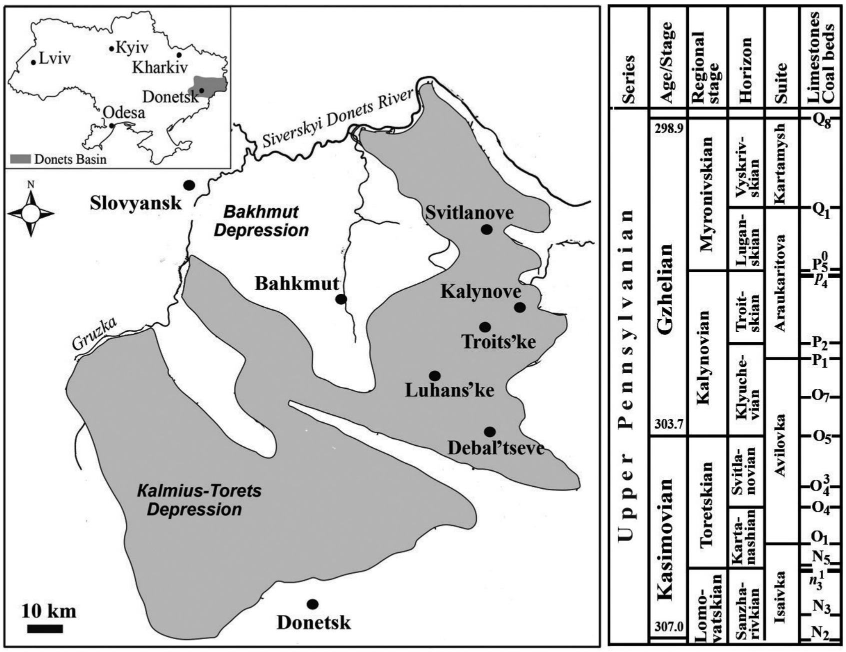

Fig. 1. Geological map of distribution of the Upper Pennsylvanian deposits in the Donets Basin (modified from the materials of State regional geological enterprise 'Donetskgeology', 1985) and Regional stratigraphic scale of the Upper Pennsylvanian of the Donets Basin [Poletaev *et al.* 2011].

Рис. 1. Геологічна карта поширення верхньопенсильванських відкладів в Донецькому басейні (модифікована за матеріалами Державного регіонального геологічного підприємства "Донецькгеологія", 1985) та регіональна стратиграфічна шкала верхнього пенсильванію Донецького басейну [Poletaev *et al.* 2011].

The Upper Pennsylvanian sequence is represented by the nearshore-marine and terrestrial sediments that comprises shallow-marine carbonate, coastal bay, lagoonal, lacustrine, deltaic, and fluvial facies [Zhemchuzhnikov *et al.* 1960; Feofilova 1966; Borisenko 1975, 2014; Shchegolev 1991; Poletaev *et al.* 2011].

For the environmental interpretations in this study, the Kasimovian and Gzhelian sedimentary facies are grouped into five facies associations, namely nearshore-marine/coastal lacustrine, coastal lagoonal/deltaic, deltaic-fluvial, fluvial, and coastal lagoonal/lacustrine, that correspond to coastal lowland, deltaic plain, river valley with floodplain, and lagoon coast depositional environments. The nearshore-marine/coastal lacustrine facies association consists of carbonate and siliciclastic deposits with grey unbedded mudstones and coal seams that occur below limestone beds. These facies are widespread in the Kasimovian, the lower and middle Gzhelian. In the upper Gzhelian, this facies association includes grey unbedded mudstone deposits intercalated with carbonate interbeds that occur between red strata. The coastal lagoonal/deltaic facies association is represented by the lagoonal facies including light grey and greenish grey, thinly bedded siltstones and fine-grained sandstones, as well as the deltaic facies with grey and greenish grey siltstones and greenish grey mudstone lacustrine deposits. The deltaic-fluvial facies association consists of light grey and greenish grey, thinly bedded siltstones with fine- and coarse-grained sandstones. The fluvial facies association comprises grey conglomerate beds, coarse- to fine-grained sandstones, thinly to thickly bedded siltstones, and rare mudstones. The coastal lagoonal/deltaic, deltaic-fluvial and fluvial facies associations are developed in the Kasimovian, the lower and middle Gzhelian. The coastal lagoonal/lacustrine facies association includes red-brown unbedded mudstone and siltstone deposits with blue and greenish grey spots that are widespread in the upper Gzhelian.

Material and Methods

The vegetation dynamics is described using a syntaxonomic composition of vegetation cover in the Kasimovian and Gzhelian times that was previously studied [Boyarina 2023]. The plant communities, forming the vegetation cover, were reconstructed on the basis of the phytooryctocoenoses from lacustrine, lagoonal-lacustrine, lacustrine-deltaic, deltaic, and fluvial deposits and presented in the vegetation classification that was conducted according to the Braun-Blanquet approach. The syntaxonomical changes of vegetation cover during the Kasimovian and Gzhelian times were reflected in the scheme and models of phytocoenogenesis that were proposed as a consequence of the analysis of florocoenotic complexes and phytocoenogenetic processes on the basis of vegetation orders [Boyarina 2022], because the orders, as the floristic variants of large physiognomic and ecological units (i.e. classes) in the Braun-Blanquet classification system [Braun-Blanquet 1964], most fully reflect the vegetation composition of different landscape types. Notably, the florocoenotic complexes were analysed using the diagnostic species of orders and the phytocoenogenetic processes were considered as the progressive or regressive development of plant communities at the rank of orders [Boyarina 2022].

The review of the Late Pennsylvanian vegetational cover is supported by the environmental and palaeophytocoenotic interpretations performed as the result of the analysis of plant-bearing strata with phytooryctocoenoses that reveals the facies features of deposits, the distribution features of phytooryctocoenoses in the section and the taxonomic composition of plant fossil assemblages. The characterisations of vegetation cover include the consideration of the syntaxonomic composition of vegetation, submitted in the prodromus, and the specifics of formation of new plant communities for the time intervals of the Late Pennsylvanian, which correspond to four regional stratigraphic units: Kasimovian (Toretskian), early Gzhelian (Kalynovian), middle Gzhelian (Luganskian), and late Gzhelian (Vyskrivkian). The prodromus of vegetation of each of time intervals is compiled on the basis of the combined prodromus of the Late Pennsylvanian vegetation of the Donets Basin [Boyarina 2023].

The main events of vegetational dynamics are identified in this study on the basis of the analysis of transformations of plant communities and their connection with environmental changes due to climatic and sea level fluctuations during the Late Pennsylvanian glacial-interglacial intervals of the Late Paleozoic Ice Age.

Characterisation of the Late Pennsylvanian Vegetation of the Donets Basin

1.The Kasimovian (Toretskian) vegetation

1.1. Environmental and palaeophytocoenotic interpretations

The Toretskian plant-bearing strata are represented by the deposits of four facies associations, namely nearshore-marine/coastal lacustrine, coastal lagoonal/deltaic, deltaic-fluvial, and fluvial, that indicate the distribution of plant communities within coastal lowlands, deltaic plains, floodplains, and river valley slopes (Fig. 2). The most part of the Toretskian deposits belongs to the

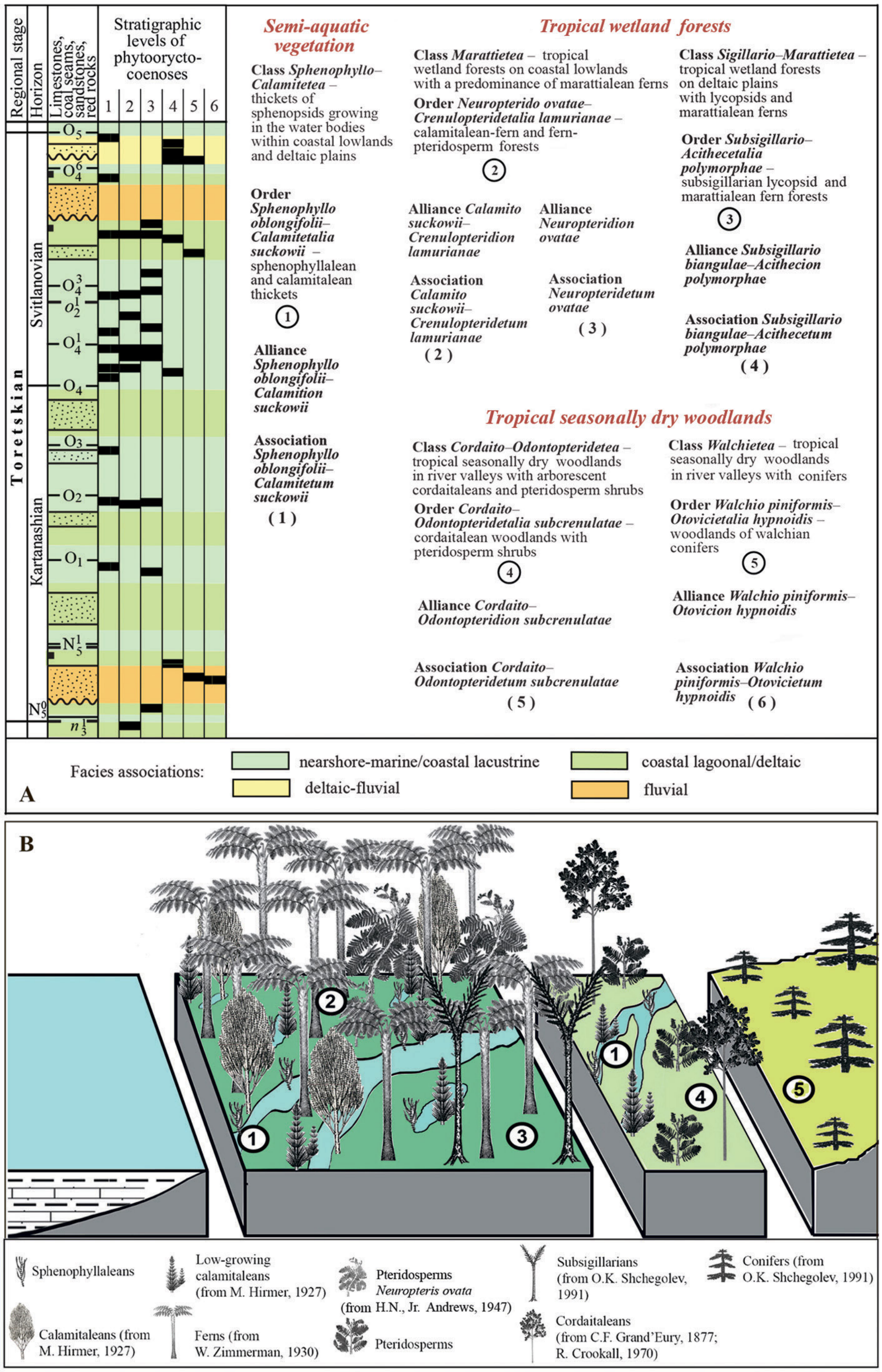

Fig. 2. Syntaxonomic composition and reconstruction of the Kasimovian (Toretskian) vegetation cover of the Donets Basin: (A) stratigraphic position and facial confinement of the phytooryctocoenoses, on the basis of which the plant associations were identified (association numbers in parentheses); (B) diagrammatic representation of the distribution of plant communities at the rank of orders of different landscape types (order numbers in a circle).

Рис. 2. Синтаксономічний склад та реконструкція рослинного покриву Донецького басейну в касимовський (торецький) час: (A) стратиграфічне положення та фаціальна належність фітооriктоценозів, на основі яких встановлені рослинні асоціації (номера асоціацій в дужках); (B) схематичне зображення поширення рослинних угруповань в ранзі порядків різних типів ландшафту (номера порядків в колі).

nearshore-marine/lacustrine facies association. These deposits contain the numerous phytooryctocoenoses with the fossil records of semi-aquatic sphenopsids and calamitalean-fern-pteridosperm communities of coastal lowlands. The interval between the O_4 and O_4^3 limestone beds is especially rich in sphenopsid and fern remains of a diverse species composition.

The semi-aquatic thickets of sphenophylls and calamitaleans were reconstructed on the basis of 11 phytooryctocoenoses in coastal lacustrine, deltaic and fluvial deposits that are more or less evenly located within the Toretskian section. The numerous plant fossils in these phytooryctocoenoses show that the semi-aquatic sphenopsids were widespread along the shores of lakes within coastal lowlands and deltaic plains. The plant associations of calamitalean-fern communities and fern-pteridosperm communities of coastal lowlands were identified on the basis of eight phytooryctocoenoses with calamitalean and fern remains from lacustrine coal-bearing beds and 10 phytooryctocoenoses with fern and pteridosperm remains from lacustrine deposits respectively. These phytooryctocoenoses with numerous plant fossils testify to the widespreading of the wetland forests, consisting of calamitalean-fern communities of the shores of lakes and fern-pteridosperm communities within coastal lowlands in the Toretskian time. The phytooryctocoenoses with plant fossils in deltaic and deltaic-fluvial facies are less represented and occur only in the lower and upper parts of the Toretskian. These plants belonged to the communities within deltaic plants and river valleys. The plant association of lycopsid-fern-pteridosperm-calamitalean communities of deltaic plains with a diverse species composition was determined on the basis of six phytooryctocoenoses from coastal lagoonal/deltaic deposits. In general, the widespread deposits of the nearshore-marine/lacustrine facies association with rich plant assemblages as well as the less common deposits of the coastal lagoonal/deltaic facies association with common and rare plant assemblages may point to the predominance of coastal lowlands and less common deltaic plains with wetland forests in the Toretskian landscapes.

The pteridosperm-cordaitalean communities, belonging to seasonally dry woodlands within floodplains and river valley slopes, were reconstructed on the basis of three phytooryctocoenoses with a poor species composition. The one phytooryctocoenos with numerous remains of conifers was found in the proluvial bed within fluvial deposits in the lower part of the Toretskian that indicate that the conifer woodlands occupied river valley slopes at times, but much of the time they grew outside sedimentation areas.

1.2. Prodromus and diagnostic species of palaeosyntaxa of the Toretskian vegetation

Class *Sphenophyllo–Calamitetea* Boyarina 2023

Thickets of semi-aquatic sphenopsids growing in water bodies within coastal lowlands and deltaic plains.

Diagnostic species: *Annularia mucronata, A. sphenophylloides*, *A.* ex gr. *stellata*, *Asterophyllites equisetiformis*, *Calamites cistii*, *C. suckowii*, *Sphenophyllum longifolium*, *Sphenophyllum oblongifolium*, and *S. verticillatum*.

Order *Sphenophyllo oblongifolii–Calamitetalia suckowii* Boyarina 2023

Sphenophyllalean and calamitalean thickets of water bodies within coastal lowlands and delta plains.

Diagnostic species: D.s. Ord. = D.s. Cl.

Alliance *Sphenophyllo oblongifolii–Calamition suckowii* Boyarina 2023

Sphenophyllalean-calamitalean communities of the shallow parts of coastal lakes and lakes within deltaic plains.

Diagnostic species: D.s. All. = D.s. Ord.

Association *Sphenophyllo oblongifolii–Calamitetum suckowii* Shchogolev et Boyarina 2023

Diagnostic species: *Annularia mucronata, A. sphenophylloides*, *A.* ex gr. *stellata*, *Asterophyllites equisetiformis*, *Calamites cistii*, *C. suckowii*, *Sphenophyllum longifolium*, *Sphenophyllum oblongifolium*, and *S. verticillatum*.

Class *Marattietea* Boyarina 2023

Tropical wetland forests on coastal lowlands with a predominance of marattialean tree ferns.

Diagnostic species: *Acitheca polymorpha*, *Annularia* ex gr. *stellata*, *Asterophyllites equisetiformis*, *Calamites suckowii*, *Cyathocarpus arboreus*, *C. cyatheus*, *Diplazites unitus*, and *Nemejcopteris feminaeformis*.

Order *Neuropterido ovatae–Crenulopteridetalia lamurianae* Boyarina 2023

Calamitalean-fern and fern-pteridosperm forests of coastal lowlands.

Diagnostic species: *Acitheca polymorpha*, *Annularia mucronata*, *A. sphenophylloides*, *A.* ex gr. *stellata*, *Asterophyllites equisetiformis*, *Calamites cistii*, *C. suckowii*, *Crenulopteris lamuriana*, *Cyathocarpus arboreus*, *C. cyatheus*, *C. lepidorachis*, *Dicksonites sterzelii*, *Diplazites unitus*, *Nemejcopteris feminaeformis*, *Neuropteris ovata*, *'Pecopteris' paleacea*, *'Pecopteris' bredovii*, *'Pecopteris' potoniei*, *Sphenopteris lebachensis*, *S. rossica*, and *S. svetlanovii*.

Alliance *Calamito suckowii–Crenulopteridion lamurianae* Boyarina 2023

Calamitalean-fern communities on lake shores within waterlogged coastal lowlands.

Diagnostic species: *Acitheca polymorpha*, *Annularia mucronata*, *A. sphenophylloides*, *A.* ex gr. *stellata*, *Asterophyllites equisetiformis*, *Calamites cistii*, *C. suckowii*, *Crenulopteris lamuriana*, *Cyathocarpus arboreus*, *C. cyatheus*, *C. lepidorachis*, *Diplazites unitus*, *Nemejcopteris feminaeformis*, *'Pecopteris' bredovii*, *'Pecopteris' potoniei*, *Sphenopteris lebachensis*, *S. rossica*, and *S. svetlanovii*.

Association *Calamito suckowii–Crenulopteridetum lamurianae*
Shchogolev et Boyarina 2023

Diagnostic species: *Acitheca polymorpha*, *Annularia mucronata*, *A. sphenophylloides*, *A.* ex gr. *stellata*, *Asterophyllites equisetiformis*, *Calamites cistii*, *C. suckowii*, *Crenulopteris lamuriana*, *Cyathocarpus arboreus*, *C. cyatheus*, *C. lepidorachis*, *Diplazites unitus*, *Nemejcopteris feminaeformis*, *'Pecopteris' bredovii*, *'Pecopteris' potoniei*, *Sphenopteris lebachensis*, *S. rossica*, and *S. svetlanovii*.

Alliance *Neuropteridion ovatae* Boyarina 2023

Fern-pteridosperm communities of coastal lowlands.

Diagnostic species: *Acitheca polymorpha*, *Crenulopteris lamuriana*, *Dicksonites sterzelii*, *Nemejcopteris feminaeformis*, *Neuropteris ovata*, *'Pecopteris' bredovii*, *'Pecopteris' paleacea*, and *Sphenopteris rossica*.

Association *Neuropteridetum ovatae* Shchogolev et Boyarina 2023

Diagnostic species: *Acitheca polymorpha*, *Crenulopteris lamuriana*, *Dicksonites sterzelii*, *Nemejcopteris feminaeformis*, *Neuropteris ovata*, *'Pecopteris' bredovii*, *'Pecopteris' paleacea*, and *Sphenopteris rossica*.

Class *Sigillario–Marattietea* Boyarina 2023

Tropical wetland forests on deltaic plains with sigillarian arborescent lycopsids and marattialean tree ferns.

Diagnostic species: *Acitheca polymorpha*, *'Pecopteris'* aff. *mironovana, Subsigillaria biangula*, *S. halensis*, *S. sulcata*, *S. weissii*, *Syringodendron angustum*, and *S. brardii*.

Order *Subsigillario–Acithecetalia polymorphae* Boyarina 2023

Subsigillarian lycopsid and marattialean fern forests of deltaic plains.

Diagnostic species: D.s. Ord. = D.s. Cl.

Alliance *Subsigillario biangulae–Acithecion polymorphae* Boyarina 2023

Lycopsid-fern-calamitalean communities of deltaic plains.

Diagnostic species: *Acitheca polymorpha*, *Annularia sphenophylloides*, *A.* ex gr. *stellata*, *Calamites* sp., *Cyathocarpus* cf. *candolleanus*, *'Pecopteris'* aff. *mironovana*, *Sigillariophylloides* sp., *Subsigillaria biangula*, *S. halensis*, *S. sulcata*, *S. weissii*, *Syringodendron angustum*, and *S. brardii*.

Association *Subsigillario biangulae–Acithecetum polymorphae*
Shchogolev et Boyarina 2023

Diagnostic species: *Acitheca polymorpha*, *Annularia sphenophylloides*, *A.* ex gr. *stellata*, *Barthelopteris germarii*, *Calamites* sp., *Cyathocarpus* cf. *candolleanus*, *Neurodontopteris auriculata*, *Odontopteris* cf. *schlotheimii*, *'Pecopteris'* aff. *mironovana*, *Sigillariophylloides* sp., *Subsigillaria biangula*, *S. halensis*, *S. sulcata*, *S. weissii*, *Syringodendron angustum*, and *S. brardii.*

Class *Cordaito–Odontopteridetea* Boyarina 2023

Tropical seasonally dry woodlands in river valleys with arborescent cordaitaleans and pteridosperm shrubs.

Diagnostic species: *Cordaites* sp., *Odontopteris subcrenulata*.

Order *Cordaito–Odontopteridetalia subcrenulatae* Boyarina 2023

Cordaitalean woodlands with pteridosperm shrubs of river valleys.

Diagnostic species: *Cordaites* cf. *borassifolia*, *C.* sp., *Odontopteris naumichana*, and *Odontopteris subcrenulata*.

Alliance *Cordaito–Odontopteridion subcrenulatae* Boyarina 2023

Cordaitean-pteridosperm communities of floodplains and river valley slopes.

Diagnostic species: D.s. All. = D.s. Ord.

Association *Cordaito–Odontopteridetum subcrenulatae* Shchogolev et Boyarina 2023

Diagnostic species: *Cordaites* cf. *borassifolia*, *C.* sp., *Odontopteris naumichana*, and *Odontopteris subcrenulata*.

Class *Walchietea* Boyarina 2023

Tropical seasonally dry woodlands in river valleys with conifers.

Diagnostic species: *Culmitzschia parvifolia*, *Otovicia hypnoides*, and *Walchia piniformis*.

Order *Walchio piniformis–Otovicietalia hypnoidis* Boyarina 2023

Walchian conifer woodlands of river valleys.

Diagnostic species: *Culmitzschia* cf. *angustifolia*, *C. hirmeri*, *C. parvifolia*, *Otovicia hypnoides*, *Samaropsis delafondii* var. *acuminata*, *S. pinnata*, *Samarospermum moravicum*, *Walchia piniformis*, and *Walchiostrobus* sp.

Alliance *Walchio piniformis–Otovicion hypnoidis* Boyarina 2023

Conifer communities of river valley slopes.

Diagnostic species: D.s. All. = D.s. Ord.

Association *Walchio piniformis–Otovicietum hypnoidis* Shchogolev et Boyarina 2023

Diagnostic species: *Culmitzschia* cf. *angustifolia*, *C. hirmeri*, *C. parvifolia*, *Otovicia hypnoides*, *Samaropsis delafondii* var. *acuminata*, *S. pinnata*, *Samarospermum moravicum*, *Walchia piniformis*, and *Walchiostrobus* sp.

1.3. Composition and phytocoenogenesis of the Toretskian vegetation

The Toretskian vegetation cover of the Donets Basin consisted of wetland forests, seasonally dry woodlands and semi-aquatic sphenopsid thickets belonging to five classes (see: Fig. 2).

The sphenopsid thickets of the shallow parts of lakes within coastal lowlands and deltaic plains were assigned to the class *Sphenophyllo–Calamitetea* with the order *Sphenophyllo oblongifolii–Calamitetalia suckowii*. The calamitaleans with the stems of *Calamites suckowii* Brongniart and the sphenophylls with the leafy shoots of *Sphenophyllum oblongifolium* (Germar et Kaulfuss) Unger dominated in these communities. The calamitaleans with the leafy shoots of *Annularia sphenophylloides* (Zenker) Gutbier and *A.* ex gr. *stellata* (Schlotheim) Wood as well as the sphenophylls with the leafy shoots of *Sphenophyllum longifolium* (Germar) Gutbier and *S. verticillatum* (Schlotheim) Zeiller were subdominats of sphenopsid thickets.

The wetland forests were widespread on sea coasts within coastal lowlands and deltaic plains. The forests, which occupied waterlogged coastal lowlands, consisted of marattialean tree ferns, calamitaleans and pteridosperm shrubs and were identified to the class *Marattietea* with the order *Neuropterido ovatae–Crenulopteridetalia lamurianae*. The latter includes two alliances. The calamitalean-fern communities of the alliance *Calamito suckowii–Crenulopteridion lamurinae* occupied the lake shores on coastal lowlands. The alliance *Neuropteridion ovatae* is represented by the communities, which were composed of tree ferns and quite common pteridosperm shrubs as evidenced by the presence of numerous remains of pteridosperms in lacustrine deposits [Boyarina 2023]. The fern-pteridosperm communities were distributed on wetlands surrounding the lakes within coastal lowlands. The forests of coastal lowlands were dominated by the ferns with the foliage of *Crenulopteris lamuriana* (Heer) Wittry et al., *Cyathocarpus arboreus* (Sternberg) Weiss, *C. hemitelioides* (Brongniart) Mosbrugger, *Nemejcopteris feminaeformis* (Schlotheim) Barthel, *Sphenopteris rossica* Zalessky, the pteridosperms with the foliage of *Neuropteris ovata* Hoffmann, and the calamitaleans with stems of *Calamites suckowii* and the foliage of *Annularia sphenophylloides*, *A.* ex gr. *stellata, Asterophyllites equisetiformis* (Sternberg) Brongniart. These wetland forests were characterised by the progressive development during the Toretskian time, as evidenced by the appearance of new fern species and an increased species abundance of some ferns, calamitaleans and pteridosperm *Neuropteris ovata*. The formation of the plant communities on coastal lowlands happened in accordance with the evolutionary progressive model of phytocoenogenesis [Boyarina 2022].

The wetland forests of deltaic plains were assigned to the class *Sigillario–Marattietea* with the order *Subsigillario–Acithecetalia polymorphae*. The lycopsid-fern forests of this order consisted of the subsigillarian arborescent lycopsids *Subsigillaria biangula* (Weiss) Shchegolev, *S. brardii* (Brongniart) Weiss emend. Shchegolev, *S. halensis* (Weiss) Shchegolev, *S. sulcata* (Ščurovskij) Shchegolev, *S. weisii* Shchegolev, *Syringodendron angustum* Shchegolev, and *S. brardii* Shchegolev; the ferns, among which *Acitheca polymorpha* (Brongniart) Schimper dominated; the calamitaleans with the foliage of *Annularia sphenophylloides*, *A.* ex gr. *stellata*, and *Asterophyllites equisetiformis*. The appearance of more than 10 new subsigillarian lycopsids in the composition of the wetland forests on deltaic plains demonstrates the progressive development of plant communities, the formation of which corresponds to the evolutionary progressive model of phytocoenogenesis [Boyarina 2022].

The seasonally dry vegetation occupied floodplains and river valley slopes. The woodland communities in river valleys were composed of arborescent cordaitaleans and pteridosperm shrubs and assigned to the order *Cordaito–Odontopteridetalia subcrenulatae* in composition of the class *Cordaito–Odontopteridetea*. The coniferous woodlands were identified as the class *Walchietea* with the order *Walchio piniformis–Otovicietalia hypnoidis*. The coniferous communities grew within river valley slopes and interfluve areas, which were obviously outside sedimentation areas during the most part of the Toretskian time.

In general, we can say that in vegetation cover of the Donets Basin in the Toretskian, the wetland marattialean fern-dominated forests of coastal lowlands prevailed, the wetland lycopsid-fern forests of deltaic plains were also relatively common, whereas the seasonally dry cordaitalean-pteridosperm and conifer woodlands of river valleys played no notable part within a sedimentation area.

2. The early Gzhelian (Kalynovian) vegetation

2.1. Environmental and palaeophytocoenotic interpretations

The Kalynovian plant-bearing strata are composed of the deposits that relate to four facies associations as the Toretskian deposits, i.e. nearshore-marine/coastal lacustrine, coastal lagoonal/deltaic, deltaic-fluvial, and fluvial (Fig. 3). However, there are differences in the distribution of certain facies that are manifested in the decrease of nearshore-marine/coastal lacustrine facies as well as the increase of coastal lagoonal/deltaic and deltaic-fluvial facies upwards on the Kalynovian section. And in addition, the distribution and species richness of plant fossil assemblages indicate also some phytocoenotic changes during the Kalynovian.

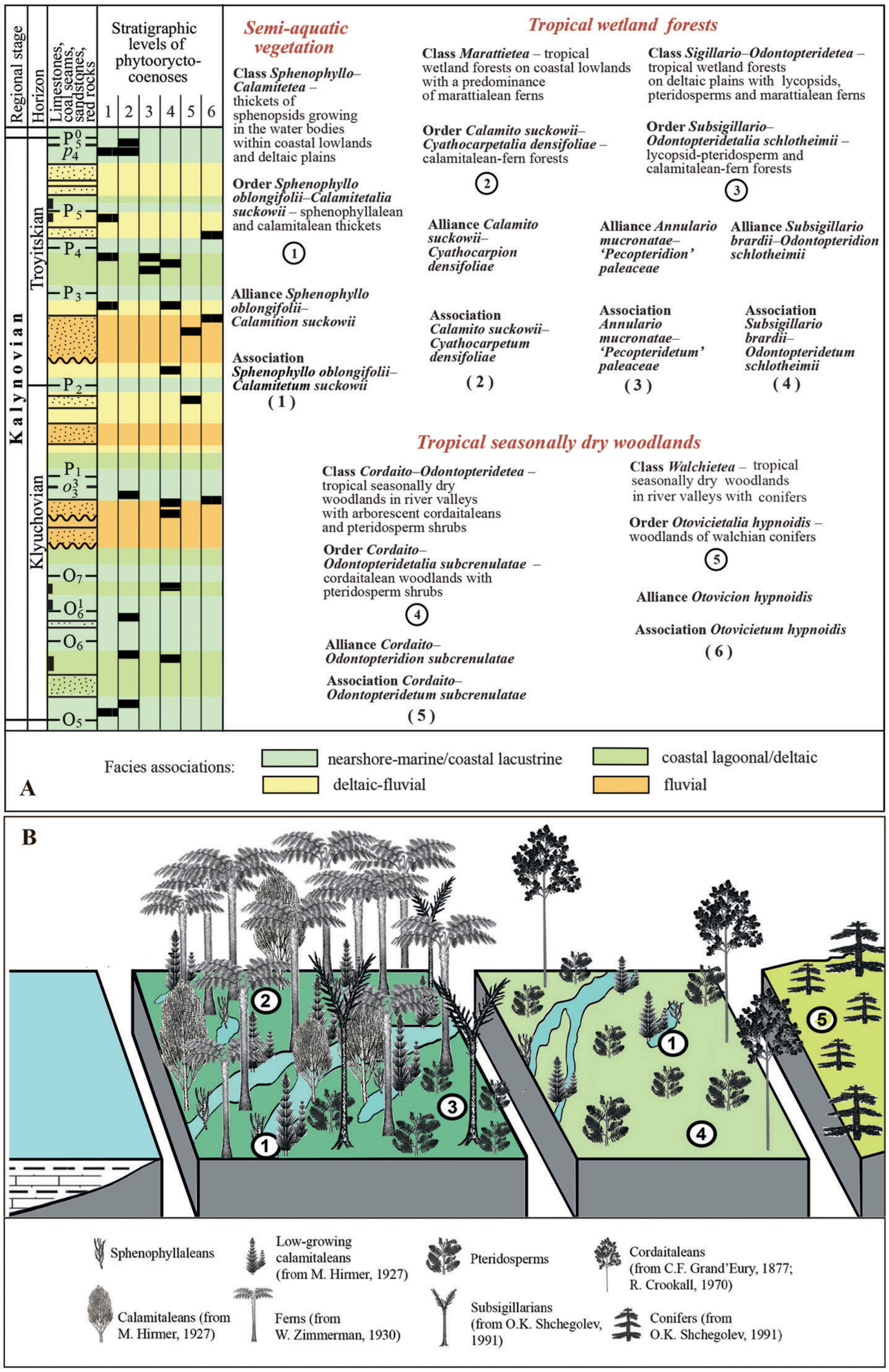

Fig. 3. Syntaxonomic composition and reconstruction of the early Gzhelian (Kalynovian) vegetation cover of the Donets Basin: (A) stratigraphic position and facial confinement of the phytooryctocoenoses, on the basis of which the plant associations were identified (association numbers in parentheses); (B) diagrammatic representation of the distribution of plant communities at the rank of orders of different landscape types (order numbers in a circle).

Рис. 3. Синтаксономічний склад та реконструкція рослинного покриву Донецького басейну в ранньогжельський (калинівський) час: (A) стратиграфічне положення та фаціальна належність фітоориктоценозів, на основі яких встановлені рослинні асоціації (номера асоціацій в дужках); (B) схематичне зображення поширення рослинних угруповань в ранзі порядків різних типів ландшафту (номера порядків в колі).

Thus, the plant association of calamitalean-fern communities with rare pteridosperms of the lake shores within coastal lowlands was identified on the basis of six phytooryctocoenoses, but at the same time four of them were found in the lower part of the Kalynovian. The decrease of coastal lacustrine strata with plant fossils in the upper part of the Kalynovian may indicate that the wetland forests of coastal lowlands were slightly reduced in the late Kalynovian. The plant associations of lycopsid-pteridosperm communities and calamitalean-fern communities with a rich species composition of deltaic plains were determined on the basis of nine phytooryctocoenoses from coastal lagoonal/deltaic deposits, and the plant fossil assemblages with the remains of lycopsids and pteridosperms are fairly evenly distributed in the section. The facies and macrofloral features of these phytooryctocoenoses show that the wetland lycopsid-fern-pteridosperm forests of deltaic plains were more widespread than calamitalean-fern forests of coastal lowlands in the late Kalynovian vegetation cover.

The seasonally dry pteridosperm-cordaitalean communities of alluvial plains are poorly represented in fossil records as in the Toretskian. The rare plant fossil assemblages in fluvial deposits, which are characterised by a poor species composition, occur in the middle part of the Kalynovian, in which deltaic-fluvial and fluvial deposits are predominant. The phytooryctocoenoses, including conifer remains, were found in greater numbers compared to the Toretskian. The conifer communities of river valley slopes were reconstructed on the basis of the conifer remains from three stratigraphic levels in deltaic-fluvial and fluvial deposits in the upper part of the Kalynovian, containing a few variegated beds, that reflect an increasing role of alluvial landscapes with some climatic drying within a sedimentation area in the late Kalynovian.

2.2. Prodromus and diagnostic species of palaeosyntaxa of the Kalynovian vegetation

Class *Sphenophyllo–Calamitetea* Boyarina 2023

Thickets of semi-aquatic sphenopsids growing in water bodies within coastal lowlands and deltaic plains.

Diagnostic species: *Annularia mucronata*, *A. sphenophylloides*, *A.* ex gr. *stellata*, *Asterophyllites equisetiformis*, *Calamites cistii*, *C. suckowii*, *Sphenophyllum longifolium*, *Sphenophyllum oblongifolium*, and *S. verticillatum*.

Order *Sphenophyllo oblongifolii–Calamitetalia suckowii* Boyarina 2023

Sphenophyllalean and calamitalean thickets of water bodies within coastal lowlands and delta plains.

Diagnostic species: D.s. Ord. = D.s. Cl.

Alliance *Sphenophyllo oblongifolii–Calamition suckowii* Boyarina 2023

Sphenophyllalean-calamitalean communities of the shallow parts of coastal lakes and lakes within deltaic plains.

Diagnostic species: D.s. All. = D.s. Ord.

Association *Sphenophyllo oblongifolii–Calamitetum suckowii*
Shchogolev et Boyarina 2023

Diagnostic species: *Annularia mucronata*, *A. sphenophylloides*, *A.* ex gr. *stellata*, *Asterophyllites equisetiformis*, *Calamites cistii*, *C. suckowii*, *Sphenophyllum longifolium*, *Sphenophyllum oblongifolium*, and *S. verticillatum*.

Class *Marattietea* Boyarina 2023

Tropical wetland forests on coastal lowlands with a predominance of marattialean tree ferns.

Diagnostic species: *Acitheca polymorpha*, *Annularia* ex gr. *stellata*, *Asterophyllites equisetiformis*, *Calamites suckowii*, *Cyathocarpus arboreus*, *C. cyatheus*, *Diplazites unitus*, and *Nemejcopteris feminaeformis*.

Order *Calamito suckowii–Cyathocarpetalia densifoliae* Boyarina 2023

Calamitalean-fern forests on coastal lowlands.

Diagnostic species: *Acitheca polymorpha*, *A. sphenophylloides*, *A.* ex gr. *stellata*, *Asterophyllites equisetiformis*, *Calamites medulatus*, *C. suckowii*, *Calamostachys germanica*, *Cyathocarpus arboreus*, *C. cyatheus*, *C. densifolius*, *C. hemitelioides*, *Diplazites unitus*, *Nemejcopteris feminaeformis*, *Odontopteris cantabrica*, *'Pecopteris' jongmansii*, *'Pecopteris' platonii*, and *'Pecopteris' truncata*.

Alliance *Calamito suckowii–Cyathocarpion densifoliae* Boyarina 2023

Calamitalean-fern communities on lake shores within coastal lowlands.

Diagnostic species: D.s. All. = D.s. Ord.

Association *Calamito suckowii–Cyathocarpetum densifoliae*
Shchogolev et Boyarina 2023

Diagnostic species: *Acitheca polymorpha*, *Annularia mucronata*, *A. sphenophylloides*, *A.* ex gr. *stellata*, *Asterophyllites equisetiformis*, *Calamites medulatus*, *C. suckowii*, *Calamostachys germanica*, *Cyathocarpus arboreus*, *C. cyatheus*, *C. densifolius*, *C. hemitelioides*, *Diplazites unitus*, *Nemejcopteris feminaeformis*, *Odontopteris cantabrica*, *'Pecopteris' jongmansii*, *'Pecopteris' platonii*, and *'Pecopteris' truncata*.

Class *Sigillario–Odontopteridetea* Boyarina 2023

Tropical wetland forests on deltaic plains with sigillarian arborescent lycopsids, pteridosperm shrubs and marattialean tree ferns.

Diagnostic species: *Annularia mucronata*, *Barthelopteris germarii*, *Calamites multiramis*, *C. suckowii*, *Cordaites* sp., *Neuropteris crassinervis*, *Neurodontopteris auriculata*, *Odontopteris schlotheimii*, *'Pecopteris' mironovana*, *'Pecopteris' paleacea*, *'Pecopteris' platonii*, *'Pecopteris' potoniei*, *Subsigillaria brardii*, *S. donetciana*, *S. fimbriata*, *S. simplex*, and *Syringodendron brardii*.

Order *Subsigillario–Odontopteridetalia schlotheimii* Boyarina 2023

Subsigillarian lycopsid-pteridosperm and calamitalean-fern forests of deltaic plains.

Diagnostic species: *Annularia mucronata*, *Asterophyllites equisetiformis*, *Barthelopteris germarii*, *Calamites multiramis*, *C. suckowii*, *Cordaites* sp., *Neuropteris crassinervis*, *Neurodontopteris auriculata*, *Odontopteris schlotheimii*, *'Pecopteris' mironovana*, *'Pecopteris' paleacea*, *'Pecopteris' platonii*, *'Pecopteris' potoniei*, *Remia* aff. *pinnatifida*, *Sphenopteris rossica*, *Sigillariostrobophyllum* sp., *Subsigillaria brardii*, *S. donetciana*, *S. fimbriata*, *S. simplex*, and *Syringodendron brardii*.

Alliance *Subsigillario brardii–Odontopteridion schlotheimii* Boyarina 2023

Lycopsid-pteridosperm-calamitalean-fern communities of deltaic plains.

Diagnostic species: *Annularia mucronata*, *Asterophyllites equisetiformis*, *Barthelopteris germarii*, *Calamites suckowii*, *Cordaites* sp., *Neuropteris crassinervis*, *Neurodontopteris auriculata*, *Odontopteris schlotheimii*, *'Pecopteris' mironovana*, *'Pecopteris' paleacea*, *'Pecopteris' platonii*, *'Pecopteris' potoniei*, *Remia* aff. *pinnatifida*, *Sphenopteris rossica*, *Sigillariostrobophyllum* sp., *Subsigillaria brardii*, *S. donetciana*, *S. fimbriata*, *S. simplex*, and *Syringodendron brardii*.

Association *Subsigillario brardii–Odontopteridetum schlotheimii* Boyarina 2023

Diagnostic species: *Annularia mucronata*, *A. sphenophylloides*, *Asterophyllites equisetiformis*, *Barthelopteris germarii*, *Calamites suckowii*, *C.* cf. *schutzeiformis*, *Cordaites* sp., *Cyathocarpus hemitelioides*, *Neuropteris crassinervis*, *Neurodontopteris auriculata*, *Odontopteris schlotheimii*, *'Pecopteris' mironovana*, *'Pecopteris' paleacea*, *'Pecopteris' platonii*, *'Pecopteris' potoniei*, *Remia* aff. *pinnatifida*, *Sphenopteris rossica*, *Sigillariostrobophyllum* sp., *Subsigillaria brardii*, *S. donetciana*, *S. fimbriata*, *S. simplex*, and *Syringodendron brardii*.

Alliance *Annulario mucronatae–'Pecopteridion' paleaceae* Boyarina 2023

Calamitalean-fern communities of deltaic lake shores.

Diagnostic species: *Annularia mucronata*, *Calamites multiramis*, *Odontopteris schlotheimii*, and *'Pecopteris' paleacea*.

Association *Annulario mucronatae–'Pecopteridetum' paleaceae* Boyarina 2023

Diagnostic species: *Annularia mucronata*, *Calamites multiramis*, *Odontopteris schlotheimii*, and *'Pecopteris' paleacea*.

Class *Cordaito–Odontopteridetea* Boyarina 2023

Tropical seasonally dry woodlands in river valleys with arborescent cordaitaleans and pteridosperm shrubs.

Diagnostic species: *Cordaites* sp., *Odontopteris subcrenulata*.

Order *Cordaito–Odontopteridetalia subcrenulatae* Boyarina 2023

Cordaitalean woodlands with pteridosperm shrubs of river valleys.

Diagnostic species: D.s. Ord. = D.s. Cl.

Alliance *Cordaito–Odontopteridion subcrenulatae* Boyarina 2023

Cordaitean-pteridosperm communities of floodplains and river valley slopes.

Diagnostic species: D.s. All. = D.s. Ord.

Association *Cordaito–Odontopteridetum subcrenulatae* Shchogolev et Boyarina 2023

Diagnostic species: *Cordaites* sp., *Odontopteris subcrenulata*.

Class *Walchietea* Boyarina 2023

Tropical seasonally dry woodlands in river valleys with conifers.

Diagnostic species: *Otovicia hypnoides*, *Walchia piniformis*.

Order *Otovicietalia hypnoidis* Boyarina 2023

Walchian conifer woodlands of river valleys.

Diagnostic species: D.s. Ord. = D.s. Cl.

Alliance *Otovicion hypnoidis* Boyarina 2023

Conifer communities of river valley slopes.

Diagnostic species: D.s. All. = D.s. Ord.

Association *Otovicietum hypnoidis* Shchogolev at Boyarina 2023

Diagnostic species: *Otovicia hypnoides*, *Walchia piniformis*.

2.3. Composition and phytocoenogenesis of the Kalynovian vegetation

The Kalynovian vegetation of the Donets Basin consisted of the wetland forests on coastal lowlands and deltaic plains, seasonally dry woodlands in river valleys and semi-aquatic sphenopsid thickets. The plant communities of the mentioned vegetation types were assigned to four new orders in the composition of three same classes as in the Toretskian time and one new class (see: Fig. 3). The semi-aquatic sphenopsids, forming the thickets in the shallow parts of lakes within coastal lowlands and deltaic plains, are characterised by the same species composition with the same dominants, and therefore belong to the same order *Sphenophyllo oblongifolii–Calamitetalia suckowii* and class *Sphenophyllo–Calamitetea* as in the Toretskian time.

The wetland forests both on coastal lowlands and deltaic plains had experienced the changes in the species composition and dominants of communities. Thus, the fern-pteridosperm communities of the alliance *Neuropteridion ovatae* disappeared from the forests of coastal lowlands. These forests began to consist of the communities of the new order *Calamito suckowii–Cyathocarpetalia densifoliae* with the alliance *Calamito suckowii–Cyathocarpion densifoliae*. The calamitalean-fern communities of this alliance were widespread on the lake shores of coastal lowlands. They included the new species of the ferns with the foliage of *Cyathocarpus densifolius* (Goeppert) Šimůnek et Ploch, *'Pecopteris' platonii* Grand'Eury, *'Pecopteris' oreopteridia* (Schlotheim) Sternberg, as well as were characterised by the domination of the ferns *Cyathocarpus densifolius* and the increased species abundance of the ferns with the foliage of *Cyathocarpus arboreus*, *'Pecopteris' bredovii* Germar, *Diplazites unitus* (Brongniart) Cleal, *Nemejcopteris feminaeformis*. These changes testify to the progressive development of the calamitalean-fern communities and the formation of these communities according to the evolutionary progressive model of phytocoenogenesis [Boyarina 2022].

Against the background of the syntaxonomic reduction of lowland forests, the communities of wetland forests within deltaic plains of the new class *Sigillario–Odontopteridetea* expanded their composition. These forests are represented by the order *Subsigillario–Odontopteridetalia schlotheimii* with two alliances. The calamitean-fern communities of the alliance *Annulario mucronatae–'Pecopteridetum' paleaceae* occupied the shores of deltaic lakes. They included the ferns with the foliage of *'Pecopteris' paleaceae* Zeiller, the calamitaleans with the stems of *Calamites multiramis* Weiss and the calamitaleans with the leafy shoots of *Annularia mucronata* Schenk. The communities consisting of lycopsids, calamitaleans, ferns and pteridosperms of the alliance *Subsigillario brardii–Odontopteridion schlotheimii* were widespread within deltaic plains. The diagnostic species of this alliance reflect the significant changes that manifested in the increase of the species diversity of calamitaleans, fens, odontopterid and neuropterid pteridosperms. Particularly, the vegetation of deltaic plains was replenished by both new pteridosperm and fern species and some species of ferns that grew within coastal lowlands in the Toretskian time. The species composition of lycopsids was supplemented with two species along with the overall decrease of species. In general, the composition of plant communities of the order *Subsigillario–Odontopteridetalia schlotheimii* was complemented by 10 species, including the endemic species *Subsigillaria simplex* Shchegolev, *S. donetciana* Shchegolev, *Pecopteris mironovana* Zalessky et Tschirkova. These phytocoenotic features indicate the progressive development and formation of the plant communities of deltaic plains under the evolutionary progressive model of phytocoenogenesis [Boyarina 2022]. And, as noted above, the increase of the number of plant fossil assemblages in more common deltaic-fluvial deposits in the upper part of the Kalynovian (Troyitskian) shows that the lycopsid-pteridosperm communities of the order *Subsigillario–Odontopteridetalia schlotheimii* of deltaic plains had become more spread than calamitalean-fern communities of coastal lowlands in the late Kalynovian (Troyitskian) time.

The vegetation of seasonally dry environments was represented by cordaitean-pteridosperm and conifer woodlands in river valleys. The reconstructed cordaitean-pteridosperm communities of river valleys demonstrate the same floristic composition as in the Toretskian. The single remains of the pteridosperms *Barthelopteris germarii* (Giebel) Zodrow et Cleal and *Taeniopteris gigantea* Schenk mentioned from the upper Toretskian and Kalynovian deposits [Shchegolev 1975], which were not included in diagnostic species, testify only to the few increased species diversities from the end of the Toretskian without the change of the phytocoenotic properties of species. And so, the seasonally dry woodlands of river valleys are assigned to the same order *Cordaito–Odontopteridetalia subcrenulatae*, as in the Toretskian time. The conifer communities of river valley slopes were identified to the new order *Otovicietalia hypnoidis* with a poorer species composition than in the Toretskian.

Consequently, in the Kalynovian time the wetland lycopsid-pteridosperm-dominated forests of deltaic plains and the wetland fern-dominated forests of coastal lowlands were widespread, while the seasonally dry cordaitalean-pteridosperm and conifer woodlands of river valleys were less represented in vegetation cover as in the Toretskian time.

3. The middle Gzhelian (Luganskian) vegetation

3.1. Environmental and palaeophytocoenotic interpretations

The Luganskian plant-bearing strata are composed of deposits belonging to four facies associations as in the Toretskian and Kalynovian, i.e. nearshore-marine/coastal lacustrine, coastal lagoonal/deltaic, deltaic-fluvial, and fluvial (Fig. 4). The same facies associations have their specifics. The Luganskian section is characterised by the continued reduction of nearshore-marine/coastal lacustrine facies and the predominance of deltaic-fluvial and fluvial facies that indicate the greater role of river environments in landscape. The differences are also observed in the distribution of plant fossils. Thus,

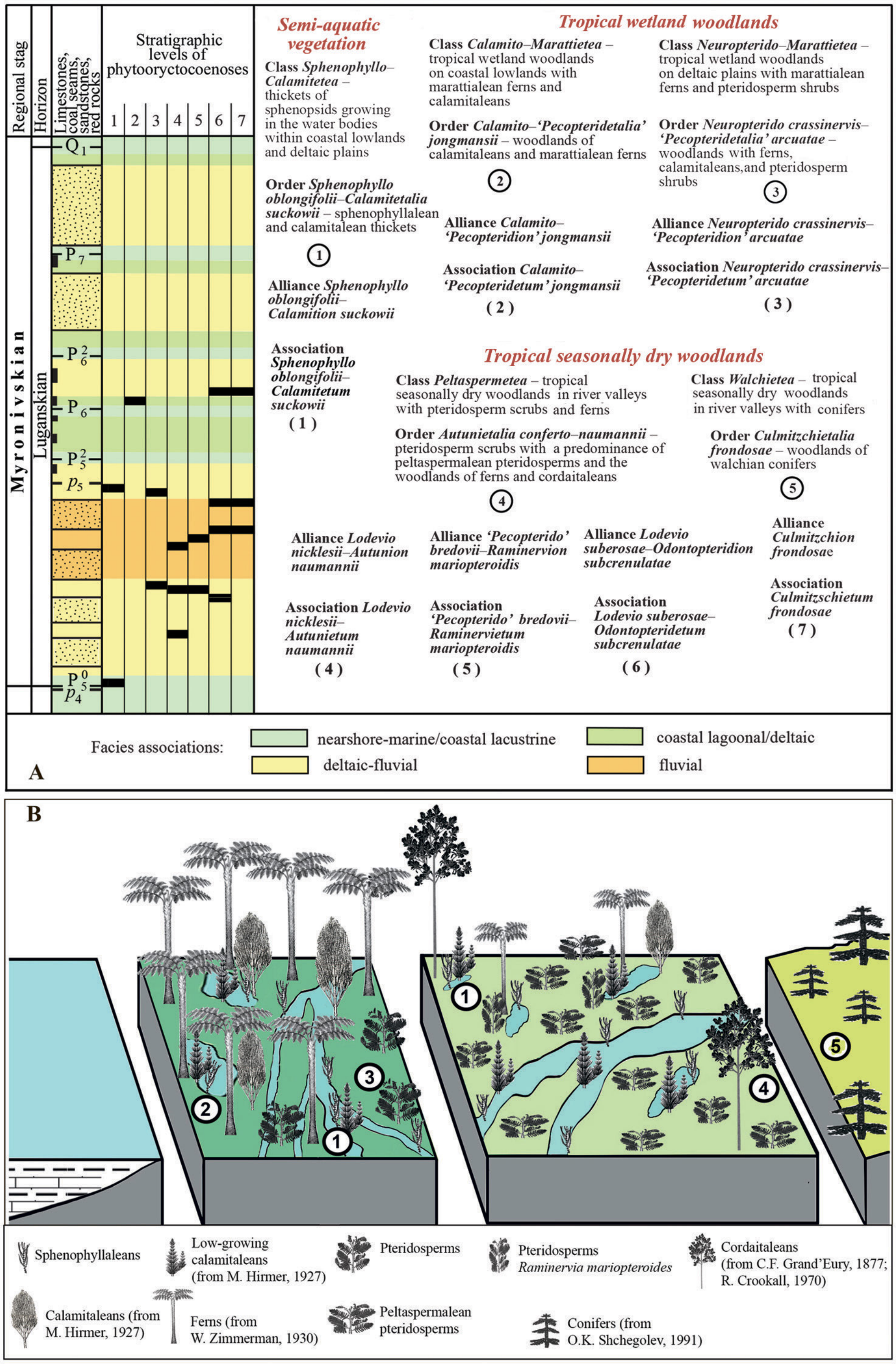

Fig. 4. Syntaxonomic composition and reconstruction of the middle Gzhelian (Luganskian) vegetation cover of the Donets Basin: (A) stratigraphic position and facial confinement of the phytooryctocoenoses, on the basis of which the plant associations were identified (association numbers in parentheses); (B) diagrammatic representation of the distribution of plant communities at the rank of orders of different landscape types (order numbers in a circle).

Рис. 4. Синтаксономічний склад та реконструкція рослинного покриву Донецького басейну в середньогжельський (луганський) час: (A) стратиграфічне положення та фаціальна належність фітоориктоценозів, на основі яких встановлені рослинні асоціації (номера асоціацій в дужках); (B) схематичне зображення поширення рослинних угруповань в ранзі порядків різних типів ландшафту (номера порядків в колі).

the plant fossil assemblages were found only in the lower part of the Luganskian, to the P_6^2 limestone. And besides, the plant remains are reduced in the deposits of the first two facies associations and abundant in the deposits of deltaic-fluvial and fluvial facies. The single plant remains in coastal lacustrine and deltaic facies testify to the reduction of wetland calamitalean-fern forests on coastal lowlands and pteridosperm-fern-calamitalean forests of deltaic plains in the Luganskian time. But at the same time, the fairly common plant fossil assemblages in deltaic-fluvial and fluvial facies contain the numerous callipterid pteridosperms together with other pteridosperms, cordaitaleans and conifers. Hence, we may conclude that the pteridosperm communities of floodplains, which were reconstructed on the basis of three phytooryctocoenoses with the large number of callipterid pteridosperm remains in lacustrine-floodplain deposits, as well as the cordaitean-pteridosperm communities of river levees and river valley slopes, which were determined on the basis of four phytooryctocoenoses from sandstone and siltstone floodplain strata, were predominant within river valleys. Based on plant fossils from two phytooryctocoenoses in lacustrine deposits within fluvial strata, the pteridosperm-fern communities of the shores of floodplain lakes were identified. The plant association of the conifer communities on river valley slopes was reconstructed on the basis of three phytooryctocoenoses from siltstone floodplain deposits. These plant fossil assemblages testify to an increasing role of the seasonally dry woodlands, including pteridosperm and conifer communities of floodplains and river valley slopes in the Luganskian vegetation cover.

3.2. Prodromus and diagnostic species of palaeosyntaxa of the Luganskian vegetation

Class *Sphenophyllo–Calamitetea* Boyarina 2023

Thickets of semi-aquatic sphenopsids growing in water bodies within coastal lowlands and deltaic plains.

Diagnostic species: *Annularia* ex gr. *stellata*, *Asterophyllites equisetiformis*, *Calamites cistii*, *C. suckowii*, *Sphenophyllum longifolium*, and *S. oblongifolium*.

Order *Sphenophyllo oblongifolii–Calamitetalia suckowii* Boyarina 2023

Sphenophyllalean and calamitalean thickets of water bodies within coastal lowlands and delta plains.

Diagnostic species: D.s. Ord. = D.s. Cl.

Alliance *Sphenophyllo oblongifolii–Calamition suckowii* Boyarina 2023

Sphenophyllalean-calamitalean communities of the shallow parts of coastal lakes and lakes within deltaic plains.

Diagnostic species: D.s. All. = D.s. Ord.

Association *Sphenophyllo oblongifolii–Calamitetum suckowii*
Shchogolev et Boyarina 2023

Diagnostic species: *Annularia* ex gr. *stellata*, *Asterophyllites equisetiformis*, *Calamites cistii*, *C. suckowii*, *Sphenophyllum longifolium*, and *S. oblongifolium*.

Class *Calamito–Marattietea* Boyarina 2023

Tropical wetland woodlands on coastal lowlands with marattialean tree ferns and calamitaleans.

Diagnostic species: *Calamites* sp., *Cyathocarpus daubreei*, *'Pecopteris' jongmansii*, *'Pecopteris' martinezii*, *'Pecopteris' monyi*, *'Pecopteris' oreopteridia*, and *Sphenopteris fayolii-mathetii*.

Order *Calamito–'Pecopteridetalia' jongmansii* Boyarina 2023

Woodlands with calamitaleans and marattialean tree ferns on coastal lowlands.

Diagnostic species: *Calamites* sp., *Cyathocarpus daubreei*, *'Pecopteris' jongmansii*, *'Pecopteris' martinezii*, *'Pecopteris' monyi*, *'Pecopteris' oreopteridia*, *Sphenopteris* cf. *castelli*, and *S. fayolii-mathetii*.

Alliance *Calamito–'Pecopteridion' jongmansii* Boyarina 2023

Calamitalean-fern communities on lake shores within coastal lowlands.

Diagnostic species: D.s. All. = D.s. Ord.

Association *Calamito–'Pecopteridetum' jongmansii* Boyarina et Shchogolev 2023

Diagnostic species: *Calamites* sp., *Cyathocarpus daubreei*, *'Pecopteris' jongmansii*, *'Pecopteris' martinezii*, *'Pecopteris' monyi*, *'Pecopteris' oreopteridia*, *Sphenopteris* cf. *castelli*, and *S. fayolii-mathetii*.

Class *Neuropterido–Marattietea* Boyarina 2023

Tropical wetland woodlands on deltaic plains with marattialean tree ferns and pteridosperm shrubs.

Diagnostic species: *Neuropteris crassinervis*, *Neurodontopteris auriculata*, and *'Pecopteris' arcuata*.

Order *Neuropterido crassinervis–'Pecopteridetalia' arcuatae* Boyarina 2023

Woodlands with tree ferns, calamitaleans, and pteridosperm shrubs on deltaic plains.

Diagnostic species: *Calamites suckowii*, *Calamites* sp., *Neuropteris crassinervis*, *Neurodontopteris auriculata*, and *'Pecopteris' arcuata*.

Alliance *Neuropterido crassinervis–'Pecopteridion' arcuatae* Boyarina 2023

Pteridosperm-fern-calamitalean communities of deltaic plains.

Diagnostic species: D.s. All. = D.s. Ord.

Association *Neuropterido crassinervis–'Pecopteridetum' arcuatae*
Shchogolev et Boyarina 2023

Diagnostic species: *Calamites suckowii*, *Calamites* sp., *Neuropteris crassinervis*, *Neurodontopteris auriculata*, and *'Pecopteris' arcuata*.

Class *Peltaspermetea* Boyarina 2023

Tropical seasonally dry woodlands in river valleys with pteridosperm scrubs and tree ferns.

Diagnostic species: *Autunia conferta*, *A. naumannii, Cordaites* sp., *Culmitzschia frondosa Dichophyllum cuneatum*, *D. flabelliferum*, *Lodevia luganica*, *L. nicklesii*, *L. suberosa*, *Neurocallipteris planchardii*, *Neurodontopteris auriculata*, *Odontopteris brardii*, *O. lingulata*, *O. schlotheimii*, *O. subcrenulata*, *Otovicia hypnoides*, *'Pecopteris' bredovii*, *Polymorphopteris subelegans*, *Raminervia mariopteroides*, *Sphenocallipteris scythica*, and *Sphenopteris fayolii*.

Order *Autunietalia conferto–naumannii* Boyarina 2023

Pteridosperm scrubs with a predominance of peltaspermalen pteridosperms and the woodlands of tree ferns and arborescent cordaitaleans in river valleys.

Diagnostic species: D.s. Ord. = D.s. Cl.

Alliance *Lodevio nicklesii–Autunion naumannii* Boyarina 2023

Pteridosperm communities of floodplains.

Diagnostic species: *Autunia conferta*, *A. naumannii*, *Dichophyllum cuneatum*, *Lodevia luganica*, *L. nicklesii*, *L. suberosa*, *Neurocallipteris planchardii*, *Neurodontopteris auriculata*, *Odontopteris lingulata*, *O. subcrenulata*, and *Polymorphopteris subelegans*.

Association *Lodevio nicklesii–Autunietum naumannii* Boyarina et Shchogolev 2023

Diagnostic species: *Autunia conferta*, *A. naumannii*, *Dichophyllum cuneatum*, *Lodevia luganica*, *L. nicklesii*, *L. suberosa*, *Neurocallipteris planchardii*, *Neurodontopteris auriculata*, *Odontopteris lingulata*, *O. subcrenulata*, and *Polymorphopteris subelegans.*

Alliance *'Pecopterido' bredovii–Raminervion mariopteroidis* Boyarina 2023

Pteridosperm-fern communities of lake shores within floodplains.

Diagnostic species: *'Pecopteris' bredovii*, *Raminervia mariopteroides*, and *Sphenopteris fayolii*.

Association *'Pecopterido' bredovii–Raminervietum mariopteroidis* Boyarina 2023

Diagnostic species: *Asterophyllites equisetiformis*, *'Pecopteris' bredovii*, *Raminervia mariopteroides*, and *Sphenopteris fayolii*.

Alliance *Lodevio suberosae–Odontopteridion subcrenulatae* Boyarina 2023

Cordaitean-pteridosperm communities of levees and river valley slopes.

Diagnostic species: *Autunia conferta*, *A. naumannii, Cordaites* sp., *Culmitzschia frondosa Dichophyllum cuneatum*, *D. flabelliferum*, *Lodevia luganica*, *L. nicklesii*, *L. suberosa*, *Neurocallipteris* cf. *planchardii*, *Neurodontopteris auriculata*, *Odontopteris brardii*, *O. schlotheimii*, *Odontopteris subcrenulata*, *Otovicia hypnoides*, and *Sphenocallipteris scythica*.

Association *Lodevio suberosae–Odontopteridetum subcrenulatae*
Boyarina et Shchogolev 2023

Diagnostic species: *Autunia conferta*, *A. naumannii, Calamites cistii*, *C. suckowii*, *Cordaites* sp., *Culmitzschia frondosa Dichophyllum cuneatum*, *D. flabelliferum*, *Lodevia luganica*, *L. nicklesii*, *L. suberosa*, *Neurocallipteris* cf. *planchardii*, *Neurodontopteris auriculata*, *Odontopteris brardii*, *O. schlotheimii*, *Odontopteris subcrenulata*, *Otovicia hypnoides*, *'Pecopteris'* cf. *platonii*, and *Sphenocallipteris scythica*.

Class *Walchietea* Boyarina 2023

Tropical seasonally dry woodlands in river valleys with conifers.

Diagnostic species: *Culmitzchia frondosa*, *Otovicia hypnoides*, *Samarospermum moravicum*, and *Walchia piniformis*.

Order *Culmitzchietalia frondosae* Boyarina 2023

Walchian conifer woodlands of river valleys.

Diagnostic species: *Culmitzchia frondosa*, *Otovicia hypnoides*, *Samaropsis bachmutiensis*, *S. spinifera*, and *Samarospermum moravicum*.

Alliance *Culmitzchion frondosae* Boyarina 2023

Conifer communities of river valley slopes.

Diagnostic species: D.s. All. = D.s. Ord.

Association *Culmitzchietum frondosae* Boyarina 2023

Diagnostic species: *Culmitzchia frondosa*, *Otovicia hypnoides*, *Samaropsis bachmutiensis*, *S. spinifera*, and *Samarospermum moravicum*.

3.3. Composition and phytocoenogenesis of the Luganskian vegetation

The Luganskian vegetation of the Donets Basin consisted of the semi-aquatic sphenopsid thickets and the woodlands of wetland and seasonally dry habitats that were assigned to five classes, three of which are new (see: Fig. 4). The foregoing prodromus reflects the transformation of vegetation cover as a whole. The main changes were the appearance of wetland woodlands on coastal lowlands and deltaic plains as well as seasonally dry peltaspermalen pteridosperm-dominated woodlands in river valleys.

The semi-aquatic vegetation of lake shores in the Luganskian time was characterised by a small reduction in species richness of the same order *Sphenophyllo oblongifolii–Calamitetalia suckowii* in the composition of the same class *Sphenophyllo–Calamitetea* as in the Toretskian and Kalynovian times.

The vegetation changes of coastal lowlands and deltaic plains, which started back in the end of the Kalynovian, were manifested in the decrease of the species diversity and species abundance of wetland forests in the beginning of the Luganskian as evidenced by sporadic fossil assemblages with rare plant remains. The decrease of the species diversity of wetland forests was accompanied by the structure simplification and dominant substitution of the plant communities on coastal lowlands and deltaic plains, reflecting the regressive development of palaeophytocoenoses, that led to the transformation of wetland forests to wetland woodlands and the formation of new communities according to the substitutionary regressive model of phytocoenogenesis [Boyarina 2022]. The significantly reduced wetland forests on coastal lowlands of the class *Marattietea* were replaced by the wetland woodlands that were recognised as the new class *Calamito–Marattietea* with the order *Calamito-'Pecopteridetalia' jongmansii*. The plant communities of this order were characterised by the decreased species diversity. And in so doing, the main role in the communities became to belong to the ferns with small pinnules (*Cyathocarpus arboreus*, *'Pecopteris' jongmansii* Wagner, *'Pecopteris' martinezii* Stockmans et Willière, *'Pecopteris' monyi* Zeiller) and the ferns, which had the pinnules with fine hairs on its surface (*Cyathocarpus daubreei* (Zeiller) De Stefani). The changed vegetation of deltaic plains constituted of the calamitalen-fern woodlands with pteridosperm shrubs of the order *Neuropterido crassinervis–'Pecopteridetalia' arcuatae* with the one alliance *Neuropterido crassinervis–'Pecopteridion' arcuatae* in the composition of the new class *Neuropterido–Marattietea*.

The seasonally dry vegetation of fluvial landscapes during the Luganskian time became widespread and had high species richness, as indicated by the numerous plant fossil assemblages with a rich floristic composition in floodplain and floodplain-lacustrine deposits. The vegetation cover of river valleys consisted of peltaspermalean pteridosperm scrubs with the woodlands of tree ferns and arborescent cordaitaleans of the new class *Peltaspermetea* including the order *Autunietalia conferto-naumannii* with three alliances. The communities of the alliance *Lodevio nicklesii–Autunion naumannii* occupied floodplains. They were dominated by the pteridosperms with the foliage of *Autunia naumannii* (Gutbier) Kerp, *A. conferta* (Sternberg) Kerp, *Lodevia nicklesii* (Zeiller) Haubold et Kerp, and *L. luganica* (Boyarina et Shchegolev) Boyarina. The plant communities of the shores of floodplain lakes belong to the alliance *'Pecopterido' bredovii-Raminervion mariopteroidis*. These communities included the pteridosperms with the callipterid foliage of *Raminervia mariopteroides* Boyarina and the ferns with the foliage of *'Pecopteris' bredovii*, *Sphenopteris fayolii* Zeiller. The alliance *Lodevio suberosae–Odontopteridion subcrenulatae* unites the communities of peltaspermalean and medullosalean pteridosperms and cordaitaleans, which inhabited river levees and river valley slopes. The appearance of evolutionary new peltaspermalean pteridosperms in the conditions of the expansion of fluvial landscapes reflects the progressive development and formation of palaeophytocoenoses under the evolutionary progressive model of phytocoenogenesis [Boyarina 2022]. The conifer communities were identified as the coniferous woodlands of the order *Culmitzschietalia frondosae*, growing on river valley slopes and interfluves.

The Luganskian vegetation cover was overall characterised by the transformation of wetland forests to wetland woodlands on coastal lowlands and deltaic plains as well as the widespreading of seasonally dry pteridosperm scrubs with a predominance of peltaspermalen pteridosperms in river valleys.

4. The late Gzhelian (Vyskrivkian) vegetation

4.1. Environmental and palaeophytocoenotic interpretations

The Vyskrivkian plant-bearing strata relate to two facies associations, namely nearshore-marine/coastal lacustrine (grey beds) and coastal lagoonal/lacustrine (red beds) (Fig. 5). The phytooryctocoenoses mainly occur in the lower part of the Vyskrivkian, to the Q_6 carbonate interbed. The plant fossil assemblages of seven phytooryctocoenoses, which were found in both grey coastal lacustrine and red lagoonal/lacustrine facies, were assigned to the plant association of semi-aquatic sphenophyll-calamitalean communities of the shallow parts of lagoons and coastal lakes. Six phytooryctocoenoses including the plant fossil assemblages with calamitaleans, ferns and pteridosperms were found in grey lacustrine deposits occasionally with carbonate beds (nearshore-marine/coastal lacustrine facies association).

These plant fossils were used for reconstruction of the calamitalean-fern communities (four assemblages) and pteridosperm-fern communities (two assemblages) of coastal lowlands. The red lagoonal/lacustrine facies bear the rare fern, pteridosperm and conifer remains that indicate the seasonally dry vegetation of lagoon coasts, including pteridosperm-fern communities and conifer communities. The plant association of pteridosperm-fern communities of the shores of lagoons and lakes was determined on the basis of five phytooryctocoenoses from lagoonal and lacustrine deposits. The phytooryctocoenosis, containing the fragment of a coniferous branch in the brownish-red sandstone

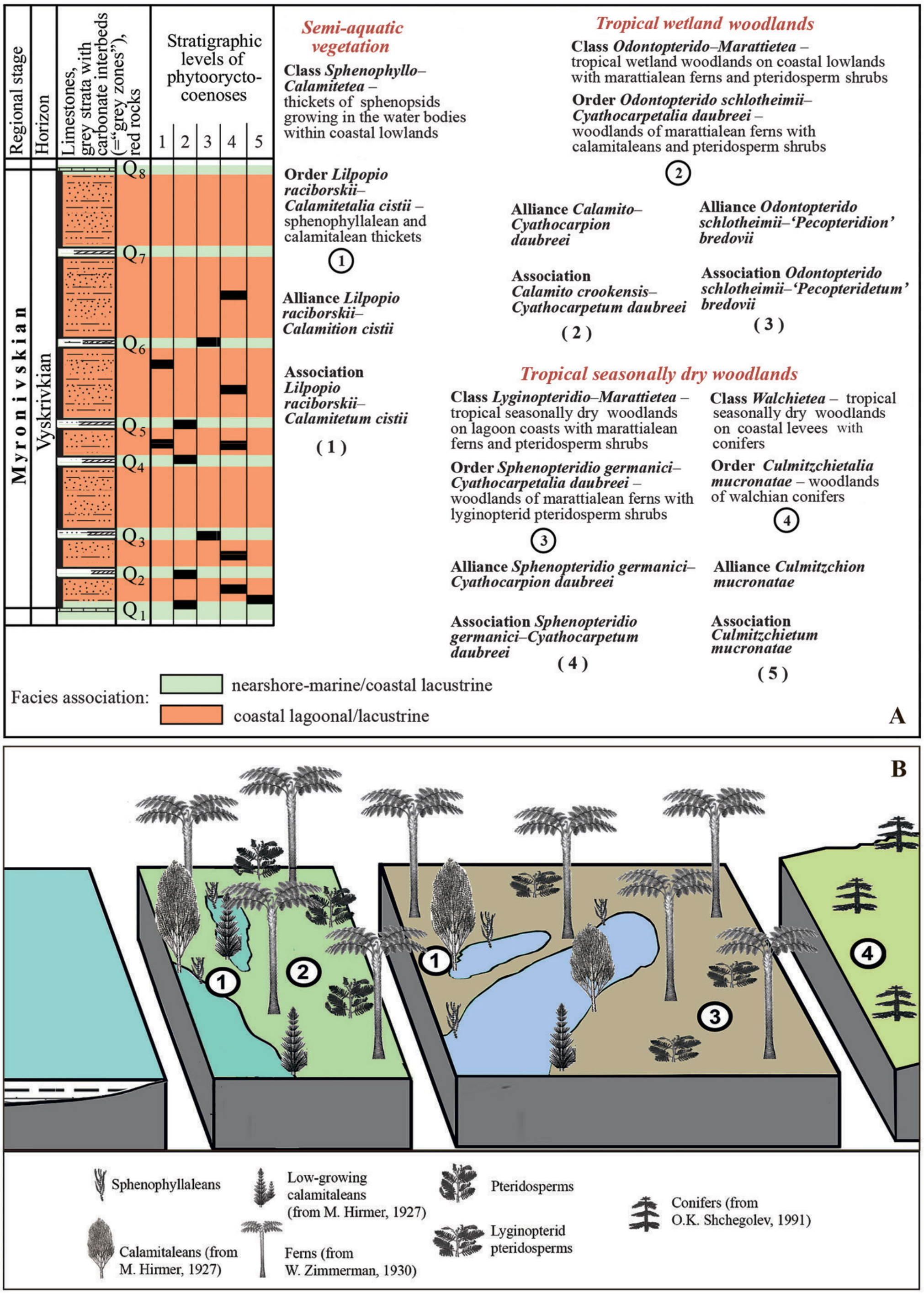

Fig. 5. Syntaxonomic composition and reconstruction of the late Gzhelian (Vyskrivkian) vegetation cover of the Donets Basin: (A) stratigraphic position and facial confinement of the phytooryctocoenoses, on the basis of which the plant associations were identified (association numbers in parentheses); (B) diagrammatic representation of the distribution of plant communities at the rank of orders of different landscape types (order numbers in a circle).

Рис. 5. Синтаксономічний склад та реконструкція рослинного покриву Донецького басейну в пізньогжельський (вискрівський) час: (A) стратиграфічне положення та фаціальна належність фітоориктоценозів, на основі яких встановлені рослинні асоціації (номера асоціацій в дужках); (B) схематичне зображення поширення рослинних угруповань в ранзі порядків різних типів ландшафту (номера порядків в колі).

bed within red lacustrine/lagoonal deposits, testifies to growth of conifer communities on coastal levees. All above-mentioned phytooryctocoenoses with rare plant fossils point to the spread of the low-density vegetation (woodlands) within coastal lowlands and lagoon coasts.

4.2. Prodromus and diagnostic species of palaeosyntaxa of the Vyskrivkian vegetation

Class *Sphenophyllo–Calamitetea* Boyarina 2023

Thickets of semi-aquatic sphenopsids growing in water bodies within coastal lowlands.

Diagnostic species: *Asterophyllites equisetiformis*, *Calamites carinatus*, *C. cistii*, *C. crookensis*, *C. multiramus*, *C. paleaceus*, *C. vandergrachtii*, *Lilpopia raciborskii*, and *Sphenophyllum verticillatum*.

Order *Lilpopio raciborskii–Calamitetalia cistii* Boyarina 2023

Sphenophyllalean and calamitalean thickets growing in water bodies within coastal lowlands.

Diagnostic species: D.s. Ord. = D.s. Cl.

Alliance *Lilpopio raciborskii–Calamition cistii* Boyarina 2023

Sphenophyllalean-calamitalean communities of the shallow parts of lagoons and coastal lakes.

Diagnostic species: D.s. All. = D.s. Ord.

Association *Lilpopio raciborskii–Calamitetum cistii* Boyarina 2023

Diagnostic species: *Asterophyllites equisetiformis*, *Calamites carinatus*, *C. cistii*, *C. crookensis*, *C. multiramus*, *C. paleaceus*, *C. vandergrachtii*, *Lilpopia raciborskii*, and *Sphenophyllum verticillatum*.

Class *Odontopterido–Marattietea* Boyarina 2023

Tropical wetland woodlands on coastal lowlands with marattialean tree ferns and pteridosperm shrubs.

Diagnostic species: *Asterophyllites equisetiformis*, *Barthelopteris germarii*, *Calamites carinatus*, *C. cistii*, *C. crookensis*, *C. multiramus*, *C. paleaceus*, *C. vandergrachtii*, *Cyathocarpus arboreus*, *C. daubreei*, *C. hemitelioides*, *Diplazites unitus, Nemejcopteris feminaeformis*, *Pecopteris plumosa*, *'Pecopteris' bredovii*, *'Pecopteris' jongmansii*, *'Pecopteris' martinezi*, *'Pecopteris' monyi*, *'Pecopteris' obliquenervis*, *'Pecopteris' potoniei*, *'Pecopteris' truncata*, *'Pecopteris'* cf. *viannae*, *Polymorphopteris subelegans*, *Odontopteris schlotheimii*, *O. subcrenulata*, and *Sphenopteris* cf. *fayolii*.

Order *Odontopterido schlotheimii–Cyathocarpetalia daubreei* Boyarina 2023

Woodlands dominated by marattialean tree ferns with subordinate calamitaleans and pteridosperm shrubs on coastal lowlands.

Diagnostic species: D.s. Ord. = D.s. Cl.

Alliance *Calamito–Cyathocarpion daubreei* Boyarina 2023

Calamitalean-fern communities of lake shores within coastal lowlands.

Diagnostic species: *Asterophyllites equisetiformis*, *Calamites carinatus*, *C. crookensis*, *C. multiramus*, *C. vandergrachtii*, *Cyathocarpus arboreus*, *C. daubreei*, *C. hemitelioides*, *Diplazites unitus, Pecopteris plumosa*, *'Pecopteris' bredovii*, *'Pecopteris' jongmansii*, *'Pecopteris' martinezi*, *'Pecopteris' obliquenervis*, *'Pecopteris' potoniei*, *'Pecopteris' truncata*, *'Pecopteris'* cf. *viannae*, and *Sphenopteris* cf. *fayolii*.

Association *Calamito crookensis–Cyathocarpetum daubreei* Boyarina 2023

Diagnostic species: *Asterophyllites equisetiformis*, *Calamites carinatus*, *C. crookensis*, *C. multiramus*, *C. vandergrachtii*, *Cyathocarpus arboreus*, *C. daubreei*, *C. hemitelioides*, *Diplazites unitus, Pecopteris plumosa*, *'Pecopteris' bredovii*, *'Pecopteris' jongmansii*, *'Pecopteris' martinezi*, *'Pecopteris' obliquenervis*, *'Pecopteris' potoniei*, *'Pecopteris' truncata*, *'Pecopteris'* cf. *viannae*, and *Sphenopteris* cf. *fayolii*.

Alliance *Odontopterido schlotheimii–'Pecopteridion' bredovii* Boyarina 2023

Pteridosperm-fern communities of coastal lowlands.

Diagnostic species: *Calamites cistii*, *C. paleaceus*, *Barthelopteris germarii*, *Nemejcopteris feminaeformis*, *Odontopteris schlotheimii*, *O. subcrenulata*, *'Pecopteris' bredovii*, *'Pecopteris' monyi*, and *Polymorphopteris subelegans*.

Association *Odontopterido schlotheimii–'Pecopteridetum' bredovii* Boyarina 2023

Diagnostic species: *Calamites cistii*, *C. paleaceus*, *Barthelopteris germarii*, *Nemejcopteris feminaeformis*, *Odontopteris schlotheimii*, *O. subcrenulata*, *'Pecopteris' bredovii*, *'Pecopteris' monyi*, and *Polymorphopteris subelegans*.

Class *Lyginopteridio–Marattietea* Boyarina 2023

Tropical seasonally dry woodlands on lagoon coasts with marattialean tree ferns and pteridosperm shrubs.

Diagnostic species: *Cyathocarpus arboreus*, *C. daubreei*, *'Pecopteris'* cf. *bioti*, *'Pecopteris' jongmansii*, *Polymorphopteris subelegans*, *Sphenocallipteris scythica*, and *Sphenopteridium germanicum*.

Order *Sphenopteridio germanici–Cyathocarpetalia daubreei* Boyarina 2023

Woodlands of marattialean tree ferns with lyginopterid pteridosperm shrubs on lagoon coasts.

Diagnostic species: D.s. Ord. = D.s. Cl.

Alliance *Sphenopteridio germanici–Cyathocarpion daubreei* Boyarina 2023

Fern-pteridosperm communities of the shores of lagoons and lakes.

Diagnostic species: D.s. All. = D.s. Ord.

Association *Sphenopteridio germanici–Cyathocarpetum daubreei* Boyarina 2023

Diagnostic species: *Calamites* sp., *Cyathocarpus arboreus*, *C. daubreei*, *'Pecopteris'* cf. *bioti*, *'Pecopteris' jongmansii*, *Polymorphopteris subelegans*, *Sphenocallipteris scythica*, and *Sphenopteridium germanicum*.

Class *Walchietea* Boyarina 2023

Tropical seasonally dry woodlands on coastal levees with conifers.

Diagnostic species: *Culmitzchietum mucronata*.

Order *Culmitzchietalia mucronatae* Boyarina 2023

Walchian conifer woodlands of coastal levees.

Diagnostic species: D.s. Ord. = D.s. Cl.

Alliance *Culmitzchion mucronatae* Boyarina 2023

Conifer communities of coastal levees.

Diagnostic species: D.s. All. = D.s. Ord.

Association *Culmitzchietum mucronatae* Boyarina 2023

Diagnostic species: *Culmitzchietum mucronata*.

4.3. Composition and phytocoenogenesis of the Vyskrivkian vegetation

The Vyskrivkian vegetation of the Donets Basin was comprised of semi-aquatic sphenopsid thickets, wetland and seasonally dry woodlands as in the Luganskian time, but with a slightly different floristic composition and other dominants (see: Fig. 5). The Vyskrivkian plant communities were assigned to four classes, two of which are new, and four new orders. The semi-aquatic sphenopsids of water bodies belong to the order *Lilpopio raciborskii–Calamitetalia cistii* of the class *Sphenophyllo–Calamitetea*. The sphenopsid thickets grew in the shallow parts of lagoons and coastal lakes. The wetland woodland communities of coastal lowlands with a relatively rich species composition were assigned to the class *Odontopterido–Marattietea* with the order *Odontopterido schlotheimii–Cyathocarpetalia daubreei* and two alliances. The calamitalean-fern communities of the alliance *Calamito–Cyathocarpion daubreei* inhabited lake shores. These communities included the ferns of a diverse species composition, among which the ferns with the foliage of *Cyathocarpus daubreei* (Zeiller) De Stefani were dominated. The pteridosperm-fern communities of the alliance *Odontopterido schlotheimii–'Pecopteridetum' bredovii* with a not very diverse species composition grew within coastal lowlands. Seasonally dry vegetation consisted of the woodlands of two classes. The fern woodlands with pteridosperm shrubs of the order *Sphenopteridio germanici–Cyathocarpetalia daubreei* in the composition of the class *Lyginopteridio–Marattietea* grew on the shores of lakes and lagoons within lagoon coasts. The ferns with the foliage of *Cyathocarpus daubreei* were more common than others. The coniferous woodlands of the order *Culmitzchietalia mucronatae* occupied, apparently, coastal levees and raised areas within lagoon coasts with better-drained substrates.

The mentioned new wetland and seasonally dry woodland communities developed in the conditions of the expansion of coastal lowlands and lagoon coasts with lakes along with the reduction of deltaic plains and river valleys. These environmental changes were accompanied by the migration of plants from decreasing to expanding landscape types, which led to the progressive development and formation of the new communities according to the migration progressive model of phytocoenogenesis [Boyarina 2022].

Vegetation dynamics and its connection with glacio-eustatic changes

The vegetation dynamics of the Donets Basin during the Late Pennsylvanian is traced in the development of two biomes, i.e. wetland forest and woodland biome and seasonally dry woodland biome. The features of the spreading of wetland and seasonally dry vegetation were related with the landscape and climatic changes that will be considered in context of glacio-eustatic sea level fluctuations, namely the changes of a relative sea level in the Donets Basin [Eros *et al.* 2012] during the glacial and interglacial intervals of the Late Paleozoic Ice Age [Fielding *et al.* 2008; Montañez & Poulsen 2013; Montañez 2022] (Fig. 6).

The formation of the Late Pennsylvanian vegetation cover in the Donets Basin occurred after the decline and loss of the wetland mixed lycopsid-dominated forests with tree ferns and pteridosperms in the latest Moscovian and the earliest Kasimovian. This time interval is compared with the end of the late Moscovian interglacial and earliest Kasimovian glacial intervals, the latter from which is mainly justified by the relative drop in sea levels [Montañez 2022]. In the Donets Basin, this glaciation corresponds to the long-term period of a relatively stable lower sea level in the late Lomovatkian (see Fig. 6) [Eros *et al.* 2012; Montañez 2022]. It should be noted that the upper part of the Lomovatkian regional stage was included in the Moscovian Stage by faunal and floral data [Poletaev *et al.* 2011] without considering the radio-isotopically calibrated age of the Moscovian–Kasimovian boundary [Davydov *et al.* 2010]. The floral changes of the Moscovian–Kasimovian (Westphalian–Stephanian) transition were identified by the disappearance of the most Westphalian flora as well as the appearance and distribution of the few Stephanian-age pteridosperms (*Neuropteris ovata*, *Odontopteris cantabrica* Wagner, *O. reichiana* Gutbier) and ferns (*Cyathocarpus* ex gr. *arboreus* (Sternberg) Weiss, *C. cyatheus* (Brongniart) Mosbrugger, *C. hemitelioides*) in coal-bearing deposits, i.e. at the base the m_9 coal seam below the N_1 limestone, at the base of the n_1 coal seam below the N_2 limestone, and at the base of the n_3 coal seam below the N_4 limestones [Fisunenko 1975, 1991, 2000]. The plant fossil assemblages occurring in lacustrine deposits in the lower part of the Toretskian regional stage (above the n_3^1 coal seam) already consist mostly of the characteristic taxa of the Stephanian flora [Shchegolev 1975].

The development of the Late Pennsylvanian (Stephanian) flora and vegetation of the Donets Basin will be regarded using the syntaxonomic composition of the Kasimovian and Gzhelian vegetation cover [Boyarina 2023]. The sequential reorganisations of the plant communities of wetland and seasonally dry habitats were generalised to the scheme and models of phytocoenogenesis [Boyarina 2022] (Fig. 7).

In the Kasimovian and early Gzhelian times, wetland forests were common within coastal lowlands and deltaic plains. The distinguishing features of the forests of deltaic plains from the forests of coastal lowlands were the presence of subsigillarian lycopsids and a greater diversity of pteridosperms. The wetland marattialean fern-dominated forests of the class *Marattietea* on coastal lowlands were represented the different orders, namely calamitalean-fern and fern-pteridosperm forests of the order *Neuropterido ovatae–Crenulopteridetalia lamurianae* in the Kasimovian and calamitalean-fern

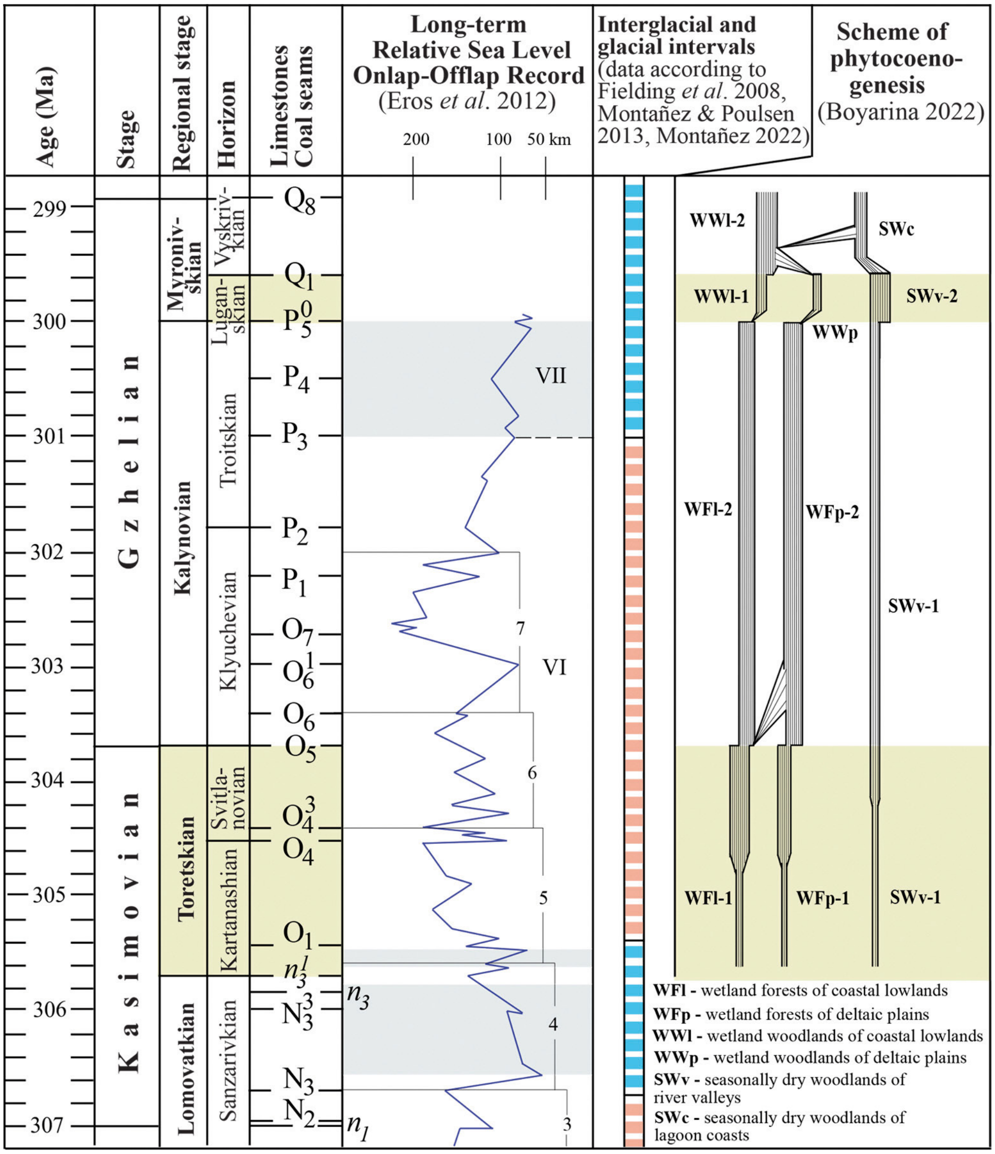

Fig. 6. Relationship among the processes of phytocoenogenesis of the Donets Basin vegetation and glacio-eustatic sea-level changes during the Late Pennsylvanian glacial and interglacial intervals.

Рис. 6. Відношення між процесами фітоценогенезу рослинності Донецького басейну та гляціо-евстатичними змінами рівня моря впродовж пізньопенсильванських гляціальних та інтергляціальних інтервалів.

forests of the order *Calamito suckowii–Cyathocarpetalia densifoliae* in the early Gzhelian. The early Gzhelian vegetation cover differed, firstly, the disappearance of dominants of the Kasimovian wetland forests—ferns *Crenulopteris lamuriana* and pteridosperms *Neuropteris ovata*, and secondly, the expanded species composition of ferns and the change of dominant ferns. The wetland subsigillarian lycopsid-marattialean fern-pteridosperm forests on deltaic plains were represented different orders and classes too. The Kasimovian lycopsid-fern-dominated forests of the class *Sigillario–Marattietea* with the order *Subsigillario–Acithecetalia polymorphae* were replaced by the early Gzhelian lycopsid-pteridosperm and calamitean-fern forests of the class *Sigillario–Odontopteridetea* with the order *Subsigillario–Odontopteridetalia schlotheimii*. The latter differed in the greater species composition of ferns and pteridosperms as well as their dominants.

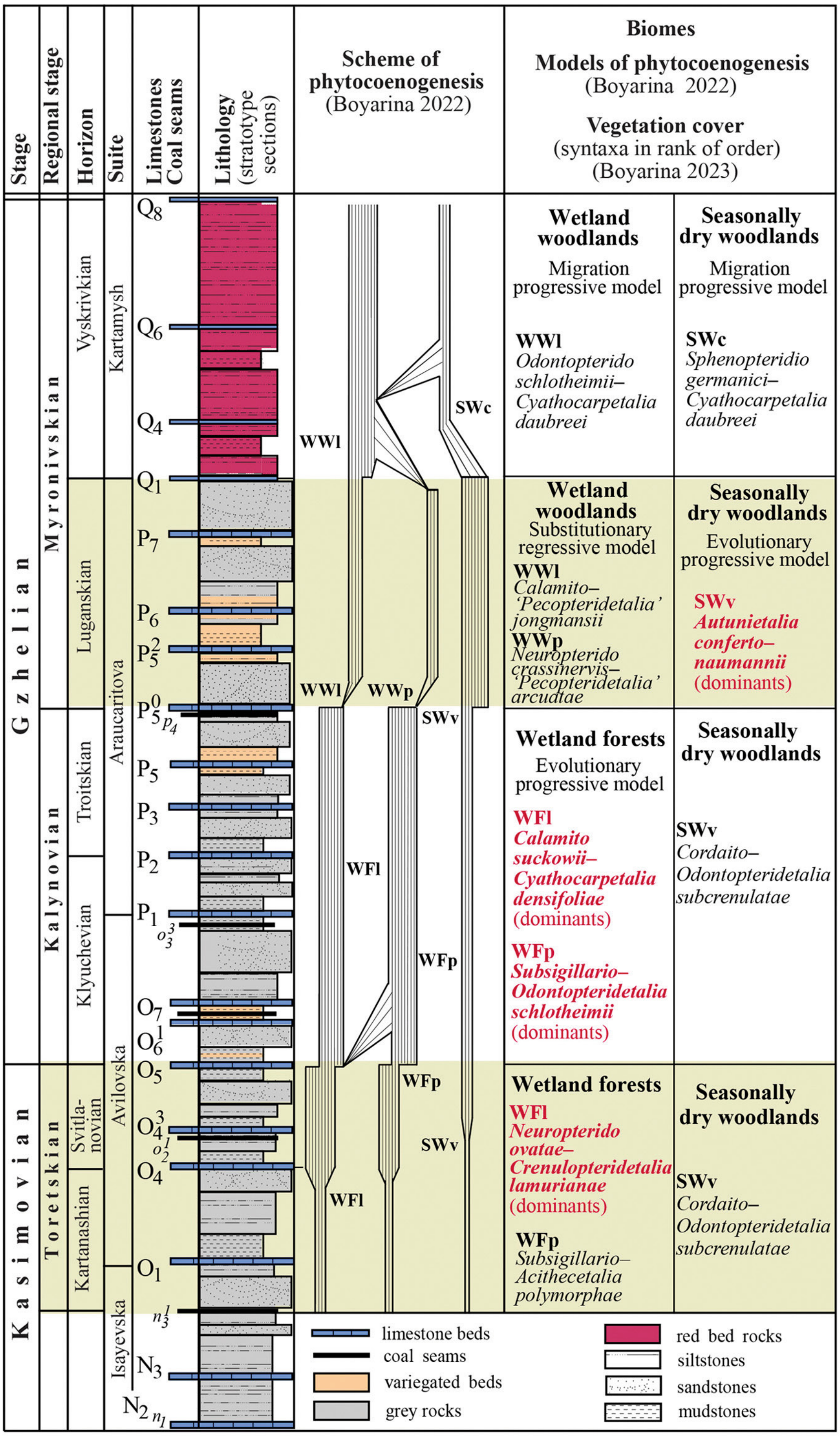

Fig. 7. Dynamics of the Late Pennsylvanian vegetation cover of the Donets Basin presented by the scheme and models of phytocoenogenesis: wetland forests (WFl) and woodlands (WWl) of coastal lowlands, wetland forests (WFp) and woodlands (WWp) of deltaic plains, seasonally dry woodlands of river valleys (SWv) and lagoon coasts (SWc).

Рис. 7. Динаміка пізньопенсильванського рослинного покриву Донецького басейну, яка представлена схемою та моделями фітоценогенезу: вологі ліси (WFl) та рідколісся (WWl) прибережних низовин, вологі ліси (WFp) та рідколісся (WWp) дельтових рівнин, сезонно-сухі рідколісся річкових долин (SWv) та лагунних узбереж (SWc).

The formation and spread of the wetland forest communities occurred in the long-term periods of relatively stable higher and lower sea levels [Eros *et al.* 2012] that were associated with the late Kasimovian through early–mid-Gzhelian interglacial interval and the late Gzhelian glacial interval [Montañez 2022] (see: Fig. 6). The rich wetland vegetation of coastal lowlands was especially widespread in the late Kasimovian (Svitlanovian), as evidenced by the large number of plant assemblages in the Svitlanovian lacustrine deposits, a spreading of which was associated with the intermediate-scale cycle at number 6 of Stage VI (sea-level stage) during a relatively stable higher sea level [Eros *et al.* 2012] (see: Figs. 2, 6). This intermediate-scale cycle includes a series of onlap–offlap events (cyclothems), i.e. frequent sea level fluctuations, resulting in the spread of coastal lowlands with a humid climate. The wide distribution of the wetland flora of such environments occurred in the early phases of transgressions from middle to late lowstand within an each glacial-interglacial (onlap-offlap after Eros *et al.* 2012) cycle [DiMichele 2014].

In contrast, the phytooryctocoenoses in deltaic deposits are more common in the lower Gzhelian (Troitskian) deposits that related with the period of a relative sea level drop (interval between the P_2-P_3 limestones) and the long-term period of relatively stable lower sea level (Stage VII) [Eros *et al.* 2012] (see: Figs. 3, 6). This leads to the following conclusions. The predomination of wetland forests of coastal lowlands in the vegetation cover took place in the late Kasimovian in the conditions of the long-term period of a relatively stable higher sea level during the first half of the late Kasimovian–early-mid-Gzhelian interglacial interval. While the wetland forests of deltaic plains became more spread in the early Gzhelian within the long-term period of a relative sea level drop in the end of the late Kasimovian–early-mid-Gzhelian interglacial interval and in the long-term period of a relatively stable lower sea level during the start of the late Gzhelian glacial interval. The latter is considered as the beginning of the late Paleozoic glaciation [Montañez 2022].

In the beginning of the middle Gzhelian (Luganskian), the wetland forests on coastal lowlands and deltaic plains were replaced by wetland woodlands that continued to grow on coastal lowlands in the late Gzhelian (Vyskrivkian). The loss of wetland forests from vegetation cover and the appearance of wetland woodlands in the middle Gzhelian (Luganskian) occurred in the condition of the reduction of coastal lowlands and deltaic plains that is indicated by decreasing nearshore-marine/coastal lacustrine and coastal lagoonal/deltaic facies while increasing fluvial deposits (see: Fig. 4).

According to the syntaxonomic composition of the middle and late Gzhelian vegetation cover, the wetland calamitalean-fern woodlands of the order *Calamito-'Pecopteridetalia' jongmansii* in composition of the class *Calamito–Marattietea*, which grew on coastal lowlands in the middle Gzhelian, were replaced by the calamitalean-fern-pteridosperm woodlands of the order *Odontopterido schlotheimii–Cyathocarpetalia daubreei* of the class *Odontopterido–Marattietea* in the late Gzhelian. The differences of the late Gzhelian order consisted in the increase in the taxonomical composition of palaeophytocoenoses due to plant migrations from deltaic plains [Boyarina 2022]. As a result of migration, the composition of the late Gzhelian woodlands had expanded by calamitaleans, ferns and pteridosperms. The middle Gzhelian woodlands on deltaic plains of the class *Neuropterido–Marattietea* with the order *Neuropterido crassinervis–'Pecopteridetalia' arcuatae* experienced the regressive development that was represented by both the disappearance of some plant species and the migration of the plants of some species to coastal lowlands, resulting in the loss of deltaic plain woodlands in the beginning of the late Gzhelian. This phytocoenotic process was caused by the reduction of deltaic and river landscapes in the late Gzhelian time, as testified by the disappearance of deltaic-fluvial and fluvial facies (see: Fig. 5).

The seasonally dry woodlands were spread in river valleys from the Kasimovian (Toretskian) until the middle Gzhelian (Luganskian) as well as on lagoon coasts in the late Gzhelian (Vyskrivkian). The cordaitean-pteridosperm woodlands of river valleys in the Kasimovian and early Gzhelian times had a similar species composition and belonged to the one class *Cordaito–Odontopteridetea* with the same order *Cordaito–Odontopteridetalia subcrenulatae*. In the middle Gzhelian, the vegetation cover in river valleys began to consist of predominant peltaspermalen pteridosperm scrubs and the less common woodlands with tree ferns and arborescent cordaitaleans of the class *Peltaspermetea* with the order *Autunietalia conferto–naumannii*. The formation of the middle Gzhelian plant communities took place in the conditions of the wide spreading of river landscapes. In the late Gzhelian time, the seasonally dry woodlands consisted of tree ferns and pteridosperm shrubs of the class *Lyginopteridio–Marattietea* with the order *Sphenopteridio germanici–Cyathocarpetalia daubreei* that were formed within expanding lagoon coasts against the background of the reduction of river landscapes and the spreading of temporary or seasonal rivers and streams.

The replacement of wetland forests by woodlands, a dominance of seasonally dry pteridosperm scrubs and a further vegetation development occurred after the long-term period of relatively stable lower sea level (Stage VII), in a condition of a continued sea level drop with low-amplitude sea level oscillations that led to gradual isolation of the Donets epicontinental sea [Gorak & Poletaev 1993; Poletaev *et al.* 2011; Borisenko 2014]. The mentioned changes of the middle and late Gzhelian vegetation cover also correspond to the trend of increasing equatorial aridity in Euramerica during Late Pennsylvanian [Tabor & Poulsan 2008; Fielding *et al.* 2008; Pfefferkorn *et al.* 2017]. The signs of the aridization in the Donets Basin are usually considered the lack of coal beds and an increase in the number of variegated beds, beginning with the Luganskian (above the P_5^2 limestone), and predominant red deposits in the upper Gzhelian (Vyskrivkian) [Feofilova 1966; Shchegolev 1975; Poletaev *et al.* 2011]. The formation of mentioned new plant communities and the predominance of red beds in the section were associated with the glacial interval in the end of the Late Pennsylvanian, involving the apex of late Paleozoic glaciation [Fielding *et al.* 2008; Isbell *et al.* 2012; Montañez & Poulsen 2013; Montañez 2022]. This glacial interval of the late Gzhelian with the palaeo-CO_2 falls and the greater value of O_2/CO_2 ratios (700 to 960) [Montañez *et al.* 2007; Richey *et al.* 2020; Montañez 2022] was accompanied a longer-term trend of drying during the later Pennsylvanian [Cecil *et al.* 1985; Montañez *et al.* 2007; Peyser *et al.* 2008]. Thus, specified climatic conditions in the late Gzhelian glacial interval had caused a declining role of wetland-dominated vegetation and an increasing role of seasonally dry-dominated vegetation in the Donets Basin in the end of the Late Pennsylvanian.

The considered transformations of vegetation cover, which are expressed by the sequential formations of new plant communities (phytocoenogenesis) and caused by changing environmental conditions related with glacial-interglacial events, can be identified as the events of the vegetation dynamics.

The following are the main events of vegetation reorganisations and their connection with the long-term periods of sea level oscillations during glacial-interglacial intervals of the Late Paleozoic Ice Age.

The earliest Kasimovian glacial interval

***The long-term period of relatively stable lower sea level* (*with infrequent sea level fluctuations*):**

- reduction and subsequent loss of the wetland lycopsid-dominated forests of coastal lowlands

The late Kasimovian–early-mid-Gzhelian interglacial interval

***The early phase (Toretskian) of the long-term period of relatively stable higher sea level* (*with frequent sea level fluctuations*):**

- formation (evolutionary progressive model of phytocoenogenesis) of wetland marattialean fern-dominated forests of the order *Neuropterido ovatae–Crenulopteridetalia lamurianae* on coastal lowlands
- formation (evolutionary progressive model of phytocoenogenesis) of wetland lycopsid-fern forests of the order *Subsigillario–Acithecetalia polymorphae* on deltaic plains

***The middle phase (Klyuchevian) of the long-term period of relatively stable higher sea level* (*with frequent sea level fluctuations*):**

- formation (evolutionary progressive model of phytocoenogenesis) of wetland marattialean fern-dominated forests with new dominants of the order *Calamito suckowii–Cyathocarpetalia densifoliae* on coastal lowlands

- formation (evolutionary progressive model of phytocoenogenesis) of wetland lycopsid-pteridosperm and calamitalean-fern forests with new dominants of the order *Subsigillario–Odontopteridetalia schlotheimii* on deltaic plains

The late Gzhelian glacial interval (beginning of late Paleozoic glaciation)

***The long-term period of relatively stable lower sea level* (*with infrequent sea level fluctuations, late Troitskian*):**

- reduction of wetland marattialean fern-dominated forests of the order *Calamito suckowii–Cyathocarpetalia densifoliae* on coastal lowlands
- the continued spreading in the start of the period of a relatively stable lower sea level and the subsequent reduction of wetland lycopsid-pteridosperm and calamitalean-fern forests of the order *Subsigillario–Odontopteridetalia schlotheimii* on deltaic plains

***The long-term period of relatively stable sea level drop* (*Luganskian*):**

- transformation of wetland forests to wetland woodlands:
  - loss of wetland marattialean fern-dominated forests of the order *Calamito suckowii–Cyathocarpetalia densifoliae* from vegetation cover on coastal lowlands and formation (substitutionary regressive model of phytocoenogenesis) of wetland calamitalean-fern woodlands of the order *Calamito-'Pecopteridetalia' jongmansii* on coastal lowlands
  - loss of wetland lycopsid-fern-pteridosperm forests of the order *Subsigillario–Odontopteridetalia schlotheimii* on deltaic plains and formation (substitutionary regressive model of phytocoenogenesis) of wetland woodlands of the order *Neuropterido crassinervis–'Pecopteridetalia' arcuatae* on deltaic plains
- formation (evolutionary progressive model of phytocoenogenesis) of seasonally dry peltaspermalen pteridosperm-dominated woodlands of the order *Autunietalia conferto–naumannii* in river valleys

***The long-term period of relatively stable sea level drop* (*Vyskrivkian*):**

- loss of wetland woodlands of the order *Neuropterido crassinervis–'Pecopteridetalia' arcuatae* of deltaic plains from vegetation cover
- formation (migration progressive model of phytocoenogenesis) of new wetland calamitalean-fern-pteridosperm woodlands of order *Odontopterido schlotheimii–Cyathocarpetalia daubreei* on coastal lowlands
- loss of seasonally dry woodlands of the order *Autunietalia conferto–naumannii* of river valleys from vegetation cover
- formation (migration progressive model of phytocoenogenesis) of new seasonally dry pteridosperm-fern woodlands of order *Sphenopteridio germanici–Cyathocarpetalia daubreei* on lagoon coasts.

As shown above, the specified events of the Late Pennsylvanian vegetation reorganisations were timed to different glacio-eustatic periods. The formation of new plant communities of wetland forests within coastal lowlands and deltaic plains took place in the long-term period of relatively stable higher sea level with frequent sea level fluctuations during the interglacial interval. And in doing so, the frequency of sea level fluctuations was important factor of climatic and landscape dynamics, causing the formation of new wetland forest communities with new floristic composition according to evolutionary progressive model of phytocoenogenesis. Whereas the reduction and subsequent loss of wetland lycopsid-dominated forests in the earliest Kasimovian as well as wetland marattialean fern-dominated and subsigillarian lycopsid-marattialean fern-pteridosperm forests in the middle Gzhelian (latest Troitskian and Luganskian) occurred in the long-term periods of relatively stable lower sea level with infrequent sea level fluctuations during the two glacial intervals. During the late Gzhelian glacial interval, the sustained reductions of certain landscape types led to the loss of forest communities and then woodland communities and the formation of new woodland communities according to substitutionary regressive and migration progressive models of phytocoenogenesis. While the new communities of seasonally dry woodlands, including peltaspermalen pteridosperm shrubs, were formed according to evolutionary progressive model of phytocoenogenesis in the condition of the sustained expansion of alluvial plains during the Luganskian sea level drop. The further sea level drop and increasing drying during the glacial interval in the Vyskrivkian had resulted in the reduction and loss of seasonally dry vegetation of river valleys.

Conclusions

The dynamics of the Late Pennsylvanian vegetation of the Donets Basin is reflected in the transformations of the vegetation cover, including the sequential formations of the new plant communities of two biomes, i.e. wetland forests and woodlands as well as seasonally dry woodlands. The reorganisations of plant communities were a result of changing environmental conditions related with the Late Pennsylvanian glacio-eustatic sea level changes during the Late Paleozoic Ice Age and the Late Pennsylvanian trend of increasing aridity in Euramerican Pangea.

The wetland forests were presented by the calamitalean-fern and fern-pteridosperm communities of coastal lowlands and the lycopsid-fern communities of deltaic plains in the Kasimovian, as well as the calamitalean-fern communities of coastal lowlands and the lycopsid-pteridosperm and calamitalean-fern communities within deltaic plains in the early Gzhelian. The new communities of coastal lowlands and deltaic plains were formed according to the evolutionary progressive model of phytocoenogenesis in the condition of the expansion of coastal lowlands and deltaic plains in the long-term period of a relatively stable higher sea level with frequent sea level fluctuations during the late Kasimovian–early-mid-Gzhelian interglacial interval. Wetland forests were replaced by wetland woodlands in the middle Gzhelian (Luganskian). The transformation of wetland forests to wetland woodlands according to the substitutionary regressive model of phytocoenogenesis was due to the reduction of coastal lowland and deltaic environments that was associated with the long-term period of a relatively stable sea level drop in the early phase of the late Gzhelian glacial interval. The wetland woodlands included the calamitalean-fern communities on coastal lowlands and the calamitalean-fern communities with pteridosperm shrubs on deltaic plains in the middle Gzhelian (Luganskian) and the fern-calamitalean-pteridosperm communities on coastal lowlands in late Gzhelian (Vyskrivkian).

The seasonally dry woodlands were presented by the cordaitalean-pteridosperm communities in river valleys in the Kasimovian and early Gzhelian, the peltaspermalen pteridosperm scrubs with fern-pteridosperm and cordaitalean-pteridosperm communities in river valleys in the middle Gzhelian, the calamitalean-fern and fern-pteridosperm communities on lagoon coasts in the late Gzhelian, as well as the coniferous woodlands on river valley slopes in the Kasimovian, early and middle Gzhelian, and the coniferous woodlands on coastal levees in the late Gzhelian. The formation of the new peltaspermalen pteridosperm-dominated communities in river valleys according to the evolutionary progressive model of phytocoenogenesis took place in the conditions of the expansion of river environments during the Luganskian sea level drop in the early phase of the late Gzhelian glacial interval. The late Gzhelian wetland and seasonally dry woodlands were formed according to the migration progressive model of phytocoenogenesis during the continued sea level drop in the late Gzhelian glacial interval.

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Declarations

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