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The Late Pennsylvanian vegetation of the Donets Basin, Ukraine: Syntaxonomy of plant communities

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abstract

A reconstruction and classification of Kasimovian and Gzhelian plant communities of the Donets Basin that constituted the Late Pennsylvanian vegetation cover of the region is proposed. Reconstructions of palaeophytocoenoses are based on the identification of the floristic composition of fossil assemblages and the lithological-facial features of plant-bearing strata from 69 phytooryctocoenoses that were found in more than 30 plant fossil localities and 20 boreholes within the Bahmut and Kalmius–Torets depressions. The plant remains were studed from lacustrine, swamp, deltaic, floodplain and lagoonal deposits that indicate biotopes corresponding to coastal lowlands, deltaic plains, floodplains and river valley slopes. The morphological and quantitative characteristics of plant fossils indicate that these palaeophytocoenoses in different time intervals of the Late Pennsylvanian belonged to four vegetation types, namely to coastal semi-aquatic vegetation, wetland forests, wetland woodlands and seasonally dry woodlands. The classification of plant communities was conducted using the ecological and floristic approach for vegetation classification by the Braun-Blanquet method. The identification of plant community types (syntaxa) from the lowest rank (association) to the higher ranks (alliance, order, and class) was made as a result of an analysis of the floristic composition and ecological conditions of palaeophytocoenoses. The major criteria for determining the syntaxa are the diagnostic species including characteristic and differential species, which are considered as indicators of environmental conditions. The newly compiled prodromus of Kasimovian and Gzhelian plant communities consists of 11 classes, 16 orders, 21 alliances and 21 associations. The prodromus reveals the syntaxonomic composition of the Late Pennsylvanian vegetation cover of the Donets Basin and provides an understanding of past vegetation dynamics. The syntaxonomic changes of vegetation are traced in the four time intervals that are correspond to regional stratigraphic units, namely Toretskian (Kasimovian), Kalynovian (early Gzhelian), Luganskian (middle Gzhelian), and Vyskrivskian (late Gzhelian), and are characterised by the plant associations of certain classes and orders.

Пізньопенсильванська рослинність Донецького басейну України: синтаксономія рослинних угруповань

Наталія Бояріна

Резюме. Пропонується реконструкція та класифікація касимовських та гжельських рослинних угруповань Донецького басейну, які складали пізньопенсильванський рослинний покрив. Реконструкції палеофітоценозів базуються на визначенні флористичного складу викопних рослинних комплексів та літолого-фаціальних ознак флороносних відкладів із 69 фітооріктоценозів, які виявлені в більш ніж 30 місцезнаходженнях викопних рослин та 20 свердловинах в межах Бахмутсткої та Кальміус-Торецької котловин. Рослинні рештки походять із озерних, болотних, дельтових, заплавних та лагунних відкладів, які визначають біотопи, що відповідають прибережним низовинам, дельтовим рівнинам, заплавам та схилам річкових долин. Морфологічні та кількісні ознаки залишків викопних рослин визначають належність палеофітоценозів до чотирьох рослинних типів, а саме прибережно-водної рослинності, вологих лісів, вологого та сезонно-сухого рідколісся. Класифікація рослинних угруповань проведена із застосуванням еколого-флористичного підходу до класифікації рослинності за методом Браун-Бланке. Встановлення типів рослинних угруповань (синтаксонів) від найнижчого рангу (асоціації) до вищих рангів (союзу, порядку, класу) проведено в результаті аналізу флористичного складу та екологічних умов палеофітоценозів. Основними критеріями визначення синтаксонів є діагностичні види (характерні та диференційні), які розглядаються як індикатори умов середовища. Вперше складений продромус рослинних угруповань касимовського та гжельського часів включає 11 класів, 16 порядків, 21 союз та 21 асоціацію. Продромус розкриває синтаксономічний склад пізньопенсильванського рослинного покриву Донецького басейну та дає розуміння динаміки рослинності. Синтаксономічні зміни рослинності простежуються в чотирьох часових інтервалах, а саме торецькому (касимовському), калинівському (ранньогжельському), луганському (середньогжельському) та вискрівському (пізньогжельському), які відповідають регіональним стратонам та характеризуються рослинними асоціаціями певних класів та порядків.

Ключові слова: рослинний покрив, класифікація, пізній пенсильваній, Донецький басейн.

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Introduction

The study of fossil flora and the reconstruction of the palaeophytocoenoses that made up the ancient vegetation cover provide an understanding of the vegetation of past geological epochs. The first reconstructions of peat-forming communities, forest communities of lowlands and plant communities of uplands gave initial insights into the Carboniferous vegetation cover in palaeotropical Euramerica [Gothan & Gimm 1930; Němejc 1951; Shchogolev 1964; Barthel 1976; Scott 1977, 1979]. At the same time, several techniques and approaches were proposed for conducting palaeoecological research and landscape interpretations [Radchenko 1964; Oshurkova 1974, 1987; Fissunenko 1979, 1987; Shchogolev 1985].

Subsequent studies were devoted to more detailed studies of the wetland and dryland flora of certain habitats with environmental interpretation [Iwaniw 1985; Raymond 1987; Falcon-Lang 2003; Bashforth *et al.* 2010; Elrick *et al.* 2017; etc.]. The Euramerican tropical vegetation in Pennsylvanian times is currently interpretated as a complex of wetland and seasonally dry ecosystems, or biomes [DiMichele *et al.* 2001, 2010; DiMichele 2014; Bashforth *et al.* 2016]. Studies of Late Pennsylvanian floral assemblages have shown that the major components of the Euramerican wetland vegetation, which occupied lowland areas with swamps and lakes, were marattialean ferns, sphenopsids, and some medullosalean pteridosperms [Gastaldo *et al.* 1995; DiMichele & Phillips 1988, 1994; Phillips & DiMichele 1998; DiMichele *et al.* 2001]. The seasonally dry vegetation of better-drained fluvial habitats was presented by conifers, cordaites, and peltaspermalean pteridosperms [Cridland & Morris 1963; Winston 1983; Lyons & Darrah 1989; DiMichele *et al.* 2001; Falcon-Lang *et al.* 2015].

The Carboniferous flora of the Donets Basin was studied by N. V. Grigoryev, M. D. Zalessky, E. F. Tschirkova, E. O. Novik, O. K. Shchogolev, O. P. Fissunenko, and N. I. Boyarina, whereas ancient

plant communities and vegetation of this time were first described by O. K. Shchogolev [1964, 1985, 1991], O. P. Fissunenko [1979, 1987], and N. I. Boyarina [1995, 2006c]. The study of the vegetation cover included the reconstructions and classifications of palaeophytocoenoses. Based on the late Carboniferous floral assemblages from different lithofacial deposits, the classifications of the plant communities of coastal lowlands and alluvial plains were carried out [Shchogolev 1991; Boyarina 2006c]. These first classifications were built using the dominant plant communities of certain landscape types and the life form of dominant plants. The two mentioned characteristics are the main criteria of the dominant and physiognomic approaches to vegetation classification [Aleksandrova 1969].

At present, the ecological and floristic approach by the Braun-Blanquet method [Braun-Blanquet 1951, 1964; Mirkin & Naumova 2014, 2017] ranks prominently in the classification of palaeophytocoenoses [Ignatiev 1992, 2016, 2020]. This method was applied for the first time to fossil phytocoenoses for the classification of Triassic plant communities by Retallack [1977]. In recent decades, the Braun-Blanquet approach was used to classify the Permian plant communities of the Pechora Basin, Fore-Urals and Urals [Naugolnykh 2007; Ignatiev 2020], and the middle Gzhelian palaeophytocoenoses of the Donets Basin [Boyarina 2016a, 2017].

The present paper is devoted to the classification of the Late Pennsylvanian vegetation cover of the Donets Basin by the Braun-Blanquet approach. The description of the plant communities at rank of associations as the base units in a Braun-Blanquet classification system and the prodromus of the Late Pennsylvanian vegetation are provided.

Geological setting

The Upper Pennsylvanian (upper Carboniferous) deposits are widespread in the western part of the Donets Basin and are exposed on the gully slopes within the Bahmut and Kalmius–Torets depressions (Fig. 1). This section reaches a thickness of more than 2500 metres and is represented by rhythmically alternating nearshore-marine and terrestrial facies. The Upper Pennsylvanian was divided into four suites (= formations) by limestone marker beds: Isaevska (including the group of limestones with letter N), Avilovska (limestones O), Araucaritova (limestones P), and Kartamyshska (limestones Q). A distinctive feature of these deposits is the decrease in the number of coal beds (Araucaritova Suite) and the appearance of red bed rocks that predominate in the upper part of the section (Kartamyshska Suite). Three regional stages with six horizons [Poletaev *et al*. 2011] and five megafloral zones [Boyarina 2016b] were recognised in the Kasimovian and Gzhelian of the Donets Basin (Fig. 2).

Material and Methods

The plant remains from more than 30 plant fossil localities and 20 boreholes have been collected since the 1960s and studied by O. K. Shchogolev [1960, 1964, 1975, 1985, 1991] and N. I. Boyarina [Boyarina & Shchogolev 1989; Boyarina 1994, 2006a, 2006b, 2010]. The specimens are predominantly represented by impressions and less so by poorly preserved compressions. They are currently stored at the Institute of Geological Sciences of the National Academy of Sciences of Ukraine, but will be transferred to the National Museum of Natural History of NAS of Ukraine, Kyiv. Most localities have already been described by O. K. Shchogolev and N. I. Boyarina [Shchogolev 1985, 1991; Boyarina 2006a, 2006b, 2010; Poletaev *et al*. 2011].

All studied plant fossil localities and boreholes are listed below (their numbers are used in the phytosociological tables given in the present paper). The plant-bearing beds containing separate plant assemblages within a single sedimentary stratum in some localities are designated by letters.

The list of localities is given in ascending stratigraphic order of deposits:

(***1***) Kartanash, a quarry near Kartanash railway station, nearby to the south-eastern outskirts of the urban village of Kalynove, Lugansk Oblast (interval between the n_3^1 coal seam and the N_5^1 limestone bed): Kartanash-a (siltstone beds above the n_3^1 coal seam), Kartanash-b (siltstone beds above a 37-m-thick sandstone bed), Kartanash-c (sandstone beds under the n_3^2coal seam).

(***2***) Volchanivka, a gully near the village of Volchanivka, north of Debaltsevo railway station, Donetsk Oblast (below the O_1 limestone bed).

(***3–5***) Svitlanove, a quarry near Svitlanove railway station, Lugansk Oblast:

(***3***) Svitlanove-1 (interval between the O_4 and O_4^1 limestone beds): Svitlanove-1a (siltstone beds above the O_4 limestone bed), Svitlanove-1b (mudstones under the unnamed coal bed below the O_4^1 limestone bed);

(***4***) Svitlanove-2 (interval between the O_4^2 and O_4^3 limestone beds);

(***5***) Svitlanove-3 (upper part of the interval between the O_4 and O_5 limestone beds): Svitlanove-3a (mudstone beds), Svitlanove-3b (siltstone beds), Svitlanove-3c (siltstone beds below the O_4^5 limestone bed).

(***6–8***) Chernyshove, a gully on the slope of the right tributary of the Zhelizna River:

(***6***) Chernyshove-1 (below the O_4^1 limestone bed);

(***7***) Chernyshove-2 (interval between the O_4^3 and O_4^4 limestone beds);

(***8***) Chernyshove-3 (interval between the O_4 and O_5 limestone beds).

(***9–17***) Kalynove, gullies on the left bank of the Lugan River near the urban village of Kalynove, Lugansk Oblast:

(***9***) Kalynove-1 (interval between the O_1 and O_2 limestone beds);

(***10***) Kalynove-2 (below the O_4^4 limestone bed);

(***11***) Kalynove-3 (interval between the O_4^6 and O_5 limestone beds): Kalynove-3a (sandstone and siltstone beds), Kalynove-3b (mudstones under the unnamed coal bed below the O_5 limestone bed);

(***12***) Kalynove-4 (interval between the O_5 and O_6 limestone beds): Kalynove-4a (siltstone beds in a deltaic succession), Kalynove-4b (mudstones under the unnamed coal bed below the O_6 limestone bed);

(***13***) Kalynove-5 (interval between the O_6 and O_7 limestone beds);

(***14***) Kalynove-6 (interval between the O_6^1 and O_7 limestone beds);

(***15***) Kalynove-7 (below the P_1 limestone bed): Kalynove-7a (mudstones under the o_3^3coal seam), Kalynove-7b (mudstones above the o_3^3coal seam);

(***16***) Kalynove-8 (under the p_4 coal seam);

(***17***) Kalynove-9 (below the P_5 limestone bed).

(***18***) Memrik gully, on the bank of the Vovcha River near the village of Galytsynivka, Donetsk Oblast (interval between the O_4 and O_5 limestone beds).

(***19–20***) Troyitske, a gully on the left bank of the Lugan River near the village of Troyitske, Lugansk Oblast:

(***19***) Troyitske-1 (below the P_1 limestone bed): Troyitske-1a (sandstone beds), Troyitske-1b (siltstone beds);

(***20***) Troyitske-2 (interval between the P_2 and P_3 limestone beds): Troyitske-2a (mudstone beds), Troyitske-2b (sandstone beds), Troyitske-2c (siltstone beds).

(***21***) Kravetska gully, near the village of Ivanopilia, Donetsk Oblast (below the P_3 limestone bed).

(***22***) Krasnyi Pahar, a gully near the village of Vozdvuzhenka (formerly Krasnyi Pahar), Donetsk Oblast (below the P_4 limestone bed): Krasnyi Pahar-a (siltstone beds in a lagoonal succession), Krasnyi Pahar-b (siltstone beds in a lacustrine-deltaic succession), Krasnyi Pahar-c (mudstone beds in a lacustrine-deltaic succession).

(***23***) Myronivske-1, a gully on the left bank of the Myronivsky Reservoir, near the urban village of Myronivske, Donetsk Oblast, 200 m north of the Kharkiv–Rostov-on-Don highway (below the P_5^0 limestone bed).

(***24***) Myronivske-2, the Myronivska gully, 731 km of the Bachmut–Rostov-on Don highway (above the P_6 limestone bed).

(***25–28***) Luganske, a gully on the the left bank of the Myronivsky Reservoir, near the urban village of Luganske, Donetsk Oblast:

(***25***) Luganske-1, the lower part of the gully (below the P_6 limestone bed): Luganske-1a (siltstones with mudstone beds in a lacustrine-deltaic succession), Luganske-1b (siltstone beds in a deltaic succession);

(***26***) Luganske-2, the middle and upper parts of the gully (below the P_6 limestone bed): Luganske-2a (greenish-grey mudstone bed within a lacustrine-floodplain succession), Luganske-2b (intercalation of greenish-grey mudstone and siltstone beds within a floodplain succession), Luganske-2c (lacustrine greenish-grey mudstones), Luganske-2d (lacustrine-floodplain greenish-grey siltstones intercalated with mudstones), Luganske-2e (intercalation of greenish-grey mudstone, siltstone and sandstone beds within a lacustrine-floodplain succession), Luganske-2f (intercalation of greenish-grey siltstone and sandstone beds within a floodplain succession), Luganske-2g (lacustrine-floodplain greenish-grey siltstones);

(***27***) Luganske-3, mudstones between two thin unnamed coal seams in the upper part of a gully (below the P_6 limestone bed);

(***28***) Luganske-4, a gully on the left bank of the Myronivsky Reservoir, within 2 km south of Rota railway station, Donetsk Oblast (interval between the P_6 and P_6^2 limestone beds).

(***29***) Novgorodske, a quarry near the urban village of Novgorodske, Donetsk Oblast (interval between two grey mudstone beds with the Q_1 and Q_3 carbonate interbeds).

(***30***) Keramic, a quarry near the village of Keramic, Donetsk Oblast (interval between two grey mudstone beds with the Q_1 and Q_3 carbonate interbeds).

(***31***) Kamyshevaha, a quarry near the village of Kamyshevaha, Lugansk Oblast (grey mudstone bed with the Q_3 carbonate interbed).

(***32***) Kalynove quarry, near the village of Kalynove, Pokrovsk Raion, Donetsk Oblast (interval between two grey mudstone beds with the Q_4 and Q_6 carbonate interbeds): Kalynove quarry-a (dark-grey mudstones), Kalynove quarry-b (light-grey mudstones), Kalynove quarry-c (red-brown mudstones with blue and dark-brown spots).

(***33***) Klynove, a quarry nearby to the north-eastern outskirts of the village of Klynove, Donetsk Oblast (below a grey mudstone bed with the Q_6 carbonate interbed).

(***34***) Borehole No. 743, the Corulsky dome, depth 902–903 m (interval between the O_4 and O_5 limestone beds).

(***35***) Borehole No. 811, the Chervonooskilsky dome, depth 869–872 m (interval between the O_5 and O_6 limestone beds).

(***36***) Borehole No. 239, the Kalmius–Torets depression, depth 206,3 m (interval between the O_5 and O_6 limestone beds).

(***37***) Borehole No. 232, the joint zone of the Druzhkovsko-Konstantynovska brachianticline and the Golovna anticline, depth 314 m (below the P_1 limestone bed).

(***38***) Borehole No. 7168, the Mechebilovske uplift, depth 86,5 m (below the P_1 limestone bed).

(***39***) Borehole No. 741, the Corulsky dome, depth 317 m (below the P_2 limestone bed).

(***40***) Borehole No. A-3, near the urban village of Olhivka, Donetsk Oblast, depth 182–154 m (interval between the P_1 and P_3 limestone beds).

(***41***) Borehole No. 443, near the city of Yunokomunarivsk, Donetsk Oblast, depth 337 m (below the P_3 limestone bed).

(***42***) Borehole No. 181, the Corulsky dome, depth 613 m (interval between the P_4 and P_5 limestone beds).

(***43***) Borehole No. 4453, the village of Krasnopolie, Donetsk Oblast, depth 507–508 m (above a grey mudstone bed with the Q_1 carbonate interbed).

(***44***) Borehole No. 4395, towards the south-west of the village of Vyskrivka, Lugansk Oblast, depth 137–148 m (interval between two grey mudstone beds with the Q_1 and Q_3 carbonate interbeds).

(***45***) Borehole No. 4377, towards the west of the village of Klynove, Donetsk Oblast, depth 706–712 m (interval between two grey mudstone beds with the Q_4 and Q_7 carbonate interbeds).

(***46***) Borehole No. 4385, towards the east of the village of Klynove, Donetsk Oblast, depth 322–324 m (interval between two grey mudstone beds with the Q_6 and Q_7 carbonate interbeds).

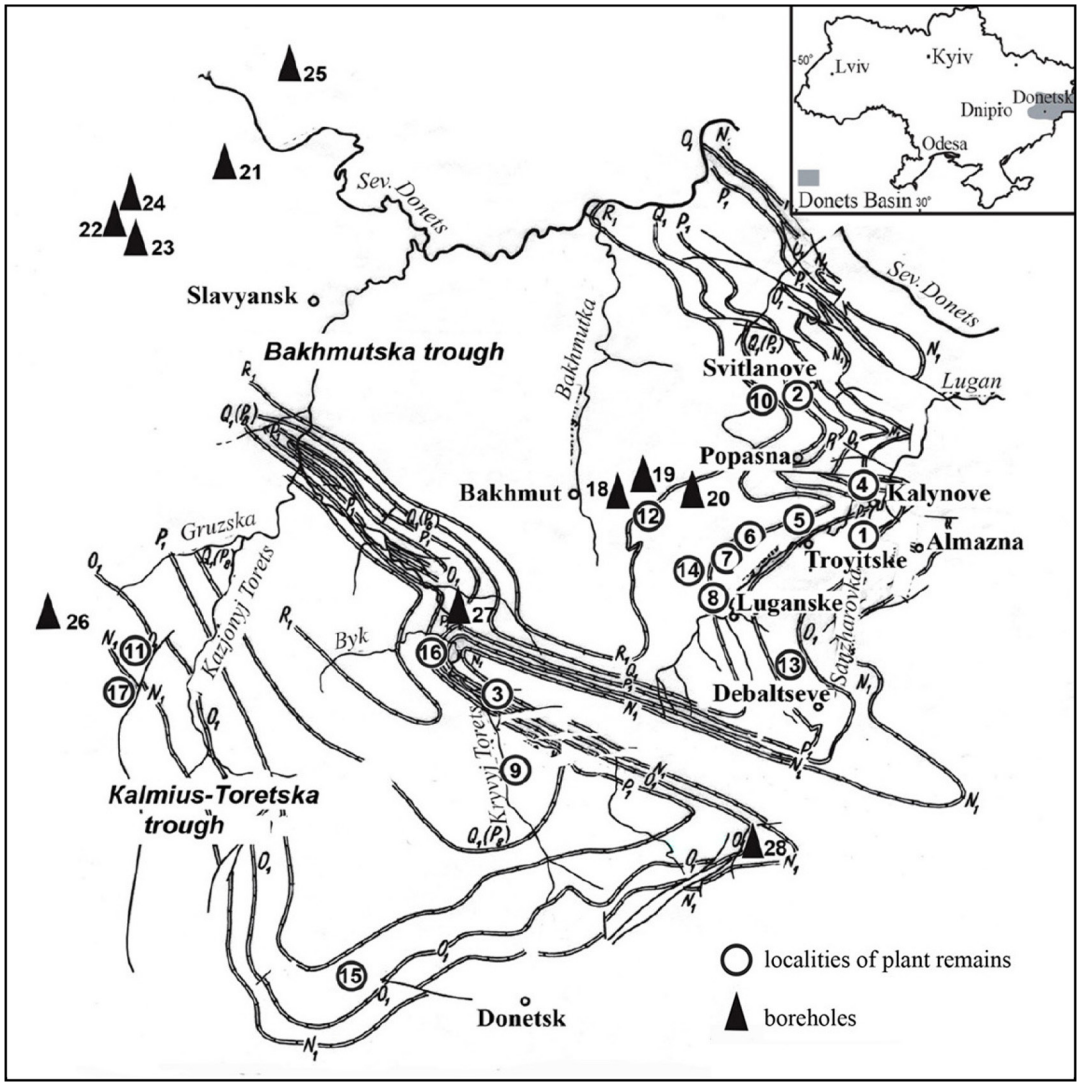

Fig. 1. Study region with the structure plan of suite limestones (from the materials of State regional geological enterprise 'Donetskgeology', 1985) and localities of plant remains. (*1*) Kartanash; (*2*) Svitlanove; (*3*) Chernyshove; (*4*) Kalynove; (*5*) Troyitske; (*6*) Krasnyi Pahar; (*7*) Myronivske; (*8*) Luhanske; (*9*) Novgorodske; (*10*) Kamyshevaha; (*11*) quarry Kalynove; (*12*) Klynove; (*13*) gully near the village of Volchanivka; (*14*) gully near Roty railway station; (*15*) gully Memryk near the village of Galytsynivka; (*16*) gully Kravetska near the village of Ivanopilie; (*17*) quarry near the village of Keramik; (*18*) borehole No. 4377; (*19*) borehole No. 4385; (*20*) borehole No. 4395; (*21*) borehole No. 4453; (*22*) borehole No. 743; (*23*) borehole No. 741; (*24*) borehole No. 181; (*25*) borehole No. 811; (*26*) borehole No. 239; (*27*) borehole No. 232; (*28*) borehole No. A-3.

Рис. 1. Схема району дослідження із структурним планом світних вапняків (за матеріалами Державного регіонального геологічного підприємства "Донецькгеологія", 1985) та положенням місцезнаходжень рослинних решток: (*1*) Картанаш; (*2*) Світланове; (*3*) Чернишове; (*4*) Калинове; (*5*) Троїцьке; (*6*) Красний Пахар; (*7*) Миронівське; (*8*) Луганське; (*9*) Новгородське; (*10*) Камишеваха; (*11*) кар'єр Калинове; (*12*) Клинове; (*13*) яр біля с. Волчанівка; (*14*) яр біля залізничної станції Роти; (*15*) яр Мемрик біля с. Галицинівка; (*16*) яр Кравецький на околиці с. Іванопіл'є; (*17*) кар'єр біля с. Керамік; (*18*) св. 4377; (*19*) св. 4385; (*20*) св. 4395; (*21*) св. 4453; (*22*) св. 743; (*23*) св. 741; (*24*) св. 181; (*25*) св. 811; (*26*) св. 239; (*27*) св. 232; (*28*) св. А-3.

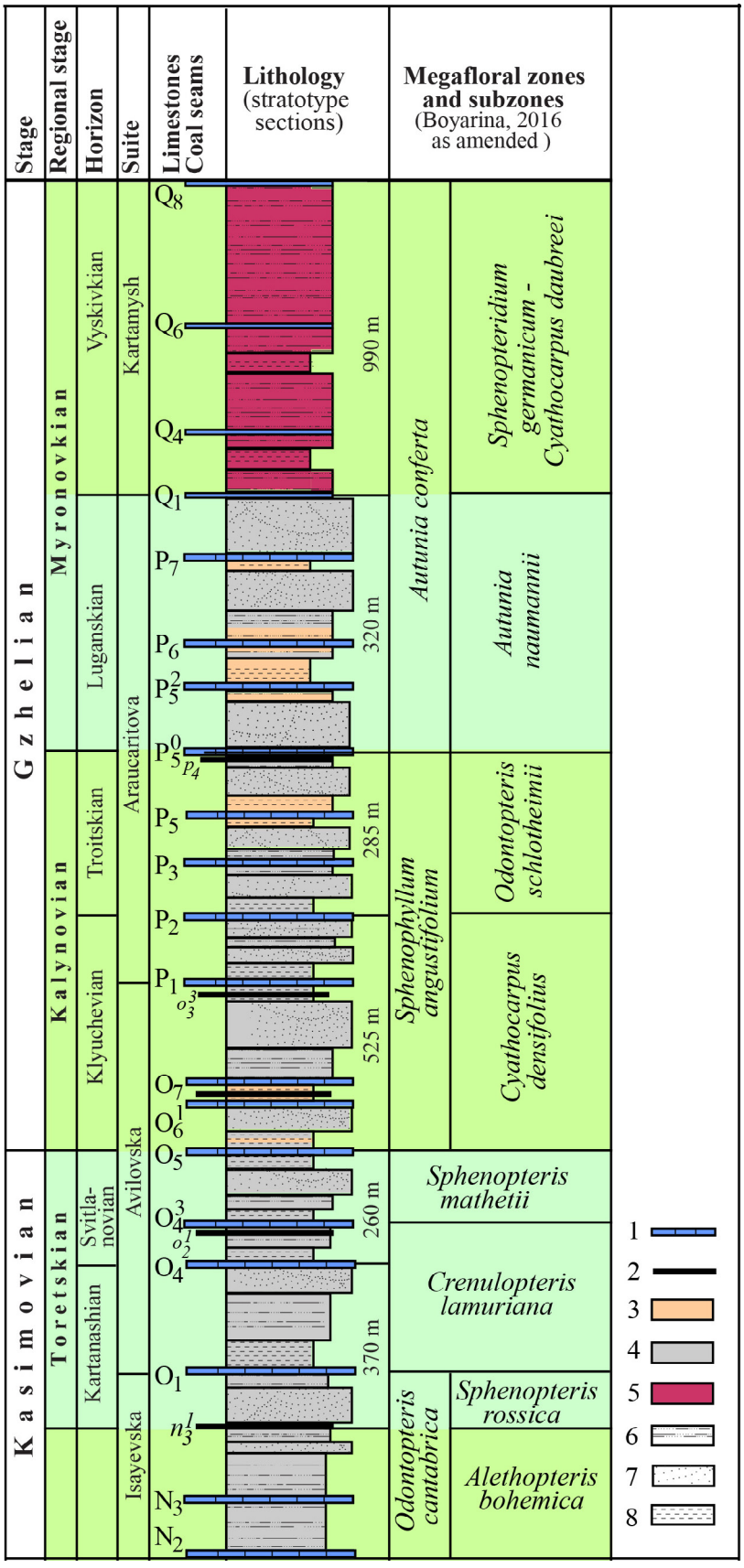

Fig. 2. Regional stratigraphical units and megafloral zones of the Upper Pennsylvanian of the Donets Basin. (*1*) limestone beds; (*2*) coal seams; (*3*) variegated beds; (*4*) grey rocks; (*5*) red bed rocks; (*6*) siltstones; (*7*) sandstones; (*8*) mudstones.

Рис. 2. Регіональні стратиграфічні підрозділи та макрофлористичні зони верхнього пенсильванію Донецького басейну. (*1*) вапнякові пласти; (*2*) вугільні прошарки; (*3*) строкатоколірні відклади; (*4*) сіроколірні породи; (*5*) червоноколірні породи; (*6*) алевроліти; (*7*) пісковики; (*8*) аргіліти.

Palaeophythosociological (palaeophytocoenological) research was carried out on the basis of 69 phytooryctocoenoses in the above-mentioned localities. The phytooryctocoenoses [Oshurkova 1974, 1987] or 'plant remain burials' after Shchogolev [1985] are sets of fossilised plant remains (fossil plant assemblages) that were buried under certain environmental conditions and are confined to rocks of specific lithology (sedimentary facies). The study of plant remains along with plant-bearing deposits was performed under the basic techniques of the analysis of phytooryctocoenoses for palaeoecological and palaeophytocoenotic interpretations that were developed by Shchogolev [1985, 1991]. The facies types were identified by the described basic terrestrial and subterrestrial types of sedimentary facies in the Carboniferous of the Donets Basin [Zhemchuzhnikov *et al.* 1960; Feofilova 1966; Borisenko 1975, 2014].

The reconstructions of plant communities were made on the basis of identifications of the floristic composition of plant fossil assemblages and the lithological and facial features of plant-bearing strata, taking into account the taphonomy of plant remains (autochthony, parautochthony, and allochthony). Megafloral data from strata less studied under lithofacial aspect are used for the palaeophytocoenological analysis too in order to obtain a more complete coverage of the vegetation composition of the Donets Basin.

The classification of Kasimovian and Gzhelian plant communities was conducted according to the ecological and floristic approach to vegetation classification by the Braun-Blanquet method described in several publications [Braun-Blanquet 1951, 1964; Whittaker 1962; Westhoff & Maarel 1973; Mirkin & Naumova 2014, 2017; Ignatiev 2016]. The classification is usally considered as consistsing of three stages: analytical, synthetic, and syntaxonomic. The study of phytooryctocoenoses and reconstruction of plant communities are related to the analytical stage. The synthetic and syntaxonomic stages include the identification and description of syntaxa.

Habitats and types of the Late Pennsylvanian vegetation of the Donets Basin

The Late Pennsylvanian plant communities have been reconstructed on the basis of plant fossil assemblages from the deposits that were interpretated as lacustrine, swamp, deltaic, floodplain and lagoonal facies. The lithological features of plant-bearing deposits indicate that the palaeophytocoenoses grew within four landscape types, namely coastal lowlands, deltaic plains, floodplains, and river valley slopes. The vegetation of coastal lowlands is reconstructed on the basis of the phytooryctocoenoses that include the remains of ferns, sphenopsids, and, less often, pteridosperms in lacustrine deposits. In the Kasimovian and lower Gzhelian, the lacustrine facies occur below limestone beds and consist of light grey unbedded mudstones with or without coal seams. The lacustrine facies with plant fossils in the upper Gzhelian (Vyskrivskian) are represented by grey unbedded mudstones intercalated with carbonate interbeds that occur between red large-scale strata. These grey intervales are interpreted as representing deposition in nearshore marine and lacustrine environments [Poletaev *et al.* 2011]. The upper Gzhelian plant fossil assemblages occur in red-brown unbedded mudstones with blue- and greenish-grey spots too. These facies are interpreted as lagoonal-lacustrine deposits. The phytooryctocoenoses including fossil subsigillarians, sphenopsids, ferns, and pteridosperms that occur in deltaic and lacustrine-deltaic deposits indicate the plant communities of deltaic plains. The deltaic facies association is restricted to the Kasimovian and lower Gzhelian. This facies association consists of light grey and greenish-grey, thinly bedded siltstones, thin grey and greenish-grey mudstone beds, fine-grained sandstones and is interpreted to represent a deltaic system [Borisenko 1975, 2014; Poletaev *et al.* 2011]. The vegetation of floodplains and river valley slopes was studied on the basis of plant fossil assemblages consisting of pteridosperms, cordaites, and conifers from fluvial deposits of the Kasimovian and lower Gzhelian. This facies association is composed of grey conglomerate beds, coar- to fine-grained sandstones, thinly to thicly bedded siltstones, rare mudstones and indicate channel and floodplain environments.

The morphological and quantitative characteristics of plant fossils and the growth forms of fossil plants indicate that the palaeophytocoenoses in different time intervals belonged to four vegetation types: coastal semi-aquatic vegetation, wetland forests, wetland woodlands, and seasonally dry woodlands. Some of them were widespread in Pennsylvanian times and are described in a number of works [e.g. DiMichele *et al*. 2001, 2005, 2009, 2010, 2014; Falcon-Lang 2003; Falcon-Lang *et al*. 2009; Bashforth *et al*. 2010; Pfefferkorn *et al*. 2017].

Syntaxonomy of the Late Pennsylvanian vegetation of the Donets Basin

The vegetation classification is based on the identification of associations that are the main units in the Braun-Blanquet classification system [Braun-Blanquet 1951, 1964]. In accordance with the Braun-Blanquet method, the major criterion for distinguishing syntaxa is their floristic composition, namely the diagnostic species, which are considered as the indicators of environmental conditions. The diagnostic species comprise characteristic and differential species. The characteristic species occur in the plant communities belonging to a single syntaxon. The differential species with a wide ecological range are common in the plant communities of several syntaxa. For the identification and characterisation of associations, phytosociological tables have been compiled. These tables are an important part of the Braun-Blanquet approach and show the quantitative data of plant fossils in all localities, arranged by abundance and constancy class of species [Braun-Blanquet 1951, 1964; Whittaker 1962; Westhoff & Maarel 1973; Mirkin & Naumova 2014, 2017; Ignatiev 2016, 2020]. In the present paper, the estimation of the abundance of a given species has been performed by the number of remains of the plants of this species in each phytooryctocoenosis: rare (1–2 specimens), common (3–8 specimens), numerous (9–15 specimens), abundant (>15 specimens). The constancy class corresponds to the percentage of phytooryctocoenoses, in which a given species is present relative to the total number of phytooryctocoenoses. In the Braun-Blanquet approach, constancy value is usually defined as: low (less than 20%), middle (21–60%) and high (61–100%). The syntaxon names in the ecological-floristic classification are given by the plant species that are present in all communities and reflect their ecology. The established associations in the Donets Basin are named by predominanting plant fossils in the phytooryctocoenoses. O. K. Shchogolev was included as the author of those associations, which were identified based on the plant fossil assemblages that he studied. The formation and typification of syntaxon names have been performed in accordance to the International Code of Phytosociological Nomenclature [Theurillat *et al*. 2021].

The various associations are typical for each of the four time intervals that correspond to regional stratigraphic units (see Fig. 2): Toretskian (Kasimovian), Kalynovian (early Gzhelian), Luganskian (middle Gzhelian) and Vyskrivskian (late Gzhelian).

1. Description of plant associations

1.1. Coastal semi-aquatic vegetation

The communities of coastal semi-aquatic plants have been studied on the basis of the plant fossil assemblages including calamitalean and sphenophyll fragments predominantly in the lacustrine deposits that occur below coal seams and within floodplain-lacustrine and lagoonal successions. The coastal semi-aquatic vegetation is represented by a single type of plant communities.

Sphenophyll-calamitalean communities of the shallow nearshore parts of lakes and lagoons were reconstructed on the basis of the remains of calamitalean leafy shoots and stems, sphenophyll leafy shoots from light grey unbedded mudstones occuring under or between coal seams (lacustrine facies), grey thinly bedded mudstones and silty mudstones lying below limestones (lacustrine-lagoonal facies that were formed under wet conditions), red thinly bedded mudstones and silty mudstones within lagoonal succession (lacustrine-lagoonal facies that were formed under seasonally dry conditions). The plant communities including sphenophylls and calamitaleans had a slighly different species composition for most of the Late Pennsylvanian, except for the late Gzhelian time, and were assigned to two associations. The names of the associations of coastal aquatic thickets are given by the species of calamitalean stems and sphenophyll leafy shoots with high and middle constancy values as well as with a high species abundance.

Association *Sphenophyllo oblongifolii–Calamitetum suckowii* Shchogolev et Boyarina ass. nov.

Toretskian, Kalynovian and Luganskian times (Tables 1–3)

Typus. Kalynove-5 (interval between the O_6 and O_7 limestone beds).

Diagnostic species. *Calamites suckowii* Brongniart, *Sphenophyllum oblongifolium* (Germar et Kaulfuss) Unger, *Calamites cistii* Brongniart, *Asterophyllites equisetiformis* (Sternberg) Brongniart, *Annularia sphenophylloides* (Zenker) Gutbier, *A. stellata* Schlotheim ex Wood, *A. mucronata* Schenk, *Sphenophyllum longifolium* (Germar) Gutbier, and *S. verticillatum* (Schlotheim) Zeiller.

Description. The association was identified by the phytooryctocoenoses from 23 localities. Both in the phytooryctocoenosis from the Kalynove-5 locality, which is the nomenclature type of this association, and in the most localities, sphenopsids occur together with ferns and pteridosperms in lacustrine and lacustrine-deltaic deposits. The rich plant assemblages in such phytooryctocoenoses include the fossil remains of both coastal semi-aquatic and terrestrial plants. Most of such assemblages are found in the Toretskian (Svitlanove-2, Svitlanove-3, Chernyshove-1, and Kalynove-2 localities) and Kalynovian (Kalynove-5 and Myronivske-1 localities) deposits. The plant assemblages with only or predominantly semi-aquatic sphenopsids and single ferns were collected in the Toretskian (borehole No. 743 and the Kalynove-3b locality), Kalynovian (Kalynove-8 and Kalynove-9 localities and borehole No. 811) and Luganskian (Luganske-3 locality) deposits. The composition of the diagnostic species of this association changed little over the Toretskian, Kalynovian and Luganskian times. These minor changes manifested in the following. The species composition of coastal semi-aquatic thickets in the Kalynovian was expanded in comparison with the Toretskian. The sphenopsids of the Luganskian differ in poorer species composition than in the Kalynovian. But at the same time, the name-giving species of this association are characterised by high and middle constancy values in all three time intervals. Among sphenopsids in all phytooryctocoenoses, the fragments of the leafy shoots of *Sphenophyllum oblongifolium*, the stems of *Calamites suckowii* and the leafy shoots of *Annularia stellata*, *Asterophyllites equisetiformis* are predominant.

Table 1. **Phytosociological table characterising the association of sphenophyll-calamitean communities of the shallow nearshore parts of lakes and lagoons in the Toretskian time**

Таблиця 1. **Фітосоціологічна таблиця, яка характеризує асоціацію угруповань клинолистів та каламітів мілких прибережних частин озер та лагун в торецький час**

Diagnostic species	Plant fossil localities								Constancy classes
	Borehole No. 743	Kalynove-2	Kalynove-3b	Svitlanove-1	Svitlanove-2	Svitlanove-3	Chernyshove-1	Volchanivka	
	Locality number								
	34	10	11	3	4	5	6	2	
	Number of species								
	7	6	2	2	5	8	5	1	
The *Sphenophyllo oblongifolii–Calamitetum suckowii* association (Toretskian)									
Calamites suckowii	r	r		r		c	r		IV
Sphenophyllum oblongifolium	r	r			r	n			III
S. longifolium						c			I
S. verticillatum	r	r			r	c			III
S. thonii subsp. *nanum*	r		c						II
S. amadokense	r						r		II
Asterophyllites equisetiformis	r	r	c				r		III
Annularia stellata		c			r	c	r	r	IV
A. sphenophylloides					r	c	r		II
A. mucronata		r				r			II
Calamites cistii				r	r	r			II
Calamostachys germanica	r								I

Legend: Number of plant remains testifying to species abundance: r, rare (1–2 specimens); c, common (3–8 specimens); n, numerous (9–15 specimens); and a, abundant (>15 specimens).
Constancy class: I, less than 20%; II, 21–40%; III, 41–60%; IV, 61–80%; V, 81–100%.

Table 2. **Phytosociological table characterising the association of sphenophyll-calamitean communities of the shallow nearshore parts of lakes and lagoons in the Kalynovian time** (legend see in Table 1)

Таблиця 2. **Фітосоціологічна таблиця, яка характеризує асоціацію угруповань клинолистів та каламітів мілких прибережних частин озер та лагун в калинівський час** (умовні позначення в Таблиці 1)

Diagnostic species	Plant fossil localities														Constancy classes
	Kalynove-5	Borehole No. 743	Kalynove-4	Kalynove-8	Kalynove-6	Kalynove-7	Borehole No. 811	Troyitske-1	Troyitske-2	Kalynove-9	Myronivske-1	Kravetska gully	Krasnyi Pahar-c	Borehole No. 239	
	Locality number														
	13	34	12	16	14	15	35	19	20	17	23	21	27	36	
	Number of species														
	5	3	1	7	1	4	7	1	3	4	6	4	3	1	
The *Sphenophyllo oblongifolii–Calamitetum suckowii* association (Kalynovian)															
Calamites suckowii	r	r		r				r			r			r	III
Sphenophyllum oblongifolium	c				c	r	r		r		r				III
S. angustifolium							r								I
S. longifolium	r			r							r	r			II
S. thonii subsp. *nanum*							r								I
S. thonii subsp. *thonii*													r		I
S. verticillatum	r														I
Calamites cistii				r			r								I
C. cruciatus										r					I
C. gigas										r					I
C. medulatus				r											I
C. multiramis													r		I
Asterophyllites equisetiformis							r		r	c	c				II
Annularia sphenophylloides		r	r	r		r					r	r			III
A. stellata	r			r		r	r			c		r			III
A. mucronata		r				r			n			r	r		II
Calamostachys tuberculata				r											I
C. germanica							r				r				I

Association *Lilpopio raciborskii –Calamitetum cistii* Boyarina ass. nov.

Vyskrivkian time (Table 3)

Typus. Klynove (below a grey mudstone bed with the Q_6 carbonate interbed).

Diagnostic species. *Calamites cistii*, *Lilpopia raciborskii* (Lilpop) Conert et Schaarschmidt, *Calamites crookensis* (Mamay et Read) Boureau, *C. vandergrachtii* Kidston et Jongmans, and *Sphenophyllum verticillatum.*

Description. The association was identified on the basis of rare plant fossils in the phytooryctocoenoses from five localities. Single sphenopsids together with ferns and pteridosperms occur in lacustrine grey siltstones and mudstones (Novgorodske and Kamyshevaha localities) and only rare sphenopsids in lacustrine-lagoon red mudstones (Klynove locality and the Kalynove quarry).

1.2. Tropical wetland forests

The wetland forest vegetation has been studied on the basis of the plant fossil assemblages from swamp, lacustrine, lacustrine deltaic, and fluvial-deltaic deposits of the Toretskian and Kalynovian regional stages. On the basis of these phytooryctocoenoses, the following plant communities were reconstructed.

Calamitalean-fern communities of the shores of lakes within coastal lowlands were reconstructed on the basis of the fragments of fern pinnae and fronds and calamitalean leafy shoots and stems from grey and light grey unbedded mudstones occuring within lagoonal-lacustrine successions with coal seams (lacustrine facies).

Table 3. **Phytosociological tables characterising the associations of sphenophyll-calamitean communities of the shallow nearshore parts of lakes and lagoons in the Luganskian and Vyskrivkian times** (legend see in Table 1)

Таблиця 3. **Фітосоціологічні таблиці, які характеризують асоціації угруповань клинолистів та каламітів мілких прибережних частин озер та лагун в луганський та вискрівський часи** (умовні позначення в Таблиці 1)

Diagnostic species	Plant fossil localities														Constancy classes
	Myronivske-2	Luganske-1b	Luganske-2b	Luganske-2c	Luganske-2d	Luganske-3	Borehole No. 741	Klynove	Kalynove quarry-a	Kalynove quarry-b	Kalynove quarry-c	Kamyshevaha	Borehole No. 4395	Novgorodske	
	Locality number														
	24	25	26	26	26	27	39	33	32	32	32	31	44	29	
	Number of species														
	1	1	1	1	1	5	4	2	3	3	1	2	1	1	
The *Sphenophyllo oblongifolii–Calamitetum suckowii* association (Luganskian)															
Calamites suckowii		r	r			r	r								III
Sphenophyllum oblongifolium						r	r								II
S. cf. *angustifolium*					r	r									II
S. longifolium							r								I
Calamites cistii	r														I
Annularia stellata						c									I
Asterophyllites equisetiformis				r		r	r								II
The *Lilpopio raciborskii–Calamitetum cistii* association (Vyskrivkian)															
Calamites cistii								r				r			II
Lilpopia raciborskii								r							I
Calamites carinatus									r						I
C. crookensis									r	r					II
C. multiramus										r					I
C. paleaceus												r			I
C. vandergrachtii									r	r					II
Sphenophyllum verticillatum											r			r	II
Asterophyllites equisetiformis													r		I

Association *Calamito suckowii–Crenulopteridetum lamurianae* Shchogolev et Boyarina ass. nov.

Toretskian time (Table 4)

Typus. Svitlanove-1b (interval between the O_4 and O_4^1 limestone beds).

Diagnostic species. *Crenulopteris lamuriana* (Heer) Wittry et al., *Calamites suckowii*, *Acitheca polymorpha* (Brongniart) Schimper, *Cyathocarpus arboreus* (Sternberg) Weiss, *C. cyatheus* (Brongniart) Mosbrugger, *C. lepidorachis* (Brongniart) Mosbrugger, *Diplazites unitus* (Brongniart) Cleal, *'Pecopteris' bredovii* Germar, *'Pecopteris' potoniei* Nemejc, *Nemejcopteris feminaeformis* (Schlotheim) Barthel, *Sphenopteris lebachensis* Weiss, *S. rossica* Zalessky, *S. svetlanovii* Shchogolev et Telichko ms., *Calamites cistii*, *Asterophyllites equisetiformis*, *Annularia mucronata*, *A. sphenophylloides*, and *A. stellata.*

Description. The association was identified on the basis of five phytooryctocoenoses from four localities. The plant assemblages include diversified ferns and calamitaleans. These fossils were mainly found in light grey mudstones that occur under or between coal seams. Only in the Kalynove-2 locality, specimens of *Crenulopteris lamuriana* were collected from dark grey mudstones. The floral assemblages are dominated by *Crenulopteris lamuriana* characterised by a high abundance and a high constancy value. The pinnae fragments of *Cyathocarpus arboreus*, *'Pecopteris' bredovii*, and *Acitheca polymorpha* are more frequent in some localities. Of the diagnostic species, *Crenulopteris lamuriana*, *Cyathocarpus arboreus*, *C. cyatheus*, *C. lepidorachis*, *'Pecopteris' bredovii*, *'Pecopteris' potoniei*, *Diplazites unitus*, *Nemejcopteris feminaeformis*, *Sphenopteris lebachensis*, *S. rossica*, and *S. svetlanovii* are characteristic species, whereas *Acitheca polymorpha* is the differential species that is known from deltaic facies too. The semi-aquatic sphenophylls are not included as diagnostic species in calamitalean-fern communities because they are the indicators of ecological condition of coastal aquatic communities.

Table 4. **Phytosociological table characterising the association of calamitean-fern communities of the lake shores within coastal lowlands in the Toretskian time** (legend see in Table 1)

Таблиця 4. **Фітосоціологічна таблиця, яка характеризує асоціацію угруповань каламітів та папоротей узбереж озер в межах прибережних рівнин в торецький час** (умовні позначення в Таблиці 1)

Diagnostic species	Plant fossil localities					Constancy classes
	Svitlanove-1b	Svitlanove-2	Svitlanove-3a	Chernyshove-1	Kalynove-2	
	Locality number					
	3	4	5	6	10	
	Number of species					
	6	8	16	11	12	
The *Calamito suckowii–Crenulopteridetum lamurianae* association (Toretskian)						
Crenulopteris lamuriana	c	n	c		c	IV
Calamites suckowii	r		r	r	r	IV
Acitheca polymorpha			c	r		II
Cyathocarpus arboreus		c			r	II
C. cyatheus		r			r	II
C. lepidorachis			r			I
'Pecopteris' bredovii	r		c	r		III
'Pecopteris' potoniei		r				I
Diplazites unitus		r	r			II
Nemejcopteris feminaeformis	r			r	r	III
Sphenopteris rossica	r		r	r	r	IV
S. lebachensis					r	I
S. svetlanovii			r			I
Calamites cistii	r	r	r	r		IV
Asterophyllites equisetiformis				r	r	II
Annularia stellata			r	r	c	III
A. mucronata			r		r	II
A. sphenophylloides		r	r	r		III
Sphenophyllum longifolium			r			I
S. oblongifolium			r		r	II
S. verticillatum		r	r		r	III
S. amadokense				r		I
Neuropteris ovata			r	c		II

Association *Calamito suckowii–Cyathocarpetum densifoliae* Shchogolev et Boyarina ass. nov.
Kalynovian time (Table 5)

Typus. Borehole No. 239 (depth 206,3 m, interval between the O_5 and O_6 limestone beds).

Diagnostic species. *Cyathocarpus densifolius* (Goeppert) Šimůnek et Ploch, *Calamites suckowii*, *Acitheca polymorpha*, *Cyathocarpus arboreus*, *C. cyatheus*, *C. hemitelioides* (Brongniart) Mosbrugger, *'Pecopteris' jongmansii* Wagner, *'Pecopteris' platonii* Grand'Eury, *'Pecopteris' truncata* (Rost) Germar, *Diplazites unitus*, *Nemejcopteris feminaeformis*, *Annularia mucronata*, *A. sphenophylloides*, *A. stellata*, *Asterophyllites equisetiformis*, *Calamostachys germanica* Weiss, and *Odontopteris cantabrica* Wagner.

Description. The association was identified by six phytooryctocoenoses from five localities. The fossil assemblages were found in the lacustrine mudstones occuring under or between coal seams. The dominant plant fossils are *Cyathocarpus densifolius*, *C. cyatheus*, and *C. arboreus* that are characteristic species too. In three localities, rare or common odontopterids together with ferns and calamitaleans are found in grey mudstones above the o_3^3 coal seam (Kalynove-7b) and in mudstone beds under coal seams (Kalynove-5 and Kalynove-7a). The pteridosperm *Odontopteris cantabrica* from these lacustrine deposits is considered as the diagnostic species of this syntaxon because it is not known in other facies, and, consequently, could have been the part of only calamitalean-fern-communities that grow near the lakes within coastal lowlands. The sphenophylls are not included as diagnostic species in calamitalean-fern-communities.

Table 5. **Phytosociological table characterising the association of calamitean-fern communities of the lake shores within coastal lowlands in the Kalynovian time** (legend see in Table 1)

Таблиця 5. **Фітосоціологічна таблиця, яка характеризує асоціацію угруповань каламітів та папоротей узбереж озер в межах прибережних рівнин в калинівський час** (умовні позначення в Таблиці 1)

Diagnostic species	Plant fossil localities						Constancy classes
	Borehole No. 239	Kalynove-4b	Kalynove-5	Kalynove-7a	Kalynove-7b	Myronivske-1	
	Locality number						
	36	12	13	15	15	23	
	Number of species						
	3	6	6	7	3	8	
The *Calamito suckowii–Cyathocarpetum densifoliae* association (Kalynovian)							
Cyathocarpus densifolius	r	c	r	c	r		V
Calamites suckowii	r		r			r	III
Acitheca polymorpha		r					I
Cyathocarpus arboreus		r	r			c	III
C. cyatheus		r				n	II
C. hemitelioides						r	I
'Pecopteris' jongmansii		r					I
'Pecopteris' platonii				r			I
'Pecopteris' truncata					r		I
Diplazites unitus				r		r	II
Nemejcopteris feminaeformis			r				I
Annularia mucronata				r			I
A. sphenophylloides		r		r		r	III
A. stellata	r		r	r			III
Asterophyllites equisetiformis						c	I
Calamostachys germanica						r	I
Odontopteris cantabrica			r	c	r		III

Fern-pteridosperm communities of coastal lowlands were reconstructed on the basis of the fragments of fern and pteridosperm pinnae and fronds from light grey and grey unbedded to thinly bedded mudstones and siltstones within lagoonal-lacustrine successions without coal seams (lacustrine facies). The depositional environment of these strata is interpreted as parts of lowlands remote from the coastline.

Association *Neuropteridetum ovatae* Shchogolev et Boyarina ass. nov.

Toretskian time (Table 6)

Typus. Gully near the village of Volchanivka (below the O_1 limestone bed).

Diagnostic species. *Neuropteris ovata* Hoffmann, *Dicksoniites sterzelii* Zeiller, *Crenulopteris lamuriana*, *Acitheca polymorpha*, *'Pecopteris' bredovii*, *'Pecopteris' paleacea* Zeiller, *Nemejcopteris feminaeformis*, *Sphenopteris rossica*, *Calamites cistii*, *C. suckowii*, *Asterophyllites equisetiformis*, *Annularia mucronata*, *A. stellata*, and *A. sphenophylloides.*

Description. The association was identified on the basis of the phytooryctocoenoses from five localities. The plant remains occur in mudstone and siltstone beds and mudstones intercalated with siltstones within lacustrine and lagoonal-lacustrine strata. They consist predominantly of *Neuropteris ovata* pteridosperms with less common calamitaleans and ferns of rich species diversity. Such composition of assemblages indicates that the pteridosperms *Neuropteris ovata* with a high species abundance were widespread within coastal lowlands along with ferns and sphenopsids with a low species abundance.

Table 6. **Phytosociological table characterising the association of pteridosperm-fern communities of coastal lowlands in the Toretskian time** (legend see in Table 1)

Таблиця 6. **Фітосоціологічна таблиця, яка характеризує асоціацію угруповань птеридоспермів та папоротей прибережних рівнин в торецький час** (умовні позначення в Таблиці 1)

Diagnostic species	Plant fossil localities					Constancy classes
	Volchanovka	Kalynove-1	Chernyshove-1	Svitlanove-3b	Memrik gully	
	Locality number					
	2	9	6	5	18	
	Number of species					
	5	3	8	3	2	
The *Neuropteridetum ovatae* association (Toretskian)						
Neuropteris ovata	a	c	n	c	r	V
Dicksoniites sterzelii	r					I
Crenulopteris lamuriana		c				I
Acitheca polymorpha			r	r		II
'Pecopteris' bredovii			r		r	II
'Pecopteris' paleacea	r					I
Nemejcopteris feminaeformis			r			I
Sphenopteris rossica			r		r	II
Calamites cistii				r		I
C. suckowii			r			I
Asterophyllites equisetiformis			r			I
Annularia mucronata	r					I
A. stellata	r		r			II
A. sphenophylloides			r			I

Lycopsid-fern-pteridosperm-calamitalean communities of deltaic plains were reconstructed on the basis of parautochthonous and less represented allochthonous remains of subsigillarian stems, fern and pteridosperm pinnae, calamitalean leafy shoots and stems in light grey and greenish-grey, thinly bedded siltstones interbedded with cross-bedded siltstones and fine-grained sandstones that underlie limestone beds (lacustrine deltaic and deltaic facies). The well-preserved fragments of fern, pteridosperm and calamitalean foliage that are concentrated in horizontally bedded siltstones indicate the plant growth within original habitats (parautochthonous floral assemblages). The portions of subsigillarian stems, small parts of fern and pteridosperm pinnae and isolated pteridosperm pinnules in siltstone beds within proluvial-deltaic successions constitute allochthonous plant assemblages.

Association *Subsigillario biangulae–Acithecetum polymorphae* Shchogolev et Boyarina ass. nov.

Toretskian time (Table 7)

Typus. Kalynove-3a (interval between the O_4^6 and O_5 limestone beds).

Diagnostic species. *Acitheca polymorpha*, *Subsigillaria biangula* (Weiss) Shchogolev, *S. halensis* (Weiss) Shchogolev, *S. sulcata* Shchogolev, *S. weissii* Shchogolev, *Syringodendron angustum* Shchogolev, *S. brardii* Shchogolev, *Sigillariophylloides* sp., *Cyathocarpus* cf. *candolleanus* (Brongniart) Weiss, *'Pecopteris'* aff. *mironovana* Zalessky et Tschirkova, *Calamites* sp., *Annularia stellata*, *A. sphenophylloides*, *Neurodontopteris auriculata* (Brongniart) Potonié, *Barthelopteris germarii* (Giebel) Zodrow et Cleal, and *Odontopteris* cf. *schlotheimii* Brongniart.

Description. The association was identified on the basis of the phytooryctocoenoses from five localities. The plant fossils occur in siltstones and fine-grained sandstones within deltaic and proluvial-deltaic successions. All plant assemblages include the fragments of subsigillarians. The phytooryctocoenosis in the Kalynove-3a locality, which is the nomenclatural type of this association, occurs in the strata consisting of intercalated siltstone and fine-grained sandstone beds that are interpeted as deltaic and proluvial-deltaic deposits. This plant assemblage includes the numerous fragments of *Acitheca polymorpha* pinnnae in siltstone beds, as well as the rare remains of subsigillarians, calamitaleans, pteridosperms, and ferns in fine-grained sandstones.

Table 7. **Phytosociological table characterising the association of lycopsid-fern-pteridosperm-calamitean communities of deltaic plains in the Toretskian time** (legend see in Table 1)

Таблиця 7. **Фітосоціологічна таблиця, яка характеризує асоціацію угруповань плаунових, папоротей, птеридоспермів та каламітів дельтових рівнин в торецький час** (умовні позначення в Таблиці 1)

Diagnostic species	Plant fossil localities					Constancy classes
	Kalynove-3a	Kartanash-c	Chernyshove-3	Svitlanove-1a	Svitlanove-3c	
	Locality number					
	11	1	8	3	5	
	Number of species					
	12	1	2	2	2	
The *Subsigillario biangullae–Acithecetum polymorphae* association (Toretskian)						
Acitheca polymorpha	n			r		II
Subsigillaria biangula	r					I
S. halensis					r	I
S. sulcata		r				I
S. weissii				r	r	II
Syringodendron angustum			r			I
S. brardii	r		r			II
Sigillariophylloides sp.	r					I
Cyathocarpus cf. *candolleanus*	r					I
'Pecopteris' aff. *mironovana*	r					I
Calamites sp.	r					I
Annularia stellata	r					I
A. sphenophylloides	r					I
Neurodontopteris auriculata	r					I
Barthelopteris germarii	r					I
Odontopteris cf. *schlotheimii*	r					I

Association *Subsigillario brardii–Odontopteridetum schlotheimii* Boyarina ass. nov.

Kalynovian time (Table 8)

Typus. Krasnyi Pahar-b (below the P_4 limestone bed).

Diagnostic species. *Odontopteris schlotheimii*, *Subsigillaria brardii* (Brongniart) Weiss emend. Shchogolev, *S. donetciana* Shchogolev, *S. fimbriata* Shchogolev, *S. simplex* Shchogolev, *Syringodendron brardii*, *Sigillariostrobophyllum* sp., *Neuropteris crassinervis* Shchogolev ms., *Neurodontopteris auriculata*, *Barthelopteris germarii*, *Cyathocarpus densifolius*, *C. hemitelioides*, *'Pecopteris' jongmansii*, *'Pecopteris' mironovana*, *'Pecopteris' paleacea*, *'Pecopteris' platonii* Grand'Eury, *'Pecopteris' potoniei* Nemejc, *Remia* aff. *pinnatifida* (Gutbier) Knight emend. Cleal, *Sphenopteris rossica*, *Calamites* cf. *schutzeiformis* Kidston et Jongmans, *C. suckowii*, *Annularia mucronata*, *A. sphenophylloides*, *A. stellata*, *Asterophyllites equisetiformis*, *Cordaites principalis* (Germar) Geinitz.

Description. The association was identified on the basis of nine phytooryctocoenoses from seven localities. The plant remains were discovered in siltstones, sandstones and less frequently in mudstones that are interpreted as lacustrine-deltaic, deltaic and proluvial-deltaic deposits. One from these phytooryctocoenoses (Krasnyi Pahar-a) include *Calamites* sp., *Annularia mucronata*, *Sphenophyllum* cf. *thonii* Mahr, *'Pecopteris' paleacea*, *'Pecopteris' potoniei* in grey unbedded lacustrine-lagoonal siltstones that contain numerous freshwater pelecypods too. The plant fossils in the Krasnyi Pahar-b locality were found in the green-grey siltstones from a lacustrine-deltaic succession. This plant assemblage is dominated by the foliage of *Odontopteris schlotheimii*. The other assemblages are predominantly represented by rare remains of subsigillarians, pteridosperms, ferns, and calamitaleans. It indicates that the plant communities of deltaic plains had a rich and diverse species composition. Of the diagnostic species of this association, subsigillarian species, the pteridosperms of *Odontopteris schlotheimii*, *Neuropteris crassinervis*, *Neurodontopteris auriculata*, *Barthelopteris germarii*, the ferns

of *'Pecopteris' mironovana*, *'Pecopteris' paleacea*, and *'Pecopteris' platonii* are characteristic species. The ferns of *Cyathocarpus densifolius*, *C. hemitelioides*, *'Pecopteris' jongmansii*, *'Pecopteris' potoniei*, *Sphenopteris rossica* and calamitaleans are differential species because they were part of the plant communities of coastal lowlands too.

Table 8. **Phytosociological table characterising the association of lycopsid-fern-pteridosperm-calamitean communities of deltaic plains in the Kalynovian time** (legend see in Table 1)

Таблиця 8. **Фітосоціологічна таблиця, яка характеризує асоціацію угруповань плаунових, папоротей, птеридоспермів та каламітів дельтових рівнин в калинівський час** (умовні позначення в Таблиці 1)

Diagnostic species	Plant fossil localities									Constancy classes
	Krasnyi Pahar-a	Krasnyi Pahar-b	Kalynove-4a	Kalynove-6	Borehole No. 7168	Troyitske-1a	Troyitske-1b	Troyitske-2c	Kravetska gully	
	Locality number									
	22	22	12	14	38	19	19	20	21	
	Number of species									
	3	6	5	4	2	2	3	1	7	
The *Subsigillario brardii–Odontopteridetum schlotheimii* association (Kalynovian)										
Odontopteris schlotheimii		a		r	r					II
Subsigillaria brardii		r			r					II
S. donetciana			r							I
S. fimbriata									r	I
S. simplex								r		I
Syringodendron brardii						r				I
Sigillariostrobophyllum sp.									r	I
Neuropteris crassinervis				r			r			II
Neurodontopteris auriculata							r			I
Barthelopteris germarii	r	r	r							II
Cyathocarpus densifolius				r						I
C. hemitelioides	r									I
'Pecopteris' jongmansii			r							I
'Pecopteris' mironovana			r							I
'Pecopteris' paleacea		r								I
'Pecopteris' platonii				r						I
'Pecopteri' potoniei		r								I
Remia aff. *pinnatifida*									r	I
Sphenopteris rossica									r	I
Calamites cf. *schutzeiformis*						r				I
C. suckowii							r			I
Annularia mucronata	r	r							r	II
A. sphenophylloides									r	I
A. stellata									r	I
Asterophyllites equisetiformis					r					I
Cordaites principalis			r							I

Calamitalean-fern community of the shores of lakes within deltaic plains was reconstructed on the basis of the fragments of calamitaleans and ferns from grey thinly bedded mudstones that occur in a deltaic succession underlying limestones (lacustrine facies).

Association *Annularia mucronatae–'Pecopteridetum' paleaceae* Boyarina ass. nov.

Kalynovian time

Typus. Krasnyi Pahar-c (below the P_4 limestone bed).

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

Description. The association was identified on the basis of one plant assemblage from lacustrine light-grey mudstones occuring in a lacustrine-deltaic succession. This assemblage includes the common remains of *Annularia mucronata*, *'Pecopteris' paleacea* and the single small fragments of the *Calamites multiramis* stems and the *Odontopteris schlotheimii* pinnae.

1.3. Tropical wetland woodlands

The wetland woodlands have been identified on the basis of the sporadic phytooryctocoenoses from Luganskian lacustrine and deltaic deposits and Vyskrivskian lacustrine-lagoonal deposits. The fossil assemblages include the rare remains of ferns, calamitaleans and pteridosperms. The occasional plant-bearing beds that contain single plant fossils in a context of the reduction in the number of coal seams in the Luganskian section and the predominance of red rocks in the Vyskrivskian section may indicate the spread of low-density forests, which are referred to as woodlands in modern geobotany. The absence of dense forests and the related lack of a significant peat accumulation in the Luganskian (middle Gzhelian) and Vyskrivskian (late Gzhelian) times are in agreement with an increasing climate aridization in the Late Pennsylvanian [Fielding *et al.* 2008; DiMichele *et al.* 2009; Pfefferkorn *et al.* 2017]. The reconstructed plant communities belong to the following types.

Calamitalean-fern communities of the shores of lakes within coastal lowlands were reconstructed on the basis of the small fragments of fern pinnae and calamitean stems from the grey and bluish-grey, thinly bedded mudstones in the lagoonal succession between limestones in the Luganskian, as well as from the grey and dark-grey, vaguely laminated mudstones intercalated with carbonate interbeds in the Vyskrivskian (lacustrine facies).

Association *Calamito–'Pecopteridetum' jongmansii* Boyarina et Shchogolev ass. nov.

Luganskian time

Typus. Luganske-4 (interval between the P_6 and P_6^2 limestone beds).

Diagnostic species. *'Pecopteris' jongmansii*, *Calamites* sp., *Cyathocarpus daubreei* (Zeiller) De Stefani, *'Pecopteris' martinezii* Stockmans et Willière, *'Pecopteris' monyi* Zeiller, *'Pecopteris' oreopteridia* (Schlotheim) Sternberg, *Sphenopteris* cf. *castelli* Zeiller, and *S. fayolii-mathetii* Zeiller.

Description. The association was identified on the basis of one phytooryctocoenosis in the Luganske-4 locality. The plant remains were found in grey to bluish-grey mudstones that occur in the lagoonal succeession consisting of an intercalation of grey mudstones, brown-grey siltstones and grey fine-grained sandstones. The fossils are represented by rare plant remains, except for the commom remains of the *'Pecopteris' jongmansii* pinnae.

Association *Calamito crookensis–Cyathocarpetum daubreei* Boyarina ass. nov.

Vyskrivskian time (Table 9)

Typus. The Kalynove quarry-a (interval between two grey mudstone beds with the Q_4 and Q_6 carbonate interbeds).

Diagnostic species. *Cyathocarpus daubreei*, *Calamites crookensis* Mamay et Read, *Cyathocarpus arboreus*, *C. hemitelioides*, *Pecopteris plumosa* (Artis) Brongniart, *'Pecopteris' bredovii*, *'Pecopteris' jongmansii*, *'Pecopteris' martinezi*, *'Pecopteris' obliquenervis* Corsin, *'Pecopteris' potoniei*, *'Pecopteris' truncata*, *'Pecopteris'* cf. *viannae* Teixeira, *Diplazites unitus*, *Sphenopteris* cf. *fayolii*, *Calamites carinatus* Sternberg, *C. multiramus*, *C. vandergrachtii* Kidston et Jongmans, and *Asterophyllites equisetiformis.*

Description. The association was identified on the basis of four phytooryctocoenoses from three localities. The fossils are presented by charred plant remains in dark grey mudstones (Kalynove quarry-a), compressed plant remains with brown organic matter in lacustrine light grey unbedded mudstones (Kalynove quarry-b) and lacustrine-lagoonal grey, vaguely laminated siltstones (Novgorodske). The taxonomically diverse plant assemblage from the Kalynove quarry-a locality is represented by rare fossils (low species abundance), except for the numerous specimens of *Cyathocarpus daubreei*. In other two localities, rare plant remains belong only to a few taxa.

Pteridosperm-fern-calamitalean communities of deltaic plains were reconstructed on the basis of the remains of fern and pteridosperm pinnae and calamitean stems from greenish-grey mudstones and siltstones within lagoonal-deltaic successions (lacustrine-deltaic and deltaic facies).

Table 9. **Phytosociological table characterising the association of calamitean-fern communities of the lake shores within coastal lowlands in the Vyskrivkian time** (legend see in Table 1)

Таблиця 9. **Фітосоціологічна таблиця, яка характеризує асоціацію угруповань каламітів та папоротей узбереж озер в межах прибережних рівнин в вискрівський час** (умовні позначення в Таблиці 1)

Diagnostic species	Plant fossil localities				Constancy classes
	Kalynove quarry-a	Kalynove quarry-b	Borehole No. 4395	Novgorodske	
	Locality number				
	32	32	44	29	
	Number of species				
	9	7	2	4	
The *Calamito crookensis–Cyathocarpetum daubreei* association (Vyskrivkian)					
Cyathocarpus daubreei	n				II
Calamites crookensis	r	r			III
Cyathocarpus arboreus		r			II
C. hemitelioides		r			II
'Pecopters' bredovii	r		r		III
'Pecopters' jongmansii	r				II
'Pecopters' martinezi	r				II
'Pecopters' obliquenervis				r	II
Pecopters plumosa		r		r	III
'Pecopters' potoniei	r				II
'Pecopters' truncata				r	II
'Pecopters' cf. *viannae*	r	r			III
Diplazites unitus				r	II
Sphenopteris cf. *fayolii*	r				II
Calamites carinatus	r				II
C. multiramus		r			II
C. vandergrachtii		r			II
Asterophyllites equisetiformis			r		II

Association *Neuropterido crassinervis–'Pecopteridetum' arcuatae* Shchogolev et Boyarina ass. nov.

Luganskian time (Table 10)

Typus. Luganske-1a (below the P_6 limestone bed).

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

Description. The association was identified on the basis of two phytooryctocoenoses in the Luganske-1 locality. The fossils occur in greenish-grey siltstones with mudstone beds (Luganske-1a, lacustrine-deltaic deposits) and in vaguely laminated micaceous siltstones (Luganske-1b, deltaic deposits). The plant remains of *Neuropteris crassinervis* are predominated in these two assemblages.

Pteridosperm-fern communities of coastal lowlands were reconstructed on the basis of the small fragments of fern and pteridosperm pinnae in the grey to greenish-grey mudstones intercalated with carbonate interbeds (lacustrine facies).

Association *Odontopterido schlotheimii–'Pecopteridetum' bredovii* Boyarina ass. nov.

Vyskrivskian time (Table 10)

Typus. Borehole No. 4377 (interval between two grey mudstone beds with the Q_4 and Q_7 carbonate interbeds).

Diagnostic species. *Odontopteris schlotheimii, 'Pecopteris' bredovii*, *'Pecopteris' monyi, Polymorphopteris subelegans* (Potonié) Wagner, *Nemejcopteris feminaeformis*, *Odontopteris subcrenulata* (Rost) Zeiller, *Barthelopteris germarii*, *Calamites cistii*, and *C. paleaceus* Stur.

Description. The association was identified on the basis of the phytooryctocoenoses from two localities. The rare plant fossils are found in lacustrine greenish-grey mudstones (borehole No. 4377)

and grey mudstones with varvelike laminations within the grey mudstone bed with the Q_3 carbonate interbed (Kamyshevaha locality). The plant remains of *'Pecopteris' bredovii* and *Odontopteris schlotheimii* are present in two phytooryctocoenoses.

Table 10. **Phytosociological tables characterising the associations of pteridosperm-fern-calamitean communities of deltaic plains in the Luganskian time and pteridosperm-fern-communities of coastal lowlands in the Vyskrivkian time** (legend see in Table 1)

Таблиця 10. **Фітосоціологічні таблиці, які характеризують асоціації угруповань птеридоспермів, папоротей та каламітів дельтових рівнин в луганський час та угруповань птеридоспермів і папоротей прибережних рівнин у вискрівський час** (умовні позначення в Таблиці 1)

Diagnostic species	Plant fossil localities				Constancy classes
	Luganske-1a	Luganske-1b	Borehole No. 4377	Kamyshevaha	
	Locality number				
	25	25	45	31	
	Number of species				
	3	3	3	8	
The *Neuropterido crassinervis–'Pecopteridetum' arcuatae* association (Luganskian)					
Neuropteris crassinervis	n	a			V
'Pecopteris' arcuata	a				III
Neurodontopteris auriculata		r			III
Calamites suckowii		r			III
Calamites sp.	r				III
The *Odontopterido schlotheimii–'Pecopteridetum' bredovii* association (Vyskrivkian)					
Odontopteris schlotheimii			r	r	V
'Pecopteris' bredovii			r	r	V
'Pecopteris' monyi			r		III
Polymorphopteris subelegans				r	III
Nemejcopteris feminaeformis				r	III
Odontopteris subcrenulata				r	III
Barthelopteris germarii				r	III
Calamites cistii				r	III
C. paleaceus				r	III

1.4. Tropical seasonally dry woodlands

The seasonally dry woodlands are reconstructed on the basis of phytooryctocoenoses that are represented by the following: the small parts of cordaite leaves and conifer shoots from floodplain and channel deposits (allochthonous remains) in the Toretskian, Kalynovian and Luganskian; the well-preserved fragments of peltaspermalean pteridosperm fronds and pinnae from floodplain-lacustrine deposits (parautochthonous remains) and small portions of pteridosperm pinnae and isolated pinnules from floodplain deposits (allochthonous floral assemblages) in the Luganskian; the small fragments of pteridosperm and fern pinnae as well as calamitaleans from lacustrine-lagoonal red-brown mudstone deposits (parautochthonous remains) and the small allochthonous remains of conifer shoots from lacustrine-lagoonal red-brown siltstone deposits intercalated with sandstones in the Vyskrivian. These macrofossils indicate that seasonally dry woodlands in the Donets Basin were widespread within fluvial landscapes during the Late Pennsylvanian time and had occupied coastal plains only at the end of the Pennsylvanian. The following communities are related to seasonally dry woodlands.

Pteridosperm-cordaitalean communities of floodplains and river valley slopes were reconstructed on the basis of the allochthonous fragments of pteridosperm pinnae, cordaitalean leaves and coniferous branches from the light-grey and greenish-grey, thinly to thicly bedded micaceous siltstones, fine-grained sandstones and silty sandstones occurring within intercalated siltstone and sandstone beds of fluvial successions (floodplain facies).

Association *Cordaito–Odontopteridetum subcrenulatae* Shchogolev et Boyarina ass. nov.

Toretskian and Kalynovian times (Table 11)

Typus. Kartanash-b (interval between the n_3^1 coal seam and the N_5^1 limestone bed).

Diagnostic species. *Odontopteris subcrenulata*, *Cordaites* sp., *C.* cf. *borassifolia* (Sternberg) Unger, and *Odontopteris naumichana* Zalessky.

Description. The association was identified on the basis of three phytooryctocoenoses from Toretskian (Kartanash-b) and Kalynovian (borehole No. 741, Troitske-2b) deposits. The Toretskian and Kalynovian plant assemblages from fluvial successions include the rare plant fossils of two name-giving species for this association. The plant remains are collected in floodplain and proluvial-floodplain strata that are comprised of ligth-grey, fine- to middle-bedded, horizontally- and cross-laminated siltstones occuring above channel middle- and coarse-grained, cross-laminated sandstones (Kartanash-b) and in fine- to middle-grained sandstones (Troitske-2b).

Table 11. **Phytosociological tables characterising the associations of pteridosperm-cordaitean communities of floodplains and river valley slopes in the Toretskian and Kalynovian times and pteridosperm-communities of floodplains in the Luganskian time** (legend see in Table 1)

Таблиця 11. **Фітосоціологічні таблиці, які характеризують асоціації угруповань птеридоспермів та кордаїтів заплав та схилів річкових долин в торецький та калинівський часи та угруповань птеридоспермів заплав в луганський час** (умовні позначення в Таблиці 1)

Diagnostic species	Plant fossil localities						Constancy classes
	Kartanash-b	Borehole No. 741	Troyitske-2b	Luganske-2g	Luganske-2b	Myronivske-2	
	Locality number						
	1	39	20	26	26	24	
	Number of species						
	7	2	2	10	6	7	
The *Cordaito–Odontopteridetum subcrenulatae* association (Toretskian and Kalynovian)							
Odontopteris subcrenulata	c	r	r				IV
Cordaites sp.	r	r	r				IV
C. cf. *borassifolia*	r						II
Odontopteris naumichana	r						II
Samaropsis pinnata	r						II
S. var. *acuminata*	r						II
Dadoxylon sp.	r						II
The *Lodevio suberosae–Odontopteridetum subcrenulatae* association (Luganskian)							
Odontopteris subcrenulata				c		r	IV
Lodevia suberosa				r	r		IV
Odontopteris brardii						r	II
O. schlotheimii				r		r	IV
Autunia conferta				c			II
A. naumannii				c			II
Lodevia nicklesii				c			II
L. luganica				r			II
Dichophyllum cuneatum				c			II
D. flabelliferum				r			II
Neurocallipteris cf. *planchardii*					r		II
Neurodontopteris auriculata					c		II
Sphenocallipteris scythica						r	II
Calamites cistii						r	II
C. suckowii					r		II
'Pecopteris' cf. *platonii*						r	II
Otovicia hypnoides						r	II
Culmitzschia frondosa					r		II
Cordaites sp.				r	r		IV

Association *Lodevio suberosae–Odontopteridetum subcrenulatae* Boyarina et Shchogolev ass. nov.

Luganskian time (Table 11)

Typus. Luganske-2g (below the P_6 limestone bed).

Diagnostic species. *Odontopteris subcrenulata*, *Lodevia suberosa* (Sterzel) Haubold et Kerp, *Neurodontopteris auriculata*, *Neurocallipteris* cf. *planchardii* (Zeiller) Cleal, Shute et Zodrow, *Odontopteris brardii* (Brongniart) Brongniart, *O. schlotheimii, Autunia conferta* (Sternberg) Kerp, *A. naumannii* (Gutbier) Kerp, *Dichophyllum cuneatum* Boyarina, *D. flabelliferum* (Weiss) Kerp et Haubold, *Lodevia nicklesii* (Zeiller) Haubold et Kerp, *L. luganica* (Boyarina et Shchogolev) Boyarina, *Sphenocallipteris scythica* (Zalessky) Kryshtofovich et Novik, *'Pecopteris'* cf. *platonii*, *Calamites cistii*, *C. suckowii*, *Cordaites* sp., *Otovicia hypnoides* (Brongniart) Kerp, Poort, Swinkels et Verwer, and *Culmitzschia frondosa* (Renault) Clement-Westerhof.

Description. The association was identified on the basis of three phytooryctocoenoses from two localities. The plant assemblages with predominantly rare remains are characterised by a rich species composition. The plant fossils occur in greenish-grey vaguely to thinly bedded mudstone and siltstone beds within a floodplain succession consisting of an intercalation of mudstones, siltstones and fine-grained sandstones. These data indicate that in the Luganskian time the plant communities of floodplains and river valley slopes continued to include odontopterid pteridosperms and cordaiteans, as well as were replenished with peltaspermean pteridosperms.

Pteridosperm communities of floodplains were reconstructed on the basis of the fragments of pteridosperm fronds and pinnae from light-grey and greenish-grey, vaguely to thinly bedded siltstones and mudstones intercalated with fine-grained sandstones and silty sandstones (floodplain-lacustrine facies).

Association *Lodevio nicklesii–Autunietum naumannii* Boyarina et Shchogolev ass. nov.

Luganskian time (Table 12)

Typus. Luganske-2d (below the P_6 limestone bed).

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

Description. The association was identified on the basis of three phytooryctocoenoses from the Luganske-2a, Luganske-2d, and Luganske-2e localities. The floral assemblages are dominated by *Autunia naumannii* and *Lodevia nicklesii*. They were collected in floodplain-lacustrine greenish-grey mudstones, siltstones with mudstone beds, mudstones intercalated with siltstones an*d* fine-grained sandstones. The peltaspermean pteridosperms *Autunia naumannii, A. conferta*, *Lodevia nicklesii* and *L. luganica* are characterised by high species abundance and constancy values.

Calamitalean-fern-pteridosperm community of the shores of floodplain lakes was reconstructed on the basis of the well-preserved remains of pteridosperm and fern fronds and pinnae, calamitalean leafy shoots from the greenish-grey massive unbedded mudstones (lacustrine facies) that occur within a floodplain succession consisting of greenish-grey, vaguely to thinly bedded siltstone and mudstone beds.

Association *'Pecopterido' bredovii–Raminervietum mariopteroidis* Boyarina ass. nov.

Luganskian time

Typus. Luganske-2c (below the P_6 limestone bed).

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

Description. The association was identified on the basis of a single phytooryctocoenosis in the Luganske-2c locality. Abundant callipterids *Raminervia mariopteroides* and a few fragments of fern pinnae were found in the greenish-grey unbedded mudstones that are interpreted as lacustrine facies.

Table 12. **Phytosociological tables characterising the associations calamitean-fern-pteridosperm communities of the shores of floodplain lakes in the Luganskian time and fern-pteridosperm-communities of lake-lagoon coasts in the Vyskrivkian time** (legend see in Table 1)

Таблиця 12. **Фітосоціологічні таблиці, які характеризують асоціації угруповань каламітів, папоротей і птеридоспермів узбереж заплавних озер в луганський час та угруповань папоротей і птеридоспермів озерно-лагунних узбереж в вискрівський час** (умовні позначення в Таблиці 1)

Diagnostic species	Plant fossil localities								Constancy classes
	Luganske-2d	Luganske-2a	Luganske-2e	Kalynove quarry-c	Borehole No. 4395	Keramic quarry	Borehole No. 4377	Borehole No. 4385	
	Locality number								
	26	26	26	32	44	30	45	46	
	Number of species								
	8	4	5	4	2	3	2	1	
The *Lodevio nicklesii–Autunietum naumannii* association (Luganskian)									
Autunia naumannii	a	c	c						V
Lodevia nicklesii	a	c							IV
Autunia conferta	r	r							IV
Lodevia luganica	r	r	r						V
L. suberosa	r								II
Dichophyllum cuneatum	r								II
Odontopteris lingulata			r						II
O. subcrenulata	r								II
Neurocallipteris planchardii	r								II
Neurodontopteris auriculata			r						II
Polymorphopteris subelegans			r						II
The *Sphenopteridio germanici–Cyathocarpetum daubreei* association (Vyskrivkian)									
Cyathocarpus daubreei				c	r	r			III
Sphenopteridium germanicum				r					I
Sphenocallipteris scythica							r		I
Cyathocarpus arboreus					r		r		II
'Pecopteris' bioti						r			I
'Pecopteris' jongmansii						r		r	II
Polymorphopteris subelegans				r					I
Calamites sp.				r					I

Pteridosperms *Raminervia mariopteroides* together with ferns were a part of the plant community that grew on the shores of floodplain lakes. *Raminervia mariopteroides* is a characteristic species of the association because it was not found in other phytooryctocoenoses.

Pteridosperm-fern communities of shores of lagoons and lakes were reconstructed on the basis of the small fragments of fern and pteridosperm pinnae, calamitalean leafy shoots and stems from the red-brown unbedded, occasionally lumpy mudstones with blue- and greenish-grey spots that occur in thick red siltstone and mudstone strata (lacustrine-lagoonal facies).

Association *Sphenopteridio germanici–Cyathocarpetum daubreei* Boyarina ass. nov.

Vyskrivskian time (Table 12)

Typus. Kalynove quarry (interval between two grey mudstone beds with the Q_4 and Q_6 carbonate interbeds).

Diagnostic species. *Cyathocarpus daubreei*, *Sphenopteridium germanicum* (Weiss) Kerp et DiMichele, *Cyathocarpus arboreus*, *'Pecopteris' bioti* Brongniart, *'Pecopteris' jongmansii*, *Polymorphopteris subelegans*, *Sphenocallipteris scythica*, and *Calamites* sp.

Description. The association was identified on the basis of the phytooryctocoenoses from five localities. The rare fern and pteridisperm remains are found in brownish-red unbedded mudstones with blue spots, brownish-red lumpy mudstones with blue and dark brown spots and brownish-red mudstones with blue-green spots that are interpreted as lacustrine-lagoonal deposits. Taking into consideration the possible conspecifity of *Sphenocallipteris scythica* (= *Sphenopteris scythica* Zalessky)

and *Sphenopteridium germanicum* (= *Sphenopteris germanica* Weiss) [Zalessky 1937], *Sphenopteridium germanicum* and *Cyathocarpus daubreei* with middle constancy values are assigned as name-giving species for this association.

Conifer communities of river valley slopes were reconstructed on the basis of the allochthonous fragments of coniferous branches and seeds from light-grey and greenish-grey, thinly to thicly bedded micaceous siltstones, fine-grained sandstones and fine-grained silty sandstones occurring within or above thick middle-grained and cross-laminated sandstone strata (floodplain facies).

Association *Walchio piniformis–Otovicietum hypnoidis* Shchogolev et Boyarina ass. nov.

Toretskian time (Table 13)

Typus. Kartanash-a (interval between the n_3^1 coal seam and the N_5^1 limestone bed).

Diagnostic species. *Otovicia hypnoides*, *Walchia piniformis* (Schlotheim) Sternberg et Clement-Westerhof, *Culmitzschia* cf. *angustifolia* (Florin) Clement-Westerhof, *C. hirmeri* (Florin) Clement-Westerhof, *C. parvifolia* (Florin) Kerp et Clement-Westerhof, *Samaropsis delafondii* (Zeiller) Florin var. *acuminata* Shchogolev, *S. pinnata* Shchogolev, *Samarospermum moravicum* (Helmhacker) Arber, and *Walchiostrobus* sp.

Description. The association was identified on the basis of the phytooryctocoenoses from the Kartanash locality and three boreholes. The numerous coniferous remains in the Kartanash locality are dominated by *Walchia piniformis*, *Otovicia hypnoides*, *Culmitzschia parvifolia*, and *C. hirmeri.* These plant fossils were collected in ligth-grey fine-grained sandstones with the interbeds of horizontally- to cross-laminated siltstones.

Table 13. **Phytosociological tables characterising the associations of conifer communities of river valley slopes and coastal levees in the Toretskian, Kalynovian and Luganskian times** (legend see in Table 1)

Таблиця 13. **Фітосоціологічні таблиці, які характеризують асоціації угруповань хвойних схилів річкових долин та прибережних валів в торецький, калинівський і луганський часи** (умовні позначення в Таблиці 1)

Diagnostic species	Plant fossil localities								Constancy classes
	Kartanash-a	Borehole No. 232	Borehole No. A-3	Borehole No. 181	Borehole No. 443	Luganske-2f	Luganske-2b	Myronivske-2	
	Locality number								
	1	37	40	42	41	26	26	24	
	Number of species								
	8	11	11	1	1	1	3	1	
The *Walchio piniformis–Otovicietum hypnoidis* association (Toretskian)									
Otovicia hypnoides	c	r	r						IV
Walchia piniformis	a			r					III
Culmitzschia cf. *angustifolia*	r								II
C. hirmeri	c								II
C. parvifolia	c								II
Samaropsis var. *acuminata*	c								II
S. pinnata	c								II
Samarospermum moravicum	c								II
The *Otovicietum hypnoidis* association (Kalynovian)									
Otovicia hypnoides		r			r				IV
Walchia piniformis			r						II
The *Culmitzschietum frondosae* association (Luganskian)									
Culmitzchia frondosa						c			II
Otovicia hypnoides								r	II
Samaropsis bachmutiensis							r		II
S. spinifera							r		II
Samarospermum moravicum							r		II

Association *Otovicietum hypnoidis* Shchogolev et Boyarina ass. nov.

Kalynovian time (Table 13)

Typus. Borehole No. 443 (below the P_3 limestone bed).).

Diagnostic species. *Otovicia hypnoides* and *Walchia piniformis.*

Description. The association was identified on the basis of the phytooryctocoenoses from three boreholes. The rare branche fragments of *Otovicia hypnoides* and *Walchia piniformis* were found in grey silty sandstones.

Association *Culmitzschietum frondosae* Boyarina ass. nov.

Luganskian time (Table 13)

Typus. Luganske-2f (below the P_6 limestone bed).

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

Description. The association was identified on the basis of three phytooryctocoenoses from two localities. The coniferous remains occur in greenish-grey siltstones intercalated with sandstones (Luganske-2f). The rare conifers *Otovicia hypnoides* in the Myronivske-2 locality are found in fine-grained sandstones. The conifer seeds were collected in the floodplain succession consisting of intercalated greenish-grey mudstone and siltstone beds (Luganske-2b).

Conifer community of coastal levees was reconstructed on the basis of the fragment of a coniferous branche from the brownish-red sandstone bed that occur within the red rocks consisting of siltstones intercalated with mudstones and rare sandstones (lacustrine-lagoonal facies). The single specimen of a coniferous branche found in unfossiliferous red strata is important for floristic characteristics. Palaeophythosociological interpretations based on this plant fossil are only hypothetical.

Association *Culmitzchietum mucronatae* Boyarina ass. nov.

Vyskrivskian time

Typus. Novgorodske (interval between two grey mudstone beds with the Q_1 and Q_3 carbonate interbeds)

Diagnostic species. *Culmitzchia mucronata* (Florin) Clement-Westerhof.

Description. The association was identified on the basis of the phytooryctocoenosis from the Novgorodske locality. A branche of *Culmitzchia* cf. *mucronata* was found in brownish-red sandstones.

2. Prodromus of the Late Pennsylvanian vegetation of the Donets Basin

2.1. Approaches to the identification of syntaxonomic units

The ecological and floristic classification of vegetation by the Braun-Blanquet method consists in the identification of plant community types (syntaxa) from the lowest rank (association) to the higher ranks (alliance, order, and class) based on the floristic composition and ecological conditions of plant communities [Braun-Blanquet 1964]. The associations as the basic units of this classification are grouped within the same landscape type into the syntaxa of higher ranks. In doing so, either floristic or ecological criteria come to the fore in the syntaxa of different ranks. Thus, classes are large physiognomic and ecological units, whereas orders are established as variants of classes according to floristic features, and alliances are the ecological variants of orders [Mirkin & Naumova 2014]. For the identification of alliances and orders, characteristic species among diagnostic species provide valid criteria [Braun-Blanquet 1964; Willner 2020]. The alliances contain its own characteristic species that are common to several or all associations of an alliance. The alliances are merged into an order, the diagnostic species of which include the characteristic species of all alliances.

The palaeophytocoenotic and palaeoecological interpretations, which have been proposed on the basis of 69 phytooryctocoenoses from the Late Pennsylvanian of the Donets Basin, allowed to identify 21 associations. According to the habitat of associations, they have been referred to 21 alliances. The

alliances of the certain landscape types have been grouped into 16 orders that differ in the set of diagnostic species in each of four time intervals of the Late Pennsylvanian (i.e. Toretskian, Kalynovian, Luganskian and Vyskrivskian) and belong to 11 classes. The latter include the orders of one or several time intervals in conformity with the types of landscape and vegetation.

Based on the described plant associations and the analysis of their characteristic species, the prodromus of plant communities was compiled that reveals the changing syntaxonomic composition of the vegetation cover of the Donets Basin of four time intervals in the Late Pennsylvanian.

2.2. Prodromus and characterisation of syntaxa

Class *Sphenophyllo–Calamitetea* Boyarina cl. nov.

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

Age: Kasimovian, Gzhelian.

Order *Sphenophyllo oblongifolii–Calamitetalia suckowii* Boyarina ord. nov.

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

Age: Kasimovian (Toretskian), early Gzhelian (Kalynovian) and middle Gzhelian (Luganskian).

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

Alliance *Sphenophyllo oblongifolii–Calamition suckowii* Boyarina all. nov.

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

Age: as for the order.

Diagnostic species: as for the order.

Association *Sphenophyllo oblongifolii–Calamitetum suckowii* Shchogolev et Boyarina ass. nov.

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

Order *Lilpopio raciborskii–Calamitetalia cistii* Boyarina ord. nov.

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

Age: late Gzhelian (Vyskrivkian).

Diagnostic species: *Calamites cistii*, *Lilpopia raciborskii*, *Calamites crookensis*, *C. vandergrachtii*, and *Sphenophyllum verticillatum.*

Alliance *Lilpopio raciborskii–Calamition cistii* Boyarina all. nov.

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

Diagnostic species: as for the order.

Association *Lilpopio raciborskii–Calamitetum cistii* Boyarina ass. nov.

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

Class *Marattietea* Boyarina cl. nov.

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

Age: Kasimovian, early Gzhelian (Kalynovian).

Order *Neuropterido ovatae–Crenulopteridetalia lamurianae* Boyarina ord. nov.

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

Age: Kasimovian (Toretskian).

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

Alliance *Calamito suckowii–Crenulopteridion lamurianae* Boyarina all. nov.

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

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

Association *Calamito suckowii–Crenulopteridetum lamurianae* Shchogolev et Boyarina ass. nov.

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

Alliance *Neuropteridion ovatae* Boyarina all. nov.

Fern-pteridosperm communities of coastal lowlands.

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

Association *Neuropteridetum ovatae* Shchogolev et Boyarina ass. nov.

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

Order *Calamito suckowii–Cyathocarpetalia densifoliae* Boyaria ord. nov.

Calamitalean-fern forests on coastal lowlands.

Age: early Gzhelian (Kalynovian).

Diagnostic species: *Cyathocarpus densifolius*, *Calamites suckowii*, *Cyathocarpus arboreus*, *C. cyatheus*, *C. hemitelioides*, *'Pecopteris' jongmansii*, *'Pecopteris' platonii*, *'Pecopteris' truncata*, *Diplazites unitus*, *Nemejcopteris feminaeformis*, *Annularia sphenophylloides*, *A. stellata*, and *Odontopteris cantabrica.*

Alliance *Calamito suckowii–Cyathocarpion densifoliae* Boyarina all. nov.

Calamitalean-fern communities on lake shores within coastal lowlands.

Diagnostic species: as for the order.

Association *Calamito suckowii–Cyathocarpetum densifoliae* Shchogolev et Boyarina ass. nov.

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

Class *Sigillario–Marattietea* Boyarina cl. nov.

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

Age: Kasimovian.

Order *Subsigillario–Acithecetalia polymorphae* Boyarina ord. nov.

Subsigillarian lycopsid and marattialean fern forests of deltaic plains.

Age: Kasimovian (Toretskian).

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

Alliance *Subsigillario biangulae–Acithecion polymorphae* Boyarina all. nov.

Lycopsid-fern-calamitalean communities of deltaic plains.

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

Association *Subsigillario biangulae–Acithecetum polymorphae* Shchogolev et Boyarina ass. nov.

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

Class *Sigillario–Odontopteridetea* Boyarina cl. nov.

Tropical wetland forests on deltaic plains with lycopsids, pteridosperms and marattialean ferns.

Age: early Gzhelian (Kalynovian).

Order *Subsigillario–Odontopteridetalia schlotheimii* Boyarina ord. nov.

Lycopsid-pteridospermalean and calamitalean-fern forests of deltaic plains.

Age: early Gzhelian (Kalynovian).

Diagnostic species: *Odontopteris schlotheimii*, *Subsigillaria brardii*, *S. donetciana*, *S. fimbriata*, *S. simplex*, *Syringodendron brardii*, *Sigillariostrobophyllum* sp., *Neuropteris crassinervis*, *Neurodontopteris auriculata*, *Barthelopteris germarii*, *'Pecopteris' mironovana*, *'Pecopteris' paleacea*, *'Pecopteris' platonii*, and *Cordaites* sp.

Alliance *Subsigillario brardii–Odontopteridion schlotheimii* Boyarina all. nov.

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

Diagnostic species: *Odontopteris schlotheimii*, *Subsigillaria brardii*, *S. donetciana*, *S. fimbriata*, *S. simplex*, *Syringodendron brardii*, *Sigillariostrobophyllum* sp., *Neuropteris crassinervis*, *Neurodontopteris auriculata*, *Barthelopteris germarii*, *'Pecopteris' mironovana*, *'Pecopteris' paleacea*, *'Pecopteris' platonii*, and *Cordaites* sp.

Association *Subsigillario brardii–Odontopteridetum schlotheimii* Boyarina ass. nov.

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

Alliance *Annulario mucronatae–'Pecopteridion' paleaceae* Boyarina all. nov.

Calamitalean-fern communities of the shores of deltaic lakes.

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

Association *Annulario mucronatae–'Pecopteridetum' paleaceae* Boyarina ass. nov.

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

Class *Calamito–Marattietea* Boyarina cl. nov.

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

Age: middle Gzhelian (Luganskian).

Order *Calamito–'Pecopteridetalia' jongmansii* Boyarina ord. nov.

Woodlands on coastal lowlands with calamitaleans and marattialean ferns.

Age: middle Gzhelian (Luganskian).

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

Alliance *Calamito–'Pecopteridion' jongmansii* Boyarina all. nov.

Calamitalean-fern communities on lake shores within coastal lowlands.

Diagnostic species: as for the order.

Association *Calamito–'Pecopteridetum' jongmansii* Boyarina et Shchogolev ass. nov.

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

Class *Neuropterido–Marattietea* Boyarina cl. nov.

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

Age: middle Gzhelian (Luganskian).

Order *Neuropterido crassinervis–'Pecopteridetalia' arcuatae* Boyarina ord. nov.

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

Age: middle Gzhelian (Luganskian).

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

Alliance *Neuropterido crassinervis–'Pecopteridion' arcuatae* Boyarina all. nov.

Pteridosperm-fern-calamitalean communities of deltaic plains.

Diagnostic species: as for the order.

Association *Neuropterido crassinervis–'Pecopteridetum' arcuatae* Shchogolev et Boyarina ass. nov.

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

Class *Odontopterido–Marattietea* Boyarina cl. nov.

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

Age: late Gzhelian (Vyskrivkian).

Order *Odontopterido schlotheimii–Cyathocarpetalia daubreei* Boyarina ord. nov.

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

Age: late Gzhelian (Vyskrivkian).

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

Alliance *Calamito–Cyathocarpion daubreei* Boyarina all. nov.

Calamitalean-fern communities of lake shores within coastal lowlands.

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

Association *Calamito crookensis–Cyathocarpetum daubreei* Boyarina ass. nov.

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

Alliance *Odontopterido schlotheimii–'Pecopteridion' bredovii* Boyarina all. nov.

Pteridosperm-fern communities of coastal lowlands.

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

Association *Odontopterido schlotheimii–'Pecopteridetum' bredovii* Boyarina ass. nov.

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

Class *Cordaito–Odontopteridetea* Boyarina cl. nov.

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

Age: Kasimovian (Toretskian) and early Gzhelian (Kalynovian).

Order *Cordaito–Odontopteridetalia subcrenulatae* Boyarina ord. nov.

Cordaitalean woodlands of river valleys with pteridosperm shrubs.

Age: as for the class.

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

Alliance *Cordaito–Odontopteridion subcrenulatae* Boyarina all. nov.

Pteridosperm-cordaitean communities of floodplains and river valley slopes.

Diagnostic species: as for the order.

Association *Cordaito–Odontopteridetum subcrenulatae* Shchogolev et Boyarina ass. nov.

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

Class *Peltaspermetea* Boyarina cl. nov.

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

Age: middle Gzhelian (Luganskian).

Order *Autunietalia conferto–naumannii* Boyarina ord. nov.

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

Age: middle Gzhelian (Luganskian).

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

Alliance *Lodevio nicklesii–Autunion naumannii* Boyarina all. nov.

Pteridosperm communities of floodplains.

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

Association *Lodevio nicklesii–Autunietum naumannii* Boyarina et Shchogolev ass. nov.

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

Alliance *'Pecopterido' bredovii–Raminervion mariopteroidis* Boyarina all. nov.

Pteridosperm-fern communities of lake shores within floodplains.

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

Association *'Pecopterido' bredovii–Raminervietum mariopteroidis* Boyarina ass. nov.

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

Alliance *Lodevio suberosae–Odontopteridion subcrenulatae* Boyarina all. nov.

Cordaitean-pteridosperm communities of levees and river valley slopes.

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

Association *Lodevio suberosae–Odontopteridetum subcrenulatae* Boyarina et Shchogolev ass. nov.

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

Class *Lyginopteridio–Marattietea* Boyarina cl. nov.

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

Age: late Gzhelian (Vyskrivkian).

Order *Sphenopteridio germanici–Cyathocarpetalia daubreei* Boyarina ord. nov.

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

Age: late Gzhelian (Vyskrivkian).

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

Alliance *Sphenopteridio germanici–Cyathocarpion daubreei* Boyarina all. nov.

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

Diagnostic species: as for the order.

Association *Sphenopteridio germanici–Cyathocarpetum daubreei* Boyarina ass. nov.

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

Class *Walchietea* Boyarina cl. nov

Coniferous woodlands of river valleys and coastal levees.

Age: Kasimovian and Gzhelian**.**

Order *Walchio piniformis–Otovicietalia hypnoidis* Boyarina ord. nov.

Walchian conifer woodlands in river valleys.

Age: Kasimovian (Toretskian).

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

Alliance *Walchio piniformis–Otovicion hypnoidis* Boyarina all. nov.

Conifer communities of river valley slopes.

Diagnostic species: as for the order.

Association *Walchio piniformis–Otovicietum hypnoidis* Shchogolev at Boyarina ass. nov.

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

Order *Otovicietalia hypnoidis* Boyarina ord. nov.

Walchian conifer woodlands in river valleys.

Age: early Gzhelian (Kalynovian).

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

Alliance *Otovicion hypnoidis* Boyarina all. nov.

Conifer communities of river valleys slopes.

Diagnostic species: as for the order.

Association *Otovicietum hypnoidis* Shchogolev at Boyarina ass. nov.

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

Order *Culmitzchietalia frondosae* Boyarina ord. nov.

Walchian conifer woodlands in river valleys.

Age: middle Gzhelian (Luganskian).

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

Alliance *Culmitzchion frondosae* Boyarina all. nov.

Conifer communities of river valley slopes.

Diagnostic species: as for the order.

Association *Culmitzchietum frondosae* Boyarina ass. nov.

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

Order *Culmitzchietalia mucronatae* Boyarina ord. nov.

Walchian conifer woodlands on coastal levees.

Age: late Gzhelian (Vyskrivkian).

Diagnostic species: *Culmitzchietum mucronata*.

Alliance *Culmitzchion mucronatae* Boyarina all. nov.

Conifer communities of coastal levees.

Diagnostic species: as for the order.

Association *Culmitzchietum mucronatae* Boyarina ass. nov.

Diagnostic species: *Culmitzchietum mucronata*.

Conclusions

The reconstruction and classification of Late Pennsylvanian plant communities were carried out based on the study of 69 phytooryctocoenoses from more than 30 plant fossil localities and 20 boreholes of the Donets Basin. The studied plant fossil assemblages were found in Kasimovian and Gzhelian lacustrine, swamp, deltaic, floodplain and lagoonal deposits.

The description of 21 plant associations and the classification of Kasimovian and Gzhelian plant communities were conducted according to the Braun-Blanquet approach to vegetation classification.

The composed prodromus of the plant communities of coastal lowlands, deltaic plains, floodplains, and river valley slopes reveals the changing syntaxonomic composition of vegetation cover of the Donets Basin in different time intervals of the Late Pennsylvanian.

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