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Analysis of the Upper Pennsylvanian phytozonal units of the Donets Basin and the Northern Caucasus using the ecostratigraphic approach

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Аналіз верхньопенсильванських фітозональних підрозділів Донецького басейну та Північного Кавказу із застосуванням екостратиграфічного підходу

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Floristic, palaeophytocoenotic and palaeoecological analyses of the Late Pennsylvanian vegetation cover of the Donets Basin and the Northern Caucasus were conducted for the time intervals of five macrofloral zones to substantiate the Upper Pennsylvanian phytozonal units in the context of palaeoecosystem changes. The vegetation cover of each basin was defined by a type of differentiation reflecting plant community distribution and developmental features of plant communities shaped by ecological niche dynamics. The vegetation cover in the Donets intracraton basin with post-rift paralic setting, where glacioeustatic sea level changes had a significant impact, was characterised by a spatial differentiation into plant communities of coastal lowlands, deltaic and floodplain plains, and river valley slopes in low-relief terrains and the emergence of new ecological niches while changing dominant landscape types. The vegetation cover in the intramontane basin of the Northern Caucasus with a fluvio-lacustrine setting, where a spatial distribution of landscapes were influenced by changes in a local base level of erosion controlled by orogenic processes, was characterised by a catenary differentiation into plant communities of lacustrine coasts, deltaic-floodplain valleys and river valley slopes in sloping terrains with increased plant species richness as a manifestation of the ecotone effect and the emergence of new ecological niches as a result of niche overlap. The time intervals of macrofloral zones are aligned with the stages of development of vegetation cover that are distinguished by progressive or regressive phytocoenotic changes and phytocoenogenetic transformations of plant communities caused by ecosystem-level factors. The analysis of the Late Pennsylvanian vegetation cover in the Donets Basin and the Northern Caucasus indicates that the different landscape and ecological conditions in different tectono-sedimentary basins determined the different types of vegetation cover differentiation, dynamics of ecological niches and diverse phytocoenotic processes. The dynamics of ecological niches and phytocoenotic processes in plant communities under conditions of different types of vegetation cover differentiation controlled the floristic composition of communities, which is reflected in stratigraphic ranges of key and characteristic taxa of macrofloral zones.

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Introduction

Ecostratigraphy is regarded as 'ecosystem stratigraphy' that relies on the connection between the evolution of the organic world and geological processes controlling the development of the biosphere as an ecosystem and reveals the relationships between the palaeocommunities of biotic groups and biostratigraphical zones (Martinsson, 1973; Krassilov et al., 1985). The ecostratigraphic studies focus on identifying the links between biotic evolution and environmental changes to determine the specific events in the development of ecosystems and their interregional correlations (Martinsson, 1973, 1980; Krassilov, 1978; Boucot, 1984; Margalef, 1986). The basis for the correlation of ecosystem events (changes) is such factors as eustatic fluctuations, orogenic processes and climatic changes, which combine evolutionary and ecological changes. The close relationship between the evolution of biotic communities and the sequence of ecological changes allows the use of ecological community analysis for more detailed biostratigraphy and the understanding of discrepancies in the dating and correlation of biostratons (Krassilov, 1977; Brenner, McHargue, 1988; Gladenkov, 1990; Olóriz et al., 1996, 2012). In this context, an important aspect of ecostratigraphic research is the reflection of the sequence of biostratons in the section as the stages (phases) of development in natural complexes (ecosystems) and the boundaries of biostratons as the transformation boundaries of ecosystems under the influence of external and internal factors in the geological past (Krassilov, 1970, 1977; Martinsson, 1973; Meyen, 1989).

The identification and analysis of palaeoecosystem changes at various hierarchical levels build on the reconstruction of palaeocommunities and the study of their dynamics. For ecostratigraphic studies of continental deposits with plant fossils, it was used the plant communities identified by traditional phytosociological methods according to plant genera and species, as well as the palaeoecological interpretations of these communities (Retallack, 1978).

Palaeophytocoenotic studies of the Late Pennsylvanian plant communities, carried out by the author in recent years in the Donets Basin (Boyarina, 2022a, 2023, 2024) and the Northern Caucasus (Boyarina, Kovalenko, 2023), allowed the analysis of the macrofloral zones in an ecostratigraphic aspect in this study. The ecostratigraphic analysis of the macrofloral zones was performed to reveal the features of vegetation development in different tectono-sedimentary basins.

Conducting such studies is significant for understanding the possible reasons of age inconsistencies of the boundaries of the some Upper Pennsylvanian macrofloral zones in the Donets Basin with paralic settings and the west European intramontane basins of the Variscan belt. The age inconsistencies were determined on the basis of radioisotope-dated zone boundaries in European basins (Knight, Wagner, 2014; Opluštil et al., 2016; Merino-Tomé et al., 2017; Knight et al., 2023) and chronostratigraphic calibration of cyclostratigraphic constructions of the Upper Pennsylvanian deposits in the Donets Basin (Davydov et al., 2010). The diachronicity of the boundaries of floral zones is due to the different stratigraphic ranges of some key taxa in different basins that are considered as a consequence of provincialism and migration time lag (Opluštil et al., 2021). To identify the factors that caused different taxon ranges, it is essential to analyse vegetation development under changing environmental conditions in various basins.

This study analyses the spatial structure and composition of vegetation in the time intervals of the Upper Pennsylvanian macrofloral zones in the Donets Basin with paralic settings and the North Caucasus with intramontane fluvio-lacustrine settings and reveals the developmental features of vegetation cover in these two basins of different tectono-sedimentary types.

Geological and facies setting

The Donets Basin and the Northern Caucasus (Fig. 1) in the Pennsylvanian were within the same floristic province of the Euramerican region and were located in its eastern part (Meyen, 1987). At the same time, these two basins represent different sedimentary types. The Donets Basin is the southeastern part of the Pripyat-Dnipro-Donets intracratonic rift system or the system of avlakogenic basins (Khayin, Mikhailov, 1985; Yakushova et al., 1988; Stovba, Stephenson, 1999). The Upper Pennsylvanian deposits of the Donets Basin, with a thickness of more than 2700 m, are post-rift paralic sedimentary strata that are composed of intercalated shallow marine, swamp, lake, delta, floodplain and channel facies (Guidebook..., 1975; Chekunov, 1994; Stovba et al., 1996; Poletaev et al., 2011). In the Northern Caucasus, the areas of sediment accumulation in the Late Pennsylvanian were grabens or

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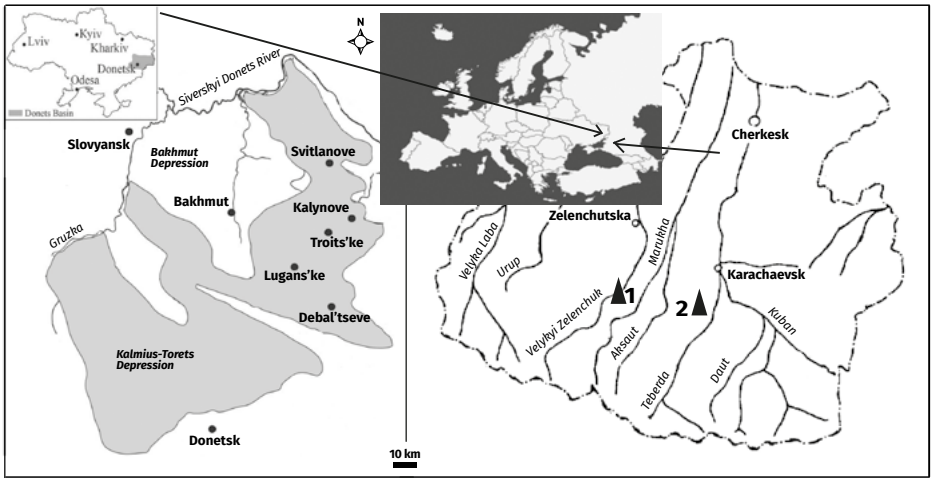

Fig. 1. Geological map of distribution of the Upper Pennsylvanian deposits in the Donets Basin (modified from the materials of State regional geological enterprise "Donetskgeology", 1985) and the map of the Northern Caucasus (Karachay-Cherkess Republic) with the localities of the Late Pennsylvanian plant fossils: 1 – Zelenchuk area (basin of the Velykyi Zelenchuk River); 2 – Teberda area (basin of the Teberda River)

semi-grabens within the continental orogenic belt, as well as the foothills of the orogenic mountain ranges (Adamia et al., 1987; Yanev, Adamia, 2010). Under the conditions of the intramontane basin, the lacustrine, fluvial and proluvial deposits were formed with thicknesses ranging from 150–200 m in the Velykyi Zelenchuk River valley to 400 m in the Teberda River valley (Belov, Kizevalter, 1962; Lunev, Reznikov, 1968; Novik, 1978; Shchegolev, 1979).

Materials and methods

The floristic analysis of the Upper Pennsylvanian macrofloral zones was conducted based on the study of collections of the fossil flora from the Donets Basin and the Northern Caucasus, which were collected in previous years by O.K. Shchegolev and the author of the present paper. The collections are stored at the Institute of Geological Sciences of the National Academy of Sciences of Ukraine under numbers NMNH PC 2216, IGS-OKS1 and IGS-OKS-NIB1. The flora description (Shchegolev, 1985, 1991; Boyarina, 1994, 2010, 2022b) and the classification of plant communities of the Donets Basin (Boyarina, 2022a, 2023, 2024), as well as the description of the flora and vegetation of the Northern Caucasus (Shchegolev, 1979; Boyarina, Kovalenko, 2023) were used for the ecostratigraphic studies.

The macrofloral zones of the Donets Basin (Boyarina, 2016) and the Northern Caucasus, which are described for the first time in the present paper, are identified on the basis of the stratigraphic distribution of key taxa of the west European macrofloral biozones (Wagner, 1984; Cleal, 1991; Wagner, Álvarez-Vázquez, 2010). To reveal the phytocoenotic and ecological-landscape features of the vegetation in the two regions, the description of the zones is supplemented by characteristic taxa that appear for the first time or have the abundant distribution within the zones of each region.

To compare the macrofloral zones of the Donets Basin and the Northern Caucasus in an ecostratigraphic aspect, the phytocoenotic and ecological-landscape affiliations of zone key and characteristic taxa were identified. The phytocoenotic affiliation indicates the type of plant communities that included the key and characteristic species of zones. The ecological and landscape affiliations indicate the type of a landscape, within which the plant communities were distributed.

Based on the palaeophytocoenotic and palaeoecological characteristics of the key and characteristic taxa of macrofloral zones, the correspondence of the time intervals of macrofloral zones to the stages of vegetation cover development was established. The stage (phase) of vegetation cover development is considered as the time interval of the spread or dominance of plant communities with a certain species composition within certain landscape types. The stages are characterised by phytocoenotic processes, which are identified as phytocoenogenetic transformations, exodynamic progressive and regressive changes in plant communities. Phytocoenogenetic transformations of palaeophytocoenoses were manifested in the formation of plant communities representing new syntaxa (Sukachev, 1942). Exodynamic changes are traditionally considered to be changes caused by external factors such as climate, relief, soils and water regime (Sukachev, 1928; Shennikov, 1964), while the increases or decreases in the species composition of communities in the absence of new dominants are identified as the progressive or regressive changes in plant communities without the formation of new syntaxa.

Floristic, phytocoenotic and ecological-landscape characteristics of the Upper Pennsylvanian macrofloral zones of the Donets Basin and the Northern Caucasus

The Donets Basin

Five macrofloral zones have been identified in the Upper Pennsylvanian deposits of the Donets Basin using palaeobotanical criteria of phytozones of the west European Stephanian Stage (Boyarina, 2016). The zone boundaries are aligned with the limestone marker beds overlapping coal seams that are the framework for intraregional correlation of sedimentary rocks in the Donets Basin. In this paper, the floristic criteria of the macrofloral zones are supplemented by the data about phytocoenotic and ecological-landscape affiliations of the key and characteristic taxa (Fig. 2) in line with the palaeophytocoenotic study and classification of the Late Pennsylvanian palaeophytocoenoses of the Donets Basin (Boyarina, 2023, 2024), as well as the time intervals of macrofloral zones are correlated with glacioeustatic sea-level changes (Eros et al., 2012) and the Late Pennsylvanian glacial and deglacial intervals (Montañez, Poulsen, 2013; Montañez, 2022).

***Odontopteris cantabrica* Zone** (n_1-N_2–O_1)

The lower boundary of the zone is drawn at the level of the n_1 coal seam under the N_2 limestone on the basis of the appearance of key taxa of *Odontopteris cantabrica* Wagner, *Alethopteris bohemica* Franke and the disappearance of *Mariopteris nervosa* (Brongniart) Zeiller (see Fig. 2). The appearance of *Sphenophyllum oblongifolium* (Germar et Kaulfuss) Unger, *Crenulopteris lamuriana* (Heer) Wagner and *Sphenopteris rossica* Zalessky (Shchegolev, 1991) in the middle and upper parts of the zone and the change of the late Westphalian flora by the early Stephanian flora above the n_3^1 coal seam (marker horizon n_3^1-N_5) (Shchegolev, 1975; Shchegolev, Kozitskaya, 1975) were the basis for subdivision of the zone into two subzones, *Alethopteris bohemica* and *Sphenopteris rossica*.

The plant fossils of key species were found in the lacustrine mudstones, indicating that these plants belonged to the calamitalean-fern-pteridosperm communities of coastal lowlands. The zone interval almost completely corresponds to the long-term period of relatively stable lower sea level (Eros et al., 2012; Boyarina, 2023), which is comparable to the earliest Kasimovian glacial interval (Montañez, Poulsen, 2013; Montañez, 2022). According to available floristic data, the wetland lycopsid-dominated forests of coastal habitats were significantly reduced in the late Lomovatkian (Fissunenko 1975, 1991, 2000) corresponding to the time interval of the lower subzone. The onset of the formation of new palaeophytocoenoses of the wetland calamitalean-fern-pteridosperm forests within coastal lowlands have been traced from the beginning of the Toretskian (n_3^1 – O_1). This time interval corresponds to the *Sphenopteris rossica* Subzone and coincides with the end of the long-term period of relatively stable lower sea level (final period of the glacial interval), which is characterised by frequent sea level fluctuations (Fig. 3).

***Crenulopteris lamuriana* Zone** (O_1–O_4^3)

The base of the *Crenulopteris lamuriana* Zone is established by the O_1 limestone (see Fig. 2). This level is characterised by the first appearance of *Nemejcopteris feminaeformis* (Schlotheim) Barthel and the disappearance of *Macroneuropteris scheuchzeri* (Hoffmann) Cleal, Shute & Zodrow. Above the O_1 limestone the common occurrence of *Cyathocarpus arboreus* (Sternberg) Weiss and the increase in abundance of *Crenulopteris lamuriana* were revealed. The additional criteria of the zone are the common occurrence of *Acitheca polymorpha* (Brongniart) Schimper in the upper part of the zone and the presence of *Sphenopteris rossica* and *Sphenophyllum oblongifolium* (Shchegolev, 1985).

The listed key and characteristic taxa of ferns belonged to the calamitalean-fern-pteridosperm communities of coastal lowlands except for the *Acitheca polymorpha* ferns, which were also part of the lycopsid-fern communities of deltaic plains. The time interval of the zone was characterised by the dominance of the wetland calamitalean-fern-pteridosperm forests of the *Neuropterido ovatae–Crenulopteridetalia lamurianae* order within coastal lowlands with the prevailing ferns *Crenulopteris lamuriana* and pteridosperms *Neuropteris ovata*. This wetland vegetation of coastal lowlands was widespread during the early phase (early Toretskian) of the long-term period of relatively stable higher sea level at the beginning of the late Kasimovian–early-middle Gzhelian deglacial interval (see Fig. 3).

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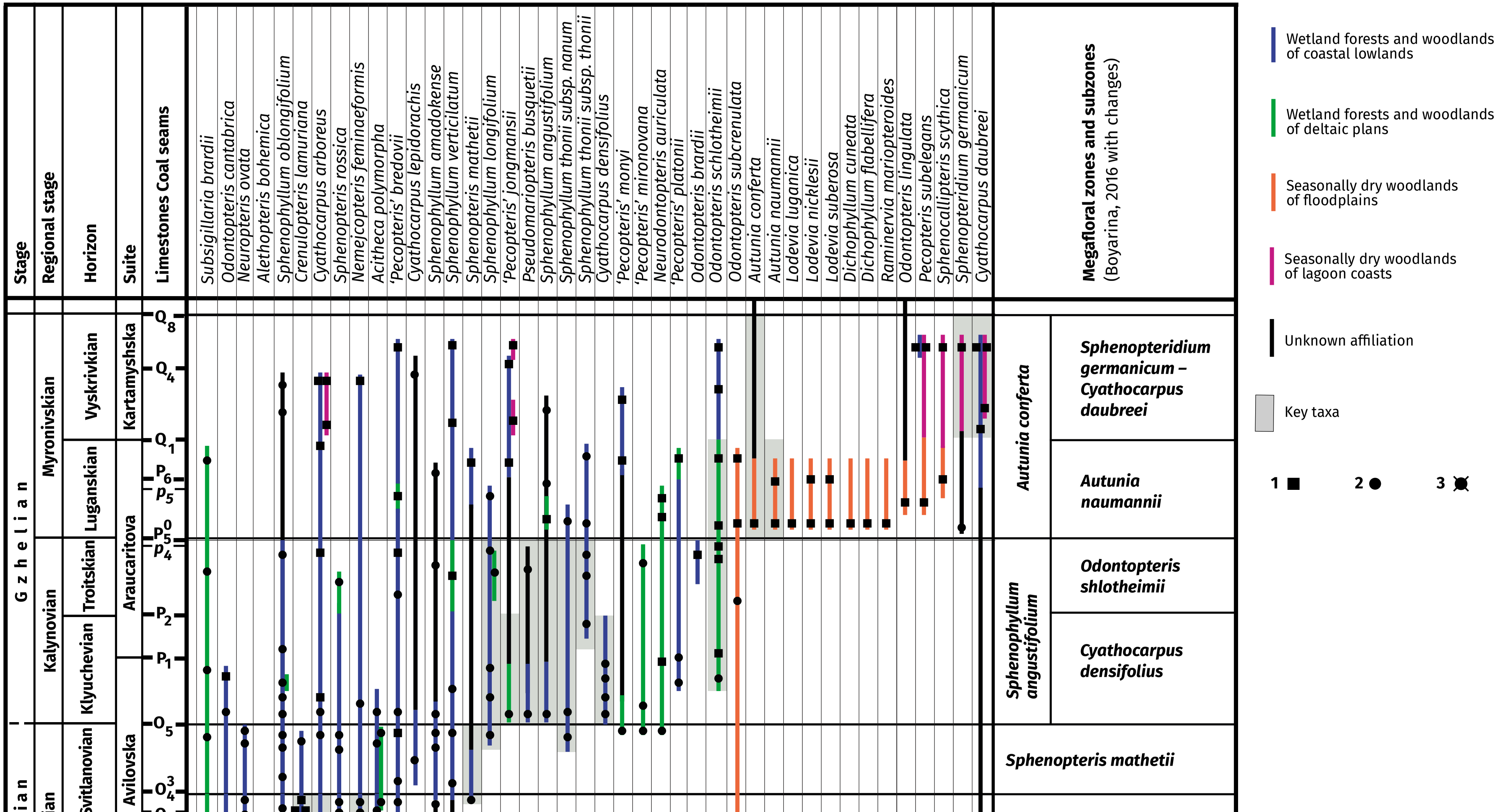

Fig. 2. Stratigraphical ranges and the phytocoenotic and landscape affiliation of the key and characteristic taxa of the Upper Pennsylvanian macrofloral zones of the Donets Basin. Stratigraphical ranges: 1 – data of the author; 2 – data of O.K. Shchegolev (1975, 1985, 1991); 3 – data of O.P. Fissunenko (1991)

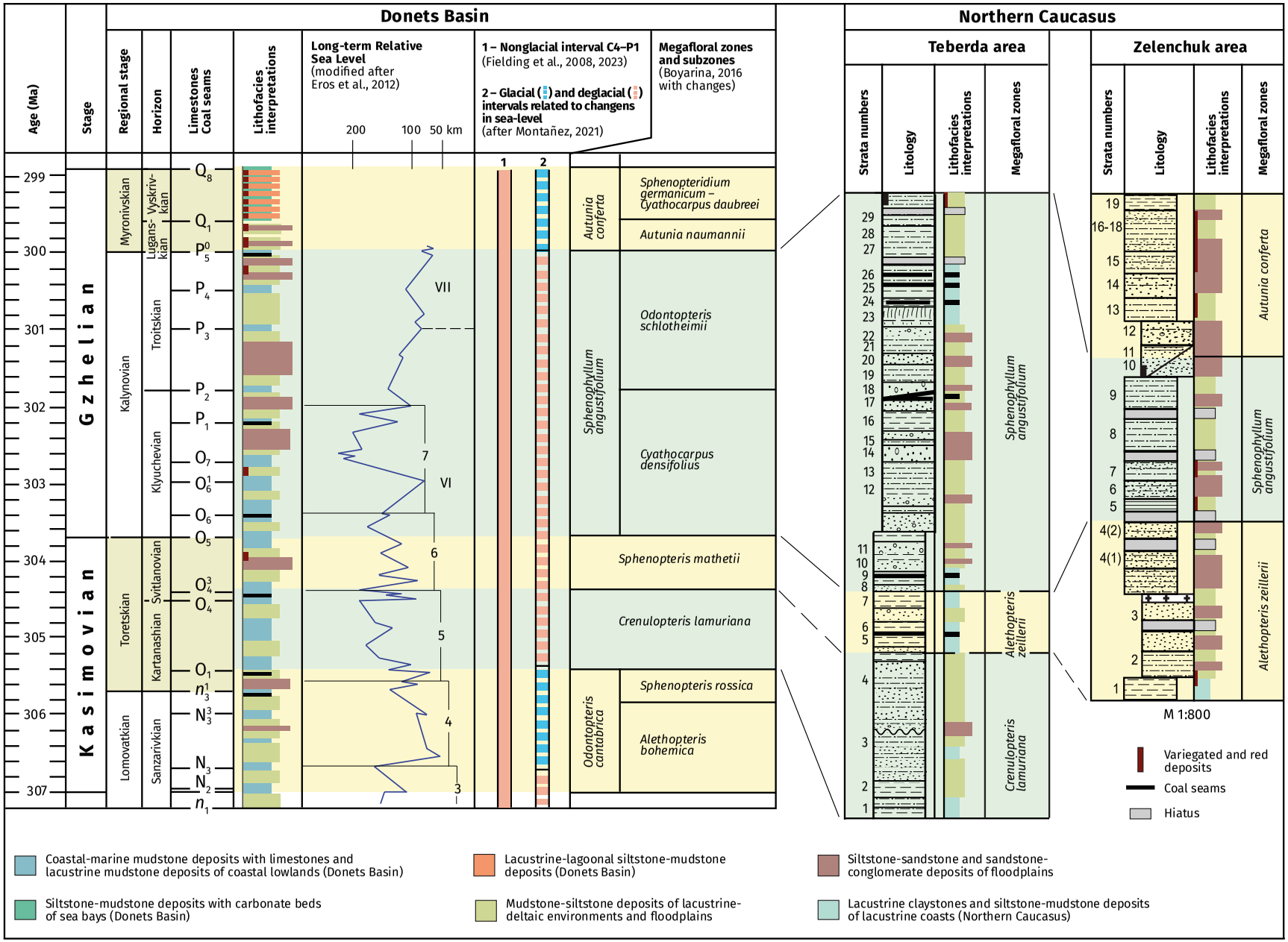

Fig. 3. Correlation of the macrofloral zones of the Donets Basin with glacioeustatic sea-level changes during the Late Pennsylvanian glacial and deglacial intervals and the comparison of lithological and facies sequences in the sections of the macrofloral zones of the Donets Basin and the Northern Caucasus

***Sphenopteris mathetii (= Alethopteris zeillerii)* Zone** (O_4^3–O_5)

In this study the lower boundary of the *Sphenopteris mathetii* Zone, which is analogous to the west European *Alethopteris zeillerii* Zone, is placed at the level of the O_4^3 limestone with the underlying o_2^1 coal seam based on the appearance of *Sphenopteris mathetii* Zeiller between interlayers of the o_2^1 coal seam (Shchegolev, 1985). The first occurrences at the upper part of the zone have the key taxa *Sphenophyllum longifolium* (Germar) Geinitz and *Sphenophyllum thonii* subsp. *nanum* Shchegolev. The zone is also characterised by the appearance of *Cyathocarpus lepidorachis* (Brongniart) Mosbrugger, "*Pecopteris*" *bredovii* Germar, "*Pecopteris*" *potoniei* Nemejc, *Diplazites unitus* (Brongniart) Cleal, the common occurrence of *Cyathocarpus hemitelioides* (Brongniart) Mosbrugger, *Sphenophyllum amadokense* Zakessky, *S. verticillatum* (Schlotheim) Zeiller, as well as the presence of *Acitheca polymorpha* and *Neuropteris ovata* Hoffmann (see Fig. 2).

The abundance plant remains of a diverse species composition were mainly found in lacustrine mudstones that indicate about wide spreading of the calamitalean-fern-pteridosperm communities of coastal lowlands. These plant communities belonged to the wetland forests of the same plant order as and in the time interval of the previous zone, namely the *Neuropterido ovatae–Crenulopteridetalia lamurianae* order (Boyarina, 2023). The forests of coastal lowlands continued to include the dominant ferns *Crenulopteris lamuriana* and pteridosperms *Neuropteris ovata*, as well as the ferns *Acitheca polymorpha*, *Sphenopteris rossica*, "*Pecopteris*" *bredovii*, and were supplemented by the ferns *Sphenopteris mathetii*, *Cyathocarpus hemitelioides*, *C. lepidorachis*, "*Pecopteris*" *potoniei*, *Diplazites unitus* and the sphenophylls *Sphenophyllum longifolium*, *S. thonii* subsp. *nanum* and *S. amadokense* Zalessky. The increase in the diversity of the forests of the same order occurred during the long-term period of relatively stable higher sea level with frequent sea level fluctuations during the late Kasimovian phase of the late Kasimovian–early-middle Gzhelian deglacial interval (see Fig. 3). Frequent sea level changes, i.e. transgressive-regressive cycles (Eros et al., 2012), led to landscape changes accompanied by the expansion of coastal lowlands with humid climatic and edaphic conditions in the early phase of a transgression, from the middle to late low sea level, during each transgressive-regressive cycle (cyclotheme) (DiMichele, 2014). These conditions caused the expansion of the wetland forests with a richer species composition, but no change in dominants.

***Sphenophyllum angustifolium* Zone** (O_5–P_5^0)

The base of the zone is established by the O_5 limestone with the underlying o_2^4 coal seam, above which the first occurrence has the index taxon. The main characteristics of the zone are the presence of *Sphenophyllum thonii* subsp. *nanum* and the appearance of *Sphenophyllum thonii* subsp. *thonii* Shchegolev, the appearance below the O_5 limestone and the abundance occurrence in the lower part of the zone of *Cyathocarpus densifolius* (Goeppert) Šimůnek et Ploch, the appearance in the middle part and the abundance occurrence in the upper part of the zone of *Odontopteris schlotheimii*, the abundance occurrence of *Sphenophyllum longifolium*, and the appearance of *Pseudomariopteris busquetii* (Zeiller) Danzé-Corsin, "*Pecopteris*" *jongmansii* Wagner, "*Pecopteris*" *platonii* Grand'Eury and also the endemic ferns of "*Pecopteris*" *mironovana* Zalessky et Tschirkova (Shchegolev, 1985). The zone is subdivided into two subzones, namely *Cyathocarpus densifolius* (O_5–P_2) and *Odontopteris schlotheimii* (P_2–P_5^0), according to the abundance occurrence of index species.

The time interval of the *Sphenophyllum angustifolium* Zone corresponds to two long-term periods of relatively stable higher and lower sea levels (Eros et al., 2012). The formation of deposits of the lower *Cyathocarpus densifolius* Subzone took place during the early Gzhelian period of relatively stable higher sea level with infrequent transgressive-regressive cycles during the late Kasimovian–early-middle Gzhelian deglacial interval (see Fig. 3). At that time, the vegetation cover was dominated by the wetland calamitalean-fern forests of coastal lowlands of the *Calamito suckowii–Cyathocarpetalia densifoliae* order including the dominant ferns *Cyathocarpus densifolius* and also the ferns *Cyathocarpus arboreus, Diplazites unitus,* and *Nemejcopteris feminaeformis.* The sedimentary rocks of the upper *Odontopteris schlotheimii* Subzone were formed during the middle Gzhelian period of falling sea level at the end of the same deglacial interval. In this time interval the reduction of coastal lowlands and the expansion of deltaic plains and floodplains occurred, as evidenced by the lithological and facies compositions of the deposits. The vegetation of the zone interval was dominated

by the calamitalean-fern and lycopsid-pteridosperm forests of the *Subsigillario–Odontopteridetalia schlotheimii* order on deltaic plains with the predominant pteridosperms *Odontopteris schlotheimii* Brongniart and the common pteridosperms *Neuropteris crassinervis* Shchogolev ms. as well as the ferns *"Pecopteris" mironovana* and *"Pecopteris" platonii* Grand'Eury. These processes are consistent with the affiliation of the key taxa of the lower subzone to the dominant plant communities of coastal lowland forests, and the key taxa of the upper subzone to the dominant plant communities of deltaic plain forests.

***Autunia conferta* Zone** (P_5^0–Q_8)

The lower boundary of the *Autunia conferta* Zone is marked by the first occurrence of the index taxon and other callipterid pteridosperms of *Autunia naumannii* (Gutbier) Kerp, *Lodevia nicklesii* (Zeiller) Haubold et Kerp, *L. suberosa* (Sterzel) Haubold et Kerp above the P_5^0 limestone (Shchogolev, 1960; Boyarina, 2010) (see Fig. 2). The zone is also characterised by the appearance of *Odontopteris lingulata* Goeppert and *Sphenopteridium germanicum* (Weiss) Kerp et DiMichele and the abundance occurrence of *Cyathocarpus daubreei* (Zeiller) De Stefani. The zone was subdivided into two subzones according to the occurrence of its index taxa: *Autunia naumannii* (P_5^0–Q_1) and *Sphenopteridium germanicum-Cyathocarpus daubreei* (Q_1–Q_8).

According to lithological and facies characteristics, the formation of deposits of this zone took place under conditions of further falling sea level (Berchenko et al., 1993; Poletaev et al., 2011) at the beginning of late Paleozoic glaciation (Fielding et al., 2008; Montañez, Poulsen, 2013; Montañez, 2022). The falling sea level during the glacial interval led to the shallowing and gradual isolation of the marine basin. In the time interval of the lower *Autunia naumannii* Subzone (P_5^0–Q_1), the seasonally dry pteridosperm woodlands of floodplains and river valley slopes of the *Autunietalia conferto–naumannii* order predominated. They included the key and characteristic taxa of the pteridosperms *Autunia conferta, A. naumannii* (Gutbier) Kerp, *Lodevia nicklesii* (Zeiller) Haubold et Kerp, *L. luganica, L. suberosa* (Sterzel) Haubold et Kerp, *Dichophyllum cuneatum*. During the time interval of the upper *Sphenopteridium germanicum–Cyathocarpus daubreei* Subzone, the plant communities of the wetland calamitalean-fern-pteridosperm woodlands of the *Odontopterido schlotheimii–Cyathocarpetalia daubreei* order on coastal lowlands and the seasonally dry fern-pteridosperm woodlands of the *Sphenopteridio germanici–Cyathocarpetalia daubreei* order on lagoon plains were widespread. These communities included the characteristic taxa of the ferns *Cyathocarpus daubreei, C. arboreus, "Pecopteris" jongmansii and the pteridosperms Sphenopteridium germanicum.*

The Northern Caucasus

The Upper Pennsylvanian plant-bearing beds of the Zelenchuk and Teberda areas of the Northern Caucasus were comparable to four macrofloral zones of the Stephanian Stage of the regional west European stratigraphic scale according to the key taxa distribution (Boyarina, Kovalenko, 2023). The deposits of the lower *Odontopteris cantabrica* Zone of the Stephanian Stage have not been identified in the Caucasus that may be a consequence of a sedimentary hiatus at the beginning of the Stephanian or erosion. Below is the description of the identified macrofloral zones on the basis of the stratigraphic distribution of the fossil floras (Shchegolev, 1979; Boyarina, Kovalenko, 2023). The floristic criteria of zones were supplemented by the ecological and phytocoenotic characteristics of their key and characteristic taxa, which were established as a result of palaeophytocoenotic analysis of fossil plant assemblages in the Northern Caucasus (Boyarina, Kovalenko, 2023).

***Crenulopteris lamuriana* Zone** (Teberda 1–4)

The zone corresponds to the plant-bearing beds 1–4 that include the key taxa of the ferns *Nemejcopteris feminaeformis* and *Cyathocarpus arboreus* (Fig. 4). This interval is also characterised by the presence of the ferns *Cyathocarpus hemitelioides*, *Acitheca polymorpha*, "*Pecopteris*" *bredovii*, "*Pecopteris*" *monyi* Zeiller, *Diplazites unitus* and the pteridosperms *Sphenocallipteris scythica* (Zalessky) Kryshtofovich et Novik, *Callipteridium gigas* (Gutbier) Weiss and *C. pteridium* (Schlotheim) Zeiller. The fossils *Crenulopteris lamuriana* are not found in the Northern Caucasus.

The plant remains of the listed species from lacustrine and deltaic deposits indicate about the similar species composition of the plant communities formed the wetland calamitalean-fern-pteridosperm forests of lacustrine coasts and deltaic valleys, in which the same ferns *Acitheca polymorpha* and *Cyathocarpus arboreus* were widespread.

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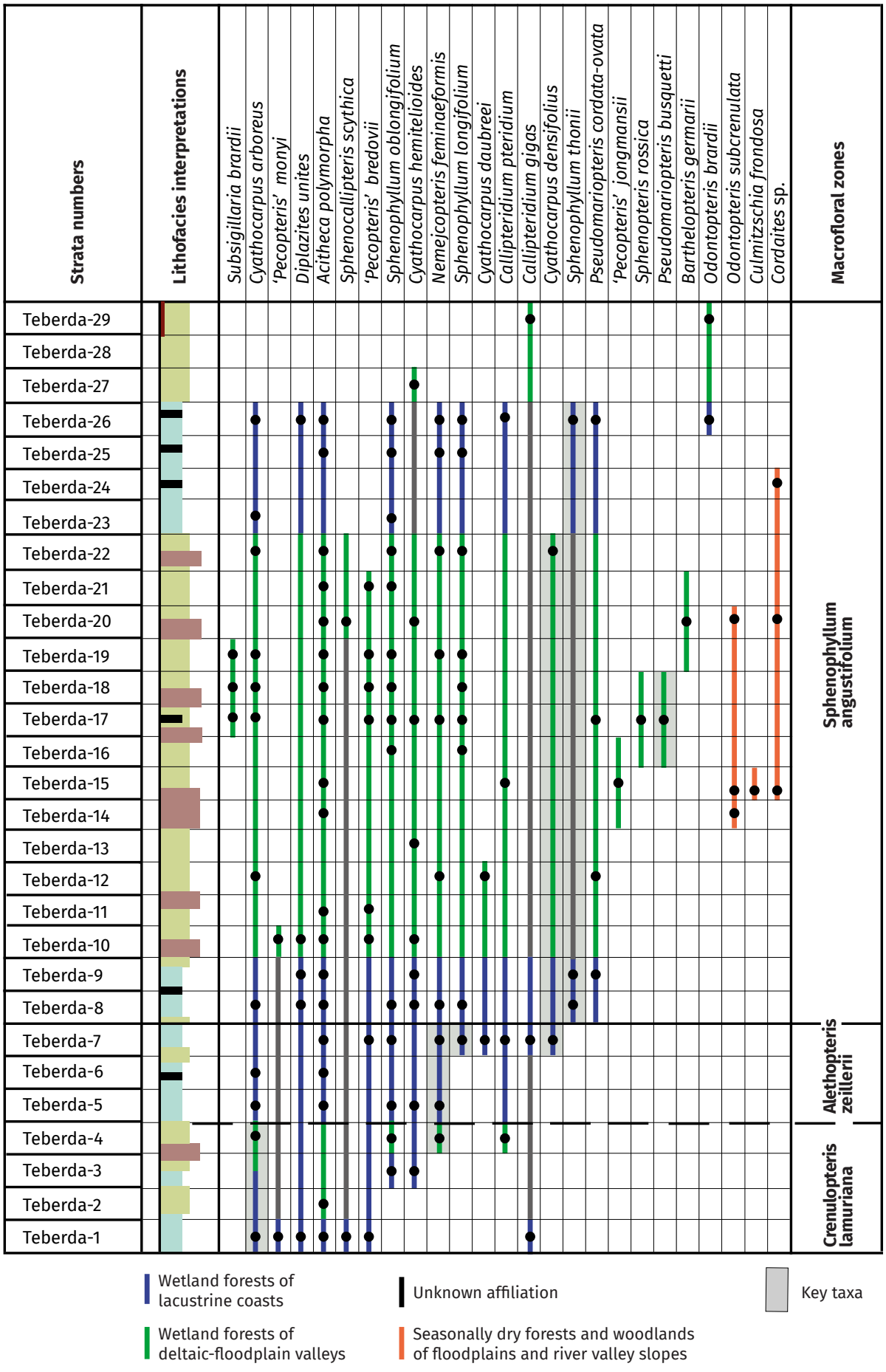

Fig. 4. Stratigraphical ranges (data of O.K. Shchegolev (1979) with additions of the author) and the phytocoenotic and landscape affiliation of the key and characteristic taxa of the Upper Pennsylvanian macrofloral zones of the Teberda area. Legend of lithofacies see Fig. 3

***Alethopteris zeillerii* Zone**

(Teberda 5–7, Zelenchuk 1–4)

In the Teberda area, the zone comprises the plant-bearing beds 5–7, including the key taxon *Sphenophyllum longifolium* in the upper part of the zone and the stratigraphically important ferns *Acitheca polymorpha*, *Cyathocarpus arboreus*, *C. hemitelioides*, "*Pecopteris*" *bredovii*, *Nemejcopteris feminaeformis* and pteridosperms *Callipteridium pteridium* (Schlotheim) Zeiller, as well as the ferns *Cyathocarpus densifolius* in the plant-bearing bed 7 (see Fig. 4). The lower boundary of the zone is conditionally delineated by lithological and facies criteria at the base of the plant-bearing bed 5. The above-mentioned fossil remains were found in lacustrine grey unlayered clay shales and siltstones. The plants of named species formed part of the calamitalean-fern-pteridosperm communities of lacustrine coasts.

This zone in the Zelenchuk area is comprised of the plant-bearing beds 1–4, and contains *Sphenophyllum longifolium* (Germar) Gutbier in the lower part and *Sphenophyllum thonii* in the upper part of zone interval (Fig. 5). The characteristic taxa of the zone are the ferns *Cyathocarpus arboreus*, *C. hemitelioides*, *Acitheca polymorpha* and the pteridosperms *Odontopteris brardii* (Brongniart) Brongniart. The fossil remains of sphenophylls were found in lacustrine grey clay shales and lacustrine-deltaic siltstones, while ferns and pteridosperms are common in deltaic-floodplain siltstones and sandstones. The plants of key and characteristic taxa belonged to the calamitalean-fern communities of lacustrine coasts and the lycopsid-calamitalean-fern-pteridosperm communities of deltaic-floodplain valleys.

The species composition of plant fossil assemblages from lacustrine, deltaic and floodplain facies suggests that the vegetation cover in the Northern Caucasus consisted of the wetland calamitalean-fern-pteridosperm forests of lacustrine coasts and the lycopsid-calamitalean-fern-pteridosperm forests of deltaic-floodplain valleys of predominantly similar species composition with slight differences. The plant communities of the lacustrine coasts in the Teberda area, in particular, had a richer species composition of ferns with the same dominant *Cya-thocarpus arboreus* and *Acitheca polymorpha* as in the time interval of the preceding zone and also included those ferns that were part of the deltaic-floodplain communities in the Zelenchuk area. However, the pteridosperm composition was different in these two areas. In general, the vegetation cover of lacustrine coasts and deltaic-floodplain valleys, which included as before the ferns *Cyathocarpus arboreus*, *Nemejcopteris feminaeformis*, *Acitheca polymorpha*, "*Pecopteris*" *bredovii* and the pteridosperms *Callipteridium pteridium*, *C. gigas*, was supplemented by the ferns *Cyathocarpus hemitelioides*, *C. daubreei*, *C. densifolius*, *Sphenopteris elaverica* Shchegolev, the pteridosperms *Odontopteris brardii*, *Dicksonites pluckenetii* (Schlotheim) Sterzel, *Pseudomariopteris cordata-ovata*, and the sphenophylls *Sphenophyllum longif*olium and *S. thonii*.

***Sphenophyllum angustifolium* Zone**

(Teberda 8–29, Zelenchuk 5–10)

The upper part of the Upper Pennsylvanian in the Teberda River basin with the plant-bearing beds 8–29 have been assigned to the *Sphenophyllum angustifolium* Zone based on the presence of the key taxa, such as the sphenophylls *Sphenophyllum thonii* Mahr, the pteridosperms *Pseudomariopteris busquetii* (Zeiller) Danzé-Corsin, emend. Krings et Kerp and the ferns *Cyathocarpus densifolius* (see Fig. 4). In addition, the characteristic taxa of the zone in the Teberda area are the ferns *Cyathocarpus arboreus, C. hemitelioides, Acitheca polymorpha,* and *"Pecopteris" bredovii,* which continued to dominate in vegetation cover as in previous times, as well as the pteridosperms *Pseudomariopteris cordato-ovata* (Weiss) Gillespie et al., *Callipteridium gigas, C. pteridium,* and the lycopods *Subsigillaria brardii* (Brongniart) Weiss emend. Shchegolev. Plant remains of mainly the same species composition were found both in lacustrine shales and in mudstone and siltstone deposits of deltaic and floodplain settings, except for the lycopods and some pteridosperms, which occur only in deltaic and floodplain deposits. These floristic and facies data indicate that the plants of key and characteristic taxa belonged to the calamitalean-fern-pteridosperm communities of lacustrine coasts and the lycopsid-calamitefern-pteridosperm communities of deltaic-floodplain valleys.

In the Zelenchuk area, the zone comprises the plant-bearing beds 5–10, which include *Sphenophyllum angustifolium* (Germar) Goeppert in the bed 5 and *Sphenophyllum thonii*. These beds are characterised by the diverse flora, namely the ferns *Acitheca polymorpha*, *Cyathocarpus arboreus*, *C. candolleanus*

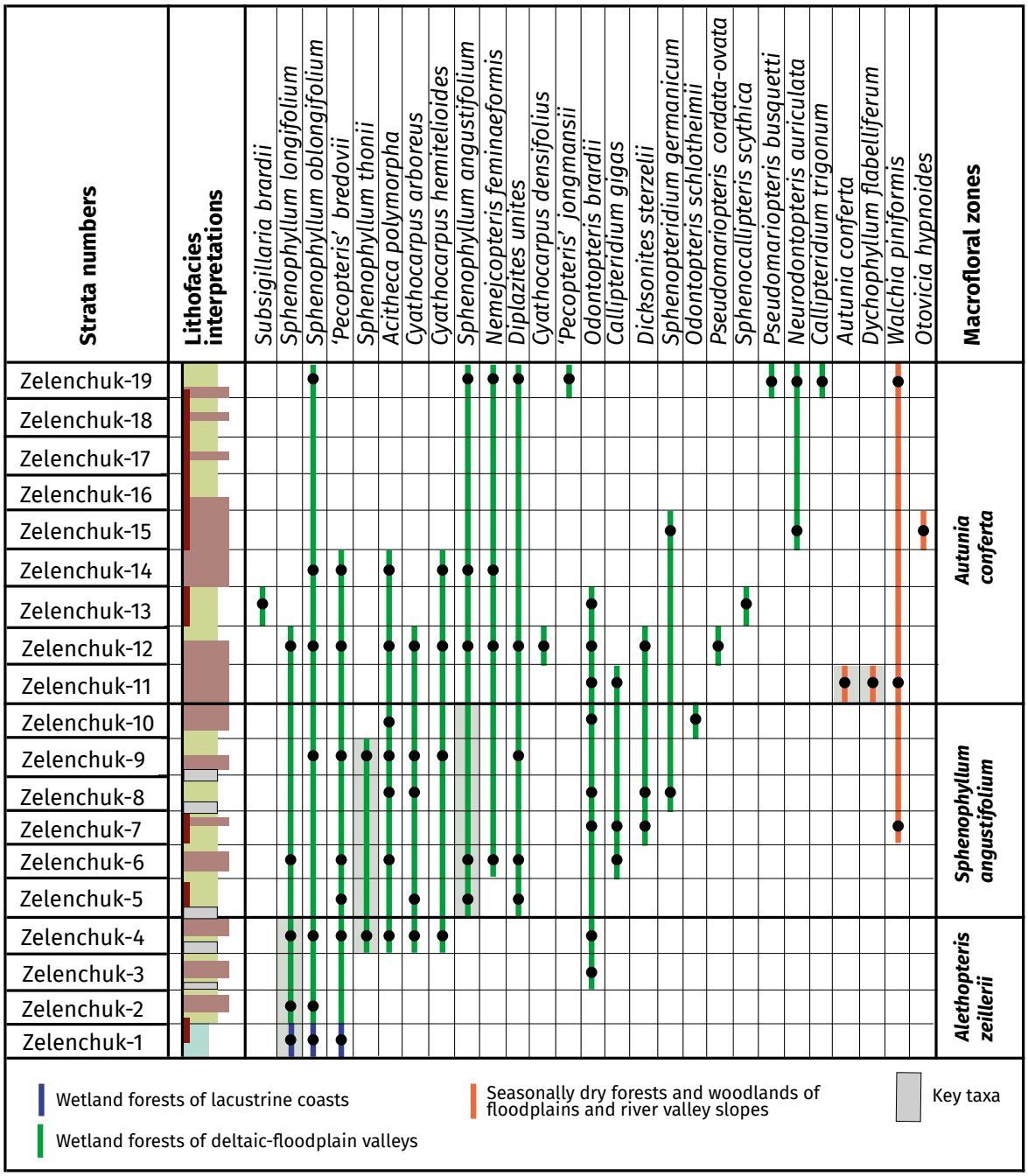

Fig. 5. Stratigraphical ranges (data of O.K. Shchegolev (1979) with additions of the author) and the phytocoenotic and landscape affiliation of the key and characteristic taxa of the Upper Pennsylvanian macrofloral zones of the Zelenchuk area. Legend of lithofacies see Fig. 3

(Brongniart) Weiss, *C. hemitelioides*, *Diplazites unitus* and the pteridosperms *Odontopteris brardii*, *O. schlotheimii*, *Dicksonites sterzelii* (Zeiller) Danzé, *Callipteridium gigas*, *Sphenopteridium germanicum* (see Fig. 5). Plant remains found in deltaic-floodplain grey mudstones and siltstones and fine-grained sandstones suggest that the plants of the listed taxa were part of the lycopsid-calamitalean-fern-pteridosperm communities of deltaic-floodplain valleys.

According to the floristic composition of plant fossil assemblages in two areas, the plant communities of both the wetland calamitalean-fern-pteridosperm forests of lacustrine coasts and the calamitalean-fern and lycopsid-pteridosperm forests of deltaic-floodplain valleys were characterised by a diverse taxonomic composition of plant communities with the same dominant ferns as in the time interval of previous zone, namely *Acitheca polymorpha*, *Cyathocarpus arboreus*, and "*Pecopteris*" *bredovii*, and also the more diverse and slightly different species composition of pteridosperms composed of *Odontopteris brardii*, *O. schlotheimii*, *Dicksonites sterzelii*, *Callipteridium gigas*, and *Sphenopteridium germanicum* in Zelenchuk area.

***Autunia conferta* Zone** (Zelenchuk 11–19)

The *Autunia conferta* Zone is defined based on the appearance of an index species. The pteridosperms *Autunia conferta* and other characteristic pteridosperms *Dichophyllum flabelliferum* (Weiss) Kerp et Haubold and *Sphenopteridium germanicum* were found in floodplain fine-grained sandstones (see Fig. 5). These pteridosperms belonged to the communities of the seasonally dry pteridosperm-conifer forests of floodplains and river valley slopes. In addition, typical for the zone are also the diverse sphenopsids, ferns, and pteridosperms that grown within deltaic-floodplain valleys. The time interval of this zone is characterised by the appearance of new communities of the seasonally dry pteridosperm forests within floodplains as well as the spread of the same wetland lycopsid-calamitalean-fern-pteridosperm forests with the same dominants within deltaic-floodplain valleys as in the previous time interval.

Comparative palaeophytocoenotic analysis of Late Pennsylvanian vegetation cover in the Donets Basin and the Northern Caucasus

The vegetation analysis was carried out based on the floristic and syntaxonomic compositions of the vegetation cover of the Donets Basin established by the author as a result of the classification of plant communities using the Braun-Blanquet method (Boyarina, 2023) and the taxonomic composition of plant communities in the Northern Caucasus basin (Boyarina, Kovalenko, 2023). The composition of the Late Pennsylvanian vegetation cover in each basin had distinctive features. The plant communities of the Donets Basin during different time intervals of the Late Pennsylvanian belonged to wetland calamitalean-fern-pteridosperm forests and calamitalean-fern woodlands, and also seasonally dry fern-pteridosperm woodlands of coastal lowlands; wetland lycopsid-calamitalean-fern-pteridosperm forests and calamitalean-fern-pteridosperm woodlands of delta plains; seasonally dry fern-pteridosperm woodlands of floodplains, and cordaitalean and coniferous woodlands of river valley slopes. According to the refined ecological and landscape interpretations in the present study, the plant communities of the Northern Caucasus were part of the wetland calamitalean-fern-pteridosperm forests of lacustrine coasts, wetland lycopsid-calamitalean-fern-pteridosperm forests of deltaic-floodplain valleys, and seasonally dry pteridosperm and coniferous forests or woodlands of floodplains and river valley slopes.

The palaeophytocoenotic and palaeoecological characteristics of the plant communities discussed above for five time intervals of macrofloral zones provide an opportunity to identify the features of the spatial structure and development of the Late Pennsylvanian vegetation cover in sedimentary basins of different types.

The vegetation cover in the Donets Basin with paralic settings was characterised by the changes in the dominance of plant communities that were associated with the landscape changes as a result of glacioeustatic sea level fluctuations. The differences in the composition of plant communities of different landscape types point to a clearly expressed spatial differentiation of vegetation cover in accordance with the landscape differentiation, namely the vegetation differentiation into the plant communities of coastal lowlands, deltaic and floodplain plains and river valley slopes. And thus, the differentiation of vegetation cove in the Donets Basin reflects the spread of the plant communities of the certain syntaxonomic type with a characteristic species composition and dominants across extensive low-relief terrains. The comparison of the time intervals of macrofloral zones with glacioeustatic sea-level changes (see Fig. 3) and the conducted analysis of plant communities show that changes of the periods of relative sea level with characteristic eustatic features (frequent or infrequent fluctuations) and climatic changes led to the changes in the spatial distribution and dominance of different types of landscapes with their characteristic plant communities. The expansion of certain types of landscapes was accompanied by the expansion of existing ecological niches and the emergence of new ecological niches. The latter played a key role in the evolution and distribution of plants and palaeophytocoenoses (Odum, 1975; DiMichele, Hook, 1992). The intensification of evolutionary changes of vegetation occurred during the periods with frequent eustatic fluctuations, which took place in the time intervals of the *Odontopteris cantabrica* Zone and the *Sphenopteris mathetii (= Alethopteris zeillerii)* Zone (see Fig. 3). In contrast, the Gzhelian stepwise changes in dominant landscapes from coastal lowlands and delta plains to river valleys and lagoonal plains occurred at the transition period from the late Kasimovian–early-middle Gzhelian deglacial interval to the late

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Paleozoic glaciation under condition of a falling sea level. These landscape changes were accompanied by the changes in the dominance of habitat-specific plant communities that are reflected by the subzones of the *Sphenophyllum angustifolium* Zone and the *Autunia conferta* Zone.

The vegetation cover in the Northern Caucasus with intramontane fluvio-lacustrine settings, overall consisting of the plant communities of lacustrine coasts and deltaic-floodplain valleys, had differences in different areas. In the Teberda area, wetland forest communities were widespread within lacustrine coasts and deltaic-floodplain valleys, whereas in the Zelenchuk area, wetland forests of deltaic-floodplain valleys prevailed. The changes of landscape settings and vegetation in intramountain basins were traditionally associated with the changes of local base level driven generally by fault- and fold-related subsidence and uplift. The lithological and facies sequences of deposits, in particular the stratigraphic position of lacustrine strata with coal interlayers within certain macrofloral zones in the Teberda area, that corresponds to the position of shallow marine strata with lacustrine and swamp sediments in the same macrofloral zones in the Donbas, can signal the possible role of glacioeustatic sea-level fluctuations in the changes of the local base level of erosion (lake levels in intramontane basins) during periods of the relatively stable higher sea level in the late Kasimovian–early-middle Gzhelian deglacial interval. However, such an impact of sea-level fluctuations could be possible, provided that there was a hydrological connectivity between the local base level of these territories and the relative sea level. But either way, the changes of the local base level of erosion played a main role in the changes of vegetation cover of the Northern Caucasus. The intramountain type of the Northern Caucasus basin within the continental orogenic belt, as well as the taphonomic features and facies affiliation of plant remains of diverse taxonomic groups discovered in Teberda and Zelenchuk areas indicate a catenary organization of vegetation cover. The geobotanical studies of the catenary arrangement of soils and plant communities have shown that the sequence of soil types (catena) influences the distribution of plant communities and is controlled by the sequence of landscape conditions according to micro-relief elements from watersheds to a local base level and, consequently, landforms, soils and vegetation reflect a catenary sequence (arrangement) from upland to lowland positions (Milne, 1935; Bushnell, 1942; Krassilov, 1972, 1977; Young, 1972). According to the lithological and facies features of deposits in the two studied basins, the landscape catenary series included lacustrine coasts, deltaic-floodplain valleys, and river valley slopes located on sloping terrains. The important aspect of this catenary series is a directional change of landscape structures along relief-related topographic and drainage gradients. The second important aspect is the mainly similar species composition of plant fossil assemblages from diverse facies (lacustrine, lacustrine-deltaic and deltaic-floodplain). This provides evidence that the plant communities of adjacent landscapes had a similar species composition and identical dominants in the intramountain basin with the catenary sequence of plant communities and the narrowly limited spatial distribution of landscape types, except in lycopsids that were limited only to deltaic settings. These phytocoenotic data and the facies sequences of deposits suggest that the dynamics of landscape types for a long time was mainly accompanied by an expansion of the ranges of plant communities and the community interaction of adjacent landscapes, which led to an increase in species diversity of plant communities without changing their dominants. The species diversity and similar species composition of plant communities of adjacent landscape types (lacustrine coasts and deltaic-floodplain valleys) were most likely a manifestation of the ecotone (edge) effect. The ecotone effect is expressed in the biological diversity of plant communities formed over long periods of time in the vegetation cover of the transition zone between two adjacent ecologically different landscape types (Odum, 1975; Holland et al., 1991). High species diversity in ecotones was contributed by the emergence of new ecological niches due to their overlap (Odum, 1975). The pronounced manifestation of the ecotone effect in the development of vegetation cover was most likely facilitated by the limited spatial distribution of these landscapes within the intramountain basin. Such features of the development of plant communities of two landscape types are traced throughout the time intervals of the macrofloral zones of *Crenulopteris lamuriana, Alethopteris zeillerii* and, especially, the *Sphenophyllum angustifolium* Zone. In addition, at this time the flora of the Northern Caucasus was also enriched by such endemic species as *"Pecopteris" angustissima* Shchegolev,

"Pecopteris" kaucasica Shchegolev, *Sphenoneuropteris elegans* Shchegolev, *S. brongniartii* Shchegolev, *Neuropteris teberdensis* Shchegolev (Shchegolev, 1979).

The different differentiation types and phytocoenotic processes of plant communities in the Donets Basin and the Northern Caucasus determined the dynamics of vegetation cover over the Late Pennsylvanian. In the development of vegetation cover in basins, several stages can be identified, which correspond to time intervals of macrofloral zones.

In the Donets Basin, the time interval of the *Odontopteris cantabrica* Zone corresponds to the transitional stage of the replacement of lycopsid-dominated forests by fern-dominated forests within coastal lowlands. The reduction in species diversity of forests with dominant lycopods (Fissunenko, 1991) indicates regressive changes in plant communities. The vegetation changes of coal-swamp environments were associated with changes of climatic conditions in the long period of the relatively stable low sea level within the early Kasimovian glacial interval in the Donets Basin. Therefore, the lower boundary of this zone marks exodynamic regressive changes, i.e. the beginning of the gradual decline of the wetland lycopsid-dominated forests.

The time interval of the *Crenulopteris lamuriana* Zone corresponds to the stage of the dominance of the wetland calamitalean-fern-pteridosperm forests of the *Neuropterido ovatae–Crenulopteridetalia lamurianae* order on coastal lowlands in the Donets Basin, as well as the stage of the dominance of the wetland calamitalean-fern-pteridosperm forests of lacustrine coasts and deltaic valleys with the dominant ferns *Acitheca polymorpha* and *Cyathocarpus arboreus* in the Teberda area of the Northern Caucasus. The lower boundaries of the zone in both regions mark phytocoenogenetic changes in vegetation cover, namely the formation and spread of new communities of wetland forests with a similar species composition of sphenopsids and ferns, but with the different fern dominants and the different taxonomic composition of pteridosperms in each of the basins. The formation of new communities in both basins was influenced by climatic conditions at the beginning of the late Kasimovian–early-middle Gzhelian deglacial interval as well as regional ecological and landscape factors. The new plant communities in the Donets Basin were formed in conditions of the emergence of new ecological niches within widespread coastal lowlands, while in the Northern Caucasus, the spread of new plant communities within lacustrine coasts and deltaic valleys was controlled by the presence of ecotones in vegetation cover.

The time interval of the *Alethopteris zeillerii (= Sphenopteris mathetii)* Zone in both basins corresponds to the stage of the increasing species diversity of the same communities as in the time interval of the previous zone. In the Donets Basin, this is the stage of the increasing species diversity of the communities of the wetland calamitalean-fern-pteridosperm forests of the *Neuropterido ovatae–Crenulopteridetalia lamurianae* order on coastal lowlands, and in the Northern Caucasus, this is the stage of the increasing species diversity of the communities of the wetland calamitalean-fern-pteridosperm forests with the dominant *Acitheca polymorpha* and *Cyathocarpus arboreus* on lacustrine coasts and the lycopsid-calamitalean-fern-pteridosperm forests with the same dominant ferns and the more common pteridosperms *Odontopteris brardii* on deltaic-floodplain valleys. Consequently, the vegetation cover in both basins was characterised by a predominantly similar species composition of ferns, but with different dominants and different composition of pteridosperms. The communities of deltaic-floodplain valleys in the Northern Caucasus included other and more diverse pteridosperms. The lower boundary of the zone in each of the basins marks the exodynamic progressive changes in the same palaeophytocoenoses. The increase in the species composition of ferns and sphenophylls belonging to the plant communities of coastal lowlands in the Donets Basin was associated with the periodic expansions of coastal lowlands accompanied by the emergence of new ecological niches during the late Kasimovian long period of the relatively stable high sea level with frequent sea-level fluctuations. In the Northern Caucasus, the increase in diversity of species composition of ferns, sphenophylls and pteridospems occurred under conditions of the expansions of lacustrine coasts in the Teberda area and deltaic-floodplain valleys in the Zelenchuk area with the emergence of new ecological niches as a result of changes of local base level.

The time interval of the *Sphenophyllum angustifolium* Zone in the Donets Basin corresponds to the stage of the formation and spread of new communities with two successive substages: the early

substage of the dominance of new communities of the wetland calamitalean-fern forests of the *Calamito suckowii–Cyathocarpetalia densifoliae* order on coastal lowlands and the late substage of the dominance of new communities of the lycopsid-calamitalean-fern-pteridosperm forests of the *Subsigillario–Odontopteridetalia schlotheimii* order on deltaic plains. The lower boundary of the zone marks the phytocoenogenetic changes of palaeophytocenoses that were presented by the formation of new communities of the wetland forests of coastal lowlands and deltaic plains with new dominants. The formation of new palaeophytocoenoses of these environments took place in the final phase of the late Kasimovian–early-middle Gzhelian deglacial interval, during which the period of the relatively higher sea level was replaced by the period of the falling sea level. The dominance of coastal lowlands in the first half of the time interval of the zone and deltaic plains in the second half of this interval played a decisive role in the spread of these two types of plant communities of different syntaxonomical types because the dominance of landscapes was accompanied by the expansion of existing and the emergence of new ecological niches within each of these landscape types. An important peculiarity in this regard is the fact that the ferns and sphenophylls of the zone key species were part of the plant communities of dominating coastal lowlands in the time interval of the lower *Cyathocarpus densifolius* Subzone, and pteridosperms of the zone key species belonged to the plant communities of the dominating deltaic plains in the time interval of the upper *Odontopteris schlotheimii* Subzone. In the Northern Caucasus, the time interval of the *Sphenophyllum angustifolium* Zone corresponds to the stage of the increasing species diversity of the plant communities with former dominants. The dominant ferns *Acitheca polymorpha* and *Cyathocarpus arboreus* and non-dominant pteridosperms *Pseudomariopteris cordata-ovata* are known in the Teberda area. The ferns *Acitheca polymorpha* and the pteridosperms *Odontopteris brardii* continued to dominate in Zelenchuk area. The lower boundary of the zone in the Northern Caucasus marks exodynamic progressive changes in paleophytocenoses. These community changes were caused by the expansion of deltaic-floodplain valleys and the emergence of new ecological niches in the Zelenchuk area. In the Teberda area, the plant communities of lacustrine coasts and deltaic-floodplain valleys had a largely similar species composition of ferns and sphenophylls, but the composition of the pteridosperms of deltaic-floodplain communities was more diverse than the communities of lacustrine coasts. The progressive changes in plant communities of the Teberda area were most probably due to a manifestation of the ecotone effect and an overlap of ecological niches.

The time interval of the *Autunia conferta* Zone in the Donets Basin corresponds to two successive stages of vegetation development. The lower *Autunia naumannii* Subzone corresponds to the stage of the formation and spread of new communities of the seasonally dry woodlands of the *Autunietalia conferto–naumannii* order of floodplains and river valley slopes, while the upper *Sphenopteridium germanicum–Cyathocarpus daubreei* Subzone – the stage of the formation and dominance of new communities of the seasonally dry fern-pteridosperm woodlands of the *Odontopterido schlotheimii–Cyathocarpetalia daubreei* order on lagoon plains. The time interval of this zone in the Northern Caucasus corresponds to the stage, which is characterised by the formation and spread of new communities of the seasonally dry forests or woodlands including callipterid pteridosperms within floodplains and river valley slopes alongside the spread of the same communities of the wetland lycopsid-calamitalean-fern-pteridosperm forests with the previous dominant *Acitheca polymorpha* and *Odontopteris brardii* in deltaic-floodplain valleys as in the previous time interval. Therefore, the lower boundaries of the zone in both regions mark the phytocoenogenetic changes of palaeophytocenoses, namely the formation and spread of new communities of the seasonally dry forests or woodlands of floodplains and river valley slopes. The wider spread of seasonally dry vegetation took place during the late Gzhelian glacial interval, which accompanied by the long-term gradual increase in aridity during the Late Pennsylvanian. However, the *Autunia conferta* Zone in the Northern Caucasus is distinguished by the more diverse flora of river landscapes, namely the presence of pteridosperms of the *Callipteridium* genus (*Callipteridium gigas*, *C. trigonum* Franke) and richer species composition of sphenophylls and ferns. This makes it possible to assume that wetter conditions were still maintained in the intramontane basin at the end of the Late Pennsylvanian.

Summarizing the above, it can be argued that the different landscape and ecological conditions in the two considered sedimentary basins determined different types of differentiation of the vegetation cover reflecting plant community distribution and developmental features of plant communties shaped by ecological niche dynamics. The vegetation cover in the Donets Basin was characterised by the spatial differentiation into plant communities in coastal lowlands, deltaic and floodplain plains, and river valley slopes in low-relief terrains and the emergence of new ecological niches under conditions of landscape expansion or change. The vegetation cover in the Northern Caucasus was marked by the catenary differentiation into plant communities of lacustrine coasts, deltaic-floodplain valleys and river valley slopes in sloping terrains with increased plant species richness as a manifestation of the ecotone effect and the emergence of new ecological niches as a result of niche overlap. The changes of landscapes occurred mainly as a consequence glacioeustatic processes in the Donets Basin and changes in the local base level with its inherent erosion processes in the Northern Caucasus against the backdrop of global climate changes and tectonic processes within continental orogenic belts. The landscape changes had an impact on vegetation cover dynamics that are reflected in the successive stages of vegetation development with the different phytocoenotic changes of plant communities. In the Donets paralic basin with the spatial differentiation of vegetation cover, the phytocoenogenetic and exodynamic progressive changes were characteristic for plant communities. In the Northern Caucasus intramontane basin with the catenary differentiation of vegetation cover, the exodynamic progressive changes in plant communities predominated as a manifestation of the ecotone effect.

Conclusions

The comparative analyses of palaeophytocoenotic and landscape data of Late Pennsylvanian vegetation in time interval of five macrofloral zones in the Donets Basin with paralic setting and the Northern Caucasus intramontane basin with fluvio-lacustrine environments showed that the different landscape and ecological conditions determined the developmental features of vegetation cover. The vegetation cover in different tectono-sedimentary basins was characterised by different types of differentiation reflecting plant community distribution, different features of plant community development shaped by dynamics of ecological niches and diverse phytocoenotic processes. The dynamics of ecological niches and phytocoenotic processes of plant communities under conditions of different types of vegetation cover differentiation controlled the floristic composition of communities, which is reflected in stratigraphic ranges of plant fossil taxa and phytostratigraphical zonation.

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Проведено флористичні, палеофітоценотичні та палеоекологічні аналізи пізньопенсильванського рослинного покриву Донецького басейну та Північного Кавказу для часових інтервалів макрофлористичних зон з метою обґрунтування верхньопенсильванських фітозональних підрозділів у контексті палеоекосистемних змін. Рослинний покрив кожного басейну відзначався типом диференціації, який відображав розташування рослинних угруповань, та особливостями розвитку рослинних угруповань, обумовленими динамікою екологічних ніш. Рослинний покрив Донецького внутрішньократонного басейну з пострифтовою паралічною седиментацією, де значний вплив мали гляціоевстатичні зміни рівня моря, характеризувався просторовою диференціацією на угруповання прибережних низовин, дельтових і заплавних рівнин і схилів річкових долин слаборельєфних місцевостей та появою нових екологічних ніш при змінах домінування типів ландшафту. Рослинний покрив міжгірського басейну Північного Кавказу з флювіально-озерними природними середовищами, де просторовий розподіл ландшафтів формувався під впливом змін місцевого базису ерозії, контрольованого орогенічнми процесами, характеризувався катенарною диференціацією на рослинні угруповання озерних узбереж, дельтово-заплавних долин і схилів річкових долин схилових місцевостей із збільшеним видовим багатством рослин як прояв екотонного ефекту та появою нових екологічних ніш у результаті перекриття ніш. Часові інтервали макрофлористичних зон скорельовані з етапами розвитку рослинного покриву, які розрізняються прогресивними або регресивними фітоценотичними змінами та фітоценогенетичними змінами рослинних угруповань, спричиненими факторами екосистемного рівня. Аналіз пізньопенсильванського рослинного покриву в кожному часовому інтервалі п'яти макрофлористичних зон Донецького басейну та Північного Кавказу свідчить, що різні ландшафтні та екологічні умови в різних тектоно-седиментаційних басейнах визначали різні типи диференціації рослинного покриву, динаміку екологічних ніш і різноманітні фітоценотичні процеси. Динаміка екологічних ніш і фітоценотичні процеси рослинних угруповань в умовах різних типів диференціації рослинного покриву контролювали флористичний склад угруповань, що відображається у стратиграфічних діапазонах ключових і характерних таксонів макрофлористичних зон.

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