

## EVOLUTION OF A MACROSUCCESSIONAL SERIES OF PALAEOPHYTOCOENOSES DURING THE PLEISTOCENE AND HOLOCENE IN BELARUS

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**ABSTRACT.** The Pleistocene and Holocene of Belarus are characterized by eight interglacials which are remarkable for the exotic elements contained in their floras and the plant communities which were present in a series of successions, each culminating in an arboreal climax. A comparison of them tells us much about the trends of each succession from the end of a glaciation (*Betula* phase), through the interglacial (initially maxima of *Pinus* and *Picea*, then *Quercus*, *Ulmus*, *Corylus*, *Alnus*, *Tilia* and *Carpinus*, finally *Abies*, *Picea* and *Pinus*) until the *Betula* phase at the beginning of the next glaciation. Overall, a number of climatic optima can be recognized. The macro-successions of the Holocene show it to be an unfinished interval with a maximum of *Pinus* indicating the present time.

A comparison of the pollen diagrams of the Eemian in Europe, associated with macrosuccessions of the plant communities, reveals striking latitudinal and longitudinal differences in their structure and the extent to which they contained exotic taxa. Palynological data thus interpreted provides an additional perspective which complements stratigraphical and palaeogeographical studies in the correlation of natural events.

**KEYWORDS:** Macrosuccessional series, palaeophytocoenoses, fossil palynoflora, exotic plants

The palynological data in Belarus characterize eight interglaciations during the Pleistocene and Holocene whose fossil floras contain specific exotic elements. They exhibit a much reduced number of taxa when compared with the flora of older epochs, e.g. the Eopleistocene (*Cryptomeria*, *Sciadopitys*, *Ginkgo*, *Podocarpus*, *Platycarya*, *Rhus*, *Nyssa*, *Engelhardtia*, *Glyptostrobus*, *Liquidambar*, *Cypressus*, *Taxodium*, *Morus*, *Eucommia*, *Sequoia*, *Rhododendron*) and the Neogene (*Palmae*, *Gleichenia*, *Libocedrus*, *Sequoiadendron*, *Cedrus*, *Keteleeria*, *Cotinus*, *Metasequoia*, *Cryptomeria*; Table 1).

The Korchevo interglaciation with one climatic optimum is the oldest of the eight interglacials. It correlates with the isotope 17 stage of the lower Pleistocene and the middle part of the Cromerian. *Celtis*, *Vitis*, *Taxus*, *Osmunda*, *Pilularia*, *Azolla filiculoides*, *Ilex*, *Picea* (sect. *Omorica*), *Pinus* (sect. *Strobis* Shaw.), *Pinus* (sect. *Cembrae*), *Betula* (sect. *Fruticosae*) made up the exotic elements of the flora.

The Byeloveza interglaciation had two climatic optima and corresponds to the isotope 15 stage and upper part of the Cromerian of the lower Pleistocene. *Taxus*, *Vitis*, *Zelkova*, *Pinus*, (sect. *Sula*), *Pinus* (sect. *Cembrae*), *Ligustrum*, *Betula* (sect. *Fruticosae*) and *Larix* were present.

The Ishkoljdj interglacial is characterized by three climatic optima which are correlated with the isotope 13 stage of the Middle Pleistocene. *Osmunda claytoniana*,

*Tilia tomentosa*, *Betula* sp. (sect. *Costatae*), *Picea* sp. (sect. *Omorica*), *Quercus pubescens*, *Ligustrum* sp., *Osmunda cinnamomea*, *Betula* sp. (sect. *Fruticosae*), *Tilia platyphyllos* and *Larix* sp. were the exotic elements of the flora at this time.

The Alexandrya interglacial had two climatic optima and corresponds to the isotope 11 stage of the Middle Pleistocene, Holsteinian. *Hedera*, *Osmunda regalis*, *O. claytoniana*, *O. cinnamomea*, *Euryale*, *Celtis*, *Buxus*, *Pinus montana*, *Pinus* sp. (sect. *Strobis*), *Pinus* sp. (sect. *Cembrae*), *Carpinus minimus*, *C. orientalis*, *Castanea*, *Myrica*, *Ligustrina*, *Tsuga*, *Carya*, *Juglans*, *Pterocarya*, *Vitis*, *Taxus*, *Picea orientalis*, *P. obovata*, *Picea* sp. (sect. *Omorica*), *Zelkova*, *Azolla filiculoides*, *Tilia tomentosa*, *T. platyphyllos*, *Eriocaulaceae*, *Ostrya*, *Ilex*, *Betula* sp. (sect. *Costatae*), *Betula* sp. (sect. *Fruticosae*), *Conogramma*, *Quercus pubescens*, *Ulmus propinqua*, *Ligustrum*, *Brasenia*, *Adiantum* and *Larix* were present in the flora.

The Smolensk interglaciation with one climatic optimum is correlated with the isotope 9 stage of the Middle Pleistocene. *Picea orientalis*, *Picea* sp. (sect. *Omorica*), *Zelkova*, *Osmunda claytoniana*, *O. cinnamomea*, *Tilia tomentosa*, *T. platyphyllos*, *Betula* sp. (sect. *Costatae*), *Betula* sp. (sect. *Fruticosae*), *Quercus pubescens*, *Pinus* sp. (sect. *Strobis*), *Ulmus propinqua*, *Ligustrum* and *Larix* represented the exotic elements of the flora.

The Shklov interglacial is characterized by three

**Table 1.** The fossil palynoflora of the Cainozoic of Belarus

**Table 1.** Continued

Plants	Horizon, index									
	Asoki	Brest	Korchevo	Byeloveza	Ishkoljdi	Alexan-drya	Smolensk	Shklov	Murava	Holocene
	N	Q <sub>1</sub>	Q <sub>1</sub>	Q <sub>1</sub>	Q <sub>2</sub>	Q <sub>2</sub>	Q <sub>2</sub>	Q <sub>2</sub>	Q <sub>3</sub>	Q <sub>4</sub>
<i>Vitis</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Pterocarya</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Juglans</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Carya</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Tsuga</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Ligustrina</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Myrica</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Castanea</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Carpinus orientalis</i> Mill.	—	—	—	—	—	—	—	—	—	—
<i>Carpinus minima</i> Szafer	—	—	—	—	—	—	—	—	—	—
<i>Pinus montana</i> Mill.	—	—	—	—	—	—	—	—	—	—
<i>Buxus</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Celtis</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Euryale</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Osmunda regalis</i> L.	—	—	—	—	—	—	—	—	—	—
<i>Hedera</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Rhododendron</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Sequoia</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Eucommia</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Morus</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Taxodium</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Cupressus</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Liquidambar</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Glyptostrobus</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Engelhardtia</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Nyssa</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Rhus</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Platycarya</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Podocarpus</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Ginkgo</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Sciadopitys</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Cryptomeria</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Metasequoia</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Cotinus</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Keteleeria</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Cedrus</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Sequoiadendron</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Libocedrus</i> sp.	—	—	—	—	—	—	—	—	—	—
<i>Gleichenia</i> sp.	—	—	—	—	—	—	—	—	—	—
Palmae	—	—	—	—	—	—	—	—	—	—

climatic optima which are correlated with the isotope 7 stage of the Middle Pleistocene. Present were *Pilularia*, *Pinus* sp. (sect. *Sula*), *Pinus* sp. (sect. *Strobus*), *Pinus* sp. (sect. *Cembrae*), *Azolla filiculoides*, *Tilia tomentosa*, *Tilia platyphyllos*, Eriocaulaceae, *Woodsia cf. manchuriensis*, *Ostrya*, *Ilex*, *Betula* sp. (sect. *Costatae*), *Betula* sp. (sect. *Fruticosae*), *Coniogramma*, *Picea* sp. (sect. *Omorica*), *Picea obovata*, *Quercus pubescens*, *Ulmus propinqua*, *Ligustrum*, *Osmunda cinnamomea*, *Adiantum* and *Larix*.

The Murava interglacial had two climatic optima and corresponds to the isotope 5 stage of the Upper Pleistocene, Eemian. *Osmunda cinnamomea*, *Brasenia*, *Betula* sp. (sect. *Fruticosae*), *Tilia platyphyllos*, *Adiantum*, *Larix* and *Picea obovata* formed the exotic elements of the flora.

The Holocene interglacial with one climatic optimum characterizes the isotope 1 stage and does not contain any exotic plants.

Table 2 shows the pollen diagrams of the various in-

Table 2. Diagram of macrosuccessions of a series of paleophytocoenoses of the Pleistocene and Holocene of Belorussia

Stratigraphic subdivisions		late glacial	early interglacial	climatic optimum of interglacial period - stages:		late interglacial	early glacial (interim cooling)
		vegetation		tundra-steppe	sm-wl woodl. woodland	thermophilous xerophytic	thermophilous /hydrophytic
surface soil samples		NAP+B		→ B → (P+Pic)	→ ( +U+T Cor+Al) → ( +F)	mixed and broad-leaved woodland	conifer.woodland
Holo-cene	Murava	Atlantic (ht-1-5)	(P+B) (Pic+P+B) (P+B) (B+P+NAP) ↗	B → P	→ U → (Co+Al) → T → ( +C+F)	→ Pic → P → B+NAp	m+w tundra-steppe
	optima	Komotovo (mr-9-10)	B → P	→ ( +U+Cor+Al T) → C	→ Pic → P → B → B+NAp		
	Shklov	Cherikov (mr-1-8)	(P+NAp) (Pic+P+NAp) (B+A+NAp) ↗	B → P	→ ( +U)(Co+Al) → T → C	→ Pic → P → (B Pic+Al) ↑	
		Chernitsy (šk-11-14)	B → P	→ ( +U)(Co+Al) → ( +C)	→ Pic → P → B → B+NAp		
		Lysaya Gora (šk-11-14)	B → P	→ Q → U → T → (Al Cor+C)	→ Pic → P → B → (B+Pic+L) ↗ (P+Pic+NAP) ↗		
		Lyuban (šk-1-5-a)	(L+Pic+NAp) (Pic+B+P+NAp) (B+AI+Q.m.+NAp) ↗ (B+NAp) ➤ (B+Q.m.+NAp) ↗	B → P	→ (Q U) → (Co+Al +T)	→ P → B → (B+P+NAp) ↗ (B+L+NAp) ➤ (P+Pic) ↗	
		Smolensk (sm-1-13-c)	(B+L+Pic+NAp) →	B → P → Pic → A+U → T → (Co+Al Q)	→ C	→ P → Pic → P → B+P	
		Neman (a-5-7)		B → P	→ U+L		
	Ishkolidj	Malaya Alexandra (a-1-4)	(B+P) (B+Hpl+NAp) ↗	→ B → P → (Pi+Al) → ( +U+Cor+Al T)	→ C	→ Ab → Pic → P → B+NAp	
		late (šk-8-10)	(B+Pic+Hpl) ↗	→ B	→ P → Pic → Al → ( +U+Cor+Al T) → C	→ Ab → Pic → P → B → B+NAp	
		middle (šk-G)		→ P	→ ( +U+Cor+Al +C +Ab) → Pic → P → B → B+NAp	→ Pic → P → B → Al > (Pic+P) ↗	
	Byeloveza	early Pushkari (išk-3-a-c)	(Pic+Pin) ➤ (P+B) ➤ L ➤ (B>(Pic+L+B+P) ➤ (P+A) ↗	B → P → (Pi+Al) → ( +U+Cor+Al T)	→ C	→ Pic → P → B → B+NAp	
		Krasnaya Dubrava (b-v-4-d-6)	(B+NAP) ➤ (L+P+NAP) ↗	→ B → P → (Pi+Al) → ( +U+Cor+Al T)	→ C	→ P → B → B+NAp	
		Borki (bv-1-4-c)	(P+Pic) →	B → P → Pic → Al → ( +U)(Co+Al T)	→ C	→ P → B → (Pic+Al+L) ↗	
		korchovo (kr-1-6)	(P+B+NAp) ➤ (B+NAp) ↗ (P+NAp) ➤ (B+NAp) ↗	B → P → Pic → Al → ( +U)(Co+Al) ➤ T → C	→ Pic → P → B → B+NAp		

NAP – grass pollen; L – Larix; Pic – Picea; Ab – Abies; P – Pinus; B – Betula; Al – Alnus; Q – Quercus; T – Tilia; U – Ulmus; C – Carpinus; F – Fagus; Cor – Corylus; Hip – Hippophaë.

terglacials of the Pleistocene and Holocene. We may infer from them the various maxima of the trees or, if we please, concentrate on the macrosuccesional series of plant communities. The latter correspond to the late glacial (periglacial), early interglacial, climatic optimum, late interglacial and early glacial (periglacial) intervals, together with the brief periods between the two or three climatic optima (Yelovicheva 1986, 1996). The palynological data from the Quaternary sediments show clearly how the plant communities evolved over millions of years as a result of the rhythmic alternation of the glacial and interglacial epochs. During the warm periods, cycles of significant vegetation development took place which may be summarized thus:

Small-leaved woodland or shrub tundra: *Betula*  
 → Coniferous and taiga woodland: *Pinus* → *Picea* →  
 Mixed and broad-leaved woodland: *Quercus* with *Ulmus*  
 → *Tilia* → *Carpinus* with *Alnus* and *Corylus*  
 → Coniferous and taiga woodland: *Picea* → *Pinus*  
 → Small-leaved woodland or shrub tundra: *Betula*.

The optimum of the Holocene will show a new macrosuccesional series:

*Ulmus* → *Tilia* → *Quercus* → *Carpinus*.

The complete macrosuccesional series of communities (culminating in *Carpinus*) occurred in the following interglacials (all optima except where otherwise shown) Korchevo, Byeloveza (second optimum only), Ishkoljdi, Alexandrya, Smolensk, Sklov (second and third optima only) and Murava. It was characterized by a thermophilous/xerophytic stage of vegetation development (*Quercus*, *Ulmus* and *Tilia*) followed by a thermophilous/hydrophytic stage (*Carpinus*). The incomplete series of communities (lacking the *Carpinus* maximum) occurred in the first optima of the Byeloveza and Sklov interglacials were only the *Quercus*, *Ulmus*, *Tilia* stage was reached. The successions of *Picea* and *Alnus*, characteristic of the early period of an interglacial, are evident in the early and middle Pleistocene Korchevo, Byeloveza, Ishkoljdi, Alexandrya and Smolensk interglacials. The postoptimal successions of *Abies* occurred in the Alexandrya and Ishkoljdi.

The successive maxima of trees in the macrosuccesions are an important aid in interpreting the second and third climatic optima within a single interglacial. If the pollen diagrams show that the sequences of communities forming the successions are complete then it is reasonable to infer that the optima occurred *in situ*.

Similarities in the courses of development of the macrosuccesions of the Pleistocene interglacials and that of the Holocene tell us much about the patterns of climatic change. Furthermore, the differences in stratigraphical position of the exotic elements of the flora in the different interglacials yield information about the migration of vegetation zones. A comparison of the communities

present in the macrosuccesional series of the oldest interglacials with those of the Holocene reveal that the Holocene is an unfinished interglacial. Currently humanity is living at the end of the initial part of the Holocene interglacial (*Pinus* phase). There is a danger that an increasing instability in the Earth's biodiversity will disturb the rhythm of the transition to the next glacial. Superimposed on the natural evolution of the Holocene communities are the changes introduced by man from the end of the Atlantic, which have resulted in increased amounts of grass pollen from open sites, more cereal pollen, a reduction in the area covered by forest, and the migration xerophytes as the climate has drier and warmer. The stability of modern vegetation depends on conserving *Pinus* as a dominant in the forest landscape and extending forest communities.

Correlation of the Eemian pollen diagrams of Europe from the Netherlands to Russia shows that the stable macrosuccesional series from the Warta Glaciation to the beginning of the Würm glaciation is represented by sequence NAP → *Betula* → *Pinus* → *Quercus* → *Corylus* → *Tilia* → *Carpinus* → *Picea* → *Pinus* → *Betula* → NAP (de Beaulieu *et al.* 1998). There are, however, some variations. Maxima of *Picea* and *Pinus* with *Betula* in the preoptimum period have been found in Lithuania, Latvia, Estonia and north-west Russia. In France *Juniperus* occupied this interval too. In the Eemian optimum *Quercus* and *Ulmus* reached a joint maximum (Q + U); on some occasions the *Quercus* maximum was followed by one of *Ulmus* (Q → U) and on others the converse occurred (U → Q). In Poland and Germany *Fraxinus* was a participant in the joint *Quercus* – *Ulmus* culmination. Other anomalies of the Eemian optimum are perhaps best summarized in tabular form:

Territory	Tree genera maxima
Belarus, Russia	<i>Corylus</i> with <i>Alnus</i>
Lithuania, Latvia, Estonia	<i>Tilia</i> , <i>Corylus</i> , <i>Alnus</i> jointly
Poland, Germany	<i>Tilia</i> , <i>Taxus</i> , <i>Acer</i> jointly (instead of <i>Corylus</i> )
France	<i>Taxus</i> with <i>Buxus</i>

In the postoptimal phase *Picea* had a clear maximum in Belarus, Russia, Lithuania and Estonia, but was replaced by *Abies* in Poland, Germany and France, where a *Buxus* – *Ilex* phase was sometimes seen. It is noteworthy that, in the Eastern European plain, *Abies* – dominated communities in the postoptimal phase of interglacials were confined to the middle Pleistocene.

Looking at differences between north and south we find in Sweden *Picea* had no maxima in the preoptimum periods and during the optimum *Corylus* and *Alnus* peaked jointly. In the Ukraine the *Betula* phases were absent and *Quercus*, (rarely *Ulmus*, *Alnus* and *Tilia*) achieved a maximum in the climatic optimum of the interglacial. A similar comparison, contrasting east and

west, shows that the composition of the exotic flora was dependent on the climate of the region.

By taking a broad overview of the Eemian vegetation throughout Europe, from the Netherlands to Russia and Sweden to the Ukraine, based on the macrosuccessional series of plant communities, we can observe striking differences in the pollen diagrams and composition of exotic plants. These must be borne in the mind when comparing diagrams from the most ancient sections of the Pleistocene, particularly if they originate from different territories.

In the author's opinion the macrosuccessions from the interglacials will provide a useful perspective in the study of vegetation evolution and correlation in Europe. The general, regional and local factors are all very clearly revealed and will enable an evaluation to be

made of the value of palynological analysis in the study of palaeogeography, stratigraphy and correlation.

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