

Article

Palaeobiodiversity of Knyszyn Forest (NE Poland) Mires Based on the Late Glacial and Holocene Histories of Vascular Plant Species

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Abstract: Peat and lacustrine sediments are a valuable source of knowledge about past biodiversity. Plant macrofossil remains were identified in sediments of mires in northeastern Poland's Knyszyn Forest. Among them, the remains of species currently absent in this area, such as *Potamogeton pusillus*, *P. friesii*, *P. filiformis*, *Myriophyllum alterniflorum*, and *Cladium mariscus*, have been found. In addition, the history of *Betula humilis* and its possible correlations with another species of bush birch—*Betula nana*—were of interest. Radiocarbon dating allowed the presence of the studied species to be placed within a time frame, and it was thus established that aquatic species existed in the area under study during the Late Glacial and the turn of the Holocene. *Cladium mariscus* occurred during the Greenlandian and Meghalayan stages of the Holocene and then became intolerant of habitat changes that occurred. The coexistence of two species of birch known to exist since the Late Glacial was interrupted in the Northgrippian. *B. nana*, then disappeared from the area, and *B. humilis* continued to occur as it was more resistant to the changing environmental conditions. It must be emphasized, however, that these conclusions were made possible by the researchers' access to undisturbed deposits. The mires present in the area of study remain in good condition, providing important and relevant materials for palaeoecological research.

Keywords: mire; peat; plant macrofossil remains; Late Glacial; Holocene; northeastern Poland



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1. Introduction

Mires are specific ecosystems characterized by the presence of biogenic sediment in the substrate in the form of peat and, sometimes, gyttja. Gyttja, which is usually present in the deeper layers of the substrate, under the peat, indicates the lacustrine origin of the mire. Peat formation occurs via the combination of a few specific habitat features. The basic feature is the high hydration level of the substrate caused by slow-moving water that has a low level of oxygen. Under such these conditions, soil micro-organisms present low-activity characteristics. This, in turn, means that the vegetation covering the surface of the mire does not completely decompose after dying. This leads to the deposition of peat, a sediment mainly composed of the remains of plants. The botanical composition of peat reflects the floristic composition of the vegetation growing in the mire during a specific historical period. Such recognition is possible using the palaeobotanical method, which relies on the analysis of plant macroscopic remains (plant macrofossil remains). Since this method provides direct evidence of the occurrence of specific taxa in the past, this form of analysis can, for example, demonstrate that a specific species was more commonly extant in the area under examination in the past than it is in the present [1]. This result may be possible because of the several useful features of macrofossils present in peat. First, macroscopic plant remains can be identified to the species level in research. Second, as previously mentioned, the specific nature of the sedimentation process allows researchers to successfully recognize the local flora and vegetation. The achievement of species-level identification is particularly important in the case of taxa whose other remains are difficult to identify at this

level. This fact is applicable to the dwarf birch, *Betula nana* L., whose pollen grains are very similar to the pollen grains of tree birches. Very specific features, such as the grain diameter and pore depth ratio, must be considered when attempting to distinguish them [2]; this is almost impossible to achieve when performing a pollen analysis.

Palaeobotanical studies constitute an excellent source of information concerning sub-fossil flora, vegetation, and the entire environment. Moreover, when examining sediments formed in the Quaternary, and thus those originating from the Late Glacial and Holocene, researchers rely on the knowledge that fossil flora (also fauna) are similar or identical to modern biota and that the majority of Quaternary biota have modern counterparts [3] even though their range and scale of occurrence may have changed. For example, at present, a modern counterpart may be evident at a full-continental, partial-continental, or minor regional scale. Moreover, macrofossil data reveal both the occurrence and extinction of plant species at a particular site [4].

Such differences evident in the occurrence of species in both the past and present have been observed in the mires of Knyszyn Forest. The forest is located in northeastern Poland, which is a key area in terms of changes in the occurrence of plant species, and is connected to the climate change and environmental transformations that occurred in the postglacial period [5]. This part of Poland is also specifically important to researchers due to its unique climate. Northeastern Poland is one of the coldest regions in the country, which is reflected by the presence of boreal plant communities, such as the boreal spruce forest on peat *Sphagno girgensohnii-Piceetum* Polak. 1962 [6]. At present, this area also marks the southwestern limit of the boreal range of *Picea abies* (L.) H. Karst. [7]. Palaeobotanical studies conducted in Knyszyn Forest identified the occurrences of taxa in the past that are presently absent from the region, such as *Cladium mariscus* (L.) Pohl; three species of genus *Potamogeton*, including *P. friesii* Rupr., *P. pusillus* L., and *P. filiformis* Pers.; and *Myriophyllum alterniflorum* DC. To date, this last species does not occur farther east than Poland [8] and is endangered. *Potamogeton filiformis* is critically endangered, and *Cladium mariscus* is close to threatened [9]. *Cladium mariscus* is also protected within the European Union [10].

Therefore, the initial aims of this study were to determine the time frame and environmental conditions during which the selected species previously occurred in the Knyszyn Forest and to determine the reason for their disappearance. This group of presently absent species also includes *Betula nana*, whose occurrence and decline in northern Poland in the Late Glacial and Holocene were described by Drzymulska [11]. This study also investigated the occurrence of another species of bush birch, *B. humilis* Schrank, which was previously present in the Knyszyn Forest. While the species is currently growing in the study area, it is rare, as it is across Poland. Both *Betula humilis* and *B. nana* are treated as glacial relicts in Poland; they are endangered species that are protected by the law [9]. This study also shows that both birch species often coexisted in the past; therefore, the study's second goal was to approximate the prevalent environmental conditions at that time and thereby explain when and why the species' coexistence terminated, i.e., why *B. humilis* occurs in the area at present while *B. nana* no longer exists.

2. Materials and Methods

2.1. Study Area

The study area was located in northeastern Poland, in the Knyszyn Forest Landscape Park (Figure 1). The modern landscape there was formed via Saalian glaciation [12], occurring within the immediate neighborhood of the Weichselian glaciation area. It features numerous kames, kame terraces, and meltwater forms [13]. The climate in Knyszyn Forest is temperate transitional with a relatively low mean annual temperature of +7 °C and very high annual amplitude reaching up to 22 °C. The mean annual precipitation oscillates by approximately 570 mm. The growing season is approximately 200 days, and snow cover lasts for 85–90 days, i.e., a period that is much longer than in the middle and western regions of Poland [14].

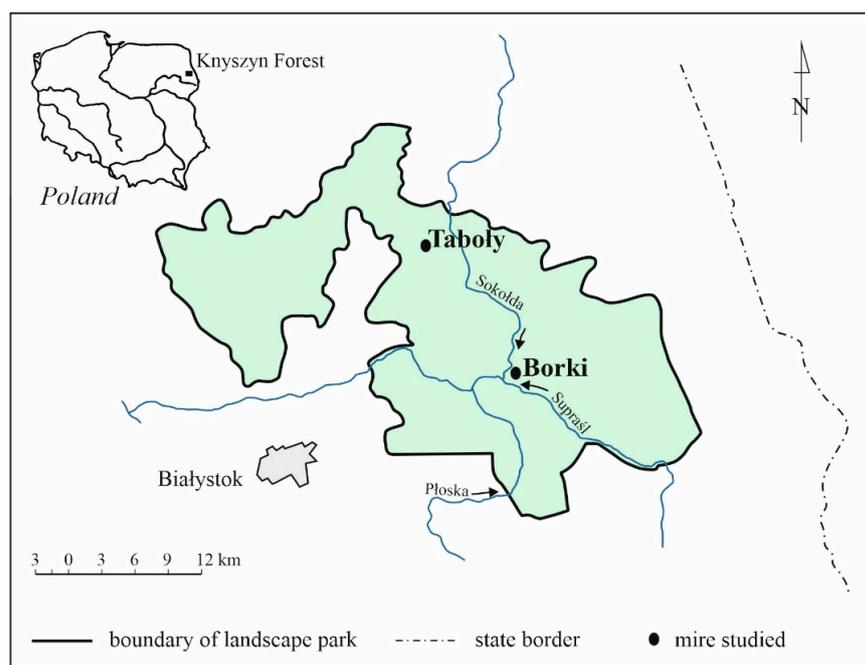


Figure 1. Location of the study area.

The vegetation in this area is characterized by the distinct participation of *Picea abies* (L.) H. Karst. in nearly all the forest areas, and there is an absence of *Fagus sylvatica* L. Boreal species other than spruce occur, including *Betula humilis* and *Oxycoccus palustris* Pers. Forest habitats cover approximately 80% of Knyszyn Forest [15].

More than 20% of Knyszyn Forest is occupied by paludal habitats with the presence of mires. The study sites, the Taboły and Borki mires, are located in these habitats (Figure 1). Both mires are protected by law as forest nature reserves and are situated in large meltwater basins (307 and 287 ha, respectively). The Borki mire has an interesting location between a plateau enclosed by kame terraces on the eastern border and the Sokółka river, separated from the mire by a 300 m wide zone of mud and alluvium at the western site. Both mires are irrigated by water from deeper water-bearing horizons. At Borki, some of these waters flow through underground fissures from the side of the neighboring Stare Biele melting basin, i.e., from the northeastern direction [16], and then they rise to the surface in the form of springs. At Taboły, the characteristic plant communities are *Sphagno girgensohnii-Piceetum* Polak, 1962 and *Thelypterido-Betuletum pubescentis* Czerw. 1972. At Borki, other than the two plant communities mentioned above, *Carici chordorrhizae-Pinetum* Paul et Lutz 1941 also occurs [6].

2.2. Field Work and Laboratory Analyses of Sediment Samples

Sediment samples utilized in our palaeobotanical study were collected from 2002–2004 via drillings created by using an Instorf sampler with a 5 cm diameter. In total, 20 and 5 cores were obtained from Taboły and Borki, respectively. The locations of the boreholes and transects formed are presented in Figure 2. The cores were sampled in the laboratory to determine macrofossil plant remains by dividing them into segments at 5–15 cm intervals. In total, 585 samples were collected in this way. To perform the analyses, 50 cm³ of sediment collected from each sample was used. The material was then boiled in distilled water with the addition of 10% KOH and then washed through a 0.2 mm sieve. Subsequently, generative (carpological) objects were picked out, placed in Petri dishes, and identified using a stereoscopic binocular microscope. To perform the analysis of the vegetative plant remains that were obtained, a light microscope was used. The detailed methodological procedure used in this study was described by Drzymulska [17]. The remains of plants were identified with reference to Grosse-Brauckmann [18,19], Katz et al. [20], Mauquoy and

van Geel [21], and the collection of macroscopic plant remains located in the Department of Palaeobiology, Faculty of Biology, University of Białystok. The vascular plant nomenclature follows that of Mirek et al. [22], and the moss nomenclature was determined according to the study of Ochyra et al. [23]. To classify the subfossil vegetation, an adequate combination of taxa remains was primarily considered, including contemporary phytocoenology [24]. This suggests that the quantitative estimation of the occurrence of a species in the community need not always be decisive for the determination of phytocoenosis [25]. Due to the scope of this study, addressing the history of the selected taxa and in order to not repeat any information, the vegetation succession history of mires was not described. Their detailed development was presented by Drzymulska [17].

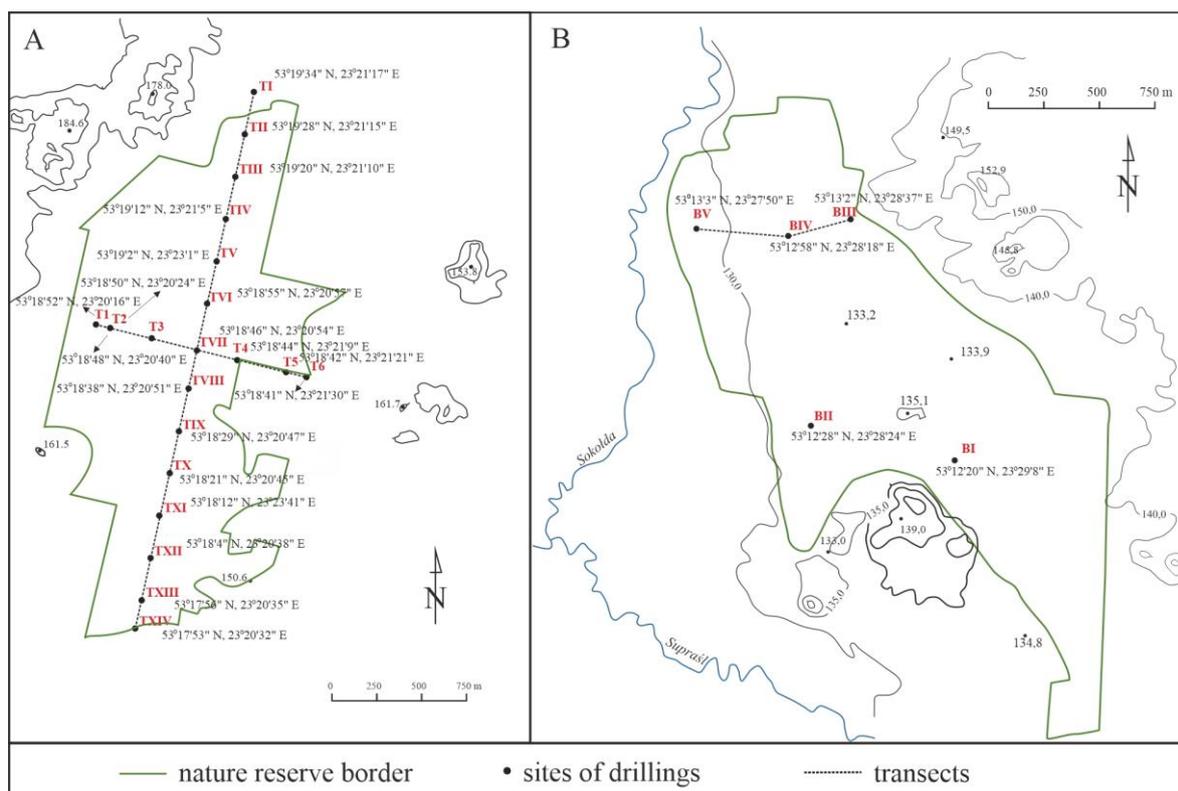


Figure 2. Sites of drillings and transects in Taboły (A) and Borki mires (B) according to [17] (slightly modified).

2.3. Determination of Sediment Age

The age of the sediments was determined via the radiocarbon dating of 36 samples in several laboratories: the Poznań Radiocarbon Laboratory (Poznań, Poland; Poz), where the AMS method was used; the Radioanalytical Laboratory at the Institute of Hygiene and Medical Ecology in Kiev (Kiev, Ukraine; Ki); and the Gliwice Radiocarbon Laboratory (Gliwice, Poland; GdA). The radiocarbon age of the samples was calibrated with OxCal 4.2.3 [26]. The chronology of the peat profiles was presented according to Litt et al. [27] with a modification by Latałowa [28] for the Late Glacial and according to Walker et al. [29] and Walker et al. [30] for the Holocene.

3. Results

The drillings and collection of the relevant materials aided the recognition of the thickness of the deposits and then the typology of the sediments present in both mires. The cores obtained from Taboły almost exclusively consisted of peat. Gyttja was present in two sites (TVII and TIX), on the bottom layer. Starting from the bottom in the TVII site, lacustrine chalk (490–460 cm) and calcareous gyttja (460–440 cm) occurred; in the TIX

site, lacustrine chalk (600–590 cm), calcareous gytija (590–570 cm), and medium-detritus gytija (570–550 cm) were present. The remaining sediment was peat-type. This was illustrated by two geological cross sections corresponding to the transects formed by the boreholes (transects TI–TXIV and T1–T6; Figures 3 and 4). The Borki sediment was peat in its entirety. Unlike in Taboły, the lacustrine phase during the mire development stage was not confirmed in Borki. The location of the drillings resulted in one geological cross section (BIII–BV; Figure 5).

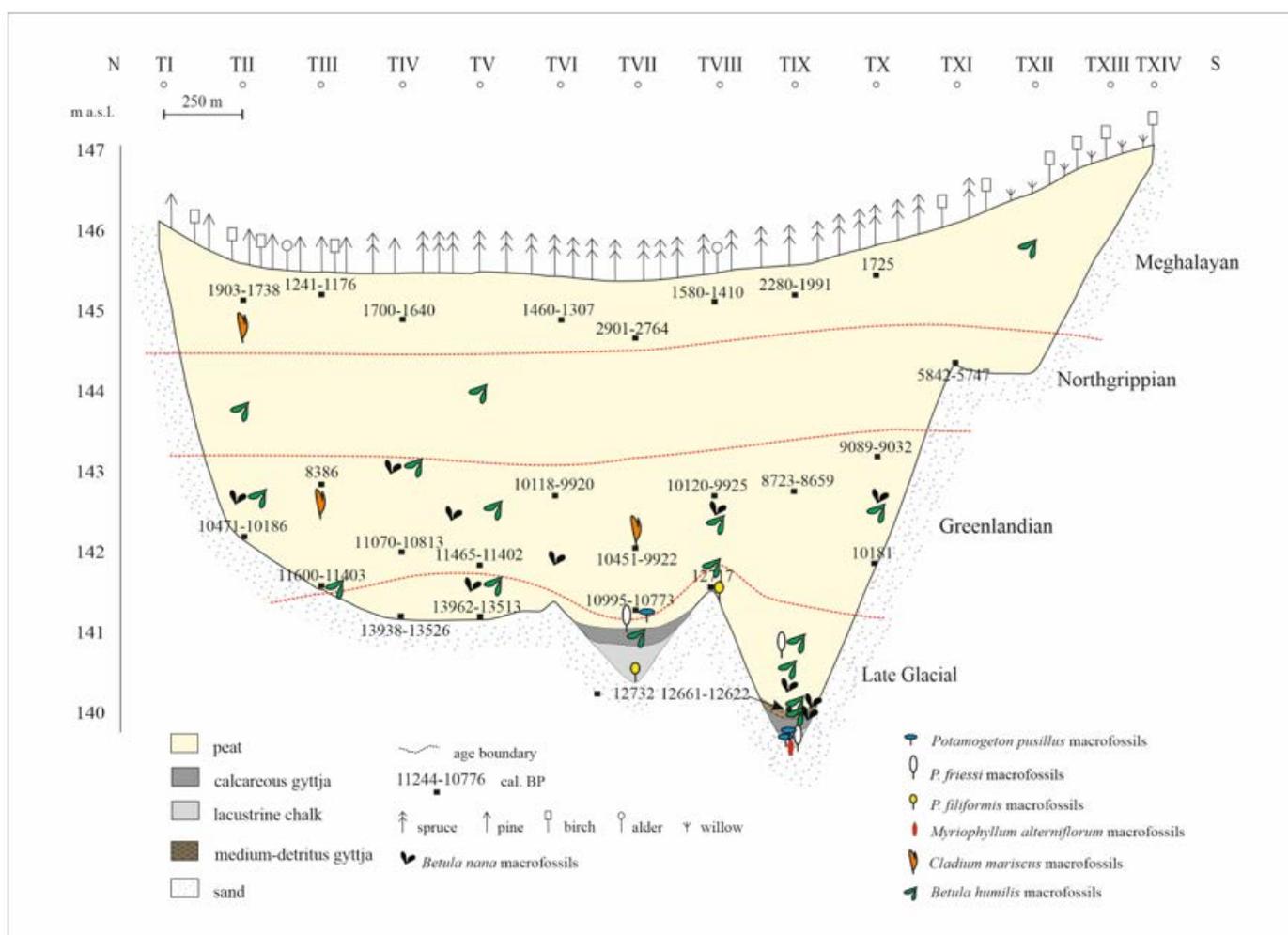


Figure 3. Longitudinal cross section of Taboły mire. Typology of sediments and location of plant remains. Cross section and placement of *Betula nana* remains as in Drzymulska [11] (modified).

The radiocarbon dating results of the samples are presented in Table 1. Our analysis indicated that the origins of the Taboły mire date back to the Late Glacial and that in Borki, peat accumulation began at the beginning of the Holocene. It was also possible to determine the age of both deposits, which—in turn—allowed for the determination of the age of the discoveries under study and the positioning of them in cross sections, as presented in Figures 3–5. Furthermore, the detailed location of the studied species remains (except those of *Betula humilis*) in deposits, their estimated ages, as well as subfossil vegetation context, are presented in Table 2.

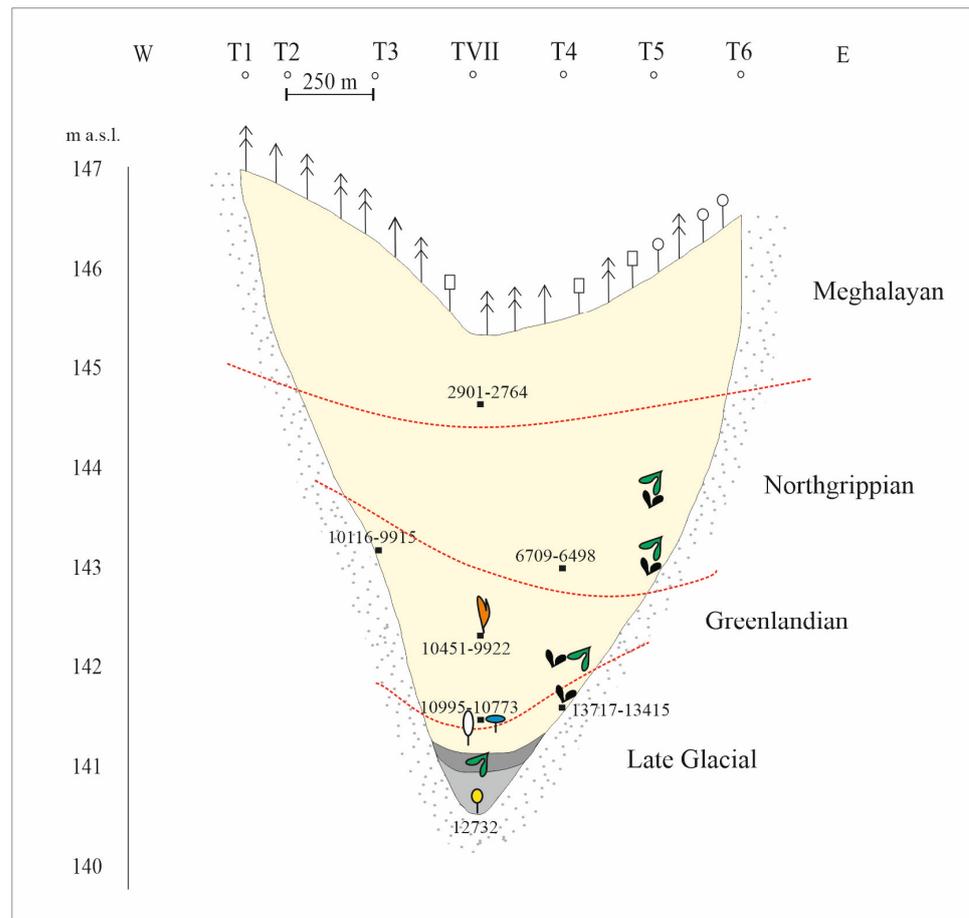


Figure 4. Transverse cross section of Taboly mire. Typology of sediments and location of plant remains. Cross section and placement of *Betula nana* remains as in Drzymulska [11] (modified). Explanations as presented in Figure 3.

Table 1. Radiocarbon dating results for the studied profiles.

Core/Depth (cm)	Dated Material	Lab Symbol of Sample	¹⁴ C BP (Before Present)	Calibrated Range 95.4% (cal. BP)
TII/35	sedge epidermis	Poz-2959	1915 ± 30	1903–1738
TII/320	coniferous wood	Poz-3177	9100 ± 50	10,471–10,186
TIII35	sedge epidermis	Poz-2960	1315 ± 30	1241–1176
TIII/245	sedge epidermis	Poz-2961	7660 ± 40	8386
TIII/385	common reed tissues	Poz-3119	10,160 ± 60	11,600–11,403
TIV/50	sedge epidermis	Poz-2962	1840 ± 30	1700–1640
TIV/363	common reed tissues	Poz-2963	9720 ± 50	11,070–10,813
TIV/422	brown moss stems	Poz-2885	11,880 ± 60	13,938–13,526
TV/365	common reed tissues	Poz-3118	10,120 ± 60	11,465–11,402
TV/425	brown moss stems	Poz-2965	11,850 ± 60	13,962–13,513
TVI/45	sedge epidermis	Poz-2966	1500 ± 30	1460–1307
TVI/270	peat moss stems	Poz-2967	9020 ± 50	10,118–9920
TVII/75	sedge epidermis	Poz-2969	2745 ± 30	2901–2764
TVII/310	brown moss stems grass epidermis	Ki-10093	9080 ± 80	10,451–9922
TVII/415	brown moss stems	Ki-10092	9700 ± 80	10,995–10,773
TVII/485	lump of sediment	Ki-10401	10,940 ± 120	12,732

Table 1. Cont.

Core/Depth (cm)	Dated Material	Lab Symbol of Sample	¹⁴ C BP (Before Present)	Calibrated Range 95.4% (cal. BP)
TVIII/37	sedge epidermis	Poz-2979	1635 ± 30	1580–1410
TVIII/265	brown moss stems	Poz-2980	9030 ± 50	10,120–9925
TVIII/385	brown moss stems	Poz-2981	10,810 ± 50	12,717
TIX/40	sedge epidermis	Poz-3115	2100 ± 30	2280–1991
TIX/280	brown moss stems	Poz-2970	8025 ± 40	8723–8659
TIX/545	brown moss stems	Poz-2972	10,710 ± 50	12,661–12,622
TX/30	coniferous wood	Poz-2973	1900 ± 30	1725
TX/275	peat moss stems	Poz-2975	8260 ± 50	9089–9032
TX/395	peat moss stems	Poz-2976	9090 ± 50	10,181
TXI/170	coniferous wood	Poz-2977	5115 ± 35	5842–5747
T3/305	peat moss stems	Poz-6327	9000 ± 50	10,116–9915
T4/245	sedge epidermis	Poz-2882	5810 ± 30	6709–6498
T4/385	brown moss stems	Poz-2883	11,670 ± 50	13,717–13,415
BIII/95	lump of peat	Gd-15646a	1850 ± 100	1537
BIII/185	lump of peat	Gd-15634	3960 ± 120	4747–4091
BIII/345	lump of peat	Gd-15636	8720 ± 140	9525–9493
BIII/450	lump of peat	Gd-30056	9730 ± 170	11,665–10,583
BIV/110	lump of peat	Gd-30060	3060 ± 90	3003
BIV/310	lump of peat	Gd-15639	9170 ± 130	10,118–9919
BV/195	lump of peat	Gd-15635	5400 ± 140	5903

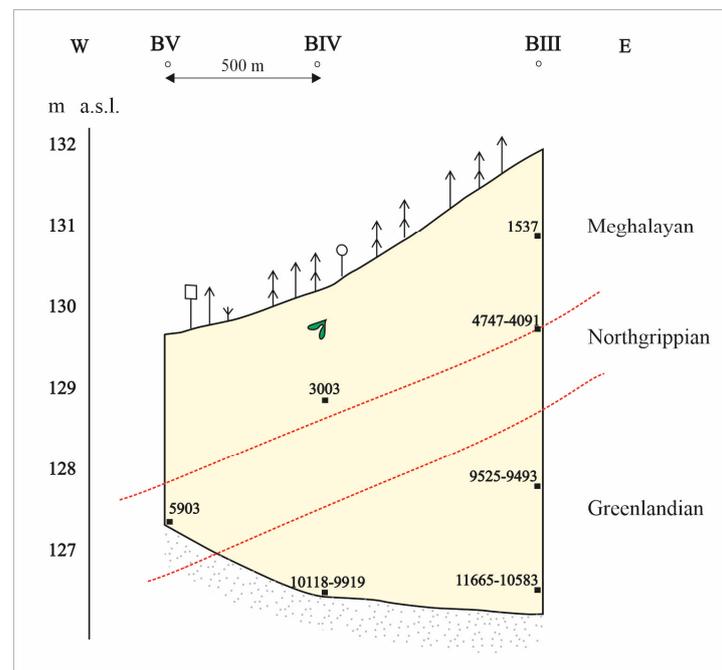


Figure 5. Cross section of Borki mire. Typology of sediments and location of plant remains. Explanations as presented in Figure 3.

Table 2. Remains of studied species in deposits, their age, and reconstruction of subfossil vegetation.

Species	Mire	Site	Depth (cm)	Remains of Studied Species	Other Remains in Sample (Pointing to Dominant Taxon/Taxa)	Subfossil Vegetation	Age
<i>Cladium mariscus</i>	Taboły	TII	90–75	roots (max. 3% in sample)	<i>Carex</i> sp. radicles (even 70% in sample), radicles of <i>Carex elata</i> , periderm of <i>Betula</i> sp., epidermis of <i>Phragmites australis</i> , single remains of <i>Sphagnum</i> sect. <i>Acutifolia</i> and <i>Sphagnum</i> sect. <i>Cuspidata</i>	in the type of contemporary <i>Magnocaricion</i>	Meghalayan
		TIII	315–255	roots (max. 5%)	<i>Carex</i> sp. radicles (even 85% in sample), epidermis of <i>Phragmites australis</i> , roots of <i>Typha</i> sp., <i>Menyanthes trifoliata</i> epidermis, remains of <i>Thelypteris palustris</i> (including sporangia)	in the type of contemporary <i>Magnocaricion</i>	Greenlandian
		TVII	320–260	roots (max. 3%), fruits (3 pieces)	<i>Carex</i> sp. radicles (even 80% in sample), sporangia of <i>Thelypteris palustris</i> , Bryales remains (including <i>Drepanocladus</i> sp.)	in the type of contemporary <i>Magnocaricion</i>	Greenlandian
<i>Potamogeton pusillus</i>	Taboły	TVII	430–420	fruits (2 pieces)	<i>Carex</i> sp. radicles (even 60% in sample); rhizodermis of <i>Equisetum fluviatile</i> ; remains of Bryales (including <i>Calliergon giganteum</i>); periderm of <i>Betula</i> sp.; deciduous wood; oogonia of Characeae (64 pieces); nuts of <i>Carex rostrata</i> , <i>Carex vesicaria</i> , and <i>Carex riparia</i> ; fruit of <i>Potamogeton friesii</i>	in the type of contemporary <i>Caricetum rostratae</i>	Late Glacial/Holocene
			580–570	fruits (2 pieces)	nuts of <i>Batrachium</i> sp. (4 pieces), fruits of <i>Potamogeton friesii</i> , <i>Nitella</i> sp. oogonium, diatoms	aquatic	Late Glacial
		TIX	600–590	one fruit	<i>Nitella</i> sp. oogonia (54 pieces), nuts of <i>Batrachium</i> sp., nuts of <i>Myriophyllum alterniflorum</i> , diatoms	aquatic	Late Glacial
<i>Potamogeton friesii</i>	Taboły	TVII	430–420	one fruit	<i>Carex</i> sp. radicles (even 60% in sample); rhizodermis of <i>Equisetum fluviatile</i> ; remains of Bryales (including <i>Calliergon giganteum</i>); periderm of <i>Betula</i> sp.; deciduous wood; oogonia of Characeae (64 pieces); nuts of <i>Carex rostrata</i> , <i>Carex vesicaria</i> , and <i>Carex riparia</i> ; fruits of <i>Potamogeton pusillus</i>	in the type of contemporary <i>Caricetum rostratae</i>	Late Glacial/Holocene
			470–460	fruits (2 pieces)	<i>Carex</i> sp. radicles (30% in sample), rhizodermis of <i>Equisetum fluviatile</i> , periderm of <i>Salix</i> sp., remains of Bryales and <i>Sphagnum</i> sp., nuts of <i>Carex vesicaria</i> (23 pieces), oogonia of <i>Nitella</i> sp., fruit of <i>Potamogeton alpinus</i> , nuts of <i>Batrachium</i> sp., fruits of <i>Myriophyllum spicatum</i> , fruit of <i>Betula humilis</i>	<i>Caricetum vesicariae</i> with Bryales	Late Glacial
		TIX	590–570	fruits (8 pieces)	<i>Nitella</i> sp. oogonium (14 pieces), nuts of <i>Batrachium</i> sp., fruits of <i>Myriophyllum alterniflorum</i> , <i>Potamogeton pusillus</i> fruits, diatoms	aquatic	Late Glacial

Table 2. Cont.

Species	Mire	Site	Depth (cm)	Remains of Studied Species	Other Remains in Sample (Pointing to Dominant Taxon/Taxa)	Subfossil Vegetation	Age
<i>Potamogeton filiformis</i>	Taboły	TVII	490–480	fruits (2 pieces)	oogonia of <i>Nitella</i> sp. (124 pieces), nuts of <i>Carex</i> sp.,	aquatic	Late Glacial
		TVIII	390–380	fruits (2 pieces)	<i>Carex</i> sp. radicles (60% in sample), rhizodermis of <i>Equisetum fluviatile</i> , remains of Bryales (including <i>Meesia triquetra</i> , <i>Helodium blandowii</i> , <i>Tomentypnum nitens</i>) and <i>Thelypteris palustris</i> , periderm of <i>Betula</i> sp., oogonia of <i>Nitella</i> sp. (10 pieces), nuts of <i>Carex vesicaria</i> , remnants of <i>Pediastrum</i> sp.	<i>Caricetum vesicariae</i> with Bryales	Late Glacial
<i>Myriophyllum alterniflorum</i>	Taboły	TIX	600–580	fruits (5 pieces)	oogonia of <i>Nitella</i> sp. (67 pieces), nuts of <i>Batrachium</i> sp., <i>Potamogeton pusillus</i> fruit, diatoms	aquatic	Late Glacial

During the plant macrofossil analysis, the remains of more than 100 plant taxa, from species to family ranks and conventional taxa, such as Bryales—represented by the remains of brown mosses—and *Betula sect. Albae*—including fruits and catkin scales of tree birches—were recognized together in both deposits. Regarding the taxa being the subject of the present study, the following remains were discovered: *Cladium mariscus*—roots (with some dark-colored surface cells) and fruits (black, and round in the cross section), *Potamogeton* ssp.—fruits (more precisely, incomplete drupes without an external part, preserved in the sediment as endocarps), *Myriophyllum alterniflorum*—fruits (single cylindrical mericarp to narrowly ovoid, abaxial surface broadly rounded), and *Betula humilis*—fruits (elliptic, widest in the middle section, often losing narrow wings in the process of fossilization) and catkin scales (cross-shaped, if undamaged). For comparison, the features of *Betula nana* remains were the following: rounder fruits with narrow wings and catkin scales in the shape of a triangle. Examples of fossil specimens of the studied species are presented in Figure 6.

Aquatic species recorded in Taboły, such as *Myriophyllum alterniflorum*, *Potamogeton pusillus*, *P. friesii*, and *P. filiformis*, were associated with the Late Glacial and with its transition to the Holocene series, such as *P. pusillus* and *P. friesii* (Figures 3 and 4). These species were not only observed in a typical aquatic environment but were also a component of sedge rush communities with *Carex vesicaria* (*P. friesii* in TIX and *P. filiformis* in TVIII) and *Carex rostrata* (*P. pusillus* in TVII and *P. friesii* in TVII) (Table 2).

Cladium mariscus occurred in communities of tall sedges in a form of contemporary *Magnocaricion elatae* alliance, and it was present in Taboły in the Greenlandian (TIII and TVII sites) and Meghalayan (TII site) stages (Figures 3 and 4). The low percentage of its remains suggests that this species was not a dominant component of plant communities but rather an admixture (Table 2).

The remains of *Betula humilis* were identified mainly in Taboły. In Borki, they were observed only in the BIV site (Table 3, Figures 3–5). This species occurred in several plant communities, some of which were similar to contemporary ones—such as *Magnocaricion elatae*, *Scheuchzerio-Cariceta nigrae* Tüxen 1937, *Caricetum vesicariae* Chouard 1924, and *Alnion glutinosae* Malcuit 1929—and they were noted in different parts of the Taboły mire at different times. Plant communities that were difficult to classify were also identified, including a *Carex-Sphagnum sect. Sphagnum + Pinus* community, known from the Meghalayan stage of the Holocene from Borki (BIV site); a community of *Sphagnum palustre-Carex* in Taboły in the Greenlandian stage (TX site); and a community of sedge-brown moss and brown moss with scrubby birches in Taboły (TV and TIX sites) in the Late Glacial (Table 3). It was also

noted that during the Late Glacial, in the Greenlandian, and probably even at the beginning of the Northgrippian stage, both bush birches often occurred in the mire side by side, or at least in the same age interval (Figure 3, Figure 4, and Figure 7). This information provides us with the following picture of co-occurrence: in the Late Glacial—TV and TIX sites; in the Greenlandian stage—TII, TIV, TV, TVIII, TX, and T4 sites; and in the Northgrippian stage—T5 site.

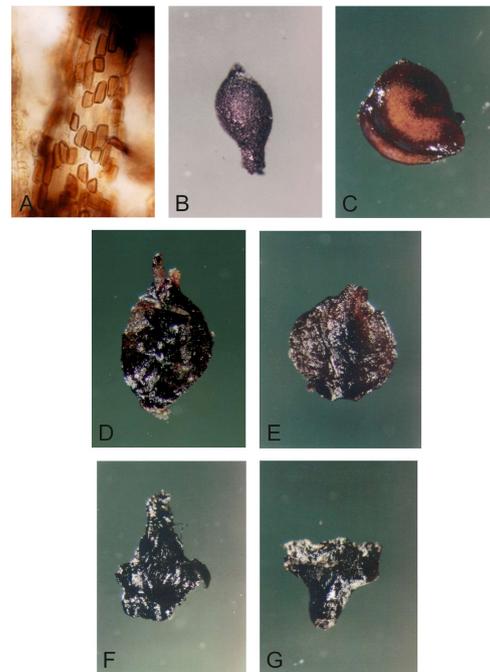


Figure 6. Macrofossils: *Cladium mariscus* root ((A); ×370); *Cladium mariscus* fruit ((B); ×72); *Potamogeton filiformis* fruit, details in the text ((C); ×45); *Betula humilis* fruit, no wings ((D); ×72); *Betula nana* fruit, no wings ((E); ×72); *Betula humilis* catkin scale, not complete ((F); ×45); *Betula humilis* catkin scale, not complete ((G); ×45) (photos by D. Drzymulska).

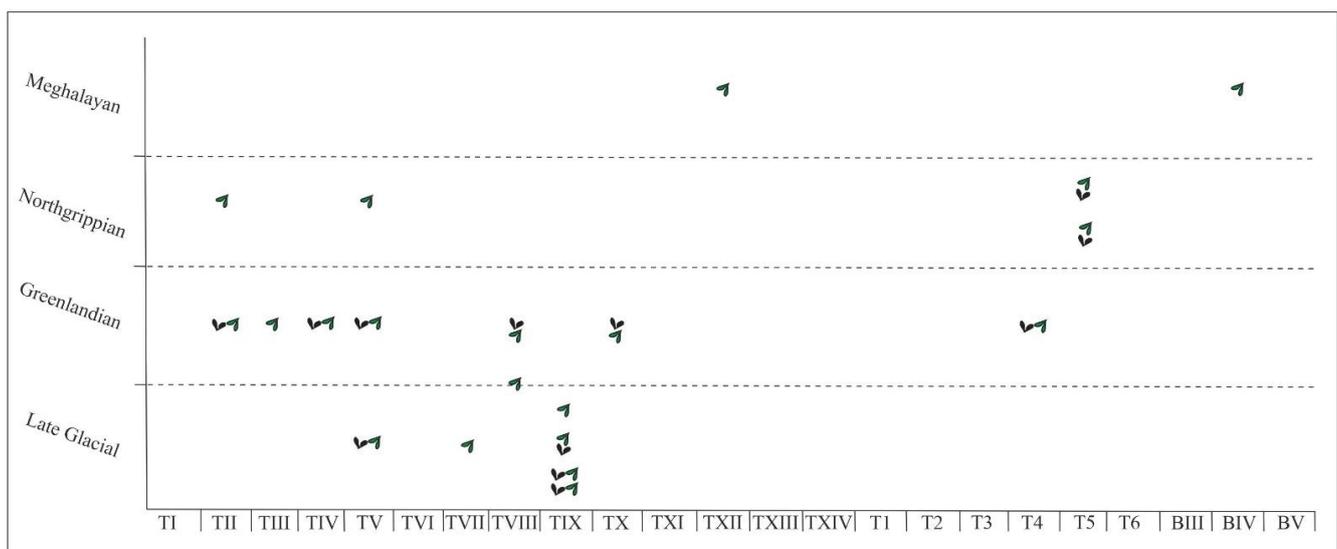


Figure 7. Occurrence of *Betula humilis* with indication of coexistence with *Betula nana*. Placement of *Betula nana* remains similar to Drzymulska [11] (modified). Marks as presented in Figure 3.

Table 3. Details of *Betula humilis* macrofossils evident in the studied deposits. * *Betula nana* was present at the same age interval, not in the same sample.

Mire	Site	Depth (cm)	Remains	Other Remains in Sample (Pointing to Dominant Taxon/Taxa)	Occurrence of <i>Betula nana</i> in the Same Layer	Subfossil Vegetation	Age	
<i>Betula humilis</i>	Taboły	TII	210–180	fruits	<i>Carex</i> sp. radicles (even 60% in sample), radicles of <i>Carex elata</i> and <i>Carex rostrata</i> , epidermis of <i>Phragmites australis</i> , rhizodermis of <i>Equisetum fluviatile</i> , periderm of <i>Betula</i> sp. and <i>Alnus</i> sp., epidermis of <i>Menyanthes trifoliata</i> and <i>Scheuchzeria palustris</i> , deciduous wood, remains of <i>Thelypteris palustris</i> (including sporangia), fruits of tree birches (<i>Betula</i> sect. <i>Albae</i>)	no	shrubs of the alliance <i>Alnion glutinosae</i>	Northgrippian
			315–270	fruits	<i>Carex</i> sp. radicles (even 75% in sample), epidermis of <i>Phragmites australis</i> , rhizodermis of <i>Equisetum fluviatile</i> , periderm of <i>Betula</i> sp., <i>Salix</i> sp. and <i>Pinus sylvestris</i> , coniferous wood, remains of <i>Thelypteris palustris</i> (including sporangia), remains of <i>Sphagnum palustre</i> , fruits of <i>Betula nana</i> and tree birches	yes		Greenlandian
		TIII	390–375	fruits	<i>Carex</i> sp. radicles (even 80% in sample), radicles of <i>Carex elata</i> , epidermis of <i>Phragmites australis</i> and <i>Menyanthes trifoliata</i> , rhizodermis of <i>Equisetum fluviatile</i> , periderm of <i>Betula</i> sp., remains of <i>Thelypteris palustris</i> , nuts of <i>Carex</i> sp.	no	in the type of contemporary <i>Magnocaricion</i>	Greenlandian
		TIV	240–210	fruits	<i>Carex</i> sp. radicles (even 80% in sample), rhizodermis of <i>Equisetum fluviatile</i> , periderm of <i>Betula</i> sp., remains of <i>Thelypteris palustris</i> (including sporangia), periderm of <i>Betula</i> sp. and <i>Alnus</i> sp., deciduous wood, fruit of <i>Betula nana</i>	yes	shrubs of the alliance <i>Alnion glutinosae</i>	Greenlandian
			195–180	fruits, catkin scales	<i>Carex</i> sp. radicles (even 85% in sample), epidermis of <i>Phragmites australis</i> , rhizodermis of <i>Equisetum fluviatile</i> , remains of <i>Thelypteris palustris</i> (including sporangia) and Bryales	no	in the type of contemporary <i>Magnocaricion</i>	Northgrippian
		TV	315–300	fruits, catkin scales	<i>Carex</i> sp. radicles (even 75% in sample), epidermis of <i>Phragmites australis</i> and <i>Menyanthes trifoliata</i> (also seeds of the last), rhizodermis of <i>Equisetum fluviatile</i> , remains of <i>Thelypteris palustris</i> (including sporangia) and Bryales, periderm of <i>Betula</i> sp., deciduous wood, fruit and catkin scale of <i>Betula nana</i>	yes	shrubs of the alliance <i>Alnion glutinosae</i>	Greenlandian
			390–375	fruits	<i>Carex</i> sp. radicles (even 70% in sample), remains of <i>Thelypteris palustris</i> (including sporangia) and Bryales, periderm of <i>Betula</i> sp., deciduous wood, fruits of <i>Betula nana</i>	yes	community of sedge-brown moss and brown moss with scrubby birches	Late Glacial
		TVII	460–450	fruits	Characeae oogonia (5 pieces), fruit of <i>Hippuris vulgaris</i>	no	aquatic	Late Glacial
		TVIII	305–290	fruits	<i>Carex</i> sp. radicles (even 50% in sample), rhizodermis of <i>Equisetum fluviatile</i> , epidermis of <i>Menyanthes trifoliata</i> , sporangia of <i>Thelypteris palustris</i> , remains of Bryales (including <i>Meesia triquetra</i> and <i>Tomentypnum nitens</i>)	yes *	in the type of contemporary <i>Scheuchzeria-Caricetea nigrae</i>	Greenlandian

Table 3. Cont.

Mire	Site	Depth (cm)	Remains	Other Remains in Sample (Pointing to Dominant Taxon/Taxa)	Occurrence of <i>Betula nana</i> in the Same Layer	Subfossil Vegetation	Age	
<i>Betula humilis</i>	Taboŷy	380–370	fruits	<i>Carex</i> sp. radicles (even 45% in sample), rhizodermis of <i>Equisetum fluviatile</i> , remains of <i>Thelypteris palustris</i> , remains of Bryales (including <i>Helodium blandowii</i> , <i>Tomentypnum nitens</i> , and <i>Aulacomnium palustre</i>), periderm of <i>Betula</i> sp., oogonia of Characeae, fruits of <i>Carex vesicaria</i> and <i>Myriophyllum spicatum</i> , remnants of <i>Pediastrum</i> sp.	no	<i>Caricetum vesicariae</i> variant with Bryales?	Late Glacial/Holocene	
		470–460	fruits	<i>Carex</i> sp. radicles (even 30% in sample), rhizodermis of <i>Equisetum fluviatile</i> , remains of <i>Thelypteris palustris</i> , remains of Bryales and <i>Sphagnum</i> sp., nuts of <i>Carex vesicaria</i> , <i>Batrachium</i> sp. and <i>Myriophyllum spicatum</i> , oogonia of <i>Nitella</i> sp., fruits of <i>Potamogeton friesii</i> and <i>P. alpinus</i>	no	<i>Caricetum vesicariae</i> variant with Bryales	Late Glacial	
		500–490	fruits	remains of Bryales (even 50% in sample), <i>Carex</i> sp. radicles, remains of <i>Sphagnum</i> sect. <i>Subsecunda</i> , epidermis of <i>Menyanthes trifoliata</i> , oogonia of <i>Nitella</i> sp.	yes *	community of sedge-brown moss and brown moss with scrubby birches	Late Glacial	
		550–540	fruits	remains of Bryales (even 60% in sample), <i>Carex</i> sp. radicles, remains of <i>Thelypteris palustris</i> , epidermis of <i>Menyanthes trifoliata</i> , fruits of <i>Carex vesicaria</i> , <i>Betula nana</i> and catkin scales of <i>Betula</i> sect. <i>Albae</i>	yes	community of sedge-brown moss and brown moss with scrubby birches	Late Glacial	
		560–550	fruits	oogonia of Characeae (2 pieces), fruits of <i>Carex pseudocyperus</i> , <i>Batrachium</i> sp. and <i>Betula nana</i>	yes	aquatic	Late Glacial	
		TX	350–340	fruits	<i>Carex</i> sp. radicles (even 60% in sample), rhizodermis of <i>Equisetum fluviatile</i> , remains of <i>Sphagnum palustre</i> and <i>Thelypteris palustris</i> , periderm of <i>Salix</i> sp., deciduous wood, nuts of <i>Betula</i> sect. <i>Albae</i>	yes *	community of <i>Sphagnum palustre</i> - <i>Carex</i>	Greenlandian
		TXII	65–55	fruits	<i>Carex</i> sp. radicles (even 90% in sample), epidermis of <i>Phragmites australis</i> , rhizodermis of <i>Equisetum fluviatile</i> , remains of <i>Thelypteris palustris</i>	no	in the type of contemporary <i>Magnocaricion</i>	Meghalayan
		T4	340–330	fruits	remains of Bryales (even 55% in sample; including <i>Helodium blandowii</i> , <i>Tomentypnum nitens</i>), <i>Carex</i> sp. radicles, remains of <i>Thelypteris palustris</i> , <i>Carex</i> sp. (including <i>Carex</i> sect. <i>Paniculatae</i>), fruits of birches (<i>Betula nana</i> and <i>Betula</i> sect. <i>Albae</i>), seeds of <i>Comarum palustre</i>	yes	in the type of contemporary <i>Scheuchzerio-Caricetea nigrae</i>	Greenlandian
		T5	210–195	fruits	<i>Carex</i> sp. radicles (even 50% in sample), rhizodermis of <i>Equisetum fluviatile</i> , remains of Bryales and <i>Thelypteris palustris</i> (including sporangia), periderm of <i>Betula</i> sp. and <i>Alnus</i> sp., deciduous wood	yes *	in the type of contemporary <i>Scheuchzerio-Caricetea nigrae</i>	Northgrippian
			270–260	catkin scales	<i>Carex</i> sp. radicles (even 85% in sample), remains of Bryales, nuts of <i>Carex vesicaria</i>	yes *	<i>Caricetum vesicariae</i> variant with Bryales	Northgrippian

Table 3. Cont.

Mire	Site	Depth (cm)	Remains	Other Remains in Sample (Pointing to Dominant Taxon/Taxa)	Occurrence of <i>Betula nana</i> in the Same Layer	Subfossil Vegetation	Age
<i>Betula humilis</i>	Borki	BIV	fruits	radicles of <i>Carex</i> (40% in sample), remains of <i>Sphagnum magellanicum</i> (even 30%) and periderm of <i>Pinus sylvestris</i> (even 25%), coniferous and deciduous wood, periderm of <i>Betula</i> sp., epidermis of <i>Phragmites australis</i> , roots of Ericaceae, remains of <i>Sphagnum palustre</i>	no	<i>Carex-Sphagnum</i> sect. <i>Sphagnum</i> + <i>Pinus</i>	Meghalayan

4. Discussion

The contemporary flora in Knyszyn Forest is well recognized in the literature [31] and includes 837 species of vascular plants, of which Holarctic species are the main group. Relevant information is provided, in this case, by floristic and phytosociological studies. On the other hand, vegetation present in a specific area in the past can be determined by using pollen analysis techniques and performing the analysis of macroscopic plant remains. Both methods have slightly different applications; however, they complement each other. Macrofossils are less readily dispersed than most types of anemophilous pollen [32]. This confers the advantage that they represent the local flora and vegetation in the studied site, and thus, they provide a more precise definition of them. On the other hand, the local dispersion of macrofossils is a disadvantage, resulting in these remains being unsuitable for regional reconstructions. There is no “macrofossil rain” comparable to regional pollen rain, and the macrofossil assemblages obtained from different areas of the same lake may differ depending on the local vegetation [33]. Thus, the choice of method depends on the purpose of the research; although sometimes, technical limitations also arise, e.g., if a type of a sediment is unsuitable for a specific type of analysis. In the case of plant macrofossil analysis, peat poses no limitations provided that it is not very dry. A special method that can be employed is the analysis of vegetative plant remains because the fundamental composition of peat is precisely that it consists of these remains; therefore, there is no risk of running out of material. The case is different for carpological analysis. Generative remains are sometimes scarce or absent from the samples. On the other hand, in the case of lacustrine sediments, only generative remains are visible.

The occurrence of three species of the *Potamogeton* genus—i.e., *P. friesii*, *P. pusillus*, and *P. filiformis*—and *Myriophyllum alterniflorum* in the area of study in the Late Glacial and during its transition to the Holocene was recognized from the fruits found in gyttja. This is evidence that these plants grew in that area. The sediments hold a record for aquatic vegetation development. These species also provide us with the possibility of reconstructing environmental and climatic conditions. The occurrence of *Myriophyllum alterniflorum* in the TIX region could indicate the possibility of a mild maritime climate [34], which would correspond to the climatic conditions of the Allerød, when the lake probably began to be developed. According to Mikulski [35], *Myriophyllum alterniflorum* is very sensitive to subzero temperatures, which is unsafe for its vegetative organs. The depth of the lake during this period could have been ca. 0.2–1.0 m [34], which is compatible with the study conducted by Kozulin et al. [36], who stated that *Myriophyllum alterniflorum* can become established when water levels remain above 30 cm. The mild climate present during the development of the lake in the TIX site was also confirmed by the occurrence of *Potamogeton friesii*, connected, at present, to an oceanic climate [35]. This species was also present in the TVII site when the climate ameliorated at the turn of the Holocene, where, admittedly, there was no longer a regular water body present during that time; however, it probably found a location in a small pond in a community of *Carex rostrata* and grew in that location together with *P. pusillus*. In the initial phase of the lake’s development of the TVII site and in the shallows of the TVIII site, *Potamogeton filiformis* occurred in the Younger Dryas. This is considered in the literature as an indicator of a cool climate [37] and

as a pioneer species occurring after the melting of dead ice [38]. In the TVIII site region, there was no gytja present at the bottom of the mire, and *Caricetum vesicariae* with brown mosses was the dominant plant community. However, it is known in the literature that such a sedge community may indicate the stagnation of water at the ground at the level of 0.2–0.3 m [34]. The disappearance of the water body in the TVII area coincided with the decrease in the water level at the turn of the Holocene in northern Poland [39]. However, in the TIX area, the lake ceased to exist during an earlier period, in the Late Glacial. Of course, the disappearance of lakes led to the withdrawal of aquatic species; however, they have not returned to Knyszyn Forest. To date, not many water bodies or brooks exist where they could exist; however, other species of *Potamogeton* are present, such as *P. crispus* L., *P. compressus* L., *P. natans* L., *P. lucens* L., and *P. alpinus* Balb., but with the absence of the *Myriophyllum* species [31].

Cladium mariscus, non-existent in Knyszyn Forest at present, occurred in the past, and it was an admixture in plant communities. This species is associated with a substrate rich in calcium compounds. However, in the event of a milder, more oceanic climate, *Cladium mariscus* can be observed to be more ecologically tolerant and also occurs in sandy substrates [40]. Approximately 160 km to the north of Knyszyn Forest—in the Suwałki Landscape Park, where the eastern border of its range is presently located in this part of Europe—the contemporary presence of *Cladium mariscus* is connected to the occurrence of calcareous sediments. Great fen-sedge is present in this location, close to the lakes Kojle and Perty. In the past, the permanent occurrence of *C. mariscus*, from ca. 9500 cal. BP, at these locations was also connected to the occurrence of calcareous deposits present in the substratum, whereas the decline in calcium carbonate content in the neighboring lake of Purwin resulted in the disappearance of *Cladium mariscus*, which occurred ca. 1700 cal. BP [41]. Several reports in the literature on the ecological requirements of *C. mariscus* emphasize the calciphilic character of this species, e.g., [10,42]. However, the remains of *Cladium mariscus* analyzed in this study were recognized in sedge peat, and no premises exist to classify this sediment as calcareous. *Cladium mariscus* was present in Taboły during the Greelandian and Meghalayan stages of the Holocene, which corresponds with the former decline of the Preboreal, Boreal, Atlantic, and even Subboreal periods. During every time period, it was a component of subfossil vegetation in the type of contemporary *Magnocaricion*. *Cladium mariscus* did not form a dense field in that location; however, it is able to do so [43]. Its coexistence with *Thelypteris palustris* is also known in the literature both at present [44] and in the past [41]. In Taboły, both these species occurred together during the early and middle Holocene periods; however, it is difficult to determine a strong correlation. Perhaps an adequate quantity of remains of both of these taxa have simply not yet been determined. Therefore, what was the reason for the withdrawal of *Cladium mariscus* from Taboły? It may be assumed that the absence of a carbonate substrate was not the only cause of this event since the species appeared and persisted for some period of time. At the TIII site, the community with *Cladium mariscus* present was replaced by shrubs of the alliance *Alnion glutinosae*. In the TVII site, *Carex riparia* occurred, and *Cladium mariscus*—known as a weak competitor [45]—could not compete with this sedge. Such specimens of *Carex riparia* creating strong competition for *C. mariscus* were determined by Gałka and Tobolski [41]. At the TII site, there was probably one more reason for the disappearance of great fen-sedge: the beginning of the oligotrophication of habitats, caused by the decreasing importance of groundwater inflow. Such oligotrophication resulted in the emergence of oligotrophic vegetation, such as *Sphagnum*, from the sections *Acutifolia* and *Cuspidata*. In the TVII site, this oligotrophication was confirmed via Meghalayan (formerly the Subboreal) dating (2901–2764 cal. BP).

The history of two bush birches located in the Knyszyn Forest is interesting. Both of these species are regarded in Poland as glacial relicts. The first of them, *Betula nana* L., is widespread at present in the arctic regions of Eurasia, Greenland, Iceland, and North America [46]. It also grows in several locations in the Alps and the Carpathians as well as in the Baltic republics [47]. However, in Poland, *B. nana* is present to date

only in three isolated locations: in northern Poland (Linje Reserve), Izerskie Mire, and Zieleniec Mire (both located in the Sudety Mountains) [47]. In these locations, it is a component of communities typical for bogs with transitional elements. The second bush birch species, *Betula humilis* Schrank, occurs in Eastern and partly Central Europe and in Western Siberia to northwestern Mongolia. The westernmost scattered sites are located in northern Germany and the Alps. The southwestern limit of the compact range runs through Poland [48]. According to Jabłońska [49], *Betula humilis* is a species closer to the class *Scheuchzeria-Caricetea nigrae* than to *Alnetea glutinosae*, to which the communities of this species were included by European authors. In recent decades, the disappearance of *B. humilis* locations in Poland has been observed as a result of the drainage and overgrowing of peatlands. Concerning the previously studied historical occurrence of both shrub birches in Knyszyn Forest, *Betula nana* was noted as being present as early as during the first Late Glacial climatic warming stage, called Bølling, at the Machnac mire. Kupryjanowicz [50] identified pollen grains discovered there as *Betula* cf. *nana*. Nutlets were recognized in Older Dryas sediments in Stare Biele—another mire in Knyszyn Forest, located close to the Borki mire [51], whereas *Betula humilis* was recognized in Stare Biele, where its remains were found at different depths; however, their age was not estimated.

During this study, a correlation in the occurrence of both bush birches' remains was noted in the Taboły mire (Figure 7). Both species were concurrently present in the mire. It is well known in the literature that, to date, such a correlation has not been recorded in Poland. *Betula nana* is more closely related to bogs, and *B. humilis* to transitional mires or even fens. In the past, they occurred together in the following communities: shrubs of the alliance *Alnion glutinosae*, phytocoenosis similar to contemporary *Scheuchzeria-Caricetea nigrae*, communities of *Sphagnum palustre-Carex*, and communities of sedge-brown moss and brown moss with scrubby birches. These phytocoenoses were connected to fens or transitional mires [17], which differs from contemporary bog associations in the literature containing dwarf birch and is more similar to the phytosociological preferences of *Betula humilis* (see [52]). Interestingly, the community of sedge-brown moss and brown moss with scrubby birches is the closest to the contemporary shrubs-sedge-brown moss community observed in Western Siberia [53]. As *Betula nana* disappeared from Knyszyn Forest during the Northgrippian stage (formerly the Atlantic period), it can be assumed that *Betula humilis* was resistant to high temperatures and endured heavy rainfall better, which can lead to waterlogging. This period of the Holocene was characterized by temperatures 1–2 °C higher than at present and by precipitation levels 10–15% higher [54]. *B. humilis* also occurred in Taboły during the Meghalayan stage (formerly the Subboreal and Subatlantic periods). In Borki, it also occurred during the Meghalayan stage (formerly the Subatlantic period), and it remains present to date. However, it is difficult to conclude that there is a definite continuity of subfossil presence because no remains have been identified in the uppermost layers of peat. The same is true for Stare Biele, where *B. humilis* still grows; however, no remains were observed in the upper layers of the tested sediment [51].

Palaeobotanical studies provide knowledge about the flora and vegetation that existed in the past. Every studied area contributes to creating a broader picture of historical environments. In addition to the data directly related to historic vegetation and plant communities formed, conclusions can be drawn about the climate in the past, including the temperature and rainfall. This is only possible due to the preservation of peat bogs in an intact, well-hydrated, non-drying state so that they do not lose their role as an archive of paleoenvironmental data. In the case of the mires studied in the present work, their paleobiodiversity seemed to be driven by climatic changes in this region of Poland which occurred from the Late Glacial to the present day. However, apart from the climatic oscillations typical in northern Poland, local changes occurring in the inflow of groundwater were certainly evident. In such conditions, the succession of vegetation and changes in the flora occurred. It seems that the development of peat deposits was not significantly influenced by human beings, which confirms their high natural value. Contemporary biodiversity is therefore a natural continuation of the processes occurring in the past.

Although, in modern times, this separation from the impact of human beings is certainly less evident.

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