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Postglacial occurrence and decline of *Betula nana* L. (dwarf birch) in northeastern Poland

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Abstract. The Late Glacial and Holocene presence of *Betula nana* L. (dwarf birch) in northeastern Poland was reconstructed through palaeoecological analyses of sediment cores from the Taboły mire located in the territory of the Knyszyńska Forest. Peat records spanning thousands of years were analysed for plant macrofossils along with radiocarbon dating. *Betula nana* was present in Taboły from ca 13 000 to ca 9000 yr BP. The presence of this species was described in the Late Glacial period, most likely in the Allerød and Younger Dryas. However, our research on the palaeoecology of dwarf birch showed that after the Late Glacial/Holocene transition, the species did not disappear from northeastern Poland and still existed in the Preboreal, Boreal and lower Atlantic periods. The occurrence of *Betula nana* was documented by the presence of generative remains (nuts and catkin scales) in sediments, which is the best evidence of its in situ position. The later disappearance of the studied species could be related to the negative effects of palaeoenvironmental conditions in the Atlantic, which resulted in a temperature increase and high precipitation, causing the waterlogging of the substratum and rendering it unsuitable for dwarf shrub that prefers severe climate conditions. The Taboły site seems to be one of separate locations of *B. nana* during the Atlantic in this part of Europe.

Key words: northeastern Poland, Late Glacial, Holocene, *Betula nana*, macrofossils.

INTRODUCTION

Mire ecosystems have a unique feature of preserving the records of past communities in the peat. Therefore peat-forming plant communities offer an opportunity to study the processes of community development and successional trends and the species composition of former phytocoenoses (Tołpa et al. 1967; Rybníček 1973). The peat archive includes macro- and microfossils that are complementary and together give a complete picture of peatland development (Rydin & Jeglum 2008). Palaeoecological studies provide information about historic environmental conditions, often revealing the past presence of taxa that are currently absent from the studied location. This is often connected with the presence of plant communities that are currently unknown or are known in other territories (Drzymulska 2006a). The changes in plant ranges were caused by climate change and its impact on edaphic conditions and vegetation distribution in the Late Glacial and Holocene, which has been well explained by a model of the glacial–interglacial cycle (Birks & Birks 2004).

Northeastern Poland is a key area for studies on the migration and the reasons for the disappearance of plants with regard to changes in climate (Gałka & Tobolski 2013). The Knyszyńska Forest, which is the study site for this research (Fig. 1), is located there.

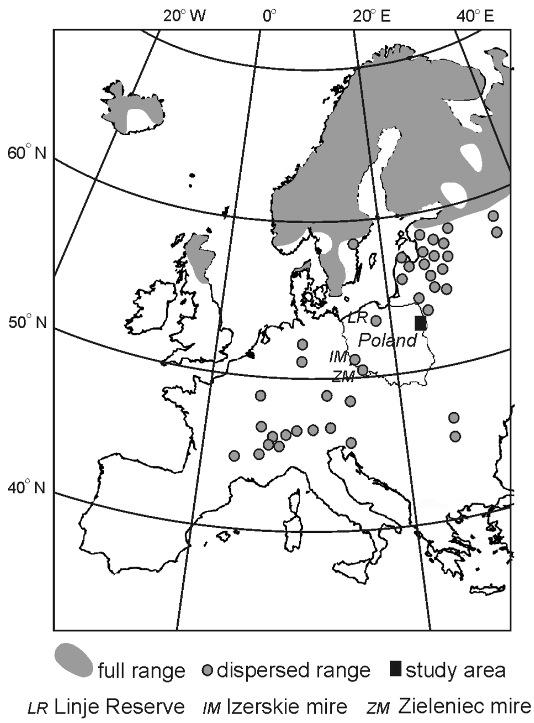

Fig. 1. Contemporary range of *Betula nana* L. in Europe (according to Polish Red Data Book of Plants; chapter: '*Betula nana* L. Dwarf birch' by Kruszelnicki & Fabiszewski 2001; slightly modified). Indication of the study area.

Over thousands of years this region has constituted a migration gate for plants in north-south-north and east-west-east directions. In addition, this part of Poland is unique due to its present-day climate. It is one of the coldest regions in Poland, which is reflected in the presence of boreal plant communities, such as boreal bog-birch forest with *Betula humilis* Schrank in the understory and boreal spruce forest in the peat (Czerwiński 1995).

Some of the most interesting macrofossils found in the sediments of this area are the remains of cold-tolerant *Betula nana* L. (dwarf birch). This species, regarded in Poland as a glacial relic, is currently widespread in the arctic regions of Eurasia, Greenland, Iceland and North America (De Groot et al. 1997). This is a highly branched shrub that often grows up to 1 m in height and is a characteristic species of open raised bog and tundra environments. When we consider the contemporary occurrence of *B. nana* in Europe as described in the Polish Red Data Book of Plants (Kruszelnicki & Fabiszewski 2001), we observe its absence in northeastern Poland (Fig. 1). The presence of dwarf birch seems natural because it occurs also in Lithuania, Latvia and Estonia. However, as no *B. nana* is found in northeastern Poland, its nearest western location is more than 300 km west, in northern Poland (Linje Reserve; LR in Fig. 1). This is one of the three contemporary isolated locations of this endangered species in Poland. The remaining two are in the Sudety Mountains (Izerskie mire and Zieleniec mire; IM and ZM, respectively, in Fig. 1). Aside from these locations, dwarf birch is still growing in several places in the Alps and the Carpathians (Kruszelnicki & Fabiszewski 2001).

The oldest postglacial presence of dwarf birch in northeastern Poland was described by Wacnik (2009) based on the pollen record from Lake Miłkowskie (Mazury Lakeland, Fig. 2), where rebuilding of vegetation (with *B. nana*) started in the Meiendorf (from ca 14 450 cal BP). In the Knyszyńska Forest, *Betula* cf. *nana* occurred (pollen grains) during the first Late Glacial climatic warming called Bølling, which was noted in sediments from the Machnacz mire (Kupryjanowicz 1991; Fig. 2). The Late Glacial and Holocene findings of *B. nana* pollen and macroremains in northeastern Poland are presented in Fig. 2.

Remains of *B. nana* include pollen grains, fruits, catkin scales, bud scales, leaves and periderm. Pollen is the most difficult to identify because the *B. nana* pollen grains are similar to those of birch trees, such as *Betula pendula* Roth and *Betula pubescens* Ehrh. Pollen grain size ranges for these species partially overlap, despite the mean values being higher for *B. nana* (Koperowa & Środoń 1965; Birks 1968). To distinguish among them, the general pollen morphology, pollen grain size and grain diameter/pore depth ratio should be taken into consideration (Birks 1968). For this reason, *B. nana* pollen grains are often identified as cf. *Betula nana*, *Betula nana*-type or they are included into a general category of *Betula* pollen. However, the nuts and the catkin scales of dwarf birch possess features distinguishing them from the nuts and catkin scales of both tree birches (*sectio Albae*) and shrubby *B. humilis* (van Dinter & Birks 1996; Felix Y. Velichkevich pers. comm. 2002). Therefore, to confirm the presence of dwarf birch in any location in the past, the recognition of macrofossils (generative remains, leaves, wood, periderm) is particularly important.

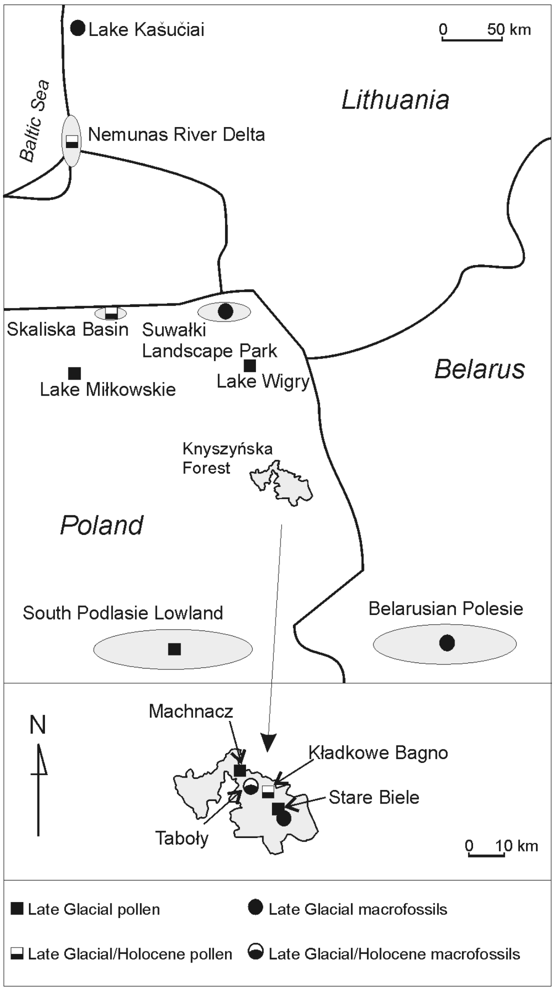

Fig. 2. Location of sites with *Betula nana* pollen and macrofossils recognized in Late Glacial and Holocene sediments of northeastern Poland.

Unfortunately, subfossil generative *B. nana* findings are not frequent, and knowledge of the distribution of this species during the postglacial period is poor. Usually, *B. nana* is mentioned as the pioneer species of the Late Weichselian landscape. We know little about its Holocene history in Poland and neighbouring countries. On two sites with *B. nana* (Linje mire and Zieleniec mire) existing in Poland, where analyses of plant macrofossils have been carried out, the continuity of duration of dwarf birch population in the Holocene has been confirmed (Kloss 2007). However, there are no publications concerning dwarf birch palaeoecology. Therefore, the key objectives of the present study are: (i) to determine the time frame of the occurrence of this species in northeastern Poland during the last approximately 13 000 years, (ii) to define subfossil plant communities containing dwarf birch, (iii) to reconstruct the palaeoenvironmental conditions of *B. nana* existence and (iv) to recognize reasons for its disappearance. For this purpose, an analysis of macrofossil plant remains and ^{14}C dating were used.

STUDY AREA

This study was conducted within the territory of northeastern Poland (Fig. 1), in the Knyszyńska Forest Landscape Park (Fig. 3A). Regional topography was formed by the Wartanian (Saalian) glaciation (Marks 2005), which produced a number of fluvioglacial features including kames, kame terraces and numerous melt-water forms. The Knyszyńska Forest region is located in the vicinity of the Vistulian (Weichselian) glaciation landscape (Pawłowska & Miodek 1993). Holocene sediments (sands, loams, fluvial gravels and peat) fill the river valleys and melt depressions.

The climate of this area is temperate transitional between maritime and continental, with a tendency towards a continental climate. The mean annual temperature is relatively low, +7 °C; however, the annual amplitude is high, up to 22 °C, and the mean annual precipitation is approximately 570 mm. The growing season is approximately 200 days long, and snow cover lasts 85–90 days, i.e., much longer than in the central and western regions of Poland (Sasinowski 1995).

A characteristic feature of vegetation in this area is the distinct presence of *Picea abies* (L.) Karsten in nearly all forest associations and the absence of *Fagus sylvatica* L. Besides spruce, other boreal species also occur, including *Betula humilis* Schrank or *Vaccinium oxycoccos* L. Forests cover approximately 80% of the Knyszyńska Forest area. The most frequent tree species are conifers: *Pinus sylvestris* L. (71%) and *Picea abies* (L.) Karsten (13%). Among deciduous trees, the main stand area is occupied by *Betula verrucosa* Ehrh. (7%), *Alnus glutinosa* (L.) Gaertner (4%) and *Quercus robur* L. (3.5%) (Żarska 1993).

More than 20% of the Knyszyńska Forest area is occupied by paludal habitats, therein mires (Okruszko 1995). One of the largest mires is Taboły, the subject of this study. This peatland, situated in a large melt-water basin (307 ha) in the northern part of the Knyszyńska Forest (Fig. 3A), is the forest nature reserve.

METHODS

Altogether, 16 cores of sediments were collected in the Taboły mire using a 5 cm diameter Russian sampler. The drillings were carried out along longitudinal and transversal transects (Fig. 3B). Cores were divided into segments 10–15 cm long. For analysis of macroscopic plant remains, 50 cm^3 from each sample of peat was used. Distilled water with an addition of 10% KOH, was used to soak the material. Next, the suspensions were boiled, rinsed in a 0.2 mm sieve, and placed in Petri dishes. For analysis of vegetative plant remains, a light microscope (Nikon Eclipse E400) was used. Generative findings were picked out of each sample. These countable remains were identified using a stereoscopic binocular microscope (Nikon SMZ 800) and were presented as absolute sums. Their identification was performed with the help of Tobolski (2000) and Felix Y. Velichkevich (personal contact at the Institute of Botany Polish Academy of Sciences, Kraków, 2002). Nuts and catkin scales of *B. nana* were identified.

The botanical composition of the analysed samples was assessed in order to describe peat units according to Tołpa et al. (1967). After that, subfossil plant communities were determined. Criteria established for contemporary phytocoenology were adapted (Oświt 1973; Pałczyński 1975), which means that a basis for the classification of the subfossil community was not the abundance of the taxa remains, but their adequate combination. Therefore, the quantitative estimation of the occurrence of a species in the community need not always be decisive for the determination of the phytocoenosis (Rybníček 1973). The subfossil plant communities from the Taboły mire were arranged in synthetic tables, in which degrees of frequencies (I–V) represent the proportion of each past taxon within individual peat samples (Drzymulska 2006a). Detailed results of the macrofossil analyses of the Taboły mire sediments have been published previously by Drzymulska (2006b, 2010, 2011).

To determine the age of the sediments and the chronozone configuration in the deposit, radiocarbon (^{14}C) dating was used. The ^{14}C samples were dated in the Poznań Radiocarbon Laboratory (Poznań, Poland; Poz) by the AMS method. Three samples were dated in the Radioanalytical Laboratory of the Institute of Hygiene and Medical Ecology in Kiev (Kiev, the Ukraine; Ki). The radiocarbon age of the samples was calibrated with OxCal 4.2.3 (Bronk Ramsey 2013). The chronology of

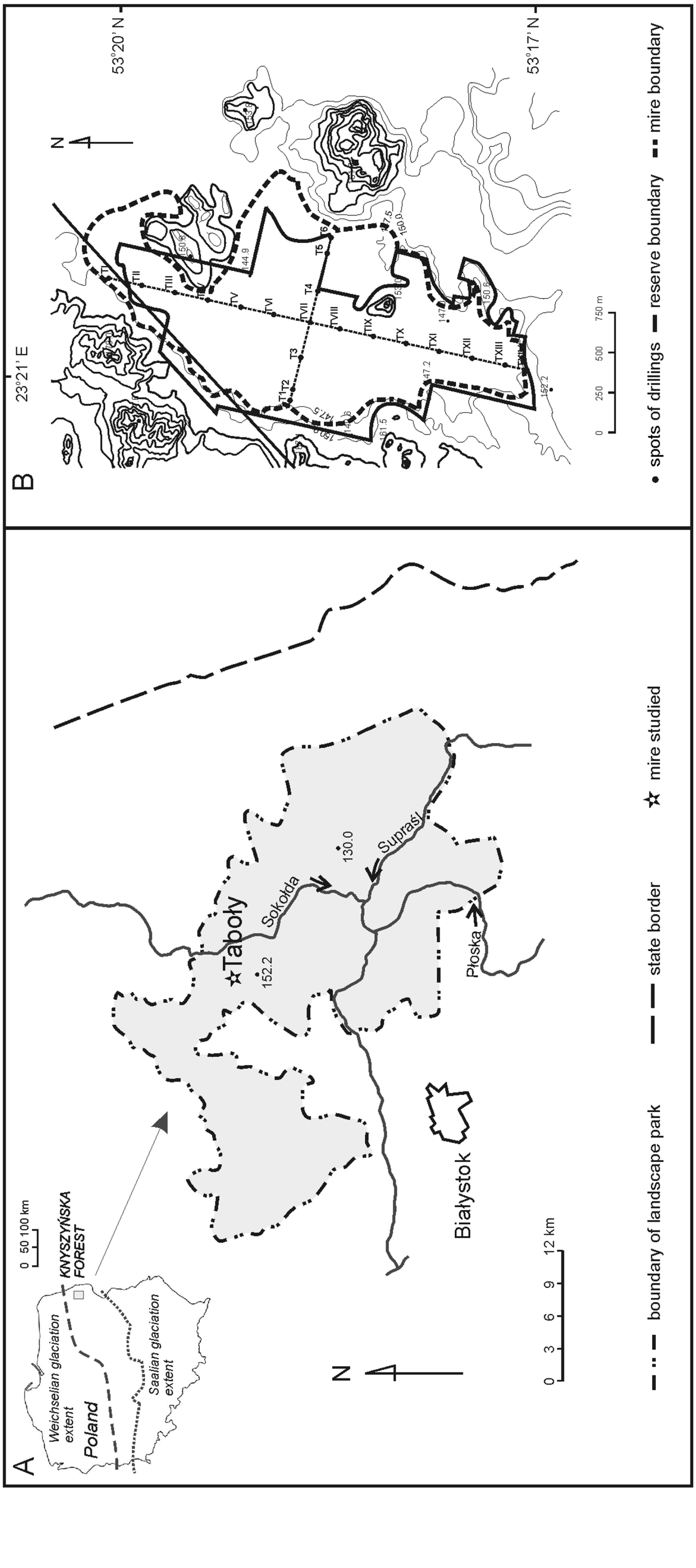

Fig. 3. A, location of the Knyszyńska Forest and the mire studied; **B**, the Taboły mire. Spots of drillings and transects.

the peat profiles was presented according to Litt et al. (2001) with a modification by Latałowa (2003) for the Late Glacial, and according to Mangerud et al. (1974), with the calibration of chronozone boundaries by Walanus & Nalepka (2010), for the Holocene.

RESULTS

The typology and distribution of the sediments were presented in two geological cross sections of the Taboły mire (Figs 4, 5). The ages of studied sediments are provided in Table 1. According to these data, biogenic accumulation started at Taboły during the decline of the Oldest Dryas (13 838–13 547 cal BP). Sediments from this time period were found in the immediate vicinity of the TIV core. In the region of TVII and TIX drillings, small water bodies existed in the Late Weichselian, which was confirmed by the presence of lacustrine sediments: at TVII – lacustrine chalk and calcareous gyttja, and in the vicinity of TIX – lacustrine chalk, calcareous gyttja and medium-detritus gyttja. Their thickness was 50 cm in both cases. In the remaining profiles, peat had accumulated directly on the mineral ground (sand). The thickest peat (550 cm) was recorded in core TIX.

During the Late Glacial, fen peat (mainly brown moss peat and sedge–brown moss peat) was the most common in the deposit, which means that brown moss communities dominated on the studied site. These phytocoenoses were present also in the Preboreal period. In the Boreal period, sedge communities and sedge communities with shrubs replaced brown mosses. In the roof of the deposit, transitional forest–herbaceous peat was observed. This peat unit is not present in the classification by Tołpa et al. (1967). A forest-brushwood + *Carex–Sphagnum* community was the parent phytocoenosis of the forest-herbaceous peat.

Betula nana was present in Taboły from ca 13 000 to ca 9000 yr BP. The occurrence of this species was connected with the Late Glacial in the vicinity of the TV, TIX and T4 drillings and with the Holocene at TII (Boreal), TIV (Boreal/Atlantic), TV (Preboreal), TVI (Preboreal), TVIII (Preboreal/Boreal), TX (Boreal) and

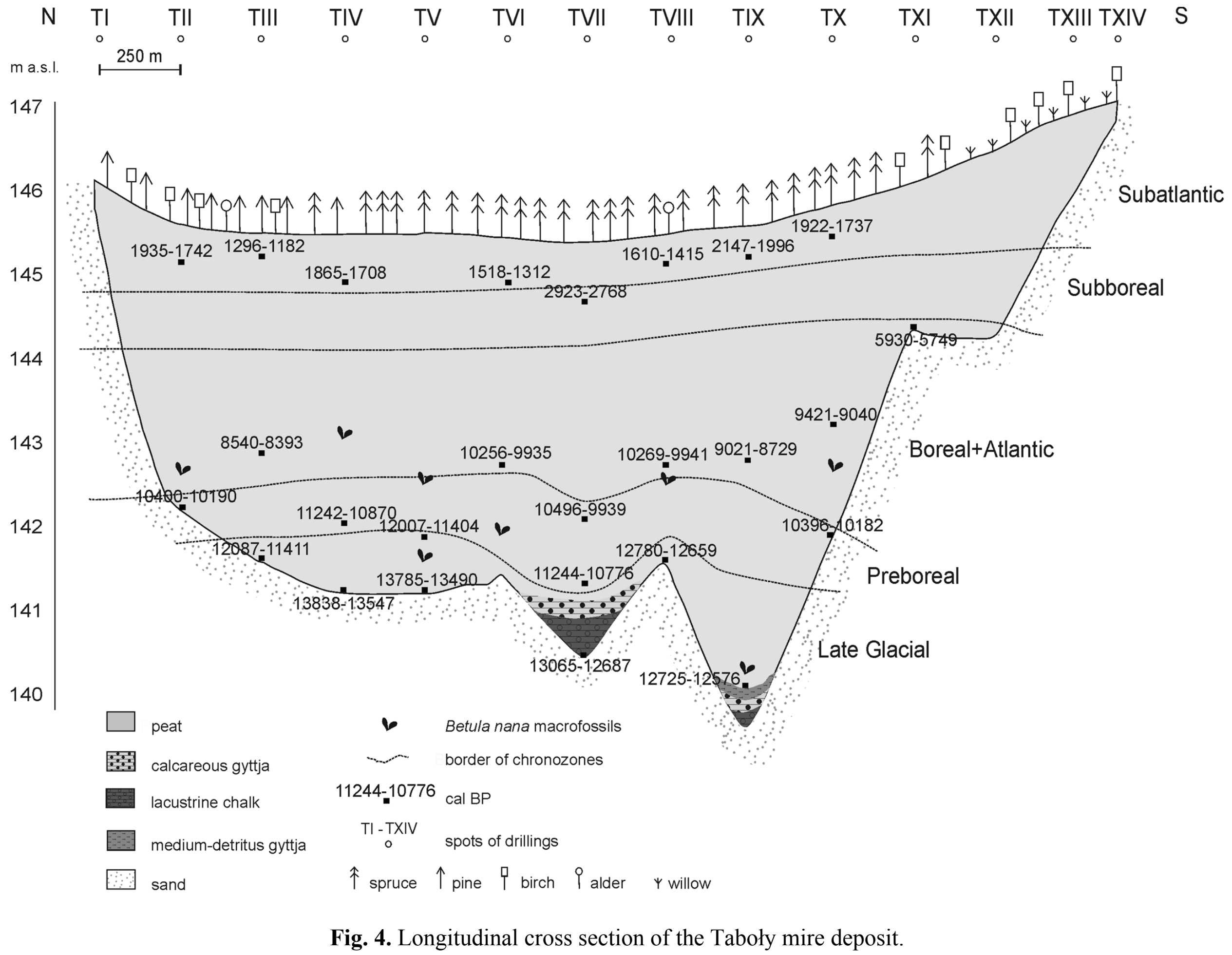

Fig. 4. Longitudinal cross section of the Taboły mire deposit.

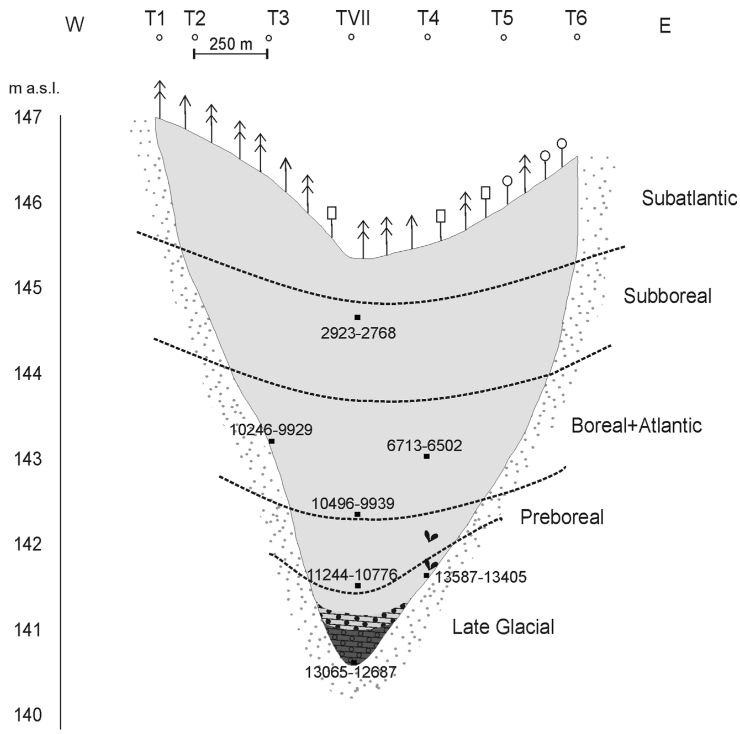

Fig. 5. Transversal cross section of the Taboły mire deposit. For explanations see Fig. 4.

Table 1. Radiocarbon datings from the studied profiles. The radiocarbon age of the samples was calibrated with OxCal 4.2.3 (Bronk Ramsey 2013)

Core/depth, cm	Dated material	Lab. No.	^{14}C BP	Calibrated range 95.4%, cal BP	Mean values of calibrated datings
TII/35	Sedge epiderm	Poz-2959	1 915 ± 30	1 935–1 742	1 838
TII/320	Coniferous wood	Poz-3177	9 100 ± 50	10 400–10 190	10 295
TIII35	Sedge epiderm	Poz-2960	1 315 ± 30	1 296–1 182	1 239
TIII/245	Sedge epiderm	Poz-2961	7 660 ± 40	8 540–8 393	8 466
TIII/385	Common reed tissues	Poz-3119	10 160 ± 60	12 087–11 411	11 749
TIV/50	Sedge epiderm	Poz-2962	1 840 ± 30	1 865–1 708	1 786
TIV/363	Common reed tissues	Poz-2963	9 720 ± 50	11 242–10 870	11 056
TIV/422	Brown moss stems	Poz-2885	11 880 ± 60	13 838–13 547	13 692
TV/365	Common reed tissues	Poz-3118	10 120 ± 60	12 007–11 404	11 705
TV/425	Brown moss stems	Poz-2965	11 850 ± 60	13 785–13 490	13 637
TVI/45	Sedge epiderm	Poz-2966	1 500 ± 30	1 518–1 312	1 415
TVI/270	Peat moss stems	Poz-2967	9 020 ± 50	10 256–9 935	10 095
TVII/75	Sedge epiderm	Poz-2969	2 745 ± 30	2 923–2 768	2 845
TVII/310	Brown moss stems, grass epiderm	Ki-10093	9 080 ± 80	10 496–9 939	10 217
TVII/415	Brown moss stems	Ki-10092	9 700 ± 80	11 244–10 776	11 010
TVII/485	Lump of sediment	Ki-10401	10 940 ± 120	13 065–12 687	12 876
TVIII/37	Sedge epiderm	Poz-2979	1 635 ± 30	1 610–1 415	1 512
TVIII/265	Brown moss stems	Poz-2980	9 030 ± 50	10 269–9 941	10 105
TVIII/385	Brown moss stems	Poz-2981	10 810 ± 50	12 780–12 659	12 719
TIX/40	Sedge epiderm	Poz-3115	2 100 ± 30	2 147–1 996	2 071
TIX/280	Brown moss stems	Poz-2970	8 025 ± 40	9 021–8 729	8 875
TIX/545	Brown moss stems	Poz-2972	10 710 ± 50	12 725–12 576	12 650
TX/30	Coniferous wood	Poz-2973	1 900 ± 30	1 922–1 737	1 829
TX/275	Peat moss stems	Poz-2975	8 260 ± 50	9 421–9 040	9 230
TX/395	Peat moss stems	Poz-2976	9 090 ± 50	10 396–10 182	10 289
TXI/170	Coniferous wood	Poz-2977	5 115 ± 35	5 930–5 749	5 839
T3/305	Peat moss stems	Poz-6327	9 000 ± 50	10 246–9 929	10 087
T4/245	Sedge epiderm	Poz-2882	5 810 ± 30	6 713–6 502	6 607
T4/385	Brown moss stems	Poz-2883	11 670 ± 50	13 587–13 405	13 496

T4 (Preboreal). The positions of dwarf birch macrofossils in the deposit are presented in Figs 4 and 5.

Betula nana was a component of some plant communities; these communities included brown mosses, herbaceous plants and other shrubs. Peat samples that contained fruits and catkin scales of dwarf birch are described as sedge peat, sedge–brown moss peat, brown moss peat, and sedge–brown moss peat with *Sphagnum*. Short descriptions of the botanical compositions of the peat layers containing remains of *B. nana*, with a designation of the peat units and the subfossil plant communities, are provided in Table 2.

Table 2. Description of the botanical composition of peat layers containing remains of *B. nana* and designation of peat units and subfossil plant communities

Core	Depth, cm	Description of plant remains	Peat unit	Subfossil community
TII	270–300	Radicles of *Carex* sp. are predominant (max. 75% in sample volume). Epiderm of *Phragmites australis* achieves a maximum of 20%. Tissues of *Thelypteris palustris*, *Pinus sylvestris*, *Alnus* sp. and *Equisetum limosum* as well as nuts of *Betula nana* and *Betula humilis* are also recognized.	Sedge peat	Alder shrub community
TIV	210–240	Radicles of *Carex* sp. achieve even 80% in a sample. Remains of *Thelypteris palustris* (max. 5% of vegetative tissues and numerous sporangia), periderm of *Alnus* sp., nuts of *Betula nana*, *Betula humilis* and *Betula sec. Albae* are recognized.	Sedge peat	Alder shrub community
TV	300–315	Remains of *Carex* sp. dominate (80%). Deciduous wood and leaves and branches of peat mosses of the *Subsecunda* section accompanying them, achieve 10% and 5%, respectively. Nuts and catkin scales of *Betula nana* and *Betula humilis*, as well as seeds of *Menyanthes trifoliata* and nuts of *Carex* sp., are recognized. Alder periderm was noted in minimal amount.	Sedge peat	Alder shrub community
	375–390	Domination of *Carex* sp. radicles (75%). Brown mosses achieve 15% of sample volume and tissues of *Thelypteris palustris* as well as deciduous wood – 5%. Nuts of *Betula nana* and *Betula* cf. *humilis* are present.	Sedge peat	Sedge–brown moss and brown moss with scrubby birch community
TVI	340–370	*Carex* sp. radicles (max. 70% in a sample) and remains of brown mosses (max. 60%) dominate. Periderm of *Betula* sp., deciduous wood and peat mosses of the *Acutifolia* section are recorded in lower percentage. Nuts of *Betula nana* are present.	Sedge peat, sedge–brown moss peat	Sedge–brown moss and brown moss with scrubby birch community
TVIII	275–290	Remains of *Carex* sp. and brown mosses (*Tomenthypnum nitens* and *Meesia triquetra*) dominate (45% and 35%, respectively). *Betula nana* nut is recognized.	Sedge–brown moss peat	Community of *Scheuchzerio–Caricetea nigrae* class
TIX	480–550	Remains of brown mosses achieve a maximum of 75% of sample volume, and radicles of *Carex* sp. – a maximum of 25%. Tissues of *Thelypteris palustris* and peat mosses are represented in smaller amounts. Nuts of *Betula nana* and *Betula humilis*, as well as catkin scales of tree birches (*sectio Albae*), seeds of *Menyanthes trifoliata*, nuts of *Carex* sp. and *Carex* cf. *pseudocyperus* are recognized.	Brown moss peat, sedge–brown moss peat	Sedge–brown moss and brown moss with scrubby birch community

Table 2. *Continued*

Core	Depth, cm	Description of plant remains	Peat unit	Subfossil community
TX	330–340	Among vegetative finds remains of *Carex* sp. (30%), *Pleurozium schreberi* (15%), brown mosses (10%), *Menyanthes trifoliata* (10%), *Sphagnum palustre* (5%) and *Sphagnum squarrosum* (5%) are present. Nuts of *Betula nana* and *Betula sec. Albae* are also recognized.	Sedge–brown moss peat with *Sphagnum*	*Sphagnum palustre–Carex* community
T4	330–340	Remains of brown mosses are dominant (max. 75%), therein *Aulacomnium palustre* (15%) and *Tomenthypnum nitens* (5%). Radicles of *Carex* sp. and tissues of *Thelypteris palustris* are noted in small amounts. Nuts of *Betula nana*, *Betula humilis*, *Betula sec. Albae*, as well as seeds of *Comarum palustre*, and nuts of *Carex vesiacaria* and *Carex sec. Paniculatae* are present.	Sedge–brown moss peat	Community of the *Scheuchzerio–Caricetea nigrae* class
	370–380	Domination of *Carex* sp. (30%) and brown mosses (45%) remains. Periderm of *Betula* sp. achieves 10% of sample volume. Tissues of *Thelypteris palustris*, Ericaceae, *Salix* sp. and deciduous wood are recorded in small percentage. Among generative finds, nuts of *Betula nana*, *Betula sec. Albae*, *Carex* sp. and seeds of *Menyanthes trifoliata* are present.	Sedge–brown moss peat	Sedge–brown moss and brown moss with scrubby birch community

DISCUSSION

The region of the Knyszyńska Forest (NE Poland), although located in the old glacial plains, was devoid of vegetation during the Plenivistulian. It was a periglacial zone, situated approximately 60 km south from the ice sheet during its maximum (Pawłowska & Miodek 1993; Fig. 3A). Amelioration of climatic conditions, in comparison with the Last Glacial Maximum, which took place during the Late Glacial period, allowed the gradual rebuilding of vegetation cover. *Betula nana* was a typical pioneer species. Its presence provides information about the local terrestrial biota, suggesting rather severe climate conditions (Wasylikowa 1964).

The oldest generative macrofossils of *B. nana* found in the studied Taboły mire were connected with the Late Glacial period (Figs 4, 5), most likely with the Allerød (TV and T4) and the Younger Dryas (TIX). Older remains (from the Older Dryas) have been observed in the nearby Stare Biele site (Fig. 2), where pollen grains of *Betula nana*-type (Kupryjanowicz 2000) and two nuts (Marek 2000) were identified. Outside the Knyszyńska Forest, the nearest Late Glacial carpological findings of dwarf birch are from the Suwałki Landscape Park (Gałka & Sznel 2013), Belorussian Polessie (Matveev et al. 1993) and western Lithuania (Lake Kašučiai; Stančikaitė et al. 2008) (Fig. 2). In each of these locations, *B. nana* was present in the Younger Dryas.

After the Late Glacial – a period that is climatically favourable for *B. nana* – abrupt and significant environmental transformations took place, joining the climatic changes with subfossil evidence of plant communities (Heikkilä et al. 2009). This transition from the Late Glacial to the Holocene interglacial caused the disappearance of Subarctic flora at the very beginning of the Holocene. During the first half of the Preboreal chronozone, *B. nana* disappeared from many locations in which this species was present in the Late Glacial. Such changes have been noted near the Knyszyńska Forest, to the north – at Lake Wigry (Kupryjanowicz 2007) and to the south – in the South Podlasie Lowland (Dobrowolski et al. 2012) (Fig. 2), and at sites located farther north, in the territories of Lithuania (Stančikaitė et al. 2008), Latvia (Ozola et al. 2010; Veski et al. 2012) and Estonia (Saarse & Rajamäe 1997).

Dwarf birch survived the Holocene climate amelioration at the Taboły site. Its presence was observed there in the Preboreal, Boreal and most likely lower Atlantic periods (TIV?; Fig. 4), which is confirmed by palynological data from the adjoining Kładkowe Bagno bog (Kupryjanowicz 2004; Fig. 2). Environmental conditions might be especially favourable for this species, and warming was not a key factor for the dwarf birch elimination. The domination of open sedge communities (shrubs present in only some places) was a likely important feature of mire (Drzymulska 2006a, 2010). *Betula nana* is a photophilous species, which prefers open spaces that are not overgrown by trees (Kruszelnicki & Fabiszewski 2001). Afforestation of the entire southern part of Belarus could be a reason for the disappearance of dwarf birch in the territory of Belorussian Polessie during the Boreal. Its pollen grains ceased to be found in the record related to this period of the Holocene (Matveev et al. 1993). However, *B. nana* was still present during the Boreal in the Skaliska Basin (Kołaczek et al. 2013) and in the Nemunas River Delta (Bitinas et al. 2002) (Fig. 2).

At the Taboły site, *B. nana* was observed in four plant communities: the alder shrub community, the sedge–brown moss and brown moss with scrubby birch community, the community of the *Scheuchzerio–Caricetea nigrae* class and the *Sphagnum palustre–Carex* community (Table 2). These phytocoenoses were connected with fens or transitional mires (Drzymulska 2006a), which is different from contemporary bog associations containing dwarf birch – *Sphagnetum magellanici* (Kruszelnicki & Fabiszewski 2001) and *Pinetum mughi betuletosum nanae* Kästner & Flössner 1933 (Holman 1996).

Most often, *B. nana* was a component of the sedge–brown moss and brown moss with scrubby birch community. This phytocoenosis was present in the mire in the Late Glacial and Preboreal and could be identified with the shrub–sedge–brown moss associations described by Liss & Berezina (1981) in Western Siberia. Its floristic composition suggests the possibility of connections with contemporary *Betuletum humilis* Fijałkowski 1959 (Pałczyński 1975; Botsch & Smagin 1993). According to Botsch & Smagin (1993), *B. nana* is one of the components of *Betuletum humilis* in the territory of northwestern Russia. Three remaining subfossil communities recognized at Taboły occurred in the older and middle Holocene.

The decline of *B. nana* in the Knyszyńska Forest most likely took place in the lower Atlantic (Kupryjanowicz 2000, 2004). This period of the Holocene was characterized by temperatures 1–2 °C higher than the present and by precipitation 10–15% higher (Ralska-Jasiewiczowa & Starkel 1999). However, in the Boreal, *B. nana* already grew in the conditions of unexpectedly high temperatures. The occurrence of *Cladium mariscus* (L.) Pohl in Taboły during this time period indicates a mean minimum July temperature of approximately 16 °C and a mean minimum January temperature of approximately –4 °C (Wasylikowa 1964). Furthermore, it has been recognized that *B. nana* is sensitive to waterlogging (Ejankowski 2008). During the Atlantic, negative factors culminated in the Knyszyńska Forest, resulting in the decline of dwarf birch. The consequences of waterlogging and high temperatures were not compensated by the occurrence of the open spaces preferred by this plant. After its decline in the Atlantic, *B. nana* never returned to this location. Dwarf birch, which is currently known from sites located to the northeast, in Lithuania, Belarus, Latvia and Estonia, has not been noted there, to my knowledge, in pollen or macrofossil records younger than the Boreal. Therefore, the identification of carpological remains of *B. nana* in sediments from this part of Europe is significant. This evidence indicates the occurrence of *B. nana* not only in the Late Glacial and the beginning of the Holocene but also during the Atlantic.

CONCLUSIONS

Betula nana appeared in northeastern Poland during the Late Glacial, when the climate ameliorated and the rebuilding of vegetation took place. The occurrence of dwarf birch was confirmed by finds of pollen grains and generative macrofossils in sediments. In the region of the Knyszyńska Forest, these findings were identified both in the Late Glacial and Holocene peat. *Betula nana* occurred at Taboły from the Allerød interstadial until the lower Atlantic period and was a component of four subfossil communities; however, none of the communities was connected with a bog, which is observed at present. One of these subfossil phytocoenoses – the sedge–brown moss and brown moss with scrubby birch community, seems to be linked with contemporary *Betuletum humilis*, which can be found in northwestern Russia. Dwarf birch disappeared in the lower Atlantic, possibly due to the negative effects of the palaeoenvironmental conditions, such as an increase in temperature, very high precipitation and waterlogging of the substratum (Ralska-Jasiewiczowa & Starkel 1988). The Taboły site is a rare location with *B. nana* in the Atlantic period in this part of Europe.

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Betula nana L. (vaevakase) jääajajärgne levik Kirde-Poolas

Danuta Drzymulska

Tuginedes Taboły soost (Knyszyńska looduskaitsealal) tehtud turbasetete paleoökoloogilistele uuringutele, tehti kindlaks vaevakase hilisjääaegne levik Poola kirdeossa ja ka hilisem esinemine Holotseenis. Uuringut toetasid taimsete makrofossiilide radiosüsinikudateeringud, mille alusel võib öelda, et *Betula nana* kasvas antud piirkonnas umbes 13 000 kuni 9000 aastat tagasi. Täpsemad paleobotaanilised uuringud näitasid, et vaevakaske leidus ka hiljem, eksisteerides siin veel preboreaalse, boreaalse ja osaliselt ka atlantilise kliimastaadiumi ajal. Seda kinnitavad vaevakase generatiivsed jäänused (tiivad, pähklikesed), mida leiti nimetatud vanusega Taboły soo setetest. Hilisemast perioodist jäänuseid enam ei leitud ja vaevakase kadumist võib põhjendada atlantilisel kliimastaadiumil toimunud temperatuuri tõusu ning sademete hulga suurenemisega, mis osutusid ebasoodsaks karmimaid kliimatingimusi eelistava vaevakase populatsiooni edasisele püsimajäämisele. Taboły soos eksisteeris vaevakask siiski üsna kaua, mida võib selle Euroopa-osa jaoks erandlikuks pidada.