



Mosses recognized as glacial relicts from their postglacial distribution in Poland

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Abstract

Some glacial relict (mosses) have survived from the Ice Age up to the present time in specific, long-lasting habitats. Mires are one of the most common ecosystems in which they are present. In this paper the past distribution of eight species of such peat-forming mosses in Poland in the past is discussed. The distribution and dates of previously published moss finds in Poland have been mapped. In almost every case the largest number of places where they were found was in northern, or more precisely northeast Poland. A significant difference in the number of known find sites for individual species and many sites of unknown age were found. The rarest moss was definitely *Cinclidium stygium* and the most frequent was *Meesia triquetra*. Data on the distribution of mosses in the Late Glacial and Holocene proved to be scarcer than expected. Only a few sites were found where the occurrence of species such as *Meesia triquetra*, *Calliergon giganteum*, *Tomentypnum nitens*, *Pseudocalliergon trifarium*, *Helodium blandowii* and *Scorpidium scorpioides* was fairly continuous for this period. Therefore, the status of these mosses as glacial relicts seems to merit some thought. Certainly, there is a further need for high resolution research on bryophyte macrofossils, combined with accurate dating.

Keywords Glacial relicts · Mosses · Late Glacial · Holocene · Poland

Introduction

The determination of whether plant species can be defined as relicts strongly depends on the evidence of their distribution in the past, because it is usually based on a comparison of modern and past distributions. Modern distribution often represents a remnant of a wider distribution in the past (Grandcolas et al. 2014). These taxa can therefore be called geographical relicts if they constitute the oldest continuous presence in the vegetation of a given area (Czubiński 1950). In the case of glacial relicts, the essence of the relict status is their presence in an area south of their typical northern range. Glacial relicts are remnants of taxa which are adapted to withstand cold, but which experienced a great reduction of their range in the postglacial period, which left

behind relict populations in enclaves where suitable conditions still existed (Jiménez-Alfaro et al. 2016). Thus, some taxa migrated into the temperate zones during the glacial periods, when the climate was presumably more suitable for them than today (Odgaard 1988). A feature of glacial relicts is their survival from the Ice Age up to the present time in specific, long-lasting habitat conditions (Holmquist 1962). In the literature the term “glacial relict” is used in reference to species that have persisted at refuge sites from the time of the Last Glacial Maximum (Horsák et al. 2010), and also to ones that had definitely arrived by the end of the Late Glacial period, and are now found in recent refuges (Holmquist 1962; Rybníček 1966). The possible distinction between relicts from glacial maxima and from interstadials is difficult because it can only be based on knowledge of their modern habitat preferences (Dítě et al. 2018). Keeping to this rule, the boreal taxa of peat mires as well as those of forest-steppe or open taiga woods should be treated as relicts of interstadials and the early Holocene, in the sense of the former Preboreal and Boreal periods. Continental taxa of zonal (climatically determined areas) of steppe and circumpolar arctic-alpine ones would be relicts of glacial maxima (Horsák et al. 2015). However, some terms used

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in the literature, like “glacial relict”, “cold-stage relict” or “postglacial relict”, seem to correspond to each other in practice (Hájková et al. 2015). Szafer (1949) pointed out the difficulty of distinguishing glacial from interglacial relicts, due to the floristic similarity of the interglacial and postglacial periods.

Dítě et al. (2018) state that glacial relicts can be considered partially light-demanding species that were regionally more common before the spread of shaded woodlands in the early and middle Holocene. Conditions in isolated refugia outside the main distributional ranges of these taxa with a specific cool microclimate meant that plants of open unwooded areas, including tundra, could survive in such places for thousands of years, and some of them are still present in the same places today. Such convenient conditions are typical especially of mires, because they have a short growing season, cold and very damp sediments and a lack of competition from tall woody vegetation (Tobolski 2003). In Poland, the long continuity of occurrence of *Betula nana* was noted by Noryśkiewicz (2005) and Kloss (2005, 2007), which had survived in the same place from the Younger Dryas up to the present at Linje mire in central northern Poland. Also, Suchan et al. (2019) noted the long-term occurrence of another glacial relict, *Rhododendron ferrugineum*, in the Karkonosze mountains on the Czech-Polish border. The whole ecosystem can also be very stable, like the calcareous fens in the western Carpathians (Hájková et al. 2015), where their local continuity from at least the beginning of the Holocene was noted. On the other hand, it is difficult to imagine that there were no changes in landscapes since the Late Glacial, and so ancient biota must have altered in some way (Hájková et al. 2015).

The calcareous fens mentioned above, also called spring-fed fens and mires in general as well as loess steppes, springs and alpine habitats, are places where glacial relicts may be present now. They often occur there in groups of many taxa consisting of plants and invertebrates (Kornaś and Medwecka-Kornaś 2002). Also, taxa now regarded as glacial relicts occurred together in the past, which is, for instance, shown by palaeoecological studies in the western Carpathians, confirming this occurrence for plants and molluscs together (Hájek et al. 2011; Hájková et al. 2015).

The status of glacial relict is assigned to a species mostly from indirect biogeographical evidence such as a modern distribution restricted to isolated areas with specific climatic or soil conditions (Dítě et al. 2018). Direct evidence that a taxon was more common in the past than today, which could suggest its status as a glacial relict, can be provided only by palaeoecological data, including the analysis of ancient plant remains. Mires are especially useful for this, because their history is recorded in the organic sediments forming them. This is due to several useful features of plant

macrofossils found in peat. First of all, these remains can often be identified to species level. Another advantage is the possibility of recognizing just local flora and vegetation, which is due to the specific nature of the deposition process. Poland, located in the temperate zone of central Europe, with numerous botanical analyses of mires, is a good place to review the state of knowledge about glacial relict mosses. This region is even more interesting because the actual date of colonization by relict taxa and their persistence at particular places are still poorly explored. Therefore, the aim of this study is to trace the fossil records of some mosses and to explore their existing status as glacial relicts.

Results and discussion

Records of mosses in the biogenic sediments of Polish mires

Eight species of mosses were selected for this review, *Calliergon giganteum*, *Pseudocalliergon trifarium*, *Cinclidium stygium*, *Helodium blandowii*, *Meesia triquetra*, *Paludella squarrosa*, *Tomentypnum nitens* and *Scorpidium scorpioides*. Currently they are rare and endangered, protected by law in Poland (except *Calliergon giganteum*), and all of them are treated as glacial relicts (Ochyra et al. 1988). Their centre of distribution is located in the boreal and arctic zones, reaching the northern edges of Eurasia and America.

In Poland, the exact number of sites where these mosses can be found is impossible to determine since there are no recent data. There is no distribution map at all for *Calliergon giganteum*. For the other six taxa, *Meesia triquetra*, *Tomentypnum nitens*, *Pseudocalliergon trifarium*, *Scorpidium scorpioides*, *Helodium blandowii* and *Paludella squarrosa*, Ochyra et al. (1988) stated that they grow mainly in scattered sites in the lowlands of Poland, especially in the north (Figs. 1a and 2a). The second largest density of sites is in the east, which does not concern *Paludella squarrosa*, and the third area is near the river Wisła (Vistula) in southern Poland, where the eighth of the considered species, the very rare *Cinclidium stygium*, is also present (Fig. 2a; Karczmarsz 1962). It should be emphasized that several dozen years after the creation of these maps, some sites where the mosses grew are now only of historical importance, because of the destruction of mires by drying out and use as farmland. The second reason may also result from the biology of the species itself. For example, *Pseudocalliergon trifarium* grows in habitats that are scarce at present, but which were present in the postglacial landscape, such as shallow peat deposits, marshland and shallow water. Therefore, the changing hydrological conditions in the Holocene did not allow this moss to survive in mires and other more

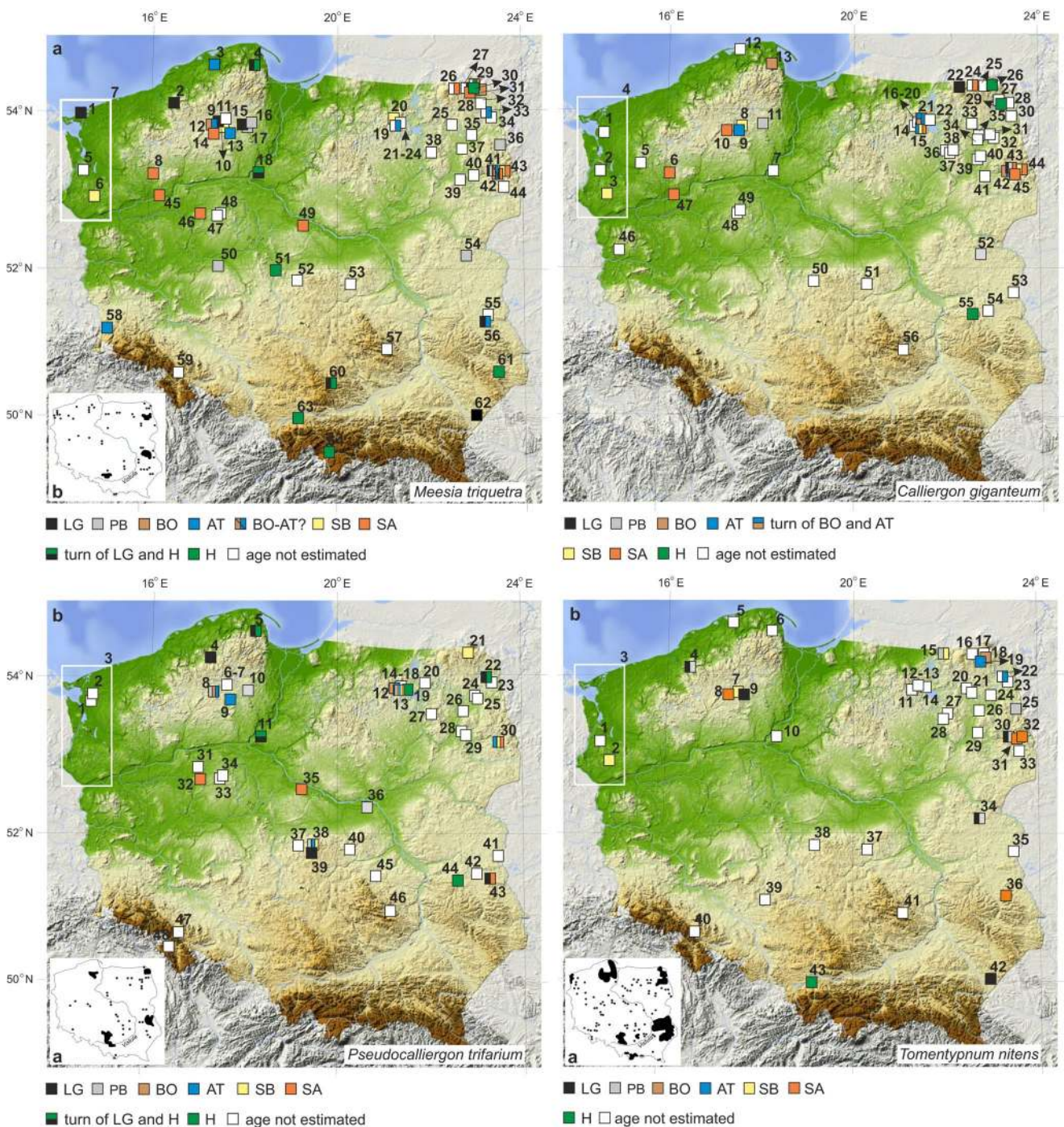


Fig. 1 Distribution of *Meesia triquetra*, *Calliergon giganteum*, *Pseudocalliergon trifarium* and *Tomentypnum nitens* in Poland; **a**, present day; **b**, in the past, based on fossil data. Abbreviations of time periods as in Table 1

competitive taxa took its place. Therefore, *P. trifarium* is now one of the mosses disappearing from the mire vegetation not only in Poland, but also throughout the Holarctic.

These mosses are quite easily identified in biogenic sediments, mostly in peat, by their characteristic morphology and features of leaves (Drzymulska 2007). In the case of *Meesia triquetra*, even a small piece of leaf with its dark cell

walls is sufficient for identification (Fig. 3a). The characteristic leaf bend should also be taken into account to recognize *Paludella squarrosa*, or specific filamentous outgrowths on the leaf base in *Helodium blandowii*. Stem leaves of *Calliergon giganteum* have a very distinct alar part of the leaf base on either side of the stalk, with cells strikingly enlarged and very strongly differentiated from the cells above (Fig. 3b).

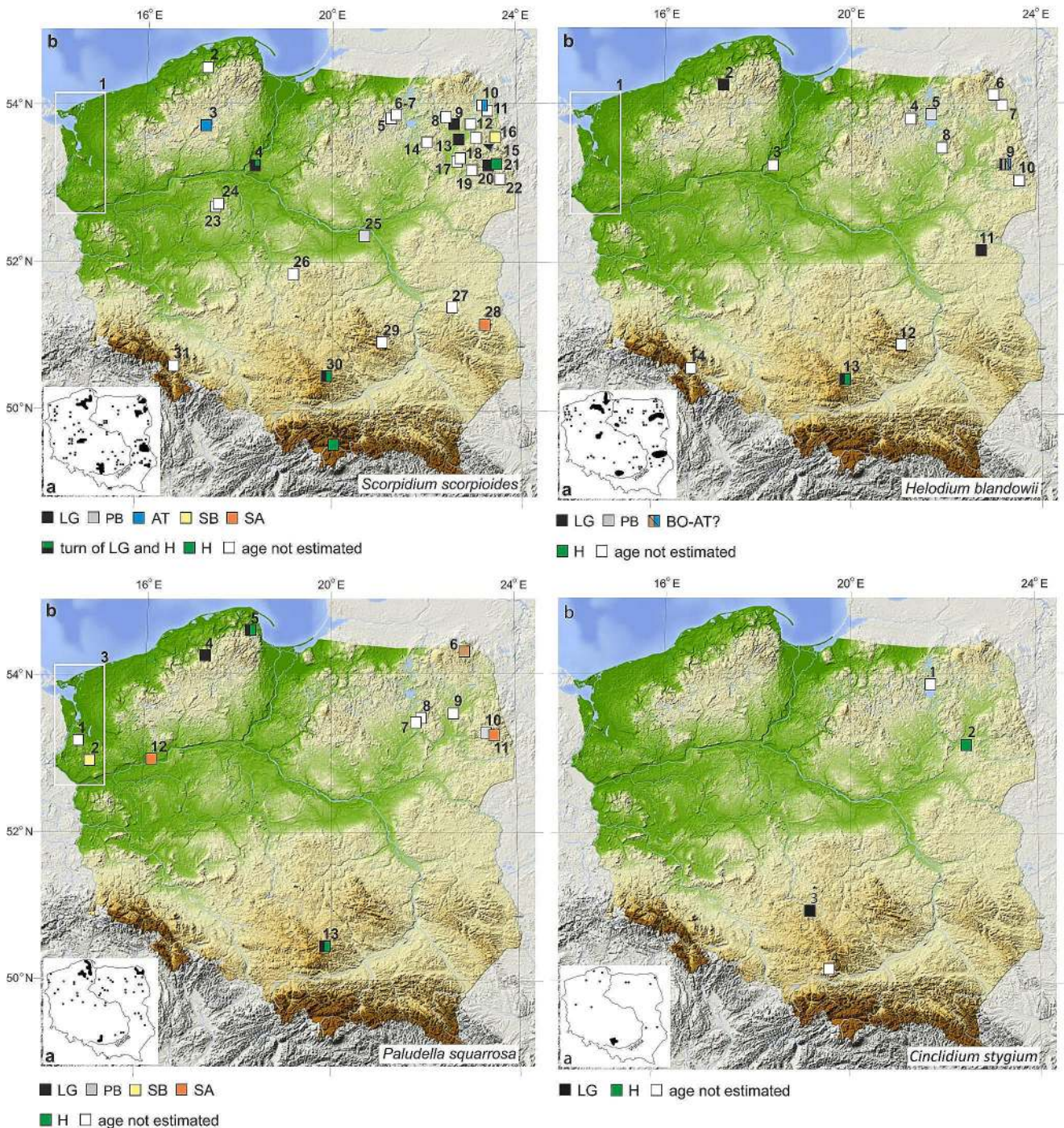


Fig. 2 Distribution of *Scorpidium scorpioides*, *Helodium blandowii*, *Paludella squarrosa* and *Cinclidium stygium* in Poland; **a**, present day; **b**, in the past, based on fossil data. Abbreviations of time periods as in Table 1

Sometimes, even entire moss specimens are fossilized, unlike vascular plants, of which only seeds, fruits or small fragments of tissues usually remain. The fossil records of these mosses have been compiled from published sources specifying the sites from where the remains were recovered and the possible date of the remains, estimated from radiocarbon dating and/or pollen analysis of the sediments.

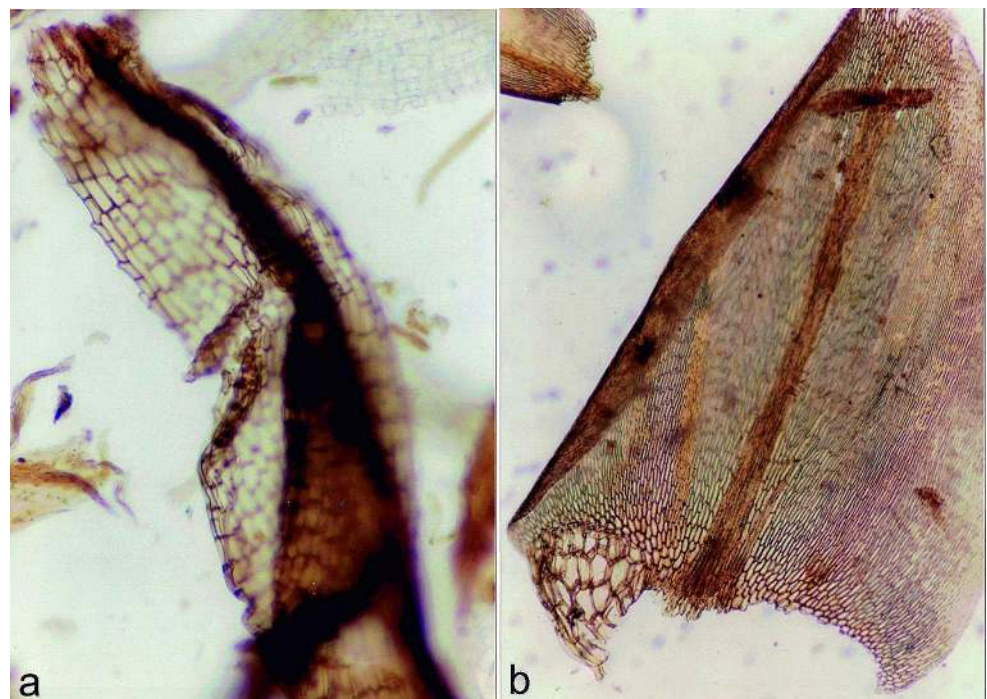
Unfortunately, sites with no such data are represented in very large numbers (Table 1), so the ages of these moss remains is not known there (Odgaard 1988). This is often because the aims of these studies did not include dating the deposits as such. Wąs (1965), for example, studied the types of moss peat, Marek (1965) the stratigraphy of alder carr bogs and Jasnowski (1957, 1959, 1962) only recognized moss

Table 1 Frequencies of particular species of relict mosses in Poland

Species	Fossil data with date							Undated sites
	LG+PB+BO	LG/H	BO-AT? BO/AT	AT+SB	SA	H	Total	
<i>Meesia triquetra</i>	10+6+2	1	2	7+5	10	8	51	24
<i>Calliergon giganteum</i>	2+3+2	0	1	4+4	8	3	27	33
<i>Pseudocalliergon trifarium</i>	6+5+3	1	0	6+4	5	4	34	24
<i>Tomentypnum nitens</i>	5+5+1	0	0	2+3	4	1	21	26
<i>Scorpidium scorpioides</i>	5+1+0	1	0	2+1	1	3	14	20
<i>Helodium blandowii</i>	4+2+0	0	1	0+0	0	1	8	9
<i>Paludella squarrosa</i>	3+1+1	0	0	0+1	2	2	10	5
<i>Cinclidium stygium</i>	1+0+0	0	0	0+0	0	1	2	2

LG, Late Glacial; PB, Preboreal; BO, Boreal; LG/H, transition of Late Glacial and Holocene; BO-AT?, presence in Boreal and/or Atlantic; BO/AT, transition of Boreal to Atlantic; AT, Atlantic; SB, Subboreal; H, Holocene

Fig. 3 **a**, *Meesia triquetra*, sub-fossil leaf, $\times 185$; **b**, *Calliergon giganteum*, subfossil leaf with one alar area on left, $\times 74$, photos by D. Drzymulska



peat and peat deposits of Poland as such. Another factor is that radiocarbon dating is expensive, while pollen analysis is very laborious and not always possible due to the type of sediment. In general, for research carried out 40 or 50 years ago, radiocarbon dating was less often done, before it became a standard procedure. However, even today, particular macrofossils such as moss remains are only occasionally dated, unless that is the specific purpose of the research, which does not seem to have been the case according to the literature. At this point, it should be clarified that the traditional divisions of the Holocene, according to Mangerud et al. (1974), have been used here because they were used in the cited sources. Relating this arrangement to the new divisions of the Holocene according to Walker et al. (2018, 2019) could result in inaccuracy or oversimplification of the

information, especially if the date of the sediment was estimated from pollen analysis. This is due to the unclear situation of Boreal and Subboreal sediments, because they could belong to both the Greenlandian and the Northgrippian, and the Northgrippian and the Meghalayan, respectively. The available published information about the past distribution of the studied group of mosses in Poland is reviewed and summarized below.

Meesia triquetra has been recorded from 64 places in the whole of Poland, with the highest density in the north, especially the north-east (Fig. 1). During the Late Glacial, this species was present at ten of them, three in Pomorze (Pomerania), Świętoujść (Latałowa and Borówka 2006), Bobolice (Osadowski et al. 2019) and Pomieczyno (Marek 1991a), and three lakes, Małe Łowne (Kowalewski et al.

2009), Trzechowskie (Słowiński et al. 2017) and Hańcza (Gałka and Sznel 2013). The other sites are Taboły in northeast Poland (Drzymulska 2006), Pawłów in the east (Pietruczuk et al. 2018) and two in the south, Wolbrom (Obidowicz 1976) and Kobylnica Wołoska (Kończek et al. 2015). It is recorded from between the Late Glacial and the Early Holocene at Linje (Kloss 2005, 2007). In the Preboreal period it was present at Borzechowo (Słowiński 2010) and in the Wda river valley (Słowiński et al. 2015), as well as in the north-east at Kuźnica (Urban et al. 2011) and Taboły (Drzymulska 2006), in the east at Radzików (Dobrowolski et al. 2012) and to the west at Grodzisko (Gałka et al. 2020). There are only two known places where *Meesia triquetra* occurred in the Boreal period, Tuchola (Lamentowicz 2005) and Perty (Gałka et al. 2015a), and two with occurrences in the Boreal and/or Atlantic, Taboły and Borki (Drzymulska 2006). During the Atlantic period, this species was present at Uroczysko Mokradła (Tomaszewska et al. 2016), at Tuchola and Zamarte (Lamentowicz 2005), at Wieliszewo in Pomorze (Pacowski 1967), at Kołowin in Mazury (Masuria) (Kloss 2005, 2007), at Suche Bagno in the region of Wigry jezioro (lake) (Kloss 2005, 2007) and at Pawłów in the east (Pietruczuk et al. 2018). There are Subboreal find sites in the Kłodawa area (Marek 1991b), at Jełonia Wyspa (Lamentowicz et al. 2007) and at Gązwa (Gałka and Lamentowicz 2014; Gałka et al. 2015b), as well as in the northeast at Stare Biele (Marek 2000). The Subatlantic sites are Kłocie Ostrowieckie (Gałka and Tobolski 2011), Rzecin (Lamentowicz et al. 2015), Kazanie (Czerwiński et al. 2021) and Stążka (Lamentowicz et al. 2013) in the west and north-west, Gąsak (Wacnik et al. 2011) in central Poland, and three places in the Pojezierze Suwalskie (Suwałki lake district), Linówek (Gałka et al. 2014), Purwin (Gałka and Apolinska 2014) and Mechacz Wielki (Żurek and Kloss 2012). *Meesia triquetra* was also recognized at Stare Biele (Marek 2000) and at Borki (Drzymulska 2006) in this period. Among the Holocene sites there are Pomieczyno (Marek 1991a), Purwin (Gałka and Tobolski 2012), Kojle (Gałka and Tobolski 2012), Wilczków (Forysiak et al. 2012), Wolbrom (Obidowicz 1976), Puścizna Ręgowiańska (Obidowicz 1990) and Uroczysko Jęzor (Urban and Tokarz 2014). However, the date is not known there. In the case of more than 20 sites there is no information about the age of the *Meesia triquetra* remains (Fig. 1).

For *Calliargon giganteum*, which has been found in 56 places (Fig. 1), its distribution is similar to that of *Meesia triquetra* but with more density in northeast Poland. There are only two Late Glacial sites, Wielkie Błoto (Karpńska-Kończek et al. 2013) and Taboły (Drzymulska 2006). In the latter place its presence was also noted in the Preboreal period. *C. giganteum* dated to this early period of the Holocene was also found by Dobrowolski et al. (2012) at

Radzików and by Słowiński et al. (2015) in the Wda valley. Boreal localities are very scarce. One of them is at Pomieczyno in Pomorze (Marek 1991a), the second at Kładkowe Bagno (Drzymulska 2006, 2008) in the north-east, near Taboły. The third one dates to the late Boreal and early Atlantic period and is located at Prawdowo in Mazury, where Kloss (1993, 2007) also recognized the Atlantic remains as at nearby Strzałowo. At Kładkowe Bagno it was also present in the Atlantic period (Drzymulska 2006), as well as at Tuchola (Lamentowicz 2005). The scarce Subboreal localities are Kłodawa area (Marek 1991b), Jełonia Wyspa (Lamentowicz et al. 2007), Strzałowo (Kloss 1993, 2007) and Stare Biele (Marek 2000). At Stare Biele and, according to Drzymulska (2006), at nearby Borki and Taboły, it also occurred in the Subatlantic. This also applies to Mechacz Wielki (Żurek and Kloss 2012) and Strzałowo (Kloss 1993, 2007). In the west and northwest of Poland it was noted from this period at Kłocie Ostrowieckie (Gałka and Tobolski 2011), Rzecin (Lamentowicz et al. 2015) and Stążka (Lamentowicz et al. 2013). During the Holocene, *C. giganteum* was present at Kojle, in the Suwałki lake district, at Sucharek, near Wigry lake (Drzymulska and Zieliński 2013) and in the Ciemięga river valley (Urban 1997). For many other sites (more than 30) no dates are available (Fig. 3b), and so it is impossible to verify when *C. giganteum* occurred there.

Pseudocalliargon trifarium was noted at 48 quite dispersed sites, with increased density in Mazury and north-eastern Poland (Fig. 1). In the Late Glacial it occurred in Pomorze, at Pomieczyno and Kramrzyny (Marek 1991a, c), at Kołowin in Mazury (Kloss 2005, 2007), at Suche Bagno in the Suwałki lake district (Kloss 2005, 2007), near Brzeziny (Lewandowska et al. 2023) in central Poland and in the east at Bagno Staw (Pietruczuk et al. 2022). Between the end of the Late Glacial and the early Holocene it was present at Linje mire (Kloss 2005, 2007). In the Preboreal period its presence was confirmed at five sites, the Wda valley (Słowiński et al. 2015), Tuchola (Lamentowicz 2005), Żabieniec (Kloss and Żurek 2010), Długie Bagno and Kołowin (Kloss 2005, 2007). At Kołowin, as well as in nearby Prawdowo (Kloss 1993), *P. trifarium* was also recognized in Boreal and Atlantic sediments. Boreal and Atlantic finds were also noted at Tuchola (Lamentowicz 2005), but only Atlantic records from nearby Zamarte (Lamentowicz 2005). Atlantic and Subboreal occurrences were recorded at Żabieniec (Kloss and Żurek 2010) and Stare Biele (Marek 2000). At the latter site there were Subatlantic finds of this moss, just as at Kołowin, where Kloss (2005, 2007) found both Subboreal and Subatlantic remains. Only Subboreal presence was noted by Gałka (2014) at Perty. From the most recent Holocene, *P. trifarium* was also noted at Kazanie (Czerwiński et al. 2021), at Gąsak (Wacnik et al.

2011) and at Pawłów (Pietruczuk et al. 2018). Holocene find sites, although undated, were described by Marek (1991a) at Pomieczyno, by Kloss (1993, 2007) at Strzałowo and Suche Bagno and by Urban (1997) in the Ciemięga valley. More than 20 find sites of this species are undated (Fig. 1).

Tomentypnum nitens was recognized from 36 sites, most of them in northeastern Poland (Fig. 1). Among them were five Late Glacial localities: Bobolice (Osadowski et al. 2019), Taboły (Drzymulska 2006), Radzików (Dobrowolski et al. 2012), Zamarte (Lamentowicz 2005) and Kobylnica Wołoska (Kończek et al. 2015). In the first three, this species was also present in the Preboreal period. Other Preboreal finds were noted at Kuźnica (Urban et al. 2011), slightly north of Taboły and further north, at Puszcza Romincka (Romincka forest) (Apolinarska et al. 2023). The only Boreal occurrence was found at Perty (Gałka et al. 2015a), and for the Atlantic at nearby Turtul (Apolinarska et al. 2022) and slightly south, at Suche Bagno (Kloss 2005, 2007). From the Subboreal period, *T. nitens* was recognized in the Kłodawa area (Marek 1991b), at Jelenia Wyspa (Lamentowicz et al. 2007) and at Puszcza Romincka (Apolinarska et al. 2023). Three Subatlantic find sites were described, at Stążka (Lamentowicz et al. 2013), Borki (Drzymulska 2006) in nearby Stare Biele (Marek 2000) and at Pawłów (Pietruczuk et al. 2018). A Holocene site was recorded by Łopatka and Gałka (2009) at Zapadź. The dates of the mosses from more than 20 sites are unknown (Fig. 1).

For *Scorpidium scorpioides*, 32 sites were found, most of them in north-eastern Poland (Fig. 2). Late Glacial remains were noted in Linje, where it was also present at the transition from the Late Glacial to the Preboreal period (Kloss 2005, 2007), in the Biebrza river valley (Oświt 1991), at Kuwasy (Żurek 1970), at Taboły (Drzymulska 2006) and at Wolbrom (Obidowicz 1976). From the Preboreal period *S. scorpioides* presence was noted by Kloss (2005, 2007) at Długie Bagno. There are no published Boreal find sites and only two from the Atlantic, Tuchola (Lamentowicz 2005) and Suche Bagno (Kloss 2005, 2007) and one for the Subboreal, at Kuźnica (Urban et al. 2011) and another from the Subatlantic, at Pawłów (Pietruczuk et al. 2018). It is known that this species was present during the Holocene at Stare Biele (Marek 2000), Wolbrom (Obidowicz 1976), Bór na Czerwonem in Podhale (Obidowicz 1978) and in the Ciemięga valley (Urban 1997). At least 20 sites where this species was present are of unknown age (Fig. 2).

Helodium blandowii has been described from 14 quite dispersed places (Fig. 2). In the Late Glacial it was present at Kramarzyny (Marek 1991c), Taboły (Drzymulska 2006), Radzików (Dobrowolski et al. 2012) and Wolbrom (Obidowicz 1976) and also in the Holocene at Wolbrom. A Preboreal find was noted by Kloss (1993) at Grabnik in Mazury and by Drzymulska (2006) at Taboły, where it also occurred

in the Boreal and/or Atlantic. Nine find sites of *H. blandowii* remains are undated (Fig. 2).

Paludella squarrosa, is known from 13 places (Fig. 2). Three of them are Late Glacial, Pomieczyno, Kramarzyny (Marek 1991a, c, respectively) and Wolbrom (Obidowicz 1976). At Kramarzyny and Wolbrom it was also present later, in the Holocene, but there are no data about the exact period. One Preboreal site was noted by Drzymulska (2006) at Taboły and there was a Boreal occurrence at Perty (Gałka and Tobolski 2012; Gałka et al. 2015a). There are no Atlantic finds. In the Kłodawa area, *P. squarrosa* occurred in the Subboreal (Marek 1991b), and in the Subatlantic at Stare Biele (Marek 2000) and at Rzecin (Lamentowicz et al. 2015). A few other find sites where this species was recognized have no dating (Fig. 2).

Cinclidium stygium was only found in four places (Fig. 2). One of them, Late Glacial, is Jezioro in the south (Fajer et al. 2012). In the case of Smolarze (Jasnowski 1957), it is known that this species was present there in the Holocene. The remains from Grabnik (Kloss 1993) and Ludwinów (Żmuda 1914) were not dated.

This review (above) indicates that the frequencies of fossil records differ for the various species. *Meesia triquetra* occurred in the greatest number of sites in Poland (Fig. 1; Table 1). The second most frequent was *Calliergon giganteum* at 56 sites (Fig. 1; Table 1). The same situation was noted for the Czech Republic and Slovakia during work on the database of plant macrofossils (Hájková et al. 2018). *Helodium blandowii* was the scarcest moss there and in Poland it was quite scarce. However, there were even fewer records of *Paludella squarrosa* and *Cinclidium stygium* in Polish studies (Table 1), but the latter was not present in the database mentioned above. In Scandinavia and the Baltic region, remains of *P. squarrosa* seem to be one of the more common moss macrofossils found in peat (Jongsdard and Birks 1995; Oksanen 2006; Birks et al. 2012; Pręskienis 2013; Kjellman et al. 2018). However, as Amon et al. (2010) noted, only a few studies of moss remains are available from Scandinavia and Estonia, and the latter are mainly *Sphagnum*.

In the case of several of the discussed mosses, the subfossil record has a fairly large similarity to their modern distribution in Poland. This is true in north-eastern Poland for *Meesia triquetra*, *Pseudocalliergon trifarium*, *Tomentypnum nitens* and *Scorpidium scorpioides* (Figs. 1 and 2). In the case of *P. trifarium*, it is also present in the east of the country and in the north, west of the Wisła (Vistula) (Fig. 1). Regarding *Calliergon giganteum*, it is known that it also occurs in north-eastern Poland today, and its presence in the past was clearly significant there. In the case of other species, the similarity is less clear, although some analogies can still be seen in *Helodium blandowii*, which also

occurs in northeast Poland (Fig. 2). On the other hand, looking at the distribution of the mosses from the point of view of their modern occurrence, it can be seen that the locations in the south, near the Wisła, are basically not reflected in subfossil sites (Figs. 1 and 2). This quite uneven spread of subfossil sites in Poland seems to reflect the distribution of mires from which the mosses were studied (Żurek 1980), and this could partly also be connected with the presence of palaeoecologists.

Although, as mentioned earlier, these mosses are quite easily recognizable by the characteristic morphological features of the various taxa, mainly by their leaves; however, although they are often present in organic sediments they may be overlooked, or just included in a general mass of mosses, unidentified to species. Also, they may simply decay away beyond recognition (Rehell and Virtanen 2015). The lack of bryophyte data is not the fault of the researcher, because it is simply impossible to identify all the plant remains in a sample. Furthermore, the number of samples that can be analysed is limited due to the time-consuming nature of the studies of the various remains and sometimes due to the poor availability of sediments. Besides that, analyses of plant remains are done with sediment samples collected with a certain resolution. In earlier studies, a 10 cm sample interval or even more was standard; at present samples are more closely spaced and the greater number of samples may make it harder to study all of them. Moreover, the sediment of a mire is usually sampled in its centre, assuming that this is probably the deepest and earliest deposit and therefore the most representative. However, there may be other kinds of deposit nearer the edge of the mire, so it is therefore easy to imagine missing some plant remains for this very reason. The next fact is that the analysed sediment samples are very small (a few cm³), so the number of taxa found may be low. Therefore, the macrofossil data cannot provide a quantitative analysis of past distribution of species (Hájková et al. 2018). On the other hand, only these analyses provide direct evidence of any past occurrence.

Glacial relict status of the mosses from their fossil records

Knowledge of the occurrence of certain species in the Late Glacial and early Holocene is a basic prerequisite for classifying them as glacial relicts (Ložek 2001). All eight of the studied mosses were present in the past and have been found in Late Glacial or early Holocene sediments as previously described, which is one of the important indices of their status as glacial relicts (Hájková et al. 2018). However, in the case of one species, *Cinclidium stygium*, such find data are very scarce (Fig. 2), in principle excluding further considerations.

The argument in favour of a given taxon being a glacial relict, and even stronger than its presence alone, is its long survival at one site, with its permanent presence recorded at a given site from the Late Glacial and/or the earliest Holocene onwards. However, the published data for the studied mosses show quite clearly that there is evidence of their chronological continuity during this period only from a few sites. *Meesia triquetra* was found only at Taboły, where it occurred in the Late Glacial, in the Preboreal and in the Boreal and/or Atlantic period (Drzymulska 2006). From other places there are fossil records for only one or two time periods, as at Tuchola with Boreal and Atlantic records (Lamentowicz 2005) and at Pawłów, from where macrofossils were recognized from the Late Glacial and only again from the Atlantic period (Pietruczuk et al. 2018). Regarding *Calliergon giganteum*, Drzymulska (2006) noted this species at Taboły from the Late Glacial until the Preboreal. Interestingly, it appeared there again in the Subatlantic period. Long-term persistence of *Pseudocalliergon trifarium* was demonstrated at Kołowin (Kloss 2005, 2007), where it occurred from the Late Glacial through the whole of the Holocene. At Tuchola it occurred continuously from the Preboreal until the Atlantic (Lamentowicz 2005), and it was present at Żabieniec from the Preboreal until the Subatlantic, although with a lack of Boreal records (Kloss and Żurek 2010). The only continuities of the occurrence of *Tomentypnum nitens* that were found were from the Late Glacial and Preboreal periods at Bobolice (Osadowski et al. 2019), at Taboły (Drzymulska 2006) and at Radzików (Dobrowolski et al. 2012). *Scorpidium scorpioides* was confirmed at Linje mire in the Late Glacial and at the transition from the Late Glacial to the Holocene (Kloss 2005, 2007). However, at Wolbrom it is only known to have been present in both the Late Glacial and the Holocene (Obidowicz 1976). *Helodium blandowii* was continuously present at Taboły, where it was noted from the Late Glacial probably until the Atlantic period (Drzymulska 2006). At Wolbrom the situation was the same as for *S. scorpioides* on this site, present in the Late Glacial and Holocene (Obidowicz 1976). The only, and not quite clear, data about the persistence of *Paludella squarrosa* were provided by Marek (1991a) for Pomieczyno and Obidowicz (1976) for Wolbrom. In both places *P. squarrosa* was present after the Late Glacial, but there is no information about which Holocene periods it was present in.

The above data indicate that only a few of these fossil records have the features of glacial relict mosses, with long-term persistence from the Late Glacial through the Holocene, or its earlier part (Fig. 4). For *Tomentypnum nitens*, three find sites were identified, Bobolice, Taboły and Radzików. One for *Calliergon giganteum* at Taboły, *Meesia triquetra* at Taboły, *Pseudocalliergon trifarium* at Kołowin

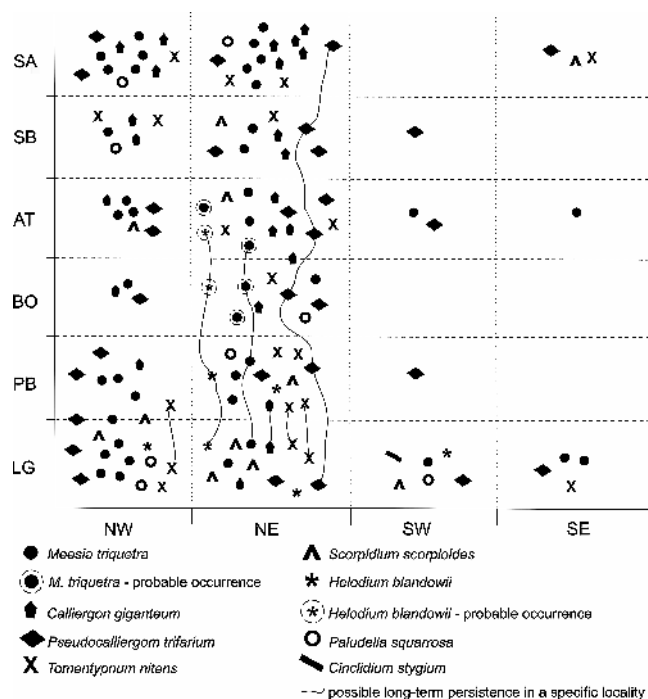


Fig. 4 Locations of dated macrofossils of the studied mosses in four parts of Poland, northwest (NW), north-east (NE), southwest (SE) and SE (southeast) according to the coordinates 52°N and 20°E as in Figs. 2 and 3; time periods unscaled, abbreviations as in Table 1

and *Helodum blandowii* at Taboły. At Wolbron the persistence of these last two moss species is uncertain. The published data about *Paludella squarrosa* are even more scarce. It occurred at Pomieczyno and Wolbrom in the Late Glacial, but whether it was present in the Preboreal period is unclear.

The analysis of the eight mosses revealed several regular patterns of occurrence. First, the remains of presumed glacial relict mosses were not very frequent in the studied sediments. Except for a few species which are often found, like *M. triquetra* or *C. giganteum*, some of them were very rare. Second, many sites were undated so they provide no information on the periods when taxa were present that can be used to assess the relict status of the mosses found there (Table 1). What is worse, there is not much chance that these sites will be studied again and moss samples dated, although it remains a distant possibility. It would certainly be very important and could provide much more information about relicts. Third, there are far more Late Glacial and early Holocene sites than from the middle Holocene, mentioned by Hájková et al. (2018) in studies of the western Carpathians, Czech and Slovak Republics, and this is apparently also confirmed for Poland (Table 1). Regarding the suggestions made by Odgaard (1988) as to the past occurrence of *Meesia triquetra* in western and central Europe, where it tended to appear just at a given stage of wetland succession, the conclusions for Poland are inconsistent. On the one hand, the rarity of this species in the Late Glacial

in Poland was not confirmed, as it had been by Odgaard in other regions. It was actually the taxon which was found in the greatest number of Late Glacial sites of a known age among all species and all time periods, as previously stated. However, it was confirmed that the Boreal period must have proved unfavourable for it, because its presence in Poland at that time is scarce (Table 1). Odgaard (1988) indicated that since the Boreal period, many rich fens have become oligotrophic and terrestrial resulting in a decrease in habitats over large areas. The author therefore questioned the status of *M. triquetra* as a glacial relict. This taxon generally tended to appear with the development of floating mats in lake basins, or at a stage when eutrophic mires turned into oligotrophic peat mires. This latter change was often caused by human activity, like clearance of woodlands around the catchment basin (Rybníček and Rybníčková 1974). From the Boreal, a decline in frequency was observed for almost all analysed species (Table 1). Did this shortage of suitable habitat for the occurrence of open fen mosses in the middle Holocene occur in Poland, as in the Carpathians? Probably not so clearly, but in Poland suitable conditions for the open fen moss species were also restricted by insufficient light under the tree canopy from the spread of woodland and by formation of ombrogenous (raised) mires, resulting in invasions by peat bog mosses (Vicherová et al. 2017). Finally, the long-term persistence of our group of mosses was noted only at a few sites, mainly in northeastern Poland (Fig. 4). This is an important area for studying the former ranges of some plants (Gałka and Tobolski 2013). For thousands of years, migrations of plant communities took place there, both those associated with western Europe and others originating from the northeastern regions of the continent and even from western Siberia (Drzymulska 2006). This part of Poland is also unusual because the modern climate there has some of the severe conditions of Scandinavia, which is reflected in the presence of boreal plant communities, such as boreal bog *Betula* (birch) woods and boreal *Picea* (spruce) forest on peat, an area in which the long term persistence of the discussed moss species can be expected. Such a confirmed distribution has already been given above, although it has not been continuous from the Late Glacial until the present day. For example, *Tomentypnum nitens* nowadays occurs in the area of Taboły, the same area where it grew in the Late Glacial and the Preboreal period, however, there is no evidence that it persisted there later. Conversely, *Meesia triquetra*, today absent at Taboły, was present there from the Late Glacial and probably until the Atlantic period. Its current absence from this area may be due to the fact that it is now wooded, and *M. triquetra* grows on open, unwooded mires (Ochyra et al. 1988). A greater occurrence of rich fen bryophytes such as *M. triquetra* in the past than at present was noted in Finland, in the area of the northern Baltic sea

(Rehell and Virtanen 2015). The reasons for this are that rich fen mosses are very sensitive both to many human activities, such as the drainage and the cessation of traditional land use in mires, and to competition from *Sphagnum* mosses. *Tomentypnum nitens* is the opposite, as in Finland it is commonly found in modern vegetation but very rarely in ancient peat. The reason may be that *T. nitens* occurs in habitats with intense humification such as bogs with *Picea* (spruce). This results in a poor state of preservation of the remains and difficulties in their identification.

Considering the discussion above, assigning the status of glacial relicts to the group of mosses on the basis of direct evidence may be quite debatable. Certainly, further analyses of ancient moss remains combined with the use of absolute dating methods are needed. Molecular studies also offer some hope, although they are rather scarce and have several disadvantages. One of them is the need for data from a wide distributional range of a taxon (Ehrich et al. 2008), and therefore such studies may be too general for the detection of local survival. Genetic structure may not be just a product of relict status since glacial times, but may show earlier migrations or more recent isolation (Wróblewska 2013). Here it is necessary to bear in mind pseudo-relicts, which are taxa brought to new sites where human actions caused changes to the environment and therefore the taxa could stay there; also wandering relicts which appear naturally in new locations without human influence. Their somewhat confusing presence was already pointed out by Szafer (1949) and even earlier by Overbeck and Schneider (1939). Interestingly, the latter researchers considered *Betula nana* to be a pseudo-relict in some of the mires of the German lowlands. *Linnaea borealis*, also considered a glacial relict in central Europe, is treated as a wandering relict at some sites (Pawlaczyk and Pawlaczyk 2002) or a pseudo-relict (Szafer 1949; Ciosek et al. 2015). The problem of the recent migration by several taxa from the boreal zone, such as *Rubus chamaemorus*, *Viola epipsila* and *Linnaea borealis*, was also addressed by Tobolski et al. (1997). They indicated that these species could have occurred at the analysed sites in Słowiński Park Narodowy, a national park on the Baltic coast, only in the late Holocene, because there were no suitable habitats for them before. For example, *R. chamaemorus* could not have grown on the Gardno-Łebsko coastal plain among the *Cladium mariscus* and then *Juncus subnodulosus* which grew there in the early Holocene, and it could only have grown after the swamp *Betula* woodland became established in the Subboreal period. The increased amount of isoetids such as *Lobelia dortmanna* in the most recent layers of sediments, which was noted by Milecka (2005) in the *Lobelia* lakes of Bory Tucholskie (Tuchola forest), can probably be treated in a similar way. The author believes that the modern presence of isoetids in the lakes which she investigated shows

that they are not relicts, but the result of successive phases of the glacial-interglacial cycle.

Considering the studied mosses, a question about their potential status as wandering relicts can also be raised. Without excluding it, the sustainability of mire ecosystems should be emphasized. Of course they could change, especially from the more fertile fens to the poorer bogs, but this is not always the case. Many taxa did not have to migrate to new places, because mires which still existed then offered them suitable habitats. Therefore, the lack of a fossil record in some of the analysed profiles could just be a result of the difficulties in research as mentioned above, and not because of a real absence of these taxa in the past. Anyway, the potential relict status of any taxon must be proven in each case by the analysis and dating of subfossils. To summarize, much incomplete data was obtained, while the number of promising records providing confirmation was lower. This indicates the need for further more detailed research to make the somewhat enigmatic term “glacial relict” more certain.

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Declarations

The author declares that there is no conflict of interest.

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