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Origin of forest plant species in Pomerania: Czubiński's hypotheses in comparison to recent research

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Abstract: More than 50 years after the time when Czubiński (1950, Bad. Fizjogr. Pol. Zach. 2(4): 339-658) published his hypotheses, the pathways and timing of Holocene migration of 16 forest species into Pomerania (NW Poland) were analysed once more. The analysis was based on recent data on distribution of the species, in the wide setting of the present-day knowledge of phytogeography, palaeobotany and palaeogeography. Czubiński's hypotheses are still valid to a large extent, but in the present paper a different arrival time of some species is postulated. This mainly results from the progress in palaeobotanical studies and new data. New hypotheses regarding the pathways and time of migration of 16 forest species into Pomerania in the Holocene were developed. The xerothermic forest species entered the territory of Pomerania probably during the Boreal period, i.e. later than Czubiński postulated. Some other species, whose arrival time in Pomerania were supposed to be connected with the beech period, apparently have occurred there at least since the Atlantic period.

Key words: chorology, geographical elements, Holocene, plant migration, Pomerania

1. Introduction

In Central Europe, the origin and dynamics of species ranges are directly linked to the question of the pathways and time of plant migration at the turn of the Late Glacial period or at the beginning of the Holocene. This problem has already been the subject of numerous palaeobotanical studies in relation to trees (Szafer 1935; Huntley & Birks 1983; Ralska-Jasiewiczowa 1983; Ralska-Jasiewiczowa *et al.* 2004). Czubiński (1950) raised numerous hypotheses concerning the immigration of forest species to Central Europe in the Holocene in his monograph on geobotanical relationships in Pomerania. That monograph for decades remained the only one discussing the questions of migration of herbaceous plants in this part of Europe. According to that author, the flora of Pomerania developed under the influence of climatic changes, associated with simultaneous edaphic changes and plant cover transformations. He postulated also an impact of barriers on the distribution of individual species. Vast ice-marginal lakes or absence of appropriate habitats might have formed such barriers. The other problems discussed by Czubiński in the work cited were the pathways of migrations and the distances from refuges. As he did not have access to complete distribution maps of all forest taxa, he formulated hypotheses concerning only selected species.

The aim of the present research was to verify the hypotheses formulated by Czubiński in 1950, after more than 50 years from their publication, basing on all currently accessible (floristic, phytosociological, ecological) data, with reference to the modern knowledge of phytogeography, palaeobotany and palaeogeography.

2. Material and methods

Considering the possible routes and the time of the forest species migration into the area of Pomerania, the criteria after Zając (1996) were adopted. The ability of a given species to migrate in a given climatic period and the connection of its range with the progress of transformation of the plant cover were taken into account. The next important criterion was the association of a given species with a defined plant community or plant formation. In determination of a hypothetical time and routes of a particular species' migration into the area investigated, its range and local distribution in Pomerania were considered. The following features were included: (*i*) ecological requirements, i.e. association with a particular forest community (or forest communities),

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(*ii*) the route and time of migration of tree species constituting this community (communities), (*iii*) available palaeobotanical data referring to the species studied, (*iv*) the history of formation, (*v*) succession and anthropogenic changes of forest communities in Pomerania, (*vi*) possibilities of inhabitation of a species studied in these communities, (*vii*) available palaeogeographic data.

The above considerations are based on the following published data: isopollen maps of tree distribution in Poland (Ralska-Jasiewiczowa 1983, Ralska-Jasiewiczowa *et al*. 2004) and in Europe (Huntley & Birks 1983) during the Holocene. In addition, results of palaeobotanical research from the area of Pomerania, especially the synthesis by Ralska-Jasiewiczowa & Latałowa (1996) and cartograms of the current forest species distribution in Pomerania (Popiela 2004) were applied. Geographical elements were distinguished according to Pawłowska's (1966) classification on the basis of range maps (Meusel *et al*. 1965; Meusel *et al*. 1978; Jalas & Suominen 1972, 1989; Jalas *et al*. 1996; Hultén & Fries 1986; Meusel & Jäger 1992). Their distribution in Poland were analysed after Zając & Zając (2001), distribution in East Germany after Benkert *et al*. (1996) and in Scandinavia after Hultén (1971). Distributional types of the forest species in Pomerania are given after Popiela (2004). Connections with plant communities for the species studied are based on the available phytosociological literature for Pomerania and original field observations. Syntaxonomic position and nomenclature follow Matuszkiewicz (2001).

3. Results and discussion

Czubiński (1950) split the studied forest species into 3 groups, with respect to the time of their immigration into Pomerania. The beginning of the Post-Glacial period favoured the spread of Eurasian species of the Boreal-Continental zone (Table 1, group 1). The following rapid temperature increase in the Holocene created optimum settlement conditions for the species characteristic for forests and forest-steppes (Table 1, group 2). Finally, the increasing oceanic influence (the humidity maximum of the Holocene along with the beginning of temperature decrease) resulted in an immigration of species related to the range of beech (Table 1, group 3). Czubiński in the work cited took under consideration climatic and edaphic factors, and only in the latest part of the Holocene also the results of human activity.

Among the species considered by him, most have ranges restricted to Europe, belonging mainly to the (Sub-)Atlantic subelement and (eastern) Central-European, and associated with different types of deciduous forests from the order *Fagetalia*. In Pomerania they show different types of distribution and fall into 3 groups: species with locations concentrated in northern, eastern and western parts of the region, respectively (Table 2).

Table 3 presents an attempt of a classification of the discussed forest species in relation to the time of their migration into the territory of Pomerania. The first 2 groups (Table 3, groups 1 and 2) include the species that most likely inhabited the area of Pomerania at the earliest time. These are the species with wide ranges in the northern hemisphere, and in Pomerania they show a similar type of distribution (Table 2); their locations concentrate in the northern part of the region. Data exist for *Empetrum nigrum*, confirming its presence in Pomerania since the Late Glacial period (Allerød and Younger Dryas), and even a wide distribution during this period (e.g. Ralska-Jasiewiczowa & Rzętkowska 1987; Latałowa 1998). That species might have been the component of the so-called Dryas flora (Iversen

Table 1. The time and pathways of migration of forest species into Pomerania according to Czubiński (1950)

No of group	Time of arrival/geologic period	Direction/status	Plant species
1	Decline of Weichselian glaciation	from north; glacial relic	*Empetrum nigrum* *Linnea borealis*
2	First post-glacial period: birch-pine and early hazel-pine period, ca. 8000 B.C.	from a refuge in south-east; terminal moraine ridges in Pomerania might have been a migration obstacle; post-glacial relic	*Isopyrum thalictroides* *Ranunculus cassubicus* *Euonymus verrucosus* *Galium schultesii*
3	Beech period: phase of thermal maximum decrease, and of simultaneous humidity maximum	residual Baltic range	*Polygonatum verticillatum* *Lunaria rediviva*
		from west or southwest	*Chrysosplenium oppositifolium* *Chaerophyllum hirsutum* (?)
		from west	*Arum maculatum* (?) *Blechnum spicant* *Carex strigosa* *Luzula sylvatica* *Lysimachia nemorum* *Veronica montana*

Explanation: (?) – uncertain, earlier location also possible

Table 2. Characteristics of forest species with respect to the affiliation to the geographical elements, distributional types, and connection with plant communities in Pomerania

Plant species	Affiliation to geographical element*	Distributional type in Pomerania**	Connection with plant communities in Pomerania
Arum maculatum	Sub-Atl-M	W	Wet forests of order *Fagetalia sylvaticae*, on stands rich in $CaCO_2$; preferring wet forests of alliances *Carpinion betuli* and *Alno-Ulmion*, especially in ass. *Ficario-Ulmetum minoris*
Blechnum spicant	C-B (m)	N	Various forests of class *Vaccinio-Piceetea*, principally in communities of order *Vaccinio-Piceetalia*; wet forests within sites of communities of *Fagetalia sylvaticae* order
Carex strigosa	Atl	W	Carr forests of alliance *Alno-Ulmion*, in patches of ass. *Carici remotae-Fraxinetum*
Chaerophyllum hirsutum	CE (m)	E	Various carr forests of alliance *Alno-Ulmion*
Chrysosplenium oppositifolium	Atl	W	Carr forests of alliance *Alno-Padion*; no phytosociological data from Pomerania
Empetrum nigrum	Atl-E-S	Ncoast	Baltic heaths of alliance *Empetrion nigri*, edges of raised bogs and transitional mires, forests of alliance *Dicrano-Pinion*; preferring coastal pine forest (ass. *Empetro nigri-Pinetum*)
Euonymus verrucosus	CE (e)	E	Forests of order *Fagetalia sylvaticae*, mainly eastern type of oak-hornbeam forest (ass. *Tilio-Carpinetum*), also xerothermic oak wood (ass. *Potentillo albae-Quercetum*)
Galium schultesii	CE (e)	E	Eastern type of oak-hornbeam forest (ass. *Tilio-Carpinetum*)
Isopyrum thalictroides	CE	E	Eastern type of oak-hornbeam forest (ass. *Tilio-Carpinetum*); no phytosociological data from Pomerania
Linnea borealis	C-B	Ncoast	Forests of class *Vaccinio-Piceetea*, often recorded in coastal pine forest (ass. *Empetro nigri-Pinetum*)
Lunaria rediviva	CE (m)	E	No phytosociological data from Pomerania
Luzula sylvatica	Sub-Atl (m)	Ncoast	No phytosociological data from Pomerania
Lysimachia nemorum	Sub-Atl (m)	Ncoast	Forests of order *Fagetalia sylvaticae*, most frequently carr forests of alliance *Alno-Ulmion*
Polygonatum verticillatum	A-A (m)	E	Various forests of order *Fagetalia sylvaticae*, forests of class *Vaccinio-Piceetea*
Ranunculus cassubicus	CE (e)	E	Oak-hornbeam forests of alliance *Carpinion betuli* (mostly in ass. *Tilio-Carpinetum*)
Veronica montana	Sub-Atl (m)	N	Forests of order *Fagetalia sylvaticae*, mainly fertile and wet forms of beech and oak-hornbeam woods

Explanations: * A-A – Arctic-Alpine subelement; Atl – Atlantic subelement; Atl-E-S – Atlantic-Euro-Siberian subelement; C-B – Circum-Boreal subelement; CE – Central European subelement; e – eastern; m – montane; Sub-Atl – Sub-Atlantic subelement; Sub-Atl-M – Sub-Atlantic-Mediterranean connective element; ** Ncoast – northern coastal; N – northern non-coastal; W – western; E – eastern

1973). Its scattered, relic range also suggest a long history of the species. *Linnea borealis*, a Circum-Boreal species having the southern limit of its range in Pomerania, also appears to be present in Pomerania at least from the Pre-Boreal onwards and some even from the Late Glacial period. Similarly to *E. nigrum*, nowadays

Table 3. Classification of forest species with respect to the time of their migration into Pomerania (after Popiela 2004, changed)

No of group	Period of migration into Pomerania	Plant species
1	Late glacial (Allerød, 11 800–11 000 ^{14}C BP)	*Empetrum nigrum*
2	Pre-Boreal (10 000–9000 ^{14}C BP) or earlier	*Linnea borealis*
3	Boreal (9000–8000 ^{14}C BP)	*Blechnum spicant* *Euonymus verrucosus* *Isopyrum thalictroides* *Luzula sylvatica* *Polygonatum verticillatum* *Ranunculus cassubicus*
4	Late Boreal (c. 8000^{14}C BP)	*Arum maculatum* *Carex strigosa* *Chaerophyllum hirsutum* *Chrysosplenium oppositifolium* *Lysimachia nemorum* *Veronica montana*
5	Atlantic (8000-5000 y BP) or earlier	*Galium schultesii* *Lunaria rediviva*

it inhabits in Pomerania mainly sunny locations in pine woods, mainly in the coastal *Empetro nigri-Pinetum*. Both species are characterised by ranges extending far northwards, and this suggests their resistance to low temperatures. *L. borealis* might have been occurring on sandy stands in light pine and birch-pine forests, in communities of the forest-tundra type. In Pomerania, park-like forest communities with willow and birch and presumably also pine in the south, appeared already during the period of climate improvement in the Bølling (about 12 400-12 000 ^{14}C BP), in the end of the Weichselian (Würm) glaciation. During the next warmer period, the Allerød (11 800-11 000 ^{14}C BP), the whole territory of Pomerania was covered by birch and birch-pine forest communities. These were open, well-lit forests with heliophilous species in the undergrowth layer (Ralska-Jasiewiczowa & Latałowa 1996; Ralska-Jasiewiczowa 1999). A rapid climate improvement took place ca. 10 300-10 200 ^{14}C BP (Ralska-Jasiewiczowa & Starkel 1999). In the Pre-Boreal (10 000-9 000 ^{14}C BP) period, Pomerania was dominated by forests composed mainly of co-dominant birch and pine. These forests were characterised by a rather open structure and occurrence of heliophilous species (Ralska-Jasiewiczowa & Latałowa 1996; Ralska-Jasiewiczowa 1999). Probably conditions in such forests favoured the spread of the discussed species. Along with the climatic optimum and development of deciduous forests, they began to withdraw from some stands. Czubiński (1950) included *Empetrum nigrum* and *Linnea borealis* into the category of glacial relics. However, it is more probable that in warm periods towards the end of Pleistocene they migrated to Pomerania from the south.

In the beginning of the Boreal period (9000-8000 ^{14}C BP), the xerothermic plants that nowadays have their northwestern range limit in Pomerania might have appeared in the study area. Czubiński (1950) assumed that *Ranunculus cassubicus, Isopyrum thalictroides, Euonymus verrucosus*, are the most typical xerothermic relics inhabiting Pomerania in the initial phases of the Post-Glacial period (Table 1). According to that author, the forest in eastern Pomerania probably had taken over the territory inhabited by esparto steppe. A fast temperature increase during the Post-Glacial period, low density of forests, and relatively high calcium content of the substrate were the factors favouring the expansion of the steppe flora (mainly during the period of pine and hazel domination) from the south-east. It seems that the above hypothesis is debatable. The species mentioned are typical forest species, which avoid non-forest formations. Therefore they must have migrated later (Table 3) than Czubiński suggested in the work cited. It appears that they have migrated from the south-east, possibly during the Boreal period. Initially, during the Boreal (9000-8000 ^{14}C BP) and the Atlantic (8000-5000 y BP) periods they might have grown in dry lime-oak forests, and subsequently in lime-hornbeam forests. It is possible that these species originated from the same migration stage. This is evidenced by similar ranges and the same (eastern) type of distribution in Pomerania (Table 2). It seems possible to include also *Galium schultesii* in this group (the same coherence of geographic range). Another possible period of migration for this species is the early Atlantic period.

The species whose time of migration Czubiński (1950) connected with the so-called 'beech period' (Table 1, group 3), seem to have occurred in Pomerania since the Boreal period. Beech arrived in the territory of Pomerania around 3 000 y BP (Latałowa *et al*. 2004), but its expansion began only after the appearance of favourable conditions. These originated after the collapse of Lusatian settlements, preceded by extensive deforestation in deciduous woodlands. When the destructive human activity ceased there, forests regenerated in the abandoned areas (Latałowa 1997; Latałowa *et al*. 2004). It seems that the discussed group of species must have been present in Pomerania much earlier (Table 3), which is suggested by the types of their general ranges and syntaxonomic connections (Table 2). Within their ranges they can occur in various types of deciduous and mixed forests (see e.g. Oberdorfer 1992), so their history should not be connected with the beech period.

A few species associated with the carr forests and wet deciduous forests of the *Fagetalia sylvaticae* order (see: Table 2) have been probably present in Pomerania for a very long time, as might be indicated by their relic ranges (*Blechnum spicant, Lysimachia nemorum*). They might have arrived in Pomerania during the Boreal period from the west (e.g. *Blechnum spicant*), or from the west and the east (*Lysimachia nemorum, Veronica montana*), perhaps together with alder. Alder appeared in Pomerania ca. 8500 ^{14}C BP from two directions: from the west and from the east (Ralska-Jasiewiczowa 1983; Ralska-Jasiewiczowa *et al*. 2004). The migrations of carr species reaching their eastern or northeastern limit of general distribution in Pomerania, e.g. *Arum maculatum, Carex strigosa* and *Chrysosplenium oppositifolium*, should be connected with the western direction. These are species with disjunct ranges and it is possible that they had wider distribution ranges during the climatic optimum of the Holocene. *A. maculatum, C. strigosa* and *Ch. oppositifolium* do not have any stands in the western part of the East German Lowland, while they occur in southern Germany in different types of forests of the order *Fagetalia sylvaticae* (Oberdorfer 1992). It is likely that these species have nowadays relict stands, which remained from widespread oak-lime tree forests during the climatic optimum.

The migration into Pomerania of some alpine species (Table 2), e.g. *Chaerophyllum hirsutum* and *Lunaria*

rediviva, seems to be connected with the Boreal or the early Atlantic periods. *L. rediviva* occurs in isolated stands in Bornholm and Scania. The geological data show that ca. 8000 BP a connection of Pomerania with Bornholm existed there (Borówka 1990). It is hence possible to conclude that this species must have had locations in Pomerania already in the Atlantic period. The immigration of the carr forest species *Ch. hirsutum* might be related to the spreading of this type of habitat towards the end of the Boreal period. It appears that the above-mentioned Alpine species represent an old group of invaders, occurring in Pomerania for a long time, which arrived from the south or the east, or from both of these directions. The type of their distribution is apparently connected to the Weichselian glaciation. These plants do not occur in the German Lowland.

Coniferous forest species (*Luzula sylvatica, Polygonatum verticillatum*) supposedly migrated into the territory of Pomerania during the early Boreal or perhaps even in the Pre-Boreal periods. They are probably relics of the old woods, but subsequently grew in various types of forests. Both species have similar patterns of distribution in Europe, which are possibly relic ranges, especially in the case of *P. verticillatum*.

4. Conclusions

The hypotheses raised by Czubiński (1950) are, to a significant extent, still valid. He managed to present the particular stages and directions of migration of some forest species into Pomerania with a great knowledge of the question and a superb intuition, especially considering the lack of information in his days. Recently new results on the time and pathways of immigration of particular tree species have been published (see e.g. Ralska-Jasiewiczowa *et al*. 2004). Moreover, the composition, spatial and temporal distribution of plant communities in Pomerania, and their anthropogenic changes have been widely studied. In the light of that study the problem of the origin, time and pathways of migration of forest species into the territory of Pomerania seems to be much more complex than supposed by Czubiński in the work cited. Especially the influence of human activity on development of forest communities is currently referred to as much more significant (see, e.g. Tobolski 1982, 1987, 1997; Latałowa 1982a, 1982b, 1992, 2001; Ralska-Jasiewiczowa & Latałowa 1996).

Palynological data show that *Empetrum nigrum* is a relic from warm periods at the turn of Pleistocene. It therefore seems a Late Glacial (Allerød and Younger Dryas) rather than a glacial relic, as suggested by Czubiński (1950). The xerothermic forest species entered the territory of Pomerania probably later than he implied in the work cited. They are associated with oak-lime forests and the time of their migration is connected with the expansion of these forest communities. The species whose arrival time in Pomerania was connected by Czubiński in the work cited with the so-called 'beech period', apparently have occurred there at least since the Atlantic period.

It is emphasised that because of the complexity of the problem and due to the fact that for the majority of the species analysed (with the exception of *Empetrum nigrum*) direct palaeobotanical data relating their presence in particular periods of the Holocene are missing, these considerations are only hypotheses and are still far from being resolved.

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