

# Analysis of distribution patterns of selected ephemeral wetland species in Western Pomerania (NW Poland, NE Germany)

Agnieszka Popiela<sup>1</sup>, Dorota Nalepka<sup>2</sup> & Andrzej Łysko<sup>3</sup>

<sup>1</sup>Department of Botany and Nature Conservation, University of Szczecin, Felczaka 3c, 71-412 Szczecin, Poland, e-mail: popiela@univ.szczecin.pl

<sup>2</sup>W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Kraków, Poland, e-mail: d.nalepka@botany.pl

<sup>3</sup>Department of Environment Protection and Development, West Pomeranian University of Technology, Szczecin, Poland, e-mail: andrzej.lysko@zut.edu.pl

**Abstract:** Phytogeographical conditions of the occurrence of 13 selected ephemeral wetland species of the *Isoëto-Nanojuncetea* class in Western Pomerania are analysed and discussed on the basis of distribution in Western Pomerania (maps are provided), distribution in Europe, general distribution range, taxonomic relations and palynological data. Present distribution patterns of the analysed taxa in Western Pomerania can thus be permanent not for a very long time and reflect the history of the settling of Pomerania by these species.

**Key words:** anthropogenic expansion, Holocene, *Isoëto-Nanojuncetea*, local distribution maps, palynological data

## 1. Introduction

Western Pomerania is the conventional name of the western part of the Baltic Sea coast. In fact, there are no officially marked borders of this region. It is a historical and geographical region along the Lower Odra River and smaller rivers flowing into the Bay of Pomerania, between Recknitz (Reknica) in the west and Łeba in the east (Fig. 1). To the west, it expands into Mecklenburg and Brandenburg, to the south into the Lubus Region and the Greater Poland Region, while to the east – into the Gdańsk (Eastern) Pomerania region. The area of Western Pomerania is an interesting land for doing phytogeographical analyses. It is a region of about 40 thousand km<sup>2</sup> situated in Central Europe, thus open to species migration but with relatively well-marked geomorphological borders: limited to the north by the seacoast of south-western Baltic and to the south, west and east by terminal moraine ranges of the Vistulian ice sheet (Gilewska 1999; Borówka *et al.* 2002).

The entire area of Western Pomerania is covered by Quaternary sediments; hence, the history of plant range formation is relatively new here. The whole region be-

came occupied by plants not earlier than after the regression of the Vistulian ice sheet (Borówka *et al.* 2002). The settling of particular species as well as the time and ways of their migration depended both on the distance from the refuges, climate fluctuations within the space of about not more than 10 000 years, formation of suitable habitats and the presence of free ecological niches. Within the discussed area, the Atlantic and continental climate effects mixed which is a probable reason why many species are found here on the periphery of their distribution ranges or have boundary posts (see e.g. Czeczottowa 1928; Czubiński 1950; Zając 1996; Popiela 2004). They belong to different habitat groups and represent different syntaxonomic groups. One of such species groups well-separated with respect to their habitat is wetland ephemerophytes occurring as the first initial stage on open soil and occupying habitats saturated with water or flooded throughout part of the vegetation season. Large liability of habitats determines a short vegetation period in species of this group and the time period from germination to giving out seeds can close even within two months. Diaspores have a long survival time and are adapted to long waiting in

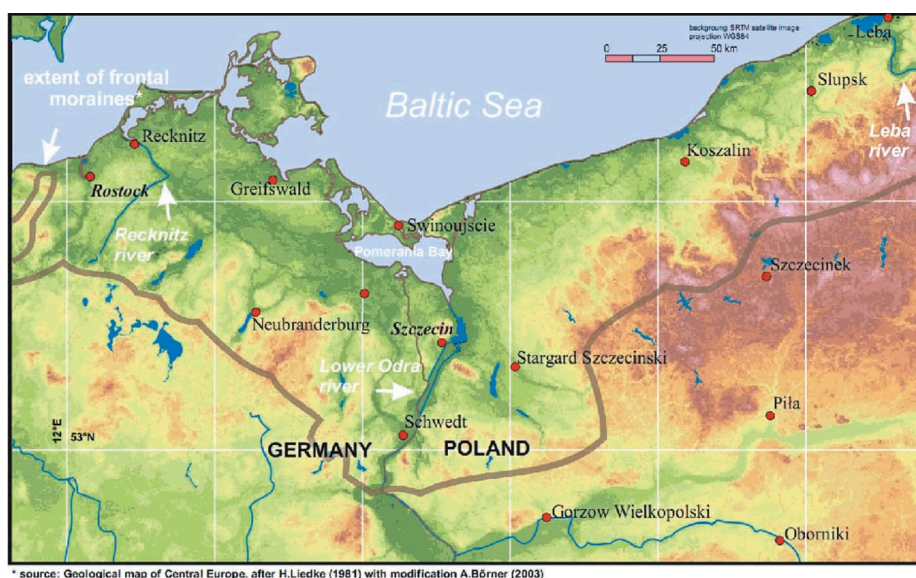


Fig. 1. Location of Western Pomerania

soil for germination-favourable conditions (see Deil 2005).

The present paper aims at analysing and discussing phytogeographical conditions of the occurrence of 13 selected ephemeral wetland species in Western Pomerania and leaving questions concerning the history of their settling open.

## 2. Method

The analysis was carried out in relation to species classified as the *Isoëto-Nanojuncetea* class and the *Nanocypertalia* order. For examinations, 13 taxa were selected with contemporary or historic locations within the area of Western Pomerania which are strictly attached to wetland habitats and do not occur outside them. Taxa with distribution ranges of undoubtedly synanthropic nature were omitted (e.g. *Plantago pauciflora*, *Juncus bufonius*, *Gypsophila muralis*, *Gnaphalium uliginosum*, *Myosurus minimus*) as well as those with a broader ecological spectrum (e.g. *Centaureum pulchellum*).

The list of the examined taxa is given below: *Carex bohemica* L., *Cyperus fuscus* L., *Elatine alsinastrum* L., *E. hexandra* Lap., *E. hydropiper* L., *E. triandra* Schkuhr., *Eleocharis acicularis* L., *E. ovata* (Roth) Roem. et Schult., *Juncus tenageia* Ehrh., *Lythrum hyssopifolia* L., *Limosella aquatica* L., *Mentha pulegium* L., *Peplis portula* L.

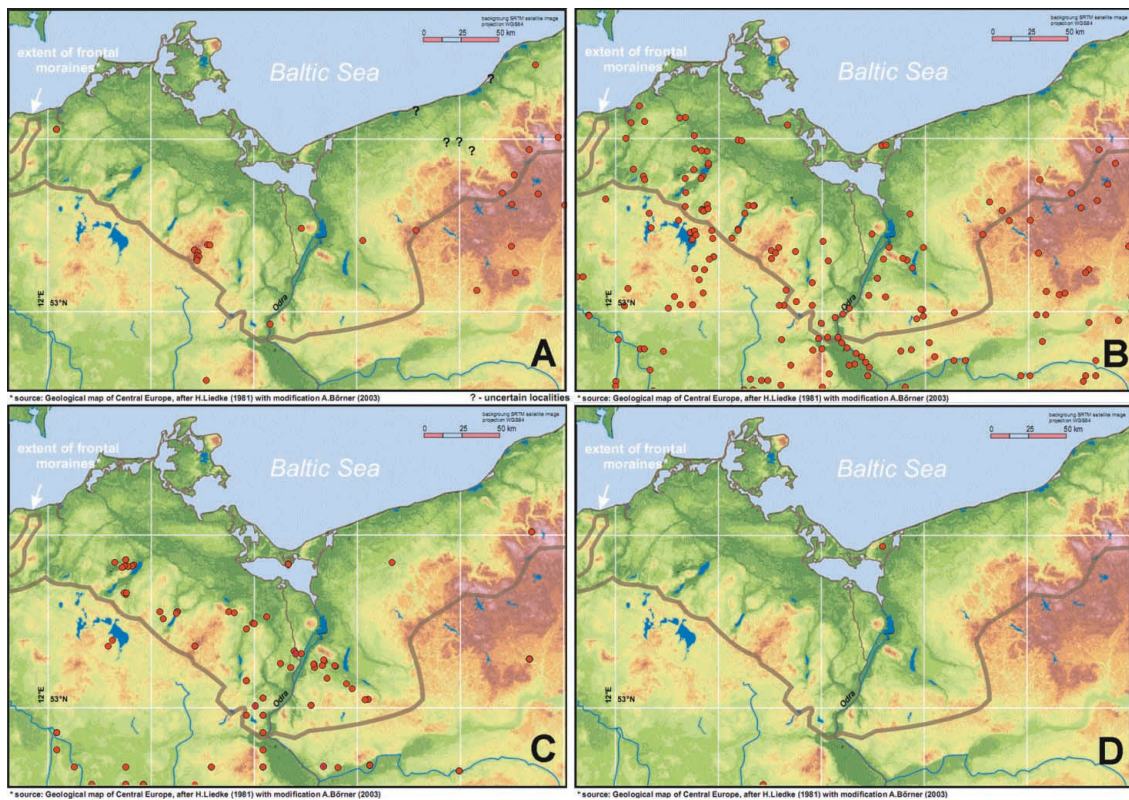
For each of the above species, the following factors were analysed: distribution in Western Pomerania, distribution in Europe, general distribution range, taxonomic relations and those analyses were supported by palaeobotanical data. Distribution maps of the examined taxa included in the paper were made by one of the

authors (A.P.) – (i) of the area within Poland boundaries based on all available published, unpublished and herbal data (Popiela 1998, 1999a, 1999b, 2001a, 2001b), while those (ii) of the area within Germany boundaries are given after Benkert *et al.* (1996) and Fukarek & Henker 2006. The world range is given on the basis of available distribution maps (Meusel *et al.* 1965, 1978; Hultén & Fries 1986; Lampe 1996).

## 3. Results and discussion

Taxonomic position, phytogeographical characteristic and distribution of the analysed species are as follows:

*Carex bohemica* (Fig. 2/A) belongs to the sub-genus *Vignea* P. Beauv. (Kük.). Kükenthal (1909) includes the species within the section of *Schellhammeria* (Moench) Kunth, into which *C. sychnocephala* Carey occurring in temperate and boreal regions of America is also included as a second species. Species of the *Schellhammeria* section, included next within the *Cyperoideae* G. Don section, have an isolated position within the genus and are well integrated with species of the monophyletic section *Ovales* Kurth (Hendricks *et al.* 2004; Ford *et al.* 2006). Species from this section are mainly distributed in North and South America, from the Arctic to Patagonia. Studies of Hipp *et al.* (2006) allow setting forth a hypothesis that the centre of diversity and, hence, the origin of taxa from the *Ovales* section (including species contained in the *Cyperoideae* section, with the exception of *C. illota* L. H. Bailey) is in the western part of North America, whereas the current distribution range of *C. bohemica* can be a result of long-distance dispersion. *C. bohemica* is a Euro-Siberian species; it has a scattered distribution in Europe,



**Fig. 2.** Distribution of *Carex bohemica* L. (A), *Cyperus fuscus* L. (B), *Elatine alsinastrum* L. (C), *Elatine hexandra* Lap. (D) in Western Pomerania

i.e. a central European one, with the occurrence centre to the north from the Alps mountain range. In Eastern Europe as well as in Siberia and the Far East, it is poorly spread (?), with single sites, mainly in river valleys. In Pomerania-Vorpommern, *C. bohemica* has been recorded along northern borders of its distribution range; single locations are observed in the Odra River valley as well as on edges of water reservoirs, mainly in areas of hummocky morainic plateaus. There are no palaeobotanical data from Western Pomerania.

*Cyperus fuscus* (Fig. 2/B) belongs to the *Fusci* Kunth. section, into which further 10, mostly annual, species originating in African steppe areas and forests, South Asian monsoon regions and South America (Kükenthal 1936; Lampe 1996) are included, apart from *C. fuscus*. The most closely related (?) – *C. difformis* L. – settles a broader home range with tropical and subtropical distribution in both hemispheres (Smith 1979). *C. fuscus* is a Euro-Siberian and Mediterranean species. Its compact home range takes up Central, Western and Southern Europe and North Africa, with single locations, mainly in the valleys of large rivers, known from Central and South-Eastern Asia. In Pomerania-Vorpommern, this species has been recorded in the northern periphery of general distribution range, mainly in the areas of hummocky morainic plateaus and, in addition, in river valleys (first of all in the Odra River valley) as well as on the Wolin and Uznam Islands. Pollen deter-

mined as: *cf. Cyperus* was present in western Pomerania (Kolczewo) and dated back to the late Holocene (Latałowa 1992).

Small family Elatinaceae (40-50 species), containing only two genera: *Bergia* L. and *Elatine* L., are probably related to the tropical family Malpighiaceae (Davis & Chase 2004). The genus *Elatine* contains about 15-25 taxa which are mainly found in temperate regions of both hemispheres (Tucker 1986). The most widespread is *E. triandra* Schuhr., found on all continents, except Antarctica. Nine species derive from Europe, whereas 12 – from the New World.

*Elatine alsinastrum* (Fig. 2/C) is the only species of the genus belonging to the sub-genus *Potamopithys* (Adanson) Seub.; it is a Euro-Siberian (Mediterranean?) taxon, with only single sites observed to the east of the Ural mountain range in river valleys of the western part of Siberia. In Europe, locations of *E. alsinastrum* have been found mainly in the central part of the continent, with their largest concentration to the north-east of the Alps mountain range. In Pomerania-Vorpommern, this taxon reaches the northern limits of its European home range, with dispersed locations of this species reported from the area of hummocky morainic plateaus or fragments of ground-morainic plateaus adjacent to them.

*Elatine hexandra* and *E. hydropiper* belong to the *Elatine* Seub. sub-genus and the section *Elatinella* Seub. *Elatine hexandra* (Fig. 2/D) is a (sub)-Atlantic species,

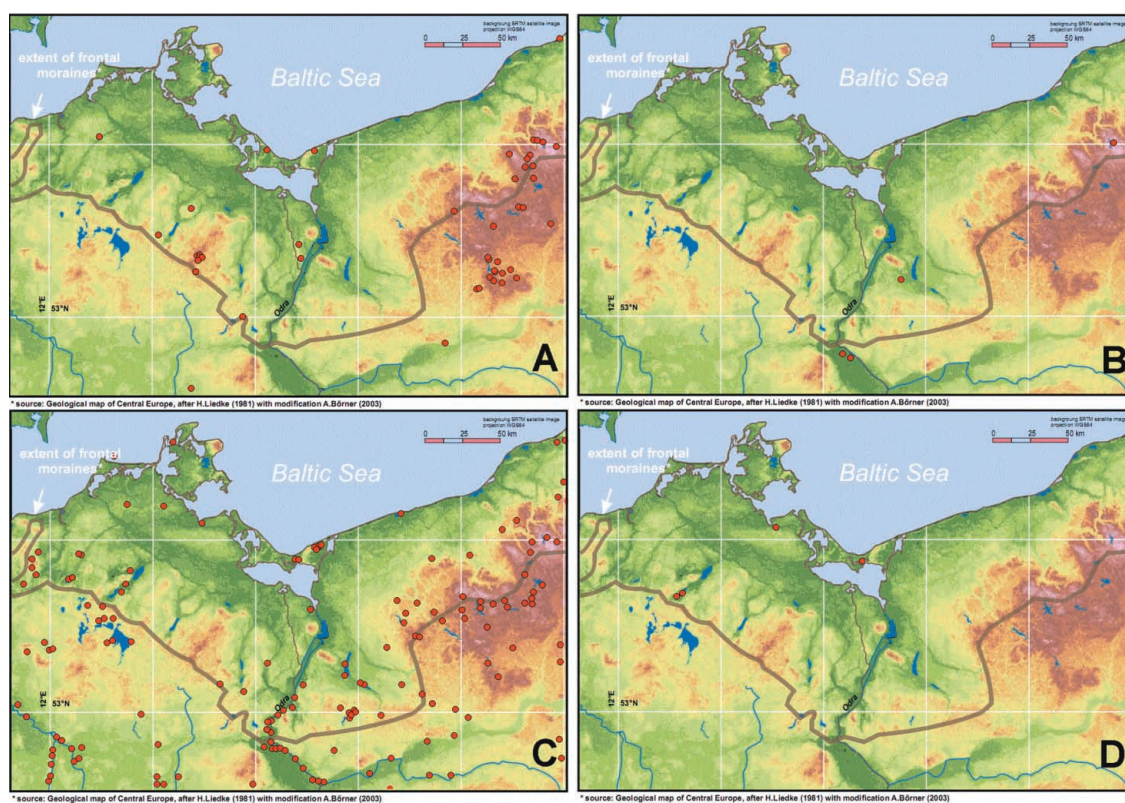
with its sites concentrated in Wales and western England and Scotland as well as in the central part of Europe, to the north of the Alps mountain range; in addition, this species has been found in scattered locations (south-western Scandinavia, Pyrenean Peninsula, drainage basin of the Upper Loire and the upper Seine). In Pomerania-Vorpommern, it had only one historic site on the Wolin Island (in the hinterland of frontal moraine heights), the most north-eastern location of this species in Central Europe.

The Euro-Siberian distribution range of *Elatine hydropiper* (Fig. 3/A) is similar to that of *E. alsinastrum* but is shifted northwards and eastwards. The core of its distribution range is in the northern part of Central Europe and southern Scandinavia, with dispersed locations found in England and Wales, the Balkan Peninsula and Eastern Europe. In Siberia, scattered locations of this species were reported in the valleys of the Irtysh, Ob and Yenisei rivers as well as at Lake Bajkal. In Pomerania-Vorpommern, *Elatine hydropiper* was recorded in single sites in the belt of hummocky morainic plateaus and sands, in the Odra River valley and in morainic areas of the Wolin and Uznam Islands.

*Elatine triandra* (Fig. 3/B) is classified into the *Elatine* Seub.sub-genus and the *Triandra* Seub. (Crypta (Nutt.) Seub section. It is a species with cosmopolite distribution range, with sites found on all continents, except Antarctica; relatively larger density of its loca-

tions is observed in Europe, South-Eastern Asia (Japan, western coasts of the Yellow and the East China Seas), South-Eastern Australia and on the eastern coast of North America. In addition, this species is reported from single sites, frequently hundreds of kilometres away from one another. In Europe, locations of *E. triandra* are concentrated in the central part of the continent (to the north of the Alps mountain range) and in the southern part of the Scandinavian Peninsula. In Pomerania-Vorpommern, two sites of *E. triandra* were observed in the Lower Odra River valley and one on the Wełtyń Plain. Pollen determined as: *Elatine* was present in western Pomerania (Kołczewo, Lake Racze sites), dating back to the late Holocene (Latałowa 1992).

The *Eleocharis* genus contains 150 species and is widespread in the world (Schultze-Motel 1966). The core distribution of this genus is in tropical and subtropical regions. Svenson (1929) includes *Eleocharis acicularis* (Fig. 3/C) in the *Acicularis* Svenson section, containing annual and perennial small-form species. A major part of taxa included here was recorded in North, Central and South America, fewer in Europe, North and East Asia, and only one in Australia (probably a synanthropic plant). From among all species of this genus, *E. acicularis* is most widespread in the northern hemisphere. It also belongs to the northernmost occurring species of wetland ephemerophytes (only *Limosella aquatica*, *Juncus bufonius* and *Gnaphalium uliginosum*



**Fig. 3.** Distribution of *Elatine hydropiper* L. (A), *Elatine triandra* Schkuhr. (B), *Eleocharis acicularis* L. (C), *Eleocharis ovata* (Roth) Roem. et Schult. (D) in Western Pomerania

have a distribution range more advanced to the north; Lampe 1996).

Macrofossils determined as: *Eleocharis* sp. were present in Poland, western Pomerania (Wolin), dating back to the late Holocene (Latałowa 1999).

*Eleocharis acicularis* is a circumboreal species, which can be found in Asia and North America, mainly in regions with cool and temperate climates. In Europe, it was recorded in the northern and central part of the continent. In Pomerania-Vorpommern, locations of this species were observed mainly in the areas of morainic and hummocky plateaus (Drawsko Lakeland, Myślibórz Lakeland, Meckleburgische Seenplatte), whereas single specimens were found in river valleys and morainic areas of the Wolin Island.

*Eleocharis ovata* (Fig. 3/D) is included by Svenson (1929) in the *Ovatae* Svenson section, together with three other annual species – *E. obtusa*, *E. engelmannii*, *E. lanceolata*., Out of them only *E. ovata* is native to Europe, while three other taxa are native to North America (see Drapalik & Mohlenbrock 1960; Lampe 1996). The distribution of *E. ovata* on that continent was reported together with the distribution of taxonomically closest *E. obtusa* (Willd.) Schult., which is not treated separately by some floras (see Roalson & Friar 2000). The home range of *E. ovata* is circumboreal, clearly zonal and almost completely limited to the southern temperate zone and does not have oceanic character. In

Asia, single records were reported mainly from the eastern part of the continent, whereas their largest concentration was recorded in Central Europe, in the valleys of large rivers. In Pomerania-Vorpommern, *E. ovata* was recorded in its northern boundary locations in Europe; historic sites of this species were known from the Wolin Island (Lucas at the Wicko Lake) as well as from the areas of hummocky morainic plateaus of the Greifswald environs and Malchiner See.

The *Juncus* genus is one of seven cosmopolite genera of the Juncaceae family originating, according to some authors, in the southern hemisphere, with the centre of diversity in South America (Drábková *et al.* 2003). *Juncus tenageia* (Fig. 4/A) belongs to the *Agathryon* sub-genus and the *Tenageia* section, which includes species of the evolutionary line containing ephemeral terophytes of wet habitat (Deil 2005). Most species of this group are stenochoric with the centre of diversity in the Mediterranean region (Drábková *et al.* 2003; Kirschner *et al.* 2004). *J. tenageia* is a central European-sub-Mediterranean species, extending over Central and Southern Europe and North Africa. Its northernmost occurrences were recorded in the Netherlands and in northern Germany and the easternmost – in the Ukraine and the Caucasus. In Pomerania-Vorpommern, this species was observed in the area of hummocky morainic and flat and undulated ground-morainic (more rarely) plateaus (e.g. the Wałcz, Pyrzyce and Wełtyń

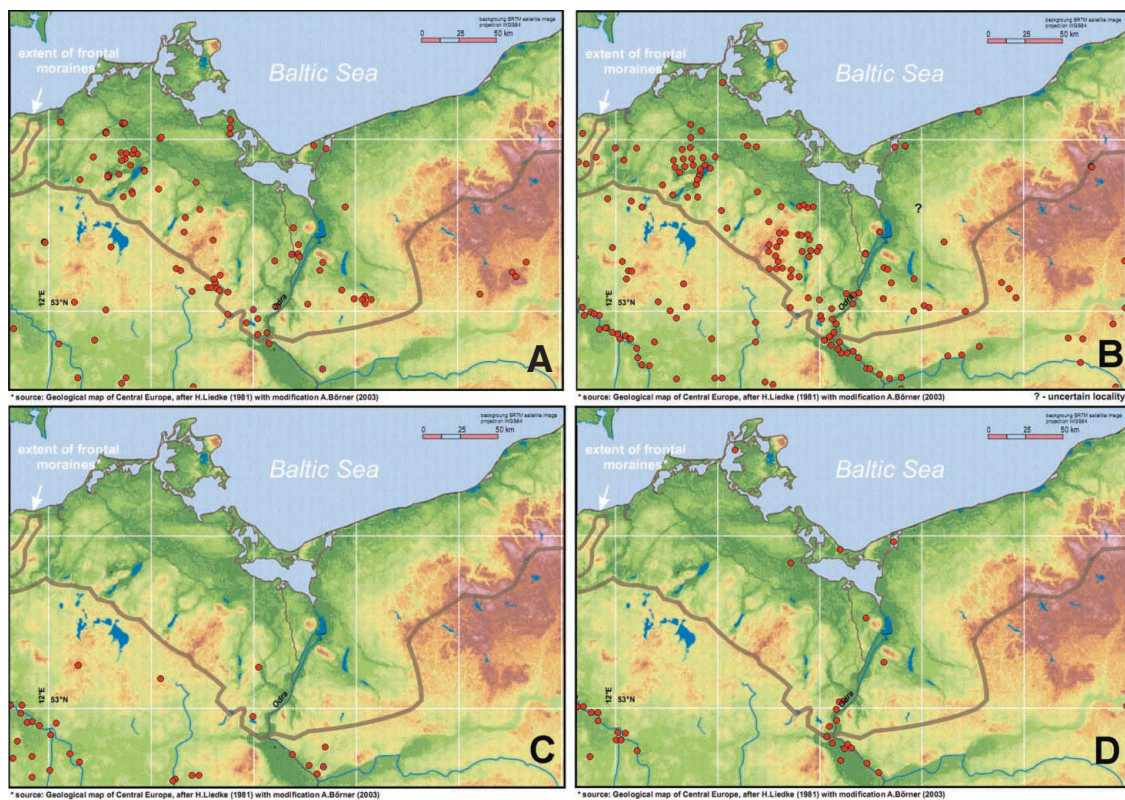


Fig. 4. Distribution of *Juncus tenageia* Ehrh.(A), *Limosella aquatica* L. (B), *Lythrum hyssopifolia* L. (C), *Mentha pulegium* L. (D) in Western Pomerania

Plains and Rückland der Mecklenburgische Seenplatte). There is no palaeobotanical data from western Pomerania.

The *Limosella* genus has almost purely extra-tropical distribution and is found in regions with temperate climates, except deserts and is characterised by an isolated taxonomic position. It is probably most closely related to species of the *Manuleeae* Bentham tribe, which is a common element of the Cape Peninsula flora (Oxelmann *et al.* 2005). The total of 15-18 species belong to the *Limosella* genus (Glück 1934). *Limosella aquatica* (Fig. 4/B) is included in the *Limosella* section, together with *L. tenella* Quezel et Cont (an endemic plant of north-western Greece), one endemic North American species (Arizona), one South American species, five South African species (two of them occur also in tropical Africa and Ethiopia) and one species with the homeland in South-Eastern Australia and South New Zealand. It is likely that ancestors of the *Limosella* genus come from South Africa, with many other species of the *Limoselleae* tribe adapted to rather dry habitats (see Kornhall & Bremer 2004). *L. aquatica* is a circumboreal species, the home range of which reaches relatively far to the north, having locations exceeding the Polar Circle. In Pomerania-Vorpommern, *L. aquatica* was mainly recorded in the southern and central part of flat and undulated ground-morainic plateaus, sandr areas (e.g. the Wełtyń Plain, the Pyrzyce Plain, the Drawsko Plain, southern part of Vorpommersches Flachland, northern part of Rückland der Mecklenburgische Seenplatte) as well as in river valleys. There is no palaeobotanical data from western Pomerania.

The *Lythrum* L. genus contains about 30 species with the core distribution in temperate and warm zones. *Lythrum hyssopifolia* (Fig. 4/C) belongs to the *Hyssopifolia* Koehne sub-genus and the *Euhyssopifolia* Koehne section, which contains annual taxa widespread in the western and central Mediterranean region as well as in the East Pontic-South Siberian or the Oriental-Turkmenian area (Koehne 1903). The distribution range of *L. hyssopifolia* includes the western, central and southern part of Europe, the Mediterranean region as well as the Irano-Turanian, the East Pontic and the South Siberian regions and, in addition, dispersed locations in Africa (to the north of the equator). Synanthropic sites of this species were recorded in North America (California), Australia, South Africa and South America (?). In Pomerania-Vorpommern, *Lythrum hyssopifolia* reaches the northern borders of its home range and has only a number of locations in the south of the examined area in the Odra River valley. There is no palaeobotanical data from western Pomerania.

The *Mentha* genus (25 species in total) is particularly rich in the western Mediterranean region. *Mentha pulegium* (Fig. 4/D) belongs to the *Pulegium* (Miller)

DC. section which, in addition, contains *M. micrantha* (Bentham) Schost (South Russia, Western Kazakhstan) and *M. daghestanica* Boriss, an endemic plant for Dagestan. Also *M. gattefossii* Maire, with a narrow limited home range in Morocco (Lampe 1996), probably belongs to this group. *M. pulegium* is a central European-Mediterranean species with the centre of occurrence in the western part of Mediterranean region. In central Europe, it occurs mainly in the valleys of large rivers; it is also recorded as a synanthropic plant in both Americas and Australia. In Pomerania-Vorpommern, *Mentha pulegium* reaches the northern borders of its occurrence in Central Europe; it has been observed in several locations, first of all in the valleys of the Odra, Penne, Dźwina and Świna Rivers. There is no palaeobotanical data from western Pomerania.

Apart from *Peplis portula* (Fig. 5), three other species are included in the *Peplis* genus: *P. diandra* Nutt. occurring in sub-Mediterranean to temperate zones of eastern America, a Pontic-sub-Siberian *P. alternifolia* Bieb., and one endemic species for Iran. The *Peplis* genus is closely related to the *Lythrum* L. genus, the south European genus *Middendorfia* Trautv and the tropical-sub-tropical genus *Amannia* L. (Lampe 1996). *P. portula* is a central European-Mediterranean species, found all over Europe, except south-eastern Spain, central and northern Scandinavia, southern Greece, southern Ukraine and northern Russia. In Pomerania-Vorpommern, locations of *P. portula* have been recorded in the areas of hummocky frontal moraines, with single sites in river valleys and on the seacoast. *Peplis portula* L. pollen determined as: *Peplis portula*, *Lythrum peplis*, *Peplis* was present in Poland, in western Pomerania (Wolin, Kołczewo), dating back to the late Holocene (Latałowa 1992, 1999).

When analysing taxonomic data as well as those referring to general and regional distribution of the species under discussion, the following regularities draw attention:

1. The prevailing majority of taxa of the group under discussion have an isolated taxonomic position, which seems to suggest – in connection with disjunctive home ranges – that ephemeral wetland flora is a plant group with a long history, originating perhaps in the Tertiary flora. Similarly, the analysis of taxonomic relations and distribution of taxa most closely related to the examined species points out to their probable very old origin and, with reference to certain taxa, to certain taxonomic isolation even at the level above species (sub-genus, genus, family). For some taxa, there is data which can confirm their long history. The *Elatinaceae* family is probably related to the tropical family *Malpighiaceae*, the common ancestor of which could appear in the Cretaceous period at the beginning of the Albian stage, i.e. 111-100 million years ago, with both families presumably

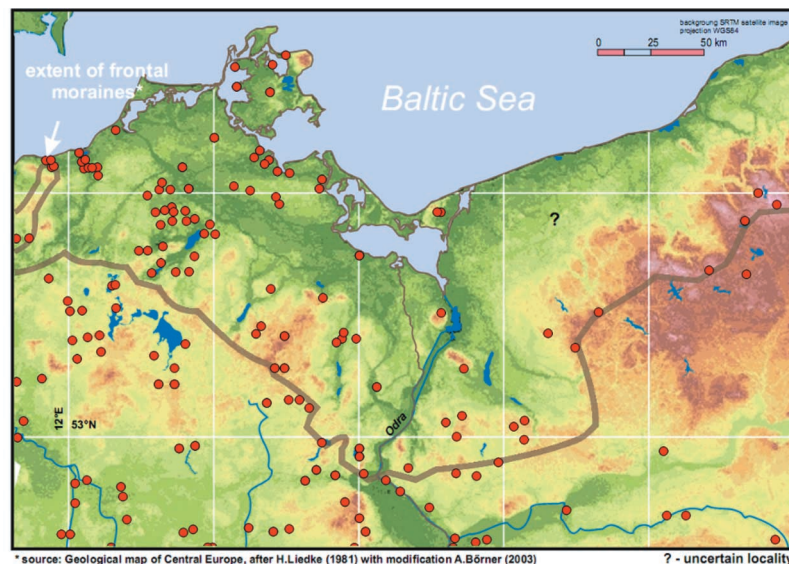


Fig. 5. Distribution of *Peplis portula* L. in Western Pomerania

separated at the end of this period, i.e. about. [113]98 [-89]/[100]-89[-85] million years ago (Davis & Chase 2004; Davis *et al.* 2005). Thus, it can be assumed that the history of the *Elatine* family in the northern hemisphere may reach back to the Mediterranean- and Madro-Tertiary flora, like that of the Juncaceae family amounting to more than 80 million years (Janssen & Bremer 2004). As far as other analysed taxa are concerned, hypotheses can be set forth on their old origin based on indirect data: some have close relatives only in tropical regions (e.g. *Limosella aquatica*, *Cyperus fuscus*), others have the centre of diversity in the Mediterranean region (e.g. *Juncus tenageia*, *Lythrum hyssopifolia*, *Mentha pulegium*) or in the western hemisphere (*Carex bohemica*, *Eleocharis acicularis*, *E. ovata*). General distribution ranges of the species of the group under examination are differentiated due to the extent of home ranges and oceanic and

zonal character but distribution of the prevailing majority of them has disjunctive character (see Table 1).

2. In Europe, the main area of occurrence of the species group under discussion (both with respect to the number of taxa and the number of locations) are the areas of the western part of the continent as well as the seacoast and islands of the western part of the Mediterranean Sea basin. To the east, the plants under discussion do not occur (*Carex bohemica*, *Elatine alsinastrum*, *E. hexandra*, *E. hydropiper*, *E. triandra*, *Eleocharis ovata*, *Juncus tenageia*, *Lythrum hyssopifolia*, *Mentha pulegium*), although they are present only in separate locations or have the character of scattered distribution range (*Limosella aquatica*, *Peplis portula*). These are species with different types of general distribution range, with some of them reaching the northern boundaries of their home range within the examined area and the distribution

**Table 1.** Selected species of the *Isoëto-Nanojuncetea* occurring in Western Pomerania – affiliation to geographical element, range border in Western Pomerania, range border in Poland

Species	Affiliation to the geographical element	European N range border in Pomerania	European range border in Poland
<i>Carex bohemica</i>	E-S	Yes	Yes
<i>Cyperus fuscus</i>	E-S-M	Yes	No
<i>Elatine alsinastrum</i>	E-S	Yes	Yes
<i>Elatine hexandra</i>	(s)Atl	No	Yes
<i>Elatine hydropiper</i>	E-S	No	Yes
<i>Elatine triandra</i>	Cosm	No	Yes
<i>Eleocharis acicularis</i>	C-B	No	No
<i>Eleocharis ovata</i>	C-B dis	Yes	Yes
<i>Juncus tenageia</i>	CE-(s)M	Yes	Yes
<i>Limosella aquatica</i>	C-B	No	No
<i>Lythrum hyssopifolia</i>	Cosm	Yes	Yes
<i>Mentha pulegium</i>	CE-M	Yes	Yes
<i>Peplis portula</i>	CE-(s)M	No	No

Explanations: C-B – Circum-Boreal sub-element, C-B dis – Circum-Boreal sub-element, disjunctive, CE-M – Central European-Mediterranean connective element, CE-(s)M – Central European-Sub-Mediterranean connective element, Cosm – Cosmopolitan connective element, E-S – Euro-Siberian sub-element, E-S-M – Euro-Siberian-Mediterranean connective element, (s)Atl – Sub-Atlantic sub-element

**Table 2.** Climatic parameters delimited range borders of selected species (after Lampe 1996)

Taxon	N border	NW border	NE border	W border	S border
<i>Carex bohemica</i>	17.5°C (16.5)***		Length of days with: >10°C – 90**, >5°C – 120**	2.5(10)°C****	Precipitation*: (250), sum of temperatures of period with average > 10°C**: 3000
<i>Cyperus fuscus</i>		17°C***			Precipitation*: 250 (100), sum of temperatures of period with average > 10°C**: 7500, length of period with >15°C**: 270
<i>Elatine hexandra</i>	Sum of temperatures period with more than 10°C**: 1500	15 (14)°C***	Length of period without frost: 180 days		Precipitation*: 600, average temperature of the warmest month: 20°C
<i>Elatine hydropiper</i>		Length of period without frost: 180 days 15°C (14°C)***	Length of period with temperatures.: 90 days > 10°C**, 120 days > 5°C**	2.5 (4)°C****	Precipitation*: 400 (200), sum of temperature of period with >10°C**: 3000 (3500)
<i>Eleocharis ovata</i>		17.5°C***			Precipitation*: (400), length of period with temperature >15°C**: 120 days
<i>Mentha pulegium</i>		15°C***	Length of period without frost: 180 days		Precipitation*: 400 (250)

Explanations: \* – sum of annual precipitation [mm], \*\* – average temperature of day, \*\*\* – average temperature of Juli, \*\*\*\* – average temperature of Januar

of others reach the Scandinavian Peninsula (see Table 2). Seven of the analysed species reach in Western Pomerania an absolute boundary of their north-western home range (*Carex bohemica*, *Cyperus fuscus*, *Elatine alsinistrum*, *Eleocharis ovata*, *Juncus tenageia*, *Lythrum hyssopifolia*, *Mentha pulegium*).

3. The group of species under discussion shows similar distribution patterns in Western Pomerania: their sites are reported in the areas of morainic plateaus of hummocky frontal moraines and undulated ground moraines as well as in the valleys of larger rivers (Odra River mostly); they avoid the areas of flat ground moraine as well as those of flood (flooded areas, first of all in the vicinity of the Szczecin Bay). A common feature of all analysed distribution ranges is concentration of locations to the south of Western Pomerania and consequently their dispersion in this area. It is a very clear distribution pattern in spite of, as showed above, separate taxonomic position, origin, general distribution and hypothetical centre of diversity of the species under examination.

4. Directly to the south of Western Pomerania, the distribution ranges of the species under discussion concentrate – with the largest number of their records and the largest populations reported in anthropogenic locations, i.e. in periodically drained fish ponds – for instance, in Lusatia, Lower Silesian Forests, or in the vicinity of Milicz. In Western Pomerania, almost all known sites have natural character, while part of them is already historic records.

The question, therefore, is: what is a possible reason for the formation of such a clear distribution pattern of the analysed species group in Western Pome-

rania? It seems that the problem of the availability of a suitable habitat can be excluded. The analysed species are taxa specialised to settle periodically flooded areas; they colonise habitats that are easily accessible, with small competition from the side of other species. It is commonly accepted that species of pioneer habitats, i.e. terophytes, spread easily if they find favourable habitat and weather conditions. Therefore, Western Pomerania – as an area with a relatively rich network of rivers and water reservoirs – is a region where, as it appears, locations of the plants under discussion should be distributed evenly. It does not appear either that climatic requirements of the species under discussion have been a reason for the distribution pattern presented above since these requirements are within climate parameters of the area of Western Pomerania (see Table 1 and Woś 1999).

In literature, a possibility of the formation of a distribution range of ephemeral wetland species through waterfowl is considered, although it is poorly documented. Only one experimentally confirmed example of exozoochoria has been known so far for *Carex bohemica* (see Deil 2005). Furthermore, when comparing maps of the passages of bird species gathering along waters (e.g. Charadriidae; see Mead *et al.* 2007) with distribution ranges of the plants discussed in Central Europe, as well as regionally within the examined area, no logical pattern can be found. Therefore, without ruling out the possibility of transmission of diaspores by birds, it appears impossible to be a main factor of the formation of such a clear distribution pattern in Western Pomerania.

Palynological and palaeobotanical data from Central Europe confirm the presence of some analysed species in Quaternary sediments; therefore, when examining



reasons for the observed clear distribution pattern of ephemeral wetland species in Western Pomerania, it is possible, as it appears, to set forth the following hypothesis:

1. The group of ephemeral wetland species under discussion is an old group of taxa which has been present in Western Pomerania at least since the Late Holocene. Present distribution pattern of the analysed taxa in Western Pomerania can thus remain permanent for a very long time (seed bank in soil) and is a reflection of history of the settling of Pomerania by these species.

2. At present, relatively frequent occurrence of the species in locations of anthropogenic origin (e.g. their large populations on periodically exposed fish pond beds; see, for instance, Pietsch 1963; Popiela 1996) suggests that the current distribution ranges in areas situated to the south of Western Pomerania have a very clear anthropogenic expansion. Probably, they would

not be so frequent by nature because their spreading and colonisation of new habitats are, for some reasons, not easy. On the other hand, they are successful when people create conditions under which they can succeed. An example in Pomerania is the site of *Elatine hydro-piper* on the Kwiecko Lake, the bed of which is being uncovered due to the operation of pumped-storage power station (Popiela *et al.* 2009).

**Acknowledgements.** Funding was provided to A. Popiela by Ministry, Department of Scientific Research project Nr PO4C03525. A. Popiela wishes to thank the keeper of Kew Herbarium for access to herbarium material and to Professor Adam Zajac for critical reading of the manuscript. We are thankful to Professor Maria Lityńska-Zajac for allowing access to her unpublished plant macrofossil database (Computer database of macroscopic plant remains from the archaeological excavations) and to Professor Małgorzata Latałowa for her very critical, extensive review of the first manuscript.

## References

- BENKERT D., FUKAREK F. & KORSCH H. (eds.). 1996. Verbreitungsatlas der Farn und Blütenpflanzen Ostdeutschlands (Mecklenburg-Vorpommern, Brandenburg, Berlin, Sachsen-Anhalt, Sachsen, Thüringen). 615 pp. Gustav Fischer Verlag, Jena-Stuttgart-Lübeck-Ulm.
- BORÓWKA R., FRIEDRICH S., HEESE T., JASNOWSKA J., KOCHANOWSKA R., OPECHOWSKI M., STANECKA E. & ZYSKA W. 2002. Nature of Pomerania. 479 pp. Oficyna in plus. Szczecin.
- CZECZOTTOWA H. 1928. The atlantic element in the flora of Poland. Rozpr. Wydz. Mat.-Przyr. PAU Ser. III, Dział A/B 65/66: 221-286.
- CZUBIŃSKI Z. 1950. Problemy geobotaniczne Pomorza. Bad. Fizjogr. Pol. Zach. 2(4): 339-658.
- DAVIS C. C. & CHASE M. W. 2004. Elatinaceae are sister to Malpighiaceae; Peridiscaceae belong to Saxifragales. *Am. J. Bot.* 91: 262-273.
- DAVIS C. C., WEBB C. O., WURDACK K. J., JARAMILLO C. A. & DONOGHUE M. J. 2005. Explosive radiation of Malpighiales supports a mid-Cretaceous origin of modern tropical rain forests. *American Naturalist* 165: E36-E65.
- DEIL U. 2005. A review on habitats, plant traits and vegetation of ephemeral wetlands – a global perspective. *Phytocoenologia* 35(2-3): 533-705.
- DRÁBKOVÁ L., KIRSCHNER J., SEBERG O., PETERSEN G. & VIČEK Č. 2003. Phylogeny of the Juncaceae based on *rbcL* sequences, with special emphasis on *Luzula* DC. and *Juncus* L. *Plant Syst. Evol.* 240: 133-147.
- DRAPALIK D. J. & MOHLENBROCK R. H. 1960. A study of *Eleocharis*, Series *Ovatae*. *American Midland Naturalist* 64(2): 339-341.
- FORD B. A., IRANPOUR M., NACZI R. C., STARR J. R. & FEROME C. A. 2006. Phylogeny of *Carex* subg. *Vignea* (Cyperaceae) based on non-coding nrDNA sequence data. *Systematic Botany* 31(1): 70-82.
- FUKAREK F. & HENKER H. (eds.) 2006. Flora von Mecklenburg-Vorpommern. 450 pp. Herausgegeben von H. Henker & Ch. Berg, Weissdornverlag Jena.
- GILEWSKA S. 1999. Rzeźba. In: L. STARKEL (eds.) *Geografia Polski. Środowisko przyrodnicze*, pp. 243-288. Wyd. Nauk. PWN, Warszawa.
- GLÜCK H. 1934. *Limosella*-Studien. *Botanische Jahrbücher für Systematic und Pflanzengeographie* 66: 488-566.
- HENDRICKS, M., MICHALSKI S., BEGEROW D., OBERWINKLER F. & HELLWIG F. H. 2004. Phylogenetic relationships in *Carex*, subgenus *Vignea* (Cyperaceae) based on ITS sequences. *Plant Syst. Evol.* 246: 109-125.
- HIPP A. L., REZNICEK A. A., ROTHROCK P. E. & WEBER J. A. 2006. Phylogeny and classification of *Carex* section *Ovales* (Cyperaceae). *Int. Plant. Sci.* 167(5): 1029-1048.
- HULTÉN E. & FRIES M. 1986. Atlas of North European Vascular Plants. North of the Tropic of Cancer. I. Introduction, taxonomic index to the maps 1-996. Maps 1-996. xvi+498 pp. Koeltz Scientific Books, Königstein.
- JANSSEN, T. & BREMER K. 2004. The age of major monocot groups inferred from 800+ *rbcL* sequences. *Bot. J. Linn. Soc.* 146: 385-398.
- KIRSCHNER J., REJDALI M. & DRÁBKOVÁ L. 2004. A new *Juncus* of the section of *Tenageia* from Morocco and Egypt. *Preslia* 76: 371-376.
- KOEHNE E. 1903. Lythraceae. In: A. ENGLER (ed.) *Das Pflanzenreich*. IV, 20(17): 1-326.
- KORNHALL P. & BREMER B. 2004. New circumscription of the tribe Limoselleae (Scrophulariaceae) that includes

- the taxa of the tribe Manuleeae. Bot. J. Linn. Soc. 146 (4): 453-467.
- KÜKENTHAL G. 1909. *Cyperaceae-Caricoideae*. In: A. ENGLER (ed.). Das Pflanzenreich. IV, 20(38): 1-824.
- KÜKENTHAL G. 1936. *Cyperaceae – Scirpoideae – Cyperae*. In: A. ENGLER (ed.). Das Pflanzenreich. IV, 20(101): 1-671.
- VON LAMPE M. 1996. Wuchsform, Wuchsrhythmus und Verbreitung der Arten der Zwergbinsengesellschaften. Dissertationes Botanicae 266: 1-351.
- LATAŁOWA M. 1992. Man and vegetation in the pollen diagrams from Wolin Island (NW Poland). Acta Palaeobot. 32(1): 123-249.
- LATAŁOWA M. 1999. Palaeoecological reconstruction of the environmental conditions and economy in early medieval Wolin – against a background of the Holocene history of the landscape. Acta Palaeobot. 39(2):183-271.
- MEAD C., OGILVIE M., JACKSON B., JACKSON J., FULLAGAR P. & OATLEY T. 2007. The atlas of bird migration: tracing the great journeys of the world's birds. 176 pp. The Natural History Museum, London.
- MEUSEL H., JÄGER E., RAUSCHERT S. & WEINERT E. 1978. Vergleichende Chorologie der zentraleuropäischen Flora. II. Text xi+418 pp., Karten pp. 259-421. Gustav Fischer Verlag, Jena.
- MEUSEL H., JÄGER E. & WEINERT E. 1965. Vergleichende Chorologie der zentraleuropäischen Flora. I. Text 583 pp., Karten 258 pp. Gustav Fischer Verlag, Jena.
- OXELMAN B., KORNHALL P., OLMSTEAD R. G. & BREMER B. 2005. Further disintegration of Scrophulariaceae. Taxon 54(2): 411-425.
- PIETSCH W. 1963. Vegetationskundliche Studien über die Zwergbinsen- und Strandlingsgesellschaften in der Nieder- und Oberlausitz. Abh. Ber. Naturkundemus. Görlitz 38, 1-80 pp.
- POPIELA A. 1996. Zbiorowiska z klasy *Isoëto-Nanojuncetea* na terenie Polski Zachodniej. Fragm. Flor. Geobot. Series Polonica 3: 289-310.
- POPIELA A. 1997. Zbiorowiska namułkowe z klasy *Isoëto-Nanojuncetea* Br. Br. et Tx. 1943 w Polsce. Monogr. Bot. 80: 1-59.
- POPIELA A. 1998. Nowe stanowiska gatunków z rodzaju *Elatine* L. w Polsce. Bad. Fizjogr. Polską Zach. Seria B-Botanika 47: 257-264.
- POPIELA A. 1999a. The distribution of character species of the *Isoëto-Nanojuncetea*-class in Poland. Part. II. *Carex bohemica*, *Eleocharis ovata* and *Juncus tenageia*. Fragm. Flor. Geobot. 44(1): 43-48.
- POPIELA A. 1999b. The distribution of character species of the *Isoëto-Nanojuncetea*-class in Poland. Part. III. *Sagina ciliata*, *S. subulata*, *Lythrum hyssopifolium* and *Mentha pulegium*. Fragm. Flor. Geobot. 44(2): 437-443.
- POPIELA A. 2001a. *Elatine alsinastrum*, *E. hexandra*, *E. hydro-piper*, *E. triandra*. *Carex bohemica*, *Cyperus fuscus*, *Eleocharis acicularis*, *E. ovata*, *Juncus capitatus*, *J. tenageia*, *Limosella aquatica*, *Lythrum hyssopifolia*, *Mentha pulegium*, *Peplis portula*. In: A. ZAJĄC & M. ZAJĄC (eds.). Distribution Atlas of Vascular Plants in Poland. Nakładem Pracowni Chorologii Komputerowej Instytutu Botaniki Uniwersytetu Jagiellońskiego, Kraków.
- POPIELA A. 2001b. The distribution of character species of the *Isoëto-Nanojuncetea*-class in Poland. Part. IV. *Limosella aquatica*, *Cyperus fuscus* and *Juncus capitatus*. Polish Botanical Journal 46(2): 155-159.
- POPIELA A. 2004. Phytogeographical aspects of distribution of forest species in the Pomerania region (NW Poland). Bot. Jahr. 125(2): 97-228.
- POPIELA A. 2005. *Isoëto-Nanojuncetea* species and plant communities occurring on their eastern distribution range (Poland). Phytocoenologia 35(2-3): 283-303.
- POPIELA A., PRAJS B. & ŁYSKO A. 2009. New data on distribution of dwarf ephemeral wetland vascular plant species and communities in the western and north-western Poland. Biodiv. Res. Conserv. 15: 41-46.
- ROALSON E. H. & FRIAR E. A. 2000. Infrageneric classification of *Eleocharis* (Cyperaceae) revisited: evidence from the internal transcribed spacer (ITS) region of nuclear ribosomal DNA. Syst. Bot. 25(2): 323-336.
- SCHULTZE-MOTEL W. 1966. *Cyperaceae*. In: Hegi G. Illustrierte Flora von Mitteleuropa 2(3): 178-180. 3 ed. Carl Hanser Verlag, München.
- SMITH A. C. 1979. Flora Vitiensis Nova. 1. Pacific Tropical Botanic Garden, Lawai, Hawaii.
- SVENSON H. K. 1929. Monographic studies in the genus *Eleocharis*. Rhodora 39: 271-272.
- TUCKER G. C. 1986. The genera of *Elatinaceae* in the southeastern United States. Journal of the Arnold Arboretum 67: 471-483.
- Woś A. 1999. Klimat Polski. 303 pp. Wyd. Nauk. PWN, Warszawa.
- ZAJĄC M. 1996. Mountain vascular plants in the Polish Lowlands. Polish Bot. Study 11: 1-92.