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Holocene history of *Cladium mariscus* (L.) Pohl in the Czech Republic. Implications for species population dynamics and palaeoecology

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ABSTRACT. The occurrence of *Cladium mariscus* (L.) Pohl (Cyperaceae), a rare species in the Czech Republic, is often considered a relict of earlier phases of the Holocene. Hitherto its relict status had only been assumed, based on analogies from other European countries. We confirm this assumption to a high degree, based on palaeobotanical finds. We argue that local occurrences of *C. mariscus* in the Czech Republic can be considered as part of an independent meta-population surviving over the entire Holocene, rather than a component of meta-populations stretching from other parts of Europe where the species is more common. In the Czech Republic *Cladium mariscus* has so far been found at 11 modern localities and at 5 fossil sites as macrofossils. Its recent localities are restricted to the last remnants of fen mires in the middle course of the Labe (Elbe) River, whereas the fossil sites occupy a much broader area. Also habitats for the species were more diverse during the past. The ecological strategies of *C. mariscus* are rather similar in the short-term perspective, as well as on a millennial scale. The species is a strong competitor forming in optimal conditions compact and uniform stands. Its clonal populations easily overcome the effect of weak or short-term disturbances such as mowing or burning. Although the occurrence of *C. mariscus* is centred on fens and fen swamps, the plant is not strictly calciphilous; rather it requires dissolved salts suppressing the accessibility of other nutrients. The spread of the species is considerably limited by its inefficient dispersal of fruits and low survival ratio of seedlings. The clear ability of *C. mariscus* to persist in existing localities is in sharp contrast with its difficulties in colonizing new habitats. Moreover, parental populations are rare and poor at present in the Czech Republic – for this reason the species cannot still keep up with the changing patterns of appearance/disappearance of vacant sites suitable for colonization and growth of the species.

KEYWORDS: pollen analysis, plant survival strategies, plant macrofossils, species extinctions, refuges, relic species, wetland palaeoecology, Czech Republic

INTRODUCTION

Great fen sedge, *Cladium mariscus* (L.) Pohl (Cyperaceae) is a rhizomatous and stoloniferous graminoid forming tall and dense stands. It is generally considered as a heliophilous and calciphilous plant of marshy fens (Conway 1942, Oberdorfer 1977, Buczek 2005). With the exception of the arctic zone, the species is distributed over the whole of Europe, but generally it seems to be in full retreat at present (Hegi 1980). In the Czech Republic, since the onset of botanical research in the first half of the 19th century, the species has been already considered as very rare. Now it is listed in the Red Data List of Vascular Plants under "critically threatened taxa" (Holub & Procházka 2000) and its community (*Cladietum marisci* Zobrist 1935) is protected as a Prirority Habitat according to EU Natura 2000 legislation (Šumberová et al. 2001).

This paper aims to contribute to an understanding of the Holocene dynamics of the species using the examples from its occurrence in the Czech Republic. Our palaeo- and actuoecological analyses focus on a study of long-term succession in fen mire habitats, with a special emphasis on plant survival strategies. Until recently, records of fossil occurrences have been almost lacking in the region, with the exception of an indirect reference to data of Rudolph (Anonymous 1925) and a find published by Čulíková (1999). Using data from our (sub)recent population and palaeoecological analyses, we propose some general hypotheses on the long-term dynamics of the species occurring in small-scale, ecologically-extreme habitats. We recognize that such long-term dynamics during the Holocene are somewhat separated from the more short-term perspectives of 'recent' population biology focused on a scale of months to tens of years.

MATERIAL AND METHODS

The paper is mostly based on a palaeoecological investigation of the valley-bottom fen mire Zahájí situated in the lower Ohře River Basin (50°22′43″N, 14°06′57″E; Fig. 1). The pollen and macrofossil record from this site covers about the last 5000 years without any apparent hiatus. The present local climate of the site is relatively warm, dry, and continental (8.3°C mean annual temperature, 496 mm mean annual precipitation), as a result of its low elevation (190 m a.s.l.) and its position under an orographic rain shadow. The site's surroundings have been densely and continuously populated since at least the Neolithic period (according to the regional component in the pollen diagram and to regional large-scale archaeological investigations; Kuna 1998, Pokorný 2005).

The results of palaeoecological analyses of the studied fossil record have given a complex picture of the development of vegetation in the surrounding region, and these data have been published separately (Pokorný 2004, 2005). The present article is devoted solely to the interpretation of the *Cladium mariscus* macrofossil finds at this site, so those interested in questions of the exact absolute dating of the profile, regional vegetation development, chronology of human impact, etc., should consult the above-mentioned articles.

Sediment sampling for pollen, sediment chemistry and macroremains analyses were performed from an open pit (profile depth from 0 to 280 cm) and by a Russian-type chamber-coring device (Jowsey 1966) from 280 cm to the bottom (570 cm).

Samples for pollen analyses were treated by acetolysis. As most sediment contained some mineral particles, the samples were pre-treated with concentrated (35%) cold hydrofluoric acid (HF) for 24 hours (Moore et al. 1991). Extracted microfossils were stained with 0.3% safranine and mounted in a glycerol-water (1:1) mixture. In each sample at least 700 pollen grains were counted. For pollen identification a reference collection and the following keys were used: Beug (2004); Faegri & Iversen (1989); and Moore et al. (1991). Pollen nomenclature follows ALPADABA (Alpine Palynological Data-Base), located at the Institute of Plant Sciences, Bern. According to some published keys (Moore et al. 1991, Beug 2004), *Cladium mariscus* pollen can be distinguished from other Cyperaceae pollen by the presence of a finger-like projection on the pollen grain. According to our observations in reference pollen material, this can also be a feature, unfortunately, of other Cyperaceae pollen grains. We think, therefore, that pollen records themselves cannot be used as a definitive proof of *Cladium mariscus* local fossil presence and that macrofossil finds of the species are necessary for a definite proof of local occurrence of the species.

Chemical analyses were performed in the Czech Geological Institute in Prague (analyst: J. Veselý). Total concentrations of metals were determined by flame atomic absorption spectroscopy (FAAS) or by volumetric titration (Al) after mineralization of homogenized samples with H_2SO_4, HNO_3, and HF (200°C, 2 hours). Total sulphur was determined by the Eschka method (ISO 334 International Standard). Silica concentration was calculated as the difference between 100% and the sum of all measured elements expressed as oxides.

After subsampling for other analyses (pollen, sediment chemistry), the remaining material was used for an investigation of plant macroremains: contiguous 10cm-long samples were cut and the volume of each determined. Macrofossils were extracted by sieving with running water, using sieves of mesh sizes 200 µm, 300 µm and 700 µm. The residue was examined under a dissecting stereomicroscope. For determination of macrofossils, a reference collection of seeds and fruits and a published keys (Kats et al. 1965, Cappers et al. 2006) were used. The plant nomenclature used is according to Flora Europaea (Tutin et al. 1964–1980). The numbers of macrofossil finds were recalculated to a standard sediment volume of 300 ml.

RESULTS

PAST AND PRESENT DISTRIBUTION OF *CLADIUM MARISCUS* IN THE CZECH REPUBLIC

The sites of past and present distribution of *Cladium mariscus* are shown together in Figure 1. They form a closed area that is limited to soft carbonaceous sediments of Mesozoic age in the Central Bohemian Basin at altitudes under 300 m a.s.l. The nearest neighbouring recent localities lie at a distance of some 150–200 km in eastern and southern Germany, Austria and Poland (Benkert et al. 1998, Haeupler et al. 1988, Schönfelder et al. 1990, Zając & Zając 2001, Gałka et al. 2007). The characteristics of individual sites in the Czech Republic and the

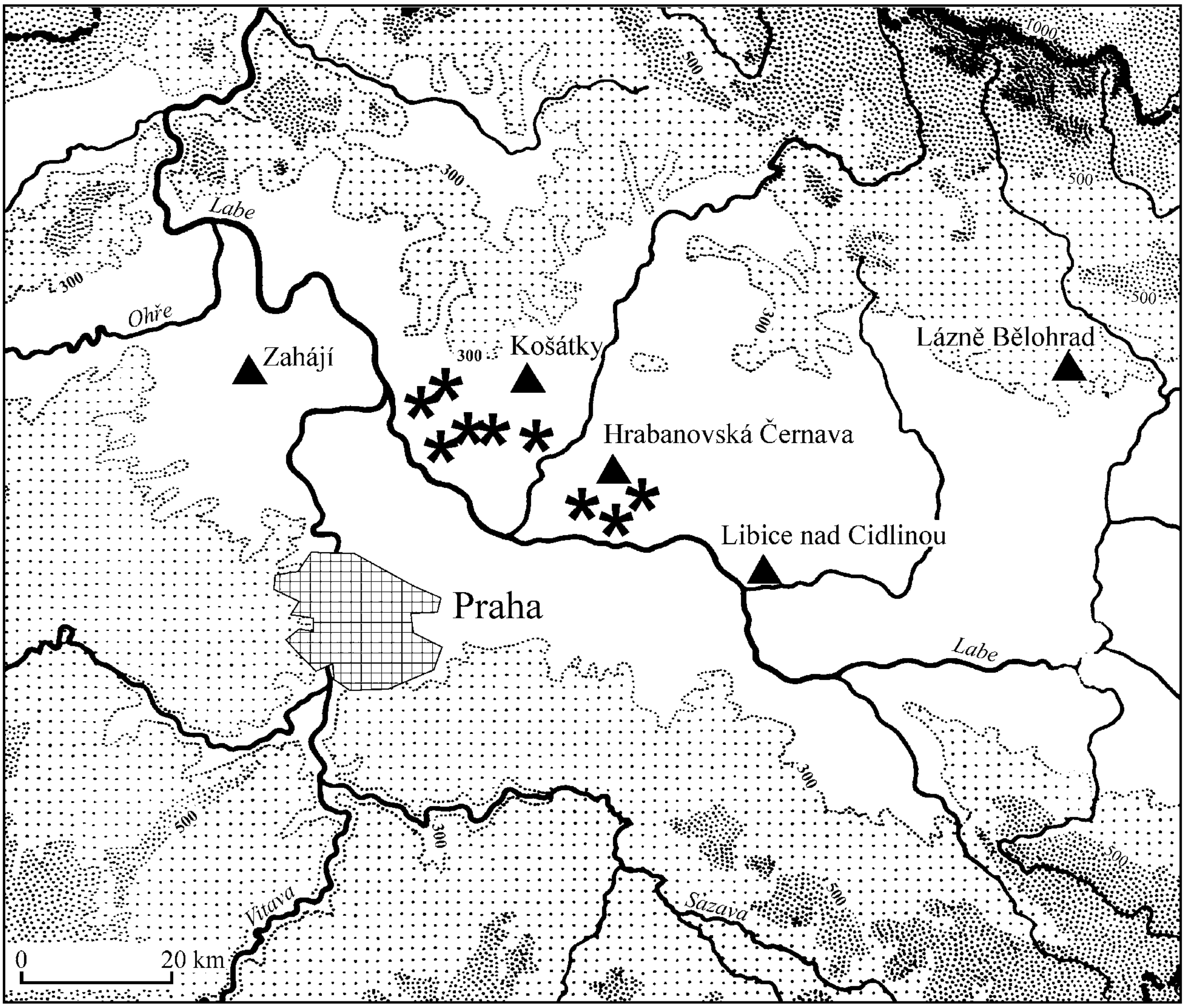

Fig. 1. Recent and historical occurrence (small star) and macrofossil finds (triangle) of *Cladium mariscus* on a map of the Bohemian Basin. Fossil sites are named

chronologies of *C. mariscus* local populations are listed in Appendix 1.

For recent or subrecent localities, we have ascribed the beginning of the occurrence either to the date of the oldest known herbarium specimen or the oldest known literature reference. Only future palaeobotanical research on these sites may alternatively confirm the history of these local populations as being much longer. (If not, such evidence should not be considered as necessarily a negative one – the absence of fossil finds may be the result of complicated patch dynamics within a wetland.)

In addition to current sites extracted from literature, Appendix 1 includes three new findings and two older, less-known findings, needing special notes. An unknown author (Anonymous 1925) referred to some palaeobotanical research by Karl Rudolph, who had performed pollen and macrofossil analyses in fen peat layers near Lázně Bělohrad (eastern Bohemia, see Fig. 1). This reference was only marginal and the find had been almost completely forgotten for more than 70 years. According to the cited reference, the author of the analyses had found fossil fruits of *C. mariscus* in the middle part of the studied sequence where pollen grains of *Picea*, *Quercus*, *Ulmus*, *Tilia*, and *Corylus* were abundant, while pollen of *Fagus* and *Abies* was absent. This note makes possible a tentative biostratigraphic dating to the Middle Holocene. The second published fossil find of *C. mariscus* (although only one single fruit) was made by Čulíková (1999) in the infilling of an Early Medieval ditch moat that formed part of a hill-fort fortification at Libice nad Cidlinou (central Bohemia, see Fig. 1). Here, *Cladium mariscus* grew locally in the waterlogged ditch with rather an intense supply of nutrients from anthropogenic waste.

PALAEOECOLOGICAL RECORD AT ZAHÁJÍ – A KEY EXAMPLE OF PAST DYNAMICS OF *CLADIUM MARISCUS*

The total depth of the studied profile is 570 cm and the basal layers date to the Late Neolithic (ca. 3000 BC). Figure 2 shows the results of pollen and macrofossil analyses. In general, the site and surrounding landscape were rather stable during prehistory. Open reed fen, alder or birch carr, pastures, fields and woodland co-existed in the landscape over all the time recorded, though their proportions changed continuously. Fen species demanding nutrient-poor ground occurred along the whole length of the profile. The human impact was generally continuous in the surrounding landscape but only episodic within the wetland itself. These events included the burning of vegetation followed by disturbance of the ground and deposition of agricultural waste, which is documented by the occurrence of charcoal particles, species of disturbed soil, crops (*Panicum* fruits) and weeds in the profile. Human activities increased considerably in the upper part of the profile (from about 1100 AD). Then massive sedimentation of flood loams occurred and, as a consequence, alluvial forest dominated by *Alnus glutinosa* and *Fraxinus* excelsior expanded, whereas most woody species decreased in the surrounding landscape.

Cladium mariscus occurred in the middle part of the profile between the depths of 200 and 250 cm. This interval roughly corresponds to the period between 0 BC/AD and 1000 AD according to calibrated radiocarbon chronology. According to the biostratigraphic subdivision of the Holocene by Firbas (1949), this covers the period from the end of the sub-Boreal to the beginning of the Younger sub-Atlantic. In archaeological terms, it corresponds to the period from the Roman Iron Age to the start of the High Middle Age. In the samples, *Cladium mariscus* has been documented by numerous subfossil fruits. In total we found 133 fruits, while the layer most rich (210 cm) contained 66 fruits per 260 ml. According to our observations in recent *C. mariscus* stands and according to a comparison with other subfossil finds (M. Hajnalová, pers. comm.), these amounts may indicate a dense stand of the species growing in optimal conditions. According to Hegi (1980), plants are mostly infertile in suboptimal habitats.

Nothing indicates the occurrence of *C. mariscus* at this site before 0 BC/AD. On the other hand, even earlier presence of the species in the mire cannot be ruled out, pointing to the general knowledge of the long-term dynamics of fen mires. In the development of central European lowland fens, gradients of water and peat chemistry, moisture, and stage of succession fluctuate dramatically; all these factors induce a certain stability of a shifting mosaic of small refuges on a scale of hundreds or thousands of years (Sádlo 2000).

The approximate 1000 years when *Cladium mariscus* dominated at Zahájí fen mire represent a distinct period in the site's development. The vegetation of that time we reconstruct as sparse birch (*Betula pubescens* and *B.pendula*) fen carr with a dense herbaceous undergrowth, dominated by *Cladium mariscus* and other tall graminoids such as *Phragmites australis*, *Carex paniculata* and *C. acutiformis*. The onset of the presence of *C. mariscus* at the site can be correlated with:

1) rise in artesian water supply; the emergence of spring water is denoted by the occurrence of *Potamogeton* cf. *Natans;*

2) change in the chemical composition (Fig. 3) of the substrate; the end of alum (hydrated sulphates) sedimentation. The change in local chemistry caused the decline of acidophilus species such as *Sphagnum*.

The decline of *Cladium mariscus* is connected with processes that are characteristic for the formation of the High Medieval cultural landscape:

1) sedimentation of nutrient-rich flood loams, caused by erosion after an extensive deforestation of the surroundings recorded by a decline in arboreal pollen;

2) ruderalization caused by increased management in the vicinity of the site (e.g. deposition of agricultural waste with pollen and macroremains of crops, ruderal species and crop weeds);

3) possibly a direct disturbance denoted by charcoal particles and nitrophilous annuals (*Ranunculus sceleratus* and *Bidens tripartita*) that emerged after trampling of the ground by stock.

We assume that chemical composition of the substrata played a crucial role in the process of the arrival and extinction of the species. Mostly the changes in alum content were of topmost importance.

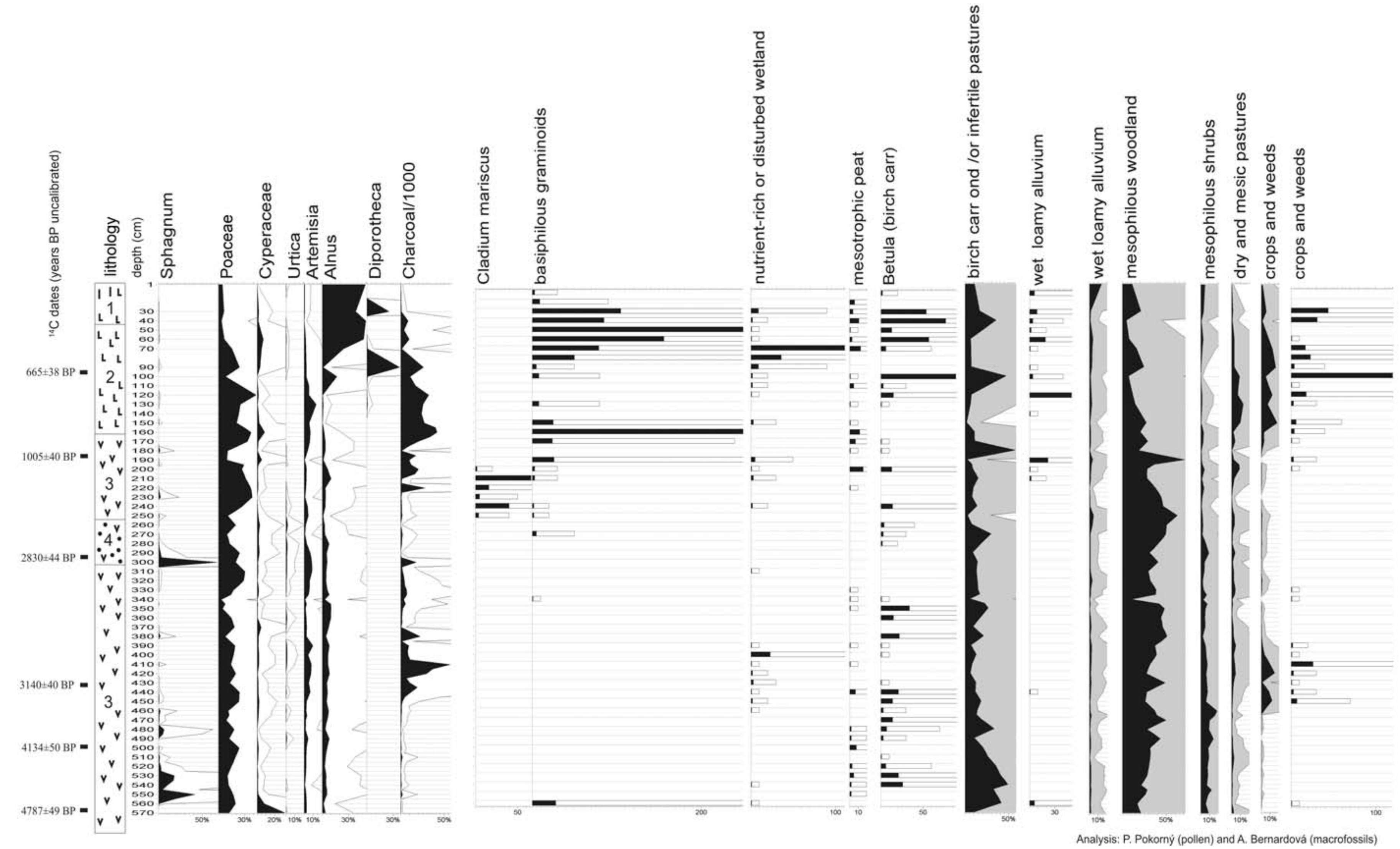

Fig. 2. Zahájí, survey pollen and macrofossil diagram, combining the results of both pollen (curves) and macrofossil (histograms) analyses. For explanation of ecological groups Appendix 2. Results of pollen analysis are expressed as percentages of the total sum that includes pollen of all terrestrial taxa. Results of the analysis of plant macrofossils are expressed in absolute numbers recalculated to a standard sediment volume of 300 ml. Description of the sediment types in a stratigraphic column: **1** – organic clay with wood remains, **2** – clayey peat with wood fragments, **3** – reed fen (*Phragmites*) peat, **4** – alum with *Phragmites* remains

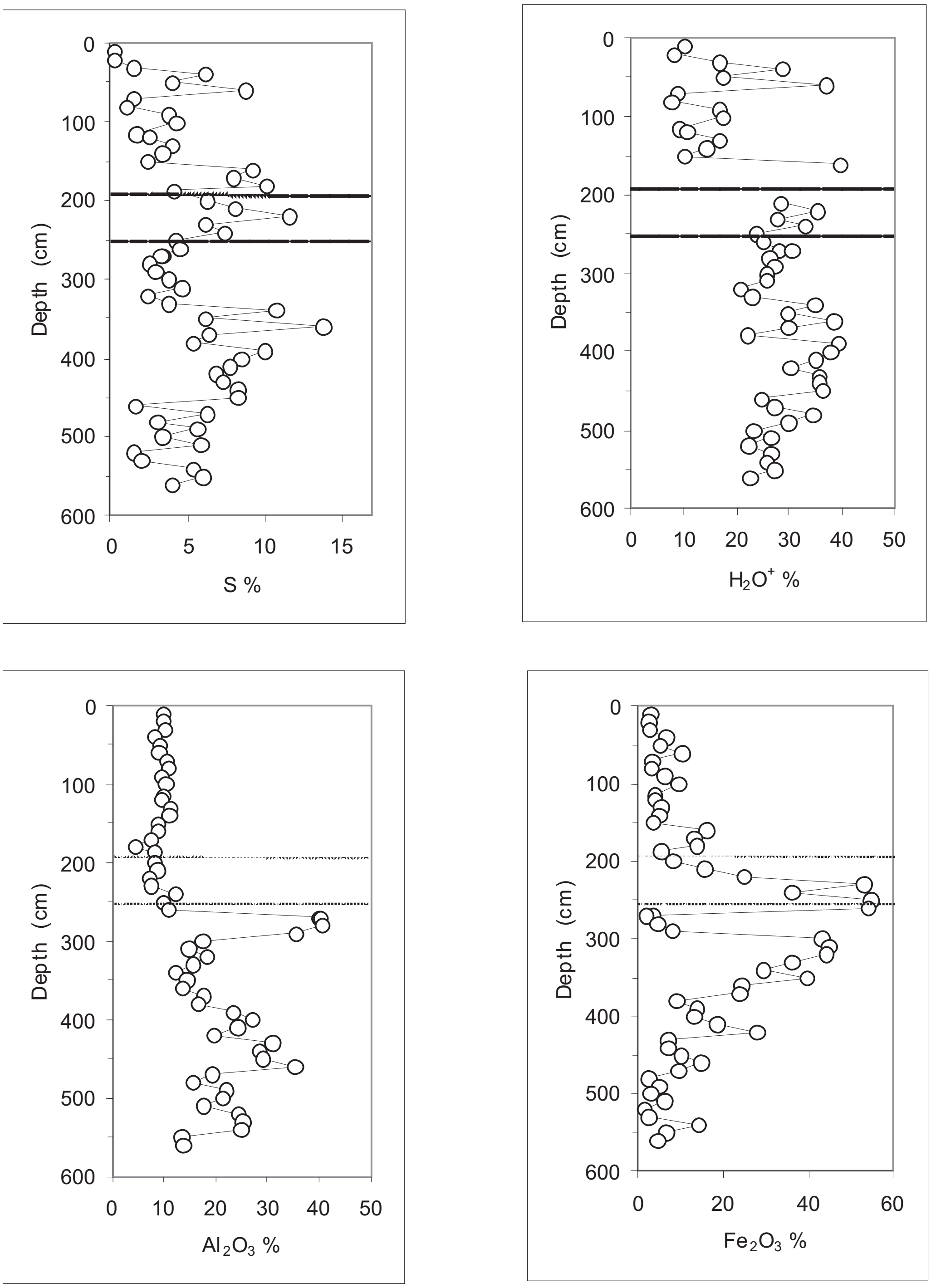

Fig. 3. Zahájí, selected data on sediment chemistry. Horizontal lines delimit a zone where *Cladium mariscus* macrofossils (fruits) are present

DISCUSSION

ALUM FEN: A DISTINCTIVE KIND OF HABITAT?

At the site of Zahájí, there is a prominent co-occurrence of *Cladium mariscus*, and unusual chemical characteristics of the substratum that is formed by organic sediment percolated by alum. An unusual species composition in the vegetation of this alum fen could be expected owing to toxic sulphate salinization. Today, alums as a substantial constituent of fen soil are extremely rare in natural localities of Central Europe though in some parts of the world they are more common (Fitzpatrick et al. 1996).

The mineral matter from the profile studied has the chemical formula app.

$K_2Fe_5(Fe, Al)_4(SO_4)_{12} . 32–36\ H_2O$ and formed about 50% of the matter analysed between 450 and 230 cm. Organic carbon percentages vary between 9 and 22% according to the amount of mineral content. Concentrations of Al_2O_3, Fe_2O_3, total S, and hydrated water are shown in Figure 3 The reaction of the mineral is slightly alkaline though its oxidized products cause acidification.

Alum in this site was probably brought up in solution from a spring of artesian water (the locality is situated on a deep neotectonic dislocation, the consequence of which is the occurrence of the springs). In the wetland, the alum flocculated, especially in the winter at lower temperatures. Alum forms a prominent gel-like layer of whitish colour in the profile.

Alum sulphates are generally toxic for plants, mainly due to the inactivation of nutrients (notably phosphorus) and hypertonization (Welch & Cooke 1999). Disturbance of alum soil causes its oxidation and a strong acidification by sulphuric acid. But the anaerobic reducing conditions maintained by a permanent groundwater stabilize the sulphates so that the soil keeps a more or less neutral pH (Fitzpatrick et al. 1996). In the site under study, acidification was prevented by the permanently damp soil or flooding by shallow and stagnant water.

In Figure 2 selected results of pollen and macrofossil analyses are depicted, showing that the vegetation of alum fen differs only slightly from its antecedent fen vegetation. A more important change to the local vegetation was caused by High Medieval eutrophication after the start of loam sedimentation. Most species of the alum fen are shared with the preceding fen swamp or the following loamy alluvium. The species composition of the alum fen resembles that of present lowland fens; reed (*Phragmites australis*) and basiphilous sedges such as *Carex paniculata* and *C. acutiformis* dominating together with *Cladium mariscus*.

Consequently, the alum fen at the Zahájí site does not show features different from other types of lowland fens in Central Europe. The ecological effect of sulphates on the site is close to that of carbonates in rich fens. Salinization may be indicated by the common occurrence of the halotolerant species *Carex otrubae* and *C. distans*, but these occur also in normal fens. Probably the inhibition of nutrients is what makes alum fen analogous to calcium-rich fens and enables the occurrence of "calciphilous" species such as *Cladium mariscus*. Though the species is generally considered calciphilous in Europe, our find in Zahájí shows that a high amount of calcium carbonate is not necessary for its establishment: Waterlogged organic soil enriched by alum sulphate is an alternative habitat. Thus the species should not be necessarily treated as calciphilous but, more generally, as one demanding salts that inhibit the uptake of other nutrients.

Gałka et al. (2007) attribute the occurrence of *Cladium mariscus* in north Poland more to specific climatic conditions than to a certain chemical composition of the substrata.

LONG-TERM DYNAMICS OF *CLADIUM MARISCUS* AS AN ECOLOGICAL STRATEGY

How to be a relict. In Central European phytogeography, the term "relict" is often used when interpreting a species' presence on extremely rare habitats or niches. The relict status of a given species is usually estimated from a general knowledge of its recent habitat dynamics, the present distribution of the taxon, as well as general knowledge of the Holocene vegetation development in the region under study. As with any historical science, study of the long-term dynamics of flora and vegetation is usually a fragile concept based on a network of indirect evidence. We believe, in general, that most of the estimations of the relict status of species are correct. Nevertheless, there is only a small number of taxa where direct palaeobotanical evidence firmly points to their relict character. In this article, we deal with one such case. In *Cladium mariscus*, the long-term dynamics of survival as a relict includes the following aspects:

Initial spread. Whereas in western and northern Europe postglacial spread of the species is known in some detail (e.g. Conway 1942, Hafsten 1965), data from the Czech Republic area were so far absent. An early onset of the species is confirmed by our recent finding made in Late Glacial layers of the Hrabanovská černava mire (see in Appendix 1).

Habitat selection. The species under study is a specialist (within a specialism–generalism continuum) and its occurrence is restricted to a small number of extreme habitats. Alkaline fens and swamps, which are its most common refuge in Central Europe, had retreated already from the early Holocene and today this is a rare and disappearing kind of habitat (Ellenberg 1982, Šumberová et al. 2001, Hájek & Rybníček 2001). Local soil conditions are generally extreme owing to, for example, flooding by anoxic stagnant water, high proportion of organic matter and minerals (mostly carbonates), and the inhibition of nutrients, especially phosphorus. By contrast the species avoids loamy or mineralized soils with nutrients freely available.

Durability of populations. At Zahájí site, *Cladium mariscus* has occurred permanently for more then a thousand years what, is time enough to be considered a good example of high population temporal stability. At the Košátky site (Appendix 1) it persisted, moreover, for even several thousands of years. At Hrabanovská černava site the species has been found within three periods since the Late Glacial to recent times, indicating the possibility of its continual occurrence for more than 12 000 years. In several (sub)recent localities, probably the same stands have persisted since the beginning of botanical research in the Czech Republic to the present.

At present the species survives mainly in blanket fens of the Czech Basin and is assessed as a relict of the Late Glacial period – considering the fact that Younger Dryas cooling was probably only weak in eastern part of Central Europe (Björck 2007.) These ecosystems are very stable on a scale of hundreds or thousands of years, despite showing considerable patch dynamics at local and short-term scales (Sádlo 2000). Their conservative character can be demonstrated by local endemism (*Pinguicula bohemica*), by the occurrence of species with an exclave distribution as *Calamagrostis stricta*, *Thesium ebracteatum*, and the now extinct *Ostericum palustre* (Culek 1995). Furthermore, *Cladium mariscus* is a vigorous competitor in optimal conditions. This highly dominating species is a typical K-strategist forming compact and uniform stands characterized by a high cover of above-ground biomass and a dense net of underground parts. The stands are well able to withstand some deterioration of conditions, if these are weak or episodic, e.g. burning, mowing or soil drainage (Conway 1942, Oberdorfer 1977, Hegi 1980). The survival of local populations can be endangered only by total and irreversible changes to their habitats.

Spreading of populations. At present-day, clonal growth considerably prevails over generative dissemination in *Cladium mariscus*. In comparison to other tall wetland graminoids, its seed production is low (Conway 1942). The round-shaped fruits are large, smooth and heavy so that they are weakly adapted to efficient long-distance dispersion. Most of them only fall down within the shadowy canopy of grown plants. According to field experiments (Roth et al. 1999), the survival of seedlings and young plants is low. The temporary occurrence of the species lasting for only several years is extremely rare. Despite a detailed floristic exploration of the Czech Republic this case has been noted at four sites only (see Appendix 1); thus indicating that, at least in the modern landscape, the species only colonizes new sites with extreme difficulty.

Generally speaking, *Cladium mariscus* populations have no problem persisting in existing localities – with the exclusion of their total doom – but they are insufficiently capable of occupying new ones. In the Czech Republic, the number of parent populations is low, and thus the species cannot keep up with the changing pattern of potential “vacant” sites as they appear and disappear.

Short-term and long-term strategies. In many species the survival strategy is scale-dependent, so that actuo-ecology gives distinct and different information from that of palaeo-ecology at the Holocene scale. For example, many R-strategists appear and disappear in their habitats, being restricted to early successional stages after some disturbance – but using this strategy they survive permanently for most of the Holocene. However, in the case of the population of *C. mariscus* in the Czech Republic, this scale-dependence appears to be rather low. Our findings on a long-term scale are well in accord with common experiences on the current ecology of the species.

Continuity of the occurrence. Available fossil data about *Cladium mariscus* are as yet insufficient for a detailed knowledge of its Holocene dynamics in the Czech Republic. But the durability of populations in some localities and occurrences in relict fen ecosystems can all be taken as a strong indication of long-term occurrences. It implies that *C. mariscus* occurred during the Holocene in the Czech Republic as an autonomous relict meta-population, rather than as a result of independent invasions from distant meta-populations. This hypothesis should be tested in the future by various methods of molecular genetics.

Causes for *Cladium mariscus* decline. Compared to its prehistoric distribution, the recent range of the species has been contracting. The remaining sites are situated in the centre of its former range, whereas localities belonging to other habitats have disappeared during later phases of the Holocene. According to the mechanisms of its decline, three clusters of sites of *C. mariscus* can be classified:

Fens of uplands – the species has as yet been found at a single site only (Lázně Bělohrad). This type of fens developed away from alkaline fens by their partial acidification during the Holocene. At the afore-mentioned site, this process was probably responsible for the decline of *C. mariscus*, the occurrence of which was restricted to the early developmental phase of the fen. The succession from rich fen to more acidic mire is also often the cause of *C. mariscus* decline in northern Europe too (Hafsten 1965, Salmina 2004).

Lowland valley fens – the species studied has hitherto been found at the sites of Zahájí and Košátecký potok. The decline of *C. mariscus* was caused by sedimentation of flood loams during the High Medieval period. These events were followed by terrestralization and eutrophication of these fens, and attenuation of springs and watercourses. In the last century, periods of agricultural impact (e.g. subsurface artificial drainage, cultivation) were interspersed with periods of abandonment of valley bottoms; this led to a dominance of terrestrial reed stands or nitrophilous woodlands. According to Ložek (2003), these Holocene dynamics seem to have occurred to most streams within the Czech Basin.

Lowland blanket fens – this cluster of lowland sites include flat fluvial plains, filled-in lake basins and palaeomeanders saturated by streams of artesian water containing a high proportion of calcium carbonate. Most findings of *C. mariscus*, including all the contemporary ones, occur in this relict ecosystem. The survival of local populations of *C. mariscus* is mainly caused by the high environmental stability of habitats. The fens endured until the 19th century, whereupon their drainage and subsequent conversion to arable land started.

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APPENDICES

Appendix 1. Recent, historical, and fossil sites of *Cladium mariscus* in the Czech Republic and dating of species occurrence

Recent localities:

1. Mělnická Vrutice, Polabská černava mire. Primary occurrence on alkaline blanket fen. Before ca 1880 AD – present.

2. Všetaty, Všetatská černava mire. Originally primary occurrence on alkaline blanket fen; today, a secondary occurrence at a waterlogged site along a railway. Before ca 1880 AD – present.

3. Ovčáry, originally probably a primary occurrence on alkaline fen on the site of a terrestrialized palaeomeander; today, a secondary occurrence at a waterlogged site along a railway (Sajvera 1952). Before 1950– present.

4. Kozly, a mire east of the village. Primary occurrence, alkaline fen at a terrestrialized palaeomeander (1934 Pohl, PRC; new finding by Novák & Rybka 2003). Before ca 1930 – present.

5. Stará Lysá, Hrabanovská černava mire. Primary occurrence on alkaline fen in the locality of documented fossil occurrence. Before 1884 – present (Polák 1884, PRC, this herbarium specimen represents the first botanical record of the species in the territory of the Czech Republic).

Subrecent localities not documented recently:

6. Mělnická Vrutice, waterlogged meadows near Přeplatil homestead. Probably secondary occurrence not far from primary sites. Population has declined as a result of eutrophication and reforestation. Before ca 1920–1960.

7. Between the villages Čečelice and Všetaty. Small lake after peat extraction (Sádlo & Červinka 2001). Small population that has declined due to unknown reasons. Before ca 1995–2002.

8. Dřísy. Secondary occurrence in waterlogged road ditch, probably connected with primary occurrence on former mire habitats. Single find,

9. Between Milovice and the village Benátská Vrutice. Secondary occurrence around a small lake after peat extraction, probably connected with primary occurrence on former mire habitats. Population declined after eutrophication and cultivation of the site. Before ca 1880–1960 AD.

10. Between the villages Milovice and Vápensko. Secondary occurrence around a small lake after peat extraction. Single find.

11. Between the villages Ostrá and Litol. Secondary occurrence, probably connected with primary one. Single find.

Fossil sites:

12. Lázně Bělohrad (Anonymous 1925), probably Middle Holocene.

13. Libice nad Cidlinou, occurrence in the ditch moat of Early Medieval hillfort (Čulíková 1999).

14. Zahájí near the village Vrbka; recently studied site, a subject of this article ca. 2000–1000 BP. Decline as a result of eutrophication after intensive management introduced at the onset of High Medieval Period.

15. Stará Lysá, Hrabanovská černava mire, recently studied site. Sub-fossil fruits of the species were recently found by L. Petr and determined by P. Pokorný in sediments dated to the Late Glacial and to Middle Holocene.

16. Košátky, old stream meander; recently studied site. Sub-fossil fruits of the species were recently found by R. Kozáková and determined by P. Pokorný in sediments dated to Middle Holocene and to Early Medieval.

Appendix 2. Description of ecological groups used in the survey pollen diagram from Fig. 2

Basiphilous graminoids excluding *Cladium mariscus* – macrofossils

Carex acutiformis, *C. distans*, *C. flacca*, *C. otrubae*, *C. paniculata*, *C.* v*ulpina*, *Juncus* cf. *subnodulosus*

Nutrient-rich or disturbed wetland – macrofossils

Alisma plantago-aquatica, *Bidens* (cf. *aquatica*), *Myosoton aquaticus*, *Persicaria lapathifolia*, *Potamogeton natans*, *Ranunculus sceleratus*, *Schoenoplectus* sp., *Solanum dulcamara*, *Stellaria palustris*, *Stachys palustris*, *Typha* sp.

Mesotrophic fen – macrofossils

Calluna vulgaris, *Carex rostrata / vesicaria*, *Comarum palustre*, *Eriophorum* sp., J*uncus* cf. *bulbosus*, *Peucedanum palustre*, *Sphagnum* sp.

Betula (birch carr) – macrofossils

Betula pendula, *B. pubescens*, *Betula* sp.

Birch carr and/or infertile pastures – pollen

Betula, *Calluna*, *Frangula*, *Salix* (*S. cinerea*)

Mineralized fen or alluvial loam – macrofossils

Ajuga reptans, *Alnus glutinosa*, *Lychnis flos-cuculi*, *Roegneria canina*, *Rubus caesius*, *R. fruticosus* s.l., *Sambucus nigra*, *S. racemosa*, *Scirpus sylvestris*

Mineralized fen or alluvial loam – pollen

Caltha, *Calystegia*, *Chaerophyllum hirsutum*, *Cuscuta europaea*, *Filipendula*, *Fraxinus*, *Heracleum*, *Lychnis*, *Lysimachia vulgaris*, *Lythrum*, *Pimpinella major*, *Rumex acetosa*, *Sambucus nigra*, *Thalictrum*, *Trollius*

Mesophilous woodland – pollen

Abies, *Acer*, *Aconitum*, *Anemone nemorosa*, *Carpinus*, *Daphne*, *Ericaceae*, *Fagus*, *Heder*a, *Lycopodium*, *Mercurialis perennis*, *Picea*, *Pinu*s, *Populus*, *Pteridium*, *Pulmonaria*, *Quercu*s, *Sambucus racemos*a, *Sorbu*s, *Stellaria holostea*, *Taxus*, *Tilia*, *Ulmus*, *Viscum*

Mesophilous shrubs – pollen

Cornus mas, *Corylus*, *Crataegus*, *Euonymus*, *Juniperus*, *Ligustrum*, *Prunus*, *Rhamnus*, *Rosa*, *Rubus*, *Viburnum opulus*

Dry and mesic pastures – pollen

Anthyllis, *Astragalus danicus*, *Centaurea jacea*, *C. scabiosa*, *Cerastium arvense*, *Chelidonium*, Cichoriidae, *Cuscuta epithymum*, *Echium*, *Eryngium*, *Genista*, *Gentianella*, *Gnaphalium*, *Helianthemum*, *Hypericum perforatum*, *Knautia*, *Medicago falcata*, *Odontites*, *Onobrychis*, *Plantago lanceolata*, *P. major*, *P. media*, *Polygonum aviculare*, Pulsatilla, *Rumex acetosella*, *Rhinanthus*, *Saxifraga granulata*-type, *Sedum*, *Serratula*, *Silene vulgaris*, *Thesium*, *Trifolium*,

Crops and weeds – pollen

*Agrostemm*a, *Ambrosia*, *Anthemi*s, *Avena*, *Cannabis sativa*, *Centaurea* cyanus, *Fagopyrum*, *Glaucium*, *Juglans*, *Marrubium*, *Papaver*, *Secale cereale*, *Zea mays*

Crops and weeds – macrofossils

Ajuga chamaepitys, *Atriplex* sp., *Cirsium* cf. *arvense*, *Chenopodium album*, *Ch. hybridum*, *Ch. polyspermum*, *Chenopodium* sp., *Euphorbia helioscopia*, *Fallopia convolvulus*, *Fumaria officinalis*, *Glaucium corniculatum*, *Hordeum vulgare*, *Hyoscyamus niger*, *Neslia paniculata*, *Panicum miliaceum*, *Polygonum aviculare*, *Reseda lutea*, Rumex acetosella, *Sonchus asper*, *Stachys arvensis*, *Stellaria media*