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QUILLWORT (*ISOËTES*), A MYSTERIOUS PLANT FROM THE CZECH REPUBLIC

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Abstract. Quillwort (*Isoëtes)* is a water fern which is a very scarce and critically endangered species in our territory mainly due to the fact that the localities are situated on the southern edge of its distribution. Proof of its occurrence in the past can be gained through palaeobotanical research of sediments which contain their micro- or megaspores. In our territory it has been found only in the Bohemian Forest (Šumava Mts). In addition to the recent plants living in Černé and Plešné Lakes, fossil findings of spores in the former lake of Stará Jímka and in sediments of Prášilské and Čertovo Lakes were recently found.

■ *Isoëtes*, lake sediments, fossil plant, Pleistocene relict, Late Glacial, Holocene, recent

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Introduction

Quillwort (*Isoëtes*) is a water plant which cannot be easily seen in its natural biotope. This is only possible for divers (Text-fig. 1), but only under exceptional circumstances because these are strictly protected plants and lake biotopes. It is a rare sub-boreal-mountainous glacial relict, which was sporadically preserved after the end of the Ice Age only in the Bohemian Forest (Šumava Mts).

Quillworts (*Isoëtes*) previously appeared many million years ago in periodic pools and oligotrophic lakes due to their ability to adapt to this environment, which thus enabled them to survive in the cold environment with lack of light, nutrients and a limited supply of carbon dioxide. On the other hand, they are very sensitive to any changes which occur in their natural habitat (Rørslett and Brettum 1989). Currently they live in our country only in two glacial lakes in the Bohemian Forest which in the last 100 years were exposed to human activity, significant acidification, eutrophication, interventions into the water regime and climate change. The Bohemian Forest quillworts are Pleistocene (glacial) relicts and a critically endangered species of our flora (Procházka 2000). The protection of these plants and the habitat, where they live, is of great importance and therefore it is vital to recognise the ecological demands and changes in the lake surroundings where they have so far occurred. Recently their life cycle and physiological demands have been examined (Husák et al. 2000). The most important result from the investigation of the Czech populations was the finding that juvenile individuals – sporophytes were absent (Lukavský et al. 1997, Husák 2001, Husák and Adamec 1998, Husák et al. 2000). The investigation enabled a comparison of these lake populations and their habitats with those from other countries (i.e. Vöge 1989, 1997a, 1997b, 1999, Szmeja 1994a, 1994b, Gacia and Ballesteros 1994). In comparison with the literature, particularly from the northern lakes, it is obvious that the viability of spores from our quillworts as well as development of new sporophytes is not optimal. The results obtained indicate the need for detailed investigation of the current situation regarding the population in situ and regular long-term monitoring (Čtvrtlíková 2004).

Quillworts (*Isoëtes*) in the Czech territory grow on the bottom of mountainous oligotrophic lakes. The studies of Bohemian Forest populations discovered in the 19th century concentrated on determination of two species in lakes, and population size was estimated only occasionally (Frič and Vávra 1898, Bociąg et al. 2007, Čtvrtlíková et al. 2009). Quillworts belong to sporophytes and thus are low down in the plant classification system (Dostál 1989, Hejný and Slavík 1988, Kubát et al. 2006). They belong in the division

Text-fig. 1. Lake quillwort (*Isoëtes lacustris* L.) in Černé Lake. Photo Bohumír Kráčmar.

(Divisio) Lycopodiophyta – clubmoss plants and therefore are closely related to the clubmoss (*Lycopodium*) and lesser clubmoss (*Selaginella*). Further they fall into the order Isoëtales (quillwort order) and the family Isoëtaceae (quillwort family). They are perennial water plants having 2 types of spores: megaspores (trilete) and microspores (monolete). Worldwide there exists altogether about 75 species of quillwort of which two grow rarely in the Czech Republic: the lake quillwort (*Isoëtes lacustris*) and the spring quillwort (*I. echinospora*) are found only in the Bohemian Forest (Hejný and Slavík 1988, Květena ČSR 1).

The spring quillwort (*Isoëtes echinospora* Durieu) has grown up to the present time in the mountainous oligotrophic Plešné lake (1 090 above sea level) on the sandy or slightly muddy bottom at a depth of up to 2 m, exceptionally at level fall it may reveal itself above the level individually or in community. The nearest spring quillwort to the Czech population is in Schwarzwald. The worldwide distribution ranges from north to north-west Europe, in western and central Europe it occurs dispersedly, to the east it penetrates into central Russia as far as the Ural Mts, sporadically it can also be found in the Upper Altai area and southern Siberia. In North America (including Greenland), on Iceland and in the Far East, the related species *Isoëtes braunii*, *I. maritima, I. asiatic* are found, connected with our spring quillwort as a sub-species or a variety (Hejný et Slavík 1988). The lake quillwort (*Isoëtes lacustris* L.) has so far grown sporadically in the mountainous oligotrophic lake of Černé (1 080 above sea level) on the sandy bottom at a depth of 3-8 m, or in the clean growths. The next nearest locality is in the Polish Giant Mts (Krkonoše Mts) in the glacial lake of Wielki Staw. In the northern part of Poland (the Pomeranian Lakeland) it is a part of the so-called Lobelia Lake (Lang 1994, Milecka 2005, Święta-Musznicka 2006) together with *Lobelia dortmanna* L. and *Littorella uniflora* L.

The total distribution covers an area in the north and north-west Europe; to the east it extends to Karelia and the middle Volga valley; in Central Europe it grows more abundantly in the north (German and Polish Lowlands), otherwise in Central and Western Europe it occurs dispersedly and it is to be sporadically found in Rumania and Bulgaria. It is considered as a separate species, *Isoëtes macrospora,* in Iceland, Greenland and North America. Further it occurs in northern Japan and on the Kurily islands.

Both our species in the Czech Republic are ranked among critically endangered plants (Hejný and Slavík 1988).

One of the oldest taxonomic classifications classifies quillwort as Isoëtinae. Only one recent family of Isoëtinaceae with one genus, *Isoëtes,* has been preserved until now (Trapl 1926). These are water plants found particularly in clean mountainous lakes. This group represents the nearest relatives of the large, fossil plants belonging to the extinct group known as the Lepidophyta. Fossil Isoëtaceae were also described, for example, from the Cretaceous and Tertiary. Since it is not possible to determine if these remains could be classified directly into the genus *Isoëtes*, it is better to use the term *Isoëtines* MÜNST (Trapl 1926).

Novák (1954) classified them into the system of pteridophyte ferns (Pteridophyta) – club-moss family (Lycopodiopsida, having 6 orders). He separated out an order, Isoëtales, and remarked that some authors classify quillwort as in the order Lepidodendrales being the youngest family that has been preserved since the Tertiary until now. According to this author, the quillwort in the recent flora differs distinctly from club-moss and spike-moss, therefore it rightly has its own order.

Isoëtes comprises about 65 species in the World today and is the last representative of the huge members of the family Sigillariaceae from the Carboniferous, representing the final link in the series of forms characterized by an increasing reduction in the plants' proportions.

Černohorský (1963) classified quillworts into the order Lepidodendrales, which contains mostly extinct tree-like types growing in the Devonian, Carboniferous and Permian (belonging to the families of Sigillariaceae and Lepidodendraceae). The quillwort family (Isoëtaceae) includes so far only one living genus, *Isoëtes*. Quillwort-like leaves form a rich rosette which are mostly fertile sporophyles. The outer leaves contain female sporangia (macrosporangium), and the internal male sporangia (microsporangium). They probably developed from Mesozoic types (Pleuromeiaceae).

In the taxonomic and paleontological literature it is possible to read that quillwort ancestors existed before the Quaternary. In recent and Quaternary research we term these plants as Pleistocene or glacial relicts because the most recent information comes from Pleistocene and Holocene sediments (Čtvrtlíková 2004, Hruška and Břízová 2007, Jankovská 2006, Mentlík et al. 2010, Květena ČSR 1988), which without doubt are direct ancestors of the present living types.

The present quillwort occurs predominantly in the northern colder areas of Scandinavia (Rørslett and Brettum 1989, Vöge 1989, 1997b), the Czech Republic is the southern most boundary of the occurrence of these plants which grow in cold glacial mountainous lakes at altitudes of about 1 000 m above sea level (Břízová and Pazdur 2007).

Methodology

Cores for the pollen analysis

The sampled sediments were 5.10 m (Stará Jímka SJ – the Bohemian Forest, CR) and 0.42 m (Wielki Staw WS – the Giant Mts, Poland) thick. All samples were analysed for pollen content and other microfossils. Sampling intervals were 5 (SJ), 2 and 1 (WS) cm. Pollen analysis strongly suggests that some contamination occurred during coring due to the downward displacement of soft, mostly organic material of mid-Holocene age into the mostly mineral Late Glacial sediments (SJ).

The samples were treated using the usual laboratory methods applied for the separation of Quaternary sporomorphs (Erdtman 1954, Faegri et al. 1964, Overbeck 1958). Pollen grains of trees and shrubs (AP – arboreal pollen) and herbs (NAP – non arboreal pollen, AP + NAP =100 %) and spores of ferns and other microfossils (spores of Bryophyta, and selected Fungi, as well as some Rhizopoda, Rotatoria, Tardigrada, etc.) were identified and counted in each sample. Identification was based on keys and pollen atlases (Reille 1992, 1995, 1998) and the pollen reference collection in Czech Geological Survey Prague. The pollen concentration was very high in all samples. Special attention

was paid to coccal green algae. Stratigraphically, the sediments were classified after Firbas (1949, 1952).

Pollen diagrams

The results are presented as a percentage pollen diagram, produced using the PC program POLPAL (Walanus and Nalepka 1999). The percentages are depicted in the pollen diagram in black. In order to show the lower percentage values, the curves of individual taxa are shown by a ten times exaggerated curve in white. The names of many plant taxa have the suffix "type" when the pollen-morphological type may belong to more than one plant taxon (e.g. *Anemone*-type). The pollen diagrams presented here were simplified, not all pollen types mentioned in the text are shown.

Palynological and palaeoalgological study

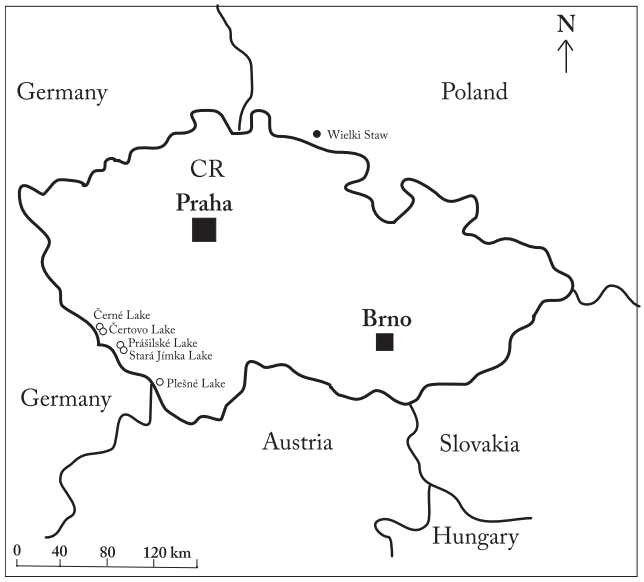
Research of organic sediments (lake and peat) was carried out as part of the investigations and projects of the Czech Geological Survey Prague and provided information for the basic geological mapping and geochemical analyses which was connected with evaluation of the natural environment. Some informative analyses led to new findings of quillwort even in localities where it cannot be found today.

Localities (Text-fig. 2)

The Bohemian Forest (Šumava Mts)

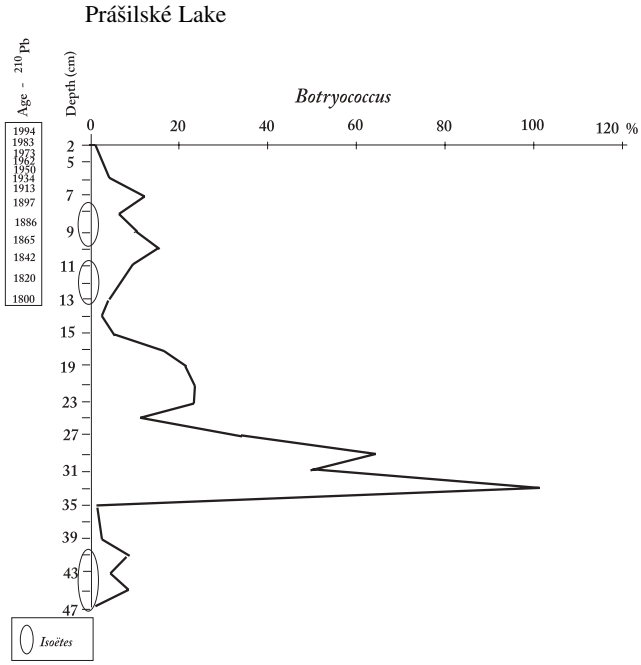
Černé Lake – the analysed lake sediment was 1.15 m thick. Occurrence of quillwort has been recorded there up to the present time. The frequency of spores in the whole profile was very low and decreasing slightly up to the present. Other pollen grains of water and wetland plants accompanied it, and belong to pondweed (*Potamogeton*) and *Butomus*-type. A very noticeable increase was exhibited by green alga of g. *Botryococcus*.

Čertovo Lake – only 8 informative samples from the sampled thickness of 0.80 m were analyzed and a few specimens of quillwort microspores were found. Water plant types were represented by pondweed (*Potamogeton*) and g. *Botryococcus*.



Text-fig. 2. Location map of the Bohemian Forest lakes (CR) and Wielki Staw Lake (Poland).

Prášilské Lake – the analysed lake sediment was 0.47 m thick. Pollen analysis and geochemical analyses were carried out using a new dating method gradually being introduced into the Czech Republic – dating ^{210} Pb (age was determined in about 0.13 m from 0.05-0.125 m, 1800-1994, Text-fig. 3). Green alga, g. *Botryococcus,* also appeared and in association with the presence of quillwort indicates a watery environment.



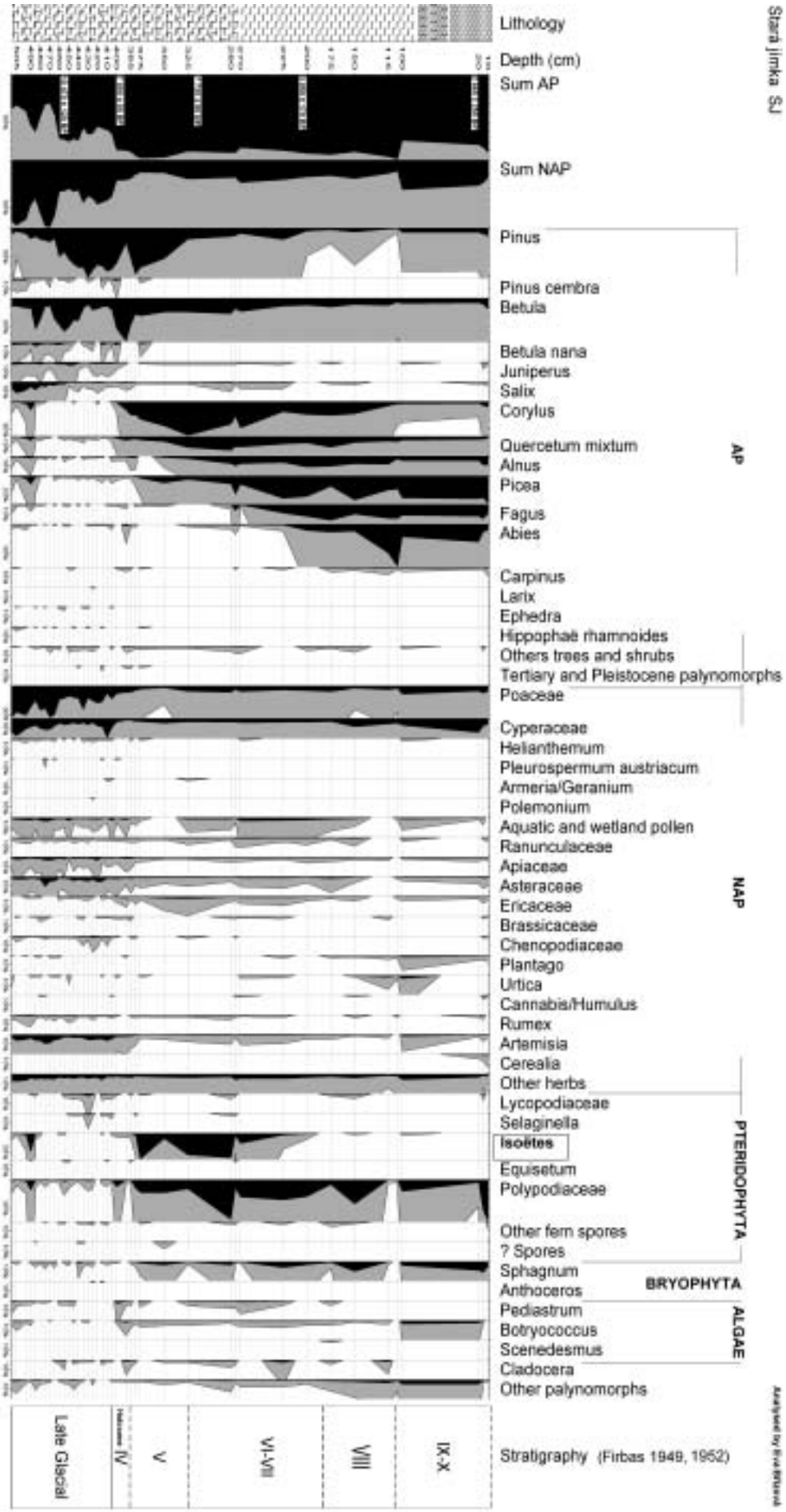
Text-fig. 3. Green alga of genus *Botryococcus* – curve occurrence (quantity %) and findings of quillwort microspores in Prášilské Lake (Analysed by E. Břízová).

Stará Jímka Lake (Text-fig. 4) – the analysed sediment from the silted lake was 5.10 m thick (sampling: by 5 cm). The water and wetland community was richer than in the above-mentioned lakes; pollen grains of duckweed (*Lemna minor*), bladderwort (*Utricularia*), water milfoil (*Myriophyllum*), pondweed (*Potamogeton*), and the sundew (*Drosera*), *Pinguicula* were found. In addition to g. *Botryococcus*, green algae were also represented by a few poorly preserved remains of g. *Pediastrum*. The existence of the lake was also supported by the presence of daphnia (Cladocera), representing the animal kingdom. Quillwort microspores were also confirmed by the discovery of some megaspores of this type (Text-fig. 5).

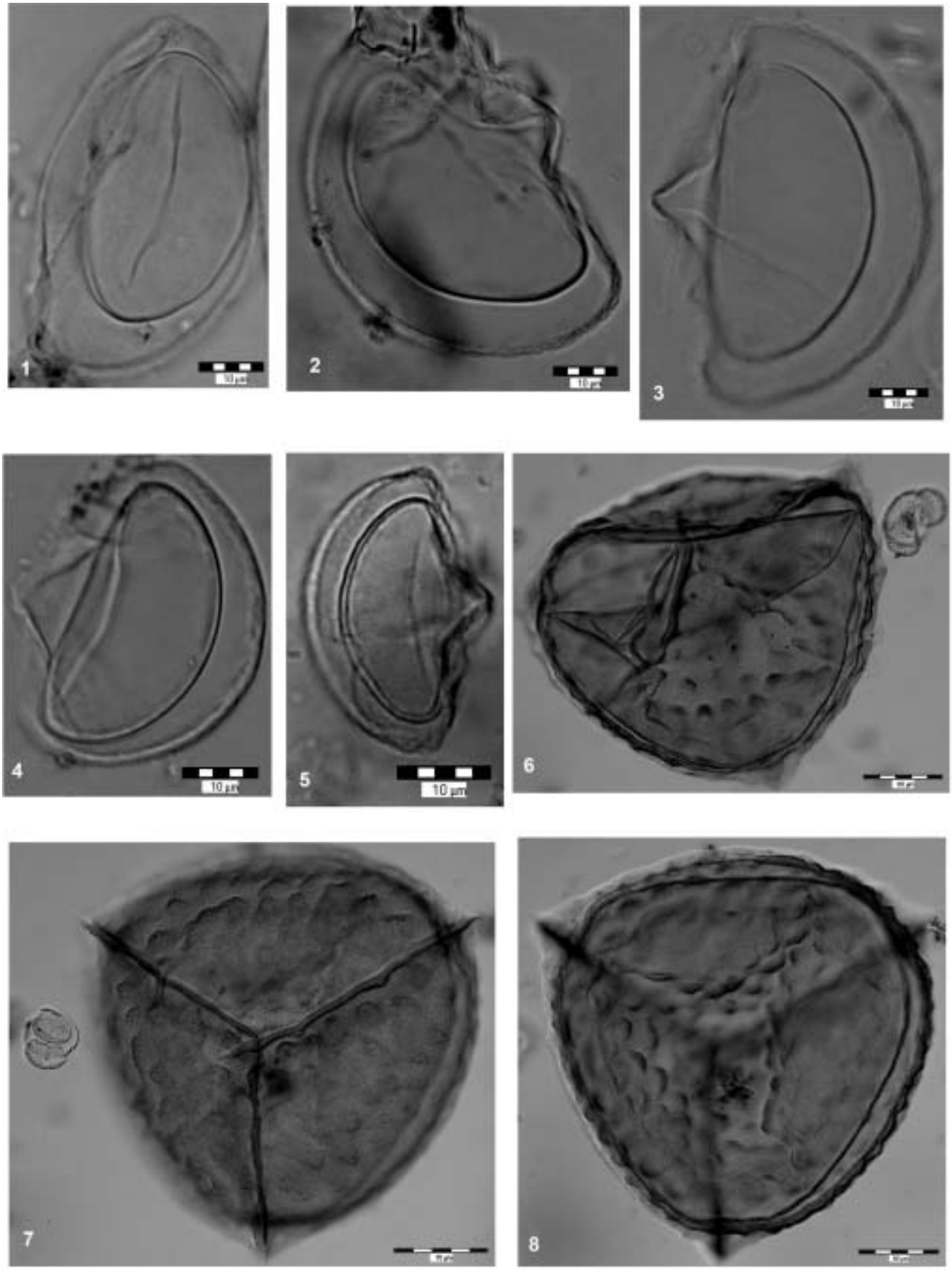
Plešné Lake – the lake sediments were analysed by Jankovská (2006). She confirmed the occurrence of spring quillwort (*Isoëtes echinospora*) accompanied by *Botryococcus pila-neglectus* and *B. braunii*. The frequency of spore findings exhibits a similar character as in sediments from Stará Jímka Lake (see Text-fig. 4).

The Giant Mts (Krkonoše Mts)

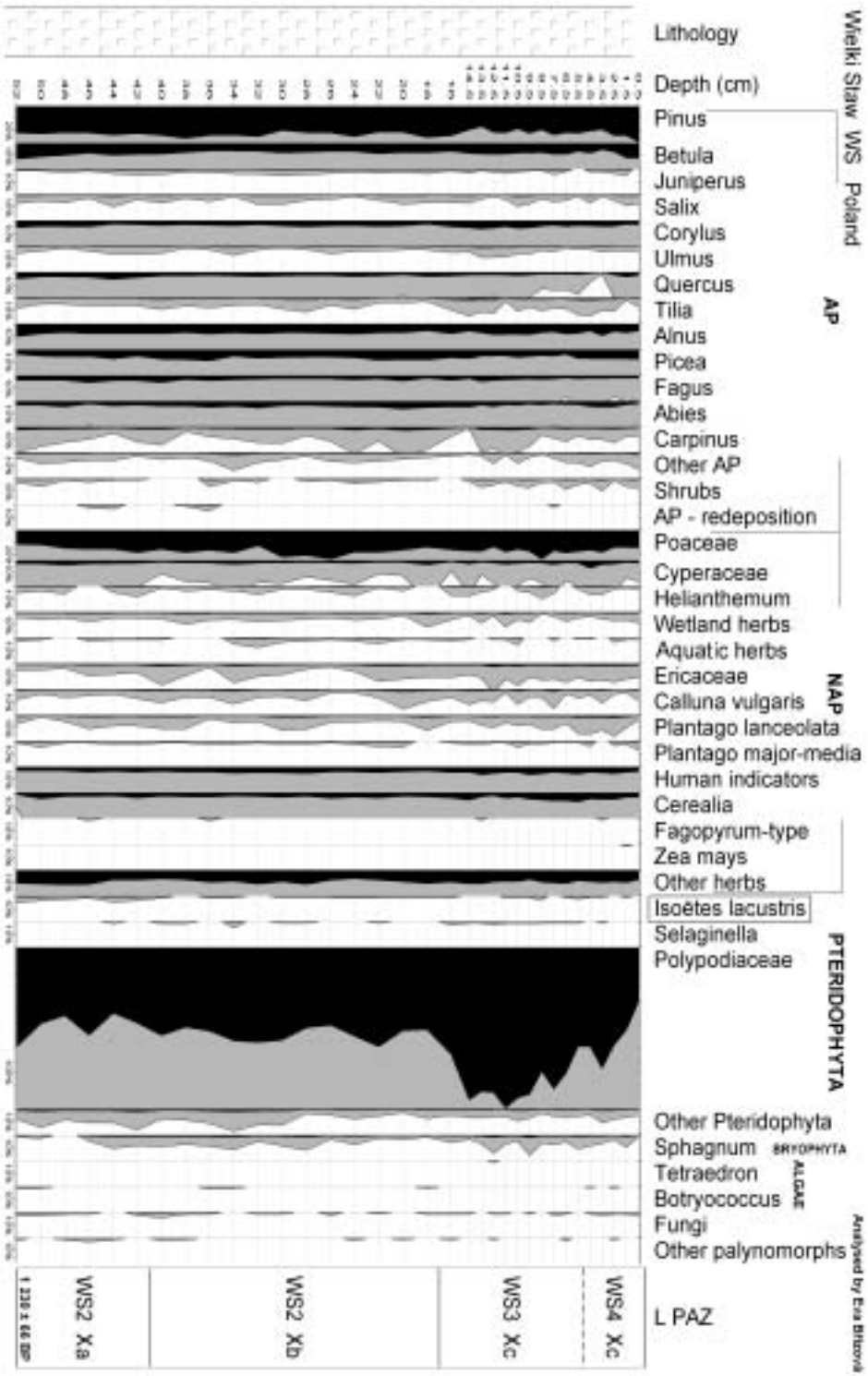
Wielki Staw Lake – the sampled lake sediment used for geochemical and dating analyses (^{210}Pb was 0.52 m thick, Text-fig. 6). The water vegetation was relatively poor; in addition to *Isoëtes lacustris,* g. *Botryococcus* and water types of g. *Sphagnum* also appeared.



Text-fig. 4. Pollen diagram from Stará Jímka Lake in the Bohemian Forest (Analysed by E. Břízová). Radiocarbon dating: Radiocarbon Laboratory Gliwice, Poland.



Text-fig. 5. Micro- and megaspores of quillwort (*Isoëtes*). Microspores: 1 – *Isoëtes lacustris*, WS 33, 2 – 3 *Isoëtes*, SJ 54, 4 – *Isoëtes*, SJ 56, 5 – *Isoëtes*, SJ 75. Megaspores: 6 – 8 *Isoëtes*, SJ 70. Localities WS Wielki Staw, SJ Stará Jímka Lake. Photo E. Břízová.



Text-fig. 6. Pollen diagram from Wielki Staw in the Giant Mts (Krkonoše Mts, Poland, Analysed by E. Břízová). Radiocarbon dating: 1 230 ± 66 BP (After Radiocarbon Laboratory).

Results of palaeobotanical study

Pollen analysis of lake sediments from a number Bohemian Forest lakes and peat bogs, and the Polish lake in the Giant Mts, significantly contributed to the detailed knowledge of quillwort (*Isoëtes*) history due to the finding of new fossil spores. This research formed part of the geological mapping of Šumava National Park (see for example Babůrek et al. 2006, 2008) and also an earlier research project (GA ČR No. 205/96/0933, Hruška et al. 1998). Quite interesting information came to light which will contribute considerably to palaeoecological research on these obscure water plants.

Currently the lake quillwort (*Isoëtes lacustris*) grows in Černé Lake in the Bohemian Forest (Text-figs 1, 5, Břízová 1996, 1999, 2004, 2007a, 2007b, 2008) and the spring quillwort (*I. echinospora*) in Plešné Lake in the Bohemian Forest (Jankovská 2006). The next nearest occurrence of *Isoëtes lacustris* is in Wielki Staw Lake in the Polish Giant Mts

(Břízová 1999, 2007b, Hruška and Břízová 2007). In the past quillworts probably also grew in other Bohemian Forest lakes. The first substantiated findings come from Stará Jímka Lake which does not exist today (Text-fig. 4). During the Holocene (10 250 years BP till now) the lake became silted up (Mentlík et al. 2010). In comparison with lakes which still exist, Černé, Čertovo, Plešné, Prášilské and Laka on our side and the Bavarian lakes of Velké and Malé Javorské and Ráchel, Stará Jímka Lake was probably relatively shallow and thus readily silted up. In its place a raised bog originated. The raised bog is situated in the shadow of the approximately 200 m high, steep, north-eastern slope of Poledník Mount (1 315 m above sea level) which is in close vicinity to Prášilské Lake (Text-fig. 3, 1 500 m to the north) at about 1 115 m above sea level. Both lakes form part of the Jezerní brook valley. Stará Jímka Lake was for a long time assumed to have been a lake but this was not supported by any proof. Only pollen and algae analyses supported this claim with factual evidence (Břízová and Havlíček 2004, Břízová and Mentlík 2006, Břízová and Pazdur 2007, Břízová et al. 2006, Mentlík et al. 2010). The end of Stará Jímka valley itself was dammed in the past with a moderate height levee and a reservoir which emerged there, and probably served for wood transportation. In addition, it was suggested that in the long distant past Stará Jímka Lake and Prášilské Lake represented one big lake, however, agin this assumption has not been proved.

The findings of microspores and megaspores contributed to a possible occurrence of quillwort in the lake sediments (Text-fig. 5). Simultaneously their spores also proved the presence of a water column during sedimentation. Detailed microscopic research on Stará Jímka Lake and other Bohemian Forest lakes confirmed that this plant grew there during the Late Glacial (15 000-10 250 years BP) and the Holocene (10 250 years BP up to the present); it also occurred in some other lakes where microspores were found only accidentally: Čertovo and Prášilské lakes (Břízová unpublished, Text-fig. 3), which might indicate that the distribution of quillwort during the Holocene was wider and they probably colonized the bottoms of numerous local lakes.

Microspores are the objects predominantly examined during pollen analysis; megaspores are much bigger and rarely appear in pollen preparations. Taking into account the small number, their determination in Stará Jímka sediments has not been possible as yet. The great number of microspores found during pollen analysis of Stará Jímka Lake (see Text-fig. 4) and Plešné Lake (Jankovská 2006) provides evidence that the maximum population of quillwort was in the Boreal (9 100-7 700 years BP) and probably upto half of the climatic optimum of the Holocene (Atlantic). The climatic optimum was the period between the years 7 700-4 500 BP when the climate in this territory was very warm and humid, it rained a lot and the vegetation developed significantly. In the Late Glacial (probably interstadial Alleröd) a larger concentration of quillwort microspores appeared, however, Jankovská (2006) presumed that there may have been contamination of sediment during sampling from the upper beds. In view of the fact that it was observed at two localities and the presence of other plants also demonstrated warming of the environment in comparison with the previous and the following period, then quillwort may indeed have grown during that period.

Much later the environmental conditions changed and this change resulted in either the total extinction of these ferns or a significant decrease in their populations. This is verified by the current investigations in Plešné and Černé lakes and in Wielki Staw Lake in the Giant Mts (Text-fig. 6).

Discussion and conclusions

It is well known that in this country today quillwort grows only in two Bohemian Forest lakes: Černé (Břízová unpublished) and Plešné (Jankovská 2006). The Šumava quillworts are Pleistocene (glacial) relicts and critically endangered species of our flora (Moravec 1963, Procházka and Štech 2002). For their protection it is necessary to know their current status and that of their environment. It will also be important for the timely prediction of various impacts on their population. However, an important and specific feature in the active protection of these rare plants will always be their secretive way of life and relative inaccessibility. The study of Bohemian Forest quillwort populations discovered in the 19th century concentrated on the accurate monitoring of both species in the lakes, only sporadically estimates of population size appeared. After the removal of the border zone during the final decade of the last century, the first underwater monitoring of the two quillwort populations occured leading to the discovery of their occurrence and distribution on the bottom of these lakes. (This was however, after the devastation of approximately one thousand plants during shooting of the fairy tale 'The Lake Queen' in 1997, Veselý, pers. comm). About 1 200 specimens of spring quillwort were estimated to inhabit Plešné Lake and about 2-3 thousand lake quillwort plants in Černé Lake.

According to current biostratigraphical research on the quillwort populations in sediments from Plešné Lake (Jankovská 2006), Stará Jímka Lake, Černé Lake, part of Čertovo, Prášilské and Wielki Staw lakes, it may be stated that these plants exhibited their greatest expansion in population size during a period of relatively high temperatures and humidity. This occured in the Boreal (IV, 9 100-7 700 years BP) and in the first half of the climatic optimum of the Holocene, in the Atlantic (VI, VII, 7 700-5 100/4 500 BP) and probably in an interstadial part of the Late Glacial (?Alleröd, III, 11 800-10 700 BP), as it is clearly demonstrated in the pollen diagrams from Plešné Lake (see Jankovská 2006) and Stará Jímka Lake. Substantially fewer specimens or only sporadic occurences were recorded in the other localities (Čertovo, Prášilské lakes, Wielki Staw Lake).

If the plant does not occur in the studied lake at the present time, its accurate determination is then very complicated. It may be done only on the basis of the possible occurrence of megaspores (they could not be precisely determined in Stará Jímka Lake).

All the lakes where quillworts appear or where microspores were found are mountainous glacial lakes situated at about 1 000 m above sea level. The water vegetation is generally poor, limited to only a limited number of forms.

Both species are slow growing, submerged perennial water herbage. The axis of the plants is formed by a secondary thickened tuberous form, from the upper part of which a rosette of quillwort-like trophosporophyles ("leaves") grow and from the lower part, a broad root system. Quillwort is a heterosporic plants; its unisexual sporangia develope on a widespread basis on the trophosporophyles. The main area of distribution of spring quillwort (circumpolar temperate boreal species with oceanic tendency) as well as the limnic quillwort (temperate boreal species) is in Northern Europe; both species grow mostly in oligotrophic to mesotrophic waters of northern lakes. Isolated localities are situated in continental Central Europe. Along the southern boundary of the area (including the Bohemian Forest) they are preserved only in a few oligotrophic mountainous glacial lakes (the Pyrenees, the Alps, the Schwarz Wald, the Bohemian Forest, the Polish Krkonoše Mts, the Pirin; for details see Procházka 2000). In the Czech Republic at present, the limnic quillwort (*Isoëtes lacustris*) occurs only in Černé Lake, and the spring quillwort (*I. echinospora*) only in Plešné Lake, both in the the Bohemian Forest. Both quillwort species from the Bohemian Forest are stress-tolerant macrophytes with adaptations for surviving in water poor in nutrients, carbon and supply of sunlight. However, if the unfavourable environmental conditions come to an end, it becomes apparent that quillwort has an insufficiently flexible growing strategy to adapt to the changes.

Quillwort grows in our territory in the mountainous lakes at the altitude of about 1 000 m above sea level; their biggest expansion was during the course of the Late Glacial and Holocene, obviously in the warmest period of the Holocene (see Text-fig. 4 and pollen diagram – Jankovská 2006). Its expansion was probably caused by a larger influx of organic material into the lake with consequently an increase in the vegetation around it (Husák et al. 2000, Čtvrtlíková 2004, Jankovská 2006). Jankovská (2006) considers the suggestion that the greatest occurrence of quillworts occured in the Late Glacial to be problematic, but quillwort microspores were also found in Stará Jímka Lake (Mentlík et al. 2010 and Text-fig. 4). However, if it is confirmed in other localities, it will probably be regarded as Late Glacial Interstadial Alleröd. Generally, vegetation always developed in the warmest phases of the Late Glacial and consequently the Holocene. On the other hand, quillwort always grew in cold waters of mountainous glacial lakes. In the literature they are characterized as glacial relicts (Čtvrtlíková 2004, Čtvrtlíková et al. 2009), which may also be termed as Pleistocene. As far as Quaternary in the Czech Republic is concerned, there is proof only from the Late Glacial and the Holocene, interglacial sediments are up to now represented only by Stonavské Lake (Břízová 1994), and quillwort did not occur there. We cannot determine if is a thermophilic plant, its principal occurrence is in the north of Europe, and the southern boundary of its extension penetrates into our territory. The situation has not been compared with occurrence in the Paleogene as I presume that it might have been a completely different species.

Considering other plants which may accompany quillwort, there are not many possibilities because it is found in relatively cold water which is poor in nutrients. There may be some green algae, for example, g. *Botryococcus* (e.g. Černé Lake, Prášilské Lake, Plešné Lake) and *Pediastrum* (e.g. Stará Jímka Lake), water types of g. *Sphagnum*, water plants such as pondweeds (*Potamogeton*) in the Wielki Staw Lake. Today they are classified as communities *Isoëtion lacustris* (Květena ČR 1, 1988).

Acknowledgements

Detailed investigations were based on the study which formed part of the the grant project: Palaeolimnological reconstruction of preindustrial acid-base properties of surface waters affected by anthropogenic acidification (GA ČR No. 205/96/0933, Hruška et al. 1998). Research continued within the geological mapping of the territory of the Giant Mts (projects of CGS 6201 and 390001) and the Bohemian Forest, being part of the Regional geology and geological mapping research scheme (MZP000257801, Babůrek et al. 2006, 2008) and the Global climatic changes research (project of CGS 323000).

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