Germination of seed of *Alisma gramineum* and its distribution in the Czech Republic

Klíčení semen druhu *Alisma gramineum* a jeho rozšíření v České republice

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The distribution of *Alisma gramineum* in the Czech Republic was determined using herbarium specimens, data in the literature and the authors' own records. Comparison of records from four periods (before 1900, 1901–1945, 1946–1970, 1971–2001) revealed that the total number of localities has not decreased, but the occurrence changed considerably both in terms of the localities and regions where the species is found. Abundant populations were observed on exposed shores of water reservoirs. It has colonized the Třeboň Basin, S Bohemia, over the last few decades. Effect of water regime, light/darkness regime and temperature on germination and dormancy was studied. *A. gramineum* is adapted to germinate in water and in the dark; germination occurs in late spring, i.e. a period of high temperature. The high variation in the germination response to particular environmental factors may be accounted for the irregular occurrence of *A. gramineum* at certain localities. Best conditions for seed production are shallow water and recently exposed shores of water reservoirs, where plants can grow and set seed within one growing season. The ability to survive in a vegetative stage is more important in deep water, but seed banks in the mud at the bottom of reservoirs is the only way the species can persist when adult plants die.

K e y w o r d s : *Alisma gramineum*, distribution, Czech Republic, dormancy, flooding, germination, life cycle, seedling survival, seeds, temperature

Introduction

Shorelines with strongly fluctuating water levels are highly variable habitats. The germination strategies of wetland plants are of crucial importance in their establishment in such sites (Leck & Brock 2000). Germination reflects adaptation to particular habitat conditions (Schütz 1999, Schütz & Rave 1999, Combroux et al. 2001), and together with seedling establishment, it is a crucial stage in the life cycle of plants. Occasional massive (but irregular) establishment from seed, survival in submerged form and irregular fluctuation in abundance are typical of *Alisma gramineum*. That seedling establishment in this species fluctuates temporally may cause changes in abundance that are associated with changes in water level. Limits to seed production may also limit its distribution.

Of the representatives of this genus occurring in Central Europe, *A. gramineum* Lej. has the most limited distribution and specialized habitat requirements, and is often considered a threatened species. It has a circumboreal distribution (Meusel et al. 1965). Its distribution in Europe is concentrated in Central and Eastern Europe except for the Carpathian Mountains. In the west, it reaches Central and Southern France, in the east a line extending from Ukraine to St. Petersburg – Hultén & Fries 1986). It grows in inland freshwater habitats.

In the Czech Republic, *A. gramineum* is sparsely distributed. It is included in the C2 category (strongly threatened taxa) of the Red List (Holub & Procházka 2000). Compared to other Central-European *Alisma* species (*A. plantago-aquatica*, *A. lanceolatum*), it is found in deeper water (Glück 1905, Hejný 1960). It typically occurs in submerged plant communities, and is a diagnostic species of the suborder *Potamenion lucentis*, i.e. communities inhabiting water depths of 1 to 2 m (Hejný in Moravec et al. 1995). *A. gramineum* has a submerged form with ribbon-like leaves, that produces emergent inflorescences and survives in a vegetative state, or can also flower under water (Glück 1905, Glück & Kirchner 1908). Little is known about seed production by this species, although this mode of reproduction is the only way of population renewal when adult plants die.

The distribution of *A. gramineum* in the Czech Republic is not well known, probably because it fluctuates in abundance, and may be overlooked, namely when submerged. The number of plant specimens in herbarium collections also depends on the activity of collectors. Although at present *A. gramineum* is thought to be declining in abundance, we previously recorded a new center of occurrence and spread in the Třeboň Basin (South Bohemia) in the 1970s. The present paper is aimed at (1) summarizing its distribution in the Czech Republic, based on a thorough field survey, herbarium collections and literature records, (2) evaluating the historical dynamics of its occurrence, and (3) describing its reproductive strategy, which accounts for the irregular records of its presence in some regions.

Material and methods

Distribution

The distribution map for *A. gramineum* was constructed using (i) herbarium collections (BRNU, BRNM, CB, CELM, GM, HR, CHOM, Museum of Jičín, LIM, LIT, MJ, MP, MZ, NJM, Museum of Příbram, OLM, PL, PR, PRC, ROZ, ZMT; abbreviations follow Vozárová & Sutorý 2001), (ii) authors' own collections and field records, (iii) herbarium specimens from private collections and information on localities provided by colleagues, and (iv) reliable data in the literature, including information on localities from Domin's material deposited in the Institute of Botany of the Academy of Sciences of the Czech Republic in Průhonice. To obtain an insight into the historical occurence of the species in particular regions, the distribution was assessed for four periods, i.e. up to the end of the 19th century; 1901–1945; 1946–1970; and 1971–2000.

Germination

Seed germination was tested repeatedly in 1982–1983, 1984–1985 and 1990–1991. As populations of *Alisma gramineum* fluctuate from year to year depending on water level and weather conditions, seed production is irregular and unpredictable. For this reason it was not possible to collect seeds from several localities at the same time and perform all germination tests in the same year. Thus the results may be influenced by different weather conditions during seed ripening and experimental winter stratification (Hroudová & Zákravský 2003). For these reasons, quantitative differences between the results obtained in different years were not evaluated statistically.

Seed used for germination was collected at the following localities: (a) the Pilský fishpond in E Bohemia, alt. 209 m, collected on 2 August 1984; this seed was used for tests performed in 1984–85; (b) the Vlkovský fishpond in S Bohemia, alt. 416 m, collected on 16 July 1990; tested in 1990–1991; (c) the flooded former sand mine near the village of Rakvice in S Moravia, alt. 162 m, collected on 7 July 1982; tested in 1982–1983.

Germination conditions were designed to cover the range of fluctuations in water level observed in natural habitats, i.e. flooded in winter drained in summer; drained in winter flooded in summer; flooded in winter and summer; drained in winter and summer. Flooded and drained treatments were used in stratification and germination tests. In addition, the effects of constant/fluctuating temperature and constant darkness were determined; response to these regimes indicates whether the seeds are able to germinate in deep water or mud, or need drained soil for germination, such as the bottoms of drained fishponds.

Stratification treatment

Two winter stratification treatments were used: (a) in water; seeds in polyethylene bottles full of distilled water were placed at a depth of about 0.3 m in a water reservoir in an experimental garden in Průhonice; (b) in aerobic (terrestrial) conditions; seeds in small nylon bags were put in a container filled with sand and placed in soil at a depth of about 1 cm in an experimental garden. Seeds were stratified from November to March, then stored in a refrigerator until germination tests were carried out. Seeds from both stratification treatments were subjected to all the germination tests except Test 1, where seeds stratified in water were compared with those that were not stratified.

Germination tests

Undamaged fully developed seeds were used in the germination tests. In all experiments, the following treatments were used:

(a) In the water treatment, 25 seeds were put in a 100 ml glass beaker containg 60 ml of distilled water.

(b) Aerobic conditions. Seeds were placed in 5 cm Petri dishes with wet filter paper. Four 5 cm Petri dishes, turned upside down, were placed in one 15 cm Petri dish and the filter paper was kept saturated with water using paper bands (Fig. 1). Each small Petri dish contained 25 seeds, giving a total of 100 seeds per big Petri dish.

Petri dishes were kept in an incubator. Seeds were inspected daily and those with radicles emerged were classed as germinated and removed. Experiments were run for about one month, until no new germination occurred. The germination experiments were performed to test:

1. The effect of different stratification treatments at a constant temperature on seed dormancy. Seeds for this experiment were collected in 1982. Some of the seed was stored dry under laboratory conditions and planted on 12 January 1983 (without prior stratification), and kept at a constant temperature of 20 °C and under a 8/16 hours light/dark regime. The remaining seeds were stratified in water during winter and then planted under the same conditions (constant temperature of 20 °C and a 8/16 hours light/dark regime). This test started on 30 June 1983.

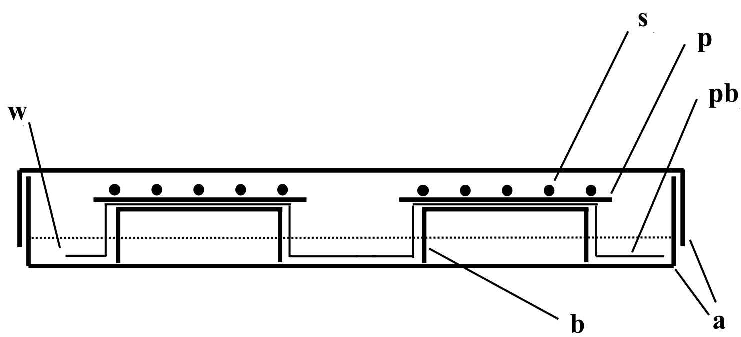

Fig. 1 – Arrangement for germinating seeds under aerobic conditions (side view): a – large Petri dish, b – small Petri dish, p – filter paper, pb – filter paper band, w – water, s – seeds.

2. The effect of different stratification treatments and a fluctuating temperature regime on seed dormancy. The seeds were collected in 1990. As in the first experiment, some of the seed was germinated without stratification, starting on 6 November 1990, but under a photoperiod regime of 8/16 hours and a temperature regime of 25 °C light /10 °C darkness. After 37 days, the temperature regime was changed to constant 25 °C. Other seeds were stratified in water and aerobic conditions during winter and germinated from 22 April 1991 under the same conditions (8/16 hours 25/10 °C, light/darkness).

3. The effect of different stratification treatments and permanent darkness. Seeds sampled in 1984 were stratified in water and aerobic conditions over the winter. From 25 June 1985, this seed was germinated at 25 °C in darkness.

4. The effect of different stratification treatments and a range of constant temperatures. Seeds sampled in 1984 were stratified in water and aerobic conditions over the winter, and from April to June 1985 germinated at 10 °C, 15 °C, 20 °C, 25 °C, 30 °C or 40 °C, and a photoperiod of 8/16 hours light/dark.

All germination experiments were replicated 3 times.

Statistical analysis

Statistical analyses were used to evaluate the differences between stratification treatments when the same germination conditions were used (Test 2a in Table 2) and between germination conditions when the same stratification treatment was used (Test 1, 2b, 3). In Test 4, the differences between stratification treatments when the same germination conditions were used and the differences between conditions of germination when one stratification treatment was used, were evaluated for each constant temperature. Data were analysed using chi-square test of independence using the program SOLO (BMDP Statistical Software 1991).

Results

Present distribution and habitat characteristics

In the Czech Republic, *A. gramineum* mainly occurs in South Bohemian fishpond basins and in river floodplains, especially in S and E Bohemia and S Moravia (Figs 2–5). The species occurs from lowlands to highlands; the highest location is near Lhenice, SW Bohemia, at ca 530 m a.s.l. The distribution range is characterized by warm to mild climate, with a mean annual temperature of 9–10 °C (S Moravia), or 8–9 °C (Bohemian lowlands), and 7–8 °C in the marginal regions of Bohemia (Götz 1966).

Comparing the area of distribution of *A. gramineum* with geological substrates (Götz 1966) shows that the species grows in predominantly mineral rich soils (on marl, cretaceous marly limestone, marly limestone, loess and loess clay, alkaline effusive rocks and their tuffs, various clays, calcareous alluvial sediments). Only in the Třeboň Basin, S Bohemia, does it grow in non-calcareous alluvial sediments.

Typical habitats for *A. gramineum* are shallow fishponds or slightly sloping shores of reservoirs where water level fluctuates from year to year and the bottoms and shores of which are periodically drained. It frequently colonizes the bottoms of fishponds drained in summer (Hadač 1935, Zapletálek 1938, Hadač & Hadač 1948, Deylová 1972). Other typical habitats, mainly in the past, were small streams or sandy silts in small rivers, oxbows, and sometimes also flooded field depressions in meadows or in former sand-pits (Rohlena 1922, Veselý 1942, 1943, 1950, Prokeš & Válek 1946, Smejkal 1950). Most of these habitats were destroyed by canalization of streams and rivers.

History

In the Czech Republic, *Alisma gramineum* was first determined by Čelakovský (1885) as *A. arcuatum* Michalet, which was the name used for the terrestrial form of *A. gramineum*. Čelakovský (1885) also correctly determined some formerly found plants of *Alisma* species, and recorded 8 localities for *A. gramineum* in Bohemia. The species was first found in the Czech Republic by F. M. Opiz, and reported in Pohl (1809). Besides the localities given by Čelakovský (1867, 1873, 1881, 1883, 1885, 1887, 1888), several other specimens of *A. gramineum* from Bohemia and Moravia were found in herbarium collections, but the data on its distribution in the 19th century are sparse (Fig. 2).

During the following period, literature data and herbarium specimens come mainly from the České Budějovice Basin in S Bohemia, and from E Bohemia and S Moravia. The species was also reported from N and Central Moravia (Smejkal 1950) and NW, N and Central Bohemia (Prokeš 1913, Rohlena 1922, Novák 1923, Baudyš 1924, Veselý 1942, 1943) (Fig. 3).

After the Second World War, there are few records (Fig. 4); *A. gramineum* is reported mainly from S Bohemia and S Moravia, by several collectors (Hadač & Hadač 1948, Smejkal 1950, Veselý 1950, Horňanský 1950, Skalický & Toman 1958, Skalický et al. 1961, Krčan & Kopecký 1959, Vaněček 1969).

Since the 1970s, new localities and spread of *A. gramineum* are recorded in the Třeboň Basin (S Bohemia) (Fig. 5). The species was not there prior to 1970s; Hejný (1948) considered *A. gramineum* as distributed in the nearby České Budějovice Basin but not in the Třeboň Basin, and an excellent botanist R. Kurka from Veselí nad Lužnicí did not find it there either. First plants were found by Z. Hroudová in 1971 at the Krajina fishpond near Vlkov nad Lužnicí, then it was collected by R. Kurka in 1977 and by S. Hejný in 1978 at fishponds in the surroundings of the village Lutová, and at other sites in the Třeboň Basin since then. The frequency of findings of this species in other regions also increased at this time (E Bohemia, repeatedly in NW Bohemia, in N and SW Moravia). This indicates that at present, *A. gramineum* is quite common in the Czech Republic.

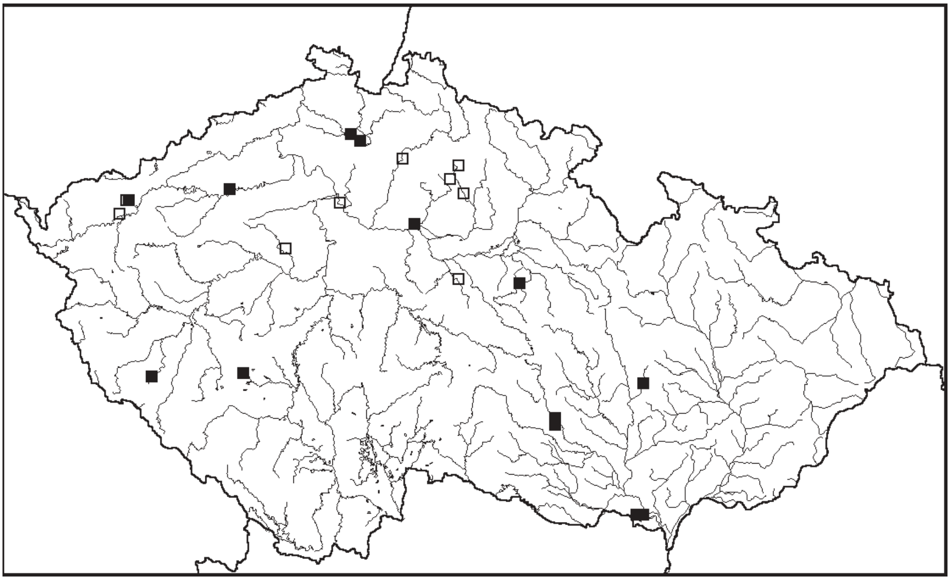

Fig. 2. – The distribution of *Alisma gramineum* in the Czech Republic in the 19th century, based on herbarium specimens (solid squares) and literature data (open squares).

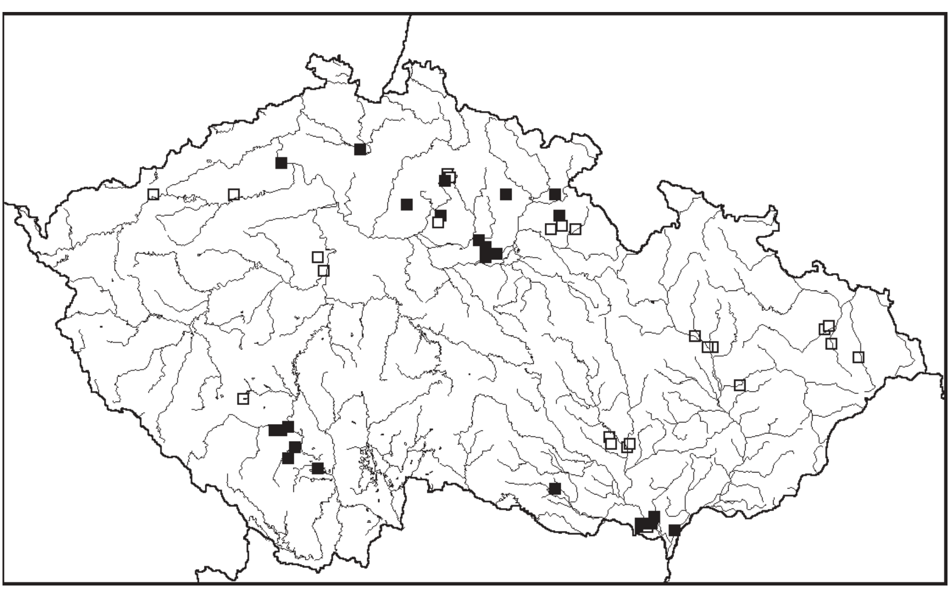

Fig. 3. – The distribution of *Alisma gramineum* in the Czech Republic over the period 1901–1945. Solid squares – herbarium specimens, open squares – literature data.

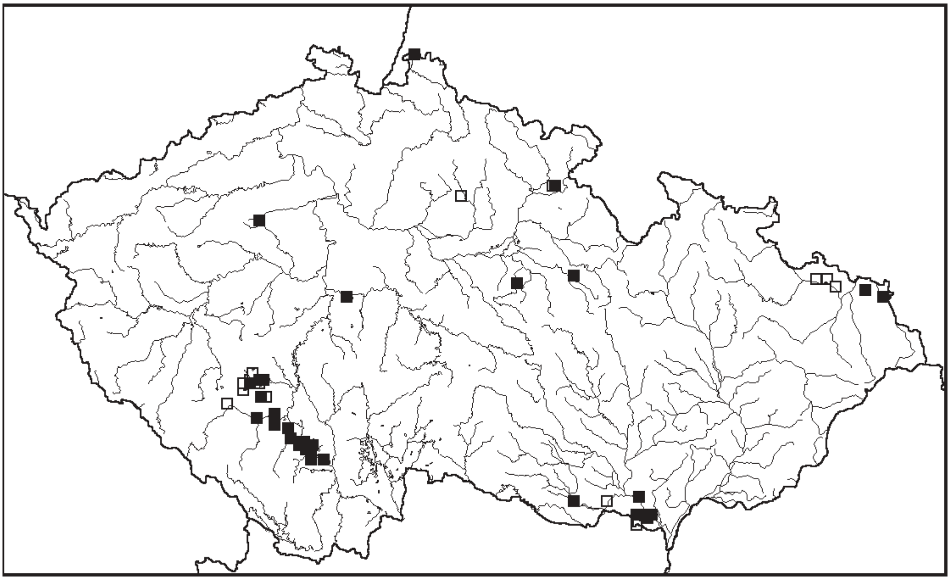

Fig. 4. – The distribution of *Alisma gramineum* in the Czech Republic over the period 1946–1970. Solid squares – herbarium specimens, open squares – literature data.

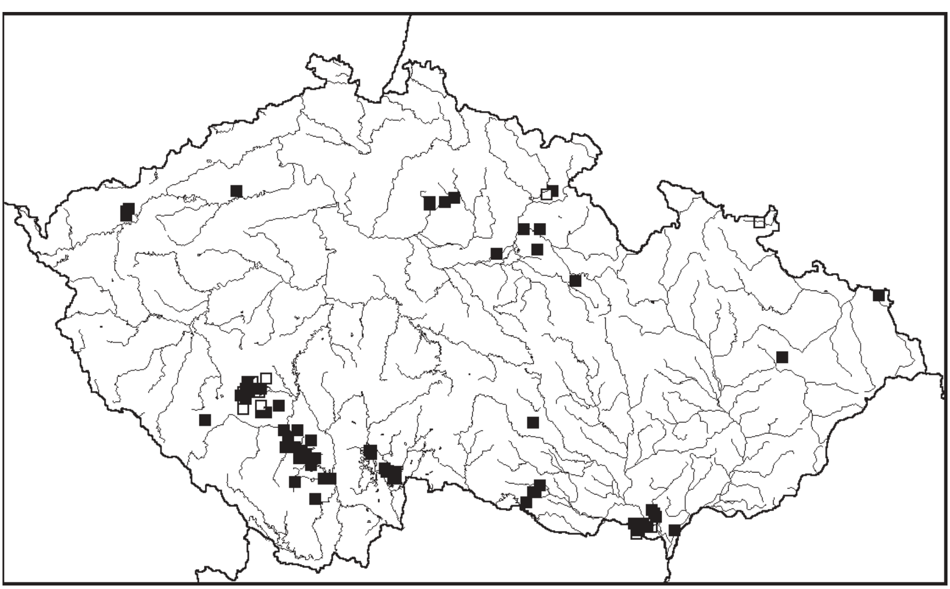

Fig. 5. – The distribution of *Alisma gramineum* in the Czech Republic over the period 1971–2000. Solid squares – herbarium specimens, open squares – literature data.

Seed germination

The percentage germination under various conditions is summarized in Table 1. Fresh seed did not germinate at all in the flooded germination regime and very poorly in aerobic conditions (Test 2a), but a relatively short period of alternating temperatures was sufficient to break the dormancy (Test 2b). In this case, placing in water under an alternating 16/8 hours of 10/25 ºC regime (i.e. with prevailing period of low temperature) might have substituted for cold wet stratification. The change from alternating temperatures to a constant high temperature induced germination, especially when seeds germinated in water (Table 2, Test 2b). In Test 1, a higher percentage of seeds not subjected to cold wet stratification also germinated in water after three months of laboratory storage than of those kept under aerobic conditions (Table 2, Test 1). No seeds germinated during stratification.

Table 1. – The percentage of *Alisma gramineum* seeds that germinated when stratified in various ways (not stratified, stratified in water or in aerobic conditions) and germinated in different conditions (aerobic, flooded). Numbers are means ± S.D. (n = 3). Locality and year of seed collection and regime under which the germination was carried out are shown for each experiment (test). + germination test was carried out after three months of dry storage in the laboratory.

		Stratification treatment					
		Not stratified		Stratified in water		Stratified in aerobic conditions	
Test no.	Seed source and germination regime	Aerobic	Flooded	Aerobic	Flooded	Aerobic	Flooded
1	Rakvice 1982/83, constant 20 °C, light/darkness	32.7±4.9+	70.0±3.3+	90.0±3.6	90.7±4.1	–	–
2a	Vlkovský 1990/91 25/10 °C, light/darkness	1.3±0.5	0	18.7±2.6	20.0±2.1	40.0±0.8	60.7±4.0
2b	dtto, changed to constant 25 °C after 37 days	7.3±1.7	86.7±2.4	–	–	–	–
3	Pilský 1985 constant 25 °C, darkness	–	–	34.0±2.16	76.7±16.7	0	1.7±2.4

Table 2. – Effect of stratification (S0 – without stratification, SW – stratified in water, SA – stratified in aerobic conditions) and germination conditions (f – flooded, a – aerobic conditions) on percentage of *Alisma gramineum* seeds that germinated (see Table 1 for values). Chi-square values and significance levels are given, significant differences are shown in bold.

Test no.	Stratification and germination conditions	Difference tested	chi^2	P
1	S0	a × f	27.4	**< 0.0001**
1	SW	a × f	0.06	0.809
2a	S0	a × f	1.01	0.316
2a	SW	a × f	0.03	0.858
2a	SA	a × f	8.82	**0.0030**
2a	a	SW × SA	10.6	**0.0011**
2a	f	SW × SA	24.8	**< 0.0001**
2b	S0	a × f	128.5	**< 0.0001**
3	SW	a × f	37.4	**< 0.0001**
3	SA	a × f	2.02	0.155
3	a	SW × SA	40.96	**< 0.0001**
3	f	SW × SA	117.69	**< 0.0001**

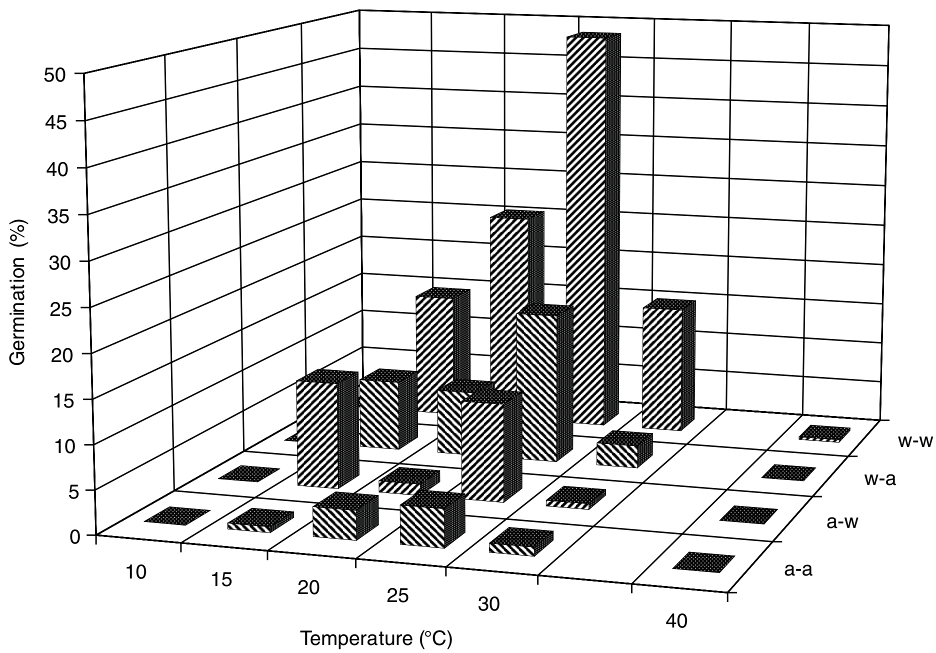

Fig. 6. – The effect of different constant temperatures on the germination of seed of *Alisma gramineum.* Different combinations of one of two modes of stratification and two conditions of germination were used at each temperature. w-w stratification and germination in water, w-a stratification in water, germination on filter paper (aerobic conditions), a-w stratification in aerobic conditions, germination in water, a-a stratification and germination under aerobic conditions.

Table 3. – Effects of stratification and germination conditions on percentage of *Alisma gramineum* seed that germinated at a range of constant temperatures (Test 4). Percentages are means ± S.D, n = 3. Different lower-case letters indicate significant differences in germination in aerobic and flooded conditions within one stratification treatment; different capital letters indicate significant differences in germination after different stratification treatments when germinated at a particular temperature. The differences were tested using chi-square test (df 1, $P < 0.05$).

Temperature (°C)	Stratification treatment			
	Stratified in aerobic conditions Conditions of germination		Stratified in water Conditions of germination	
	Aerobic	Flooded	Aerobic	Flooded
15	0.7±0.5 aA	23.4±7.6 b	8.3±1.3 B	15.0±7.8
20	3.3±1.3	1.3±1.9 A	7.7±2.5 a	25.7±11.3 bB
25	4.3±0.5 A	11.3±2.1 A	17.7±4.1 aB	48.7±6.9 bB
30	1.0±0.8	0.7±0.5 A	2.7±2.5 a	15.3±3.3 bB

Responses to flooding during stratification and germination differed: Seeds of *A. gramineum* are able to germinate when flooded during winter and submerged in the spring (Fig. 6; Table 1, Test 1, 3; Table 3). Temperature seems to be the limiting factor. In other tests, seeds germinated better after wintering in aerobic conditions (Tables 1, 2, Test 2a). Seeds germinated in the dark; in this case, wintering in water enhanced germination and significant differences were found between seeds stratified in water and under aerobic conditions (Tables 1, 2, Test 3). A significant difference was found between seeds stratified in water and germinated in flooded and aerobic conditions (Table 2, Test 3). The positive effect of flooding during stratification, as well as during germination, is increased when seed is germinated in the dark.

Seeds of *A. gramineum* do not need fluctuating day/night temperatures for germination. The optimum temperature for germination is a constant 25 °C. Seeds germinated within the temperature range 15–40 °C, with only a few seeds germinating at 40 °C if they were flooded during stratification and germination (Fig. 6, see also Moravcová et al. 2001). In seeds stratified in aerobic conditions, flooding favoured germination at low temperature (15 °C) (Table 3). After stratification in water, flooding had a significant positive effect on germination at 20 °C, 25 °C and 30 °C (Table 3). When comparing the effect of stratification in the different germination treatments (Table 3) flooding positively affected germination in the majority of cases. However, the percentage germination in the different tests done under similar conditions varied considerably. It can be concluded that flooding had a positive effect on germination, be it applied during stratification or in the course of germination, and its effect was increased when combined with the effect of temperature (Fig. 6).

Discussion

Distribution in the Czech Republic

The review of the distribution of *Alisma gramineum* in the Czech Republic gives and indication of the temporal trends in its occurrence. Populations fluctuate in time; the species was collected repeatedly for two to several years in some localities and then disappeared [e.g. Všepadelský (= Shepadler) fishpond; Čelakovský 1885 PR, 1886 PR, 1887 PR, Roubal 1900 PR], while in other localities, it persisted for a long period [e.g. Velký (= Hirschberger) fishpond near the town of Doksy; Lorinser s.d. PR in Čelakovský 1867, C. Mell ca.1910 PR, Mikuláš 1929 in Domin's material]. In some cases, *A. gramineum* is found again in a locality after a very long period of absence (e.g. Černý fishpond near the town of Ostrov n. Ohří; Ortmann 1820 PRC, Reisz 1840 PR, Hroudová 1991).

Populations also fluctuate in space. There are some centres of occurrence where *A. gramineum* has been present for a long period and is still present, although in particular localities in the same region it disappeared temporarily or was not found for a long time. This holds for the following regions: Blatná district in S Bohemia, the surroundings of the town Ostrov nad Ohří in NW Bohemia, Jičín district in NE Bohemia, and Lednice district in S Moravia.

Alisma gramineum is able to spread to suitable new habitats at new localities. In 1979, dense stands of this species developed along the shoreline of the newly constructed dam reservoir Rozkoš in E Bohemia (Krahulec 1989), although not previously reported from this site. The source was possibly the population at Počanka (Řemínek) near Doubravice (Krčan & Kopecký 1959).

The new occurrence of *A. gramineum* in the Třeboň Basin is not expansive, although the species is found occassionally at various fishponds, and the number of localities in this region is still increasing. Seeds may be spread by water birds or by fishpond management, but this has not changed over the years. Perhaps the increasing eutrophication of fishponds in this region with mineral-poor soils has favoured the establishment of seedlings of *A. gramineum*.

When comparing the past with the present distribution (Figs 2–5), a decrease in the number of localities is not detected. At present, *A. gramineum* is quite common in the Czech Republic, compared to neighbouring countries. In Poland it is scattered, concentrated in lakes and valleys of large rivers; altogether 88 localities are known, but there are few recent records (Wayda 1996). In Bavaria (Germany), *A. gramineum* is a rare species, occurring in lowlands and in floodplains of large rivers. More than a half of the localities in this country disappeared before 1945; at present, it is found at 17 localities (Schönfelder & Bresinsky 1990). In E Germany, *A. gramineum* is also rare and occurs mainly in the floodplain of lower Odra river, rarely also along the Labe river, and in lakes; 37 localities are known at present, 13 localities have disappeared (Benkert et al. 1998). In Austria (Oberösterreich region), *A. gramineum* is an extinct species (Strauch et al. 1997).

The number of reported localities may, at least in part, reflect the intensity of floristic research over the last decades, and this must be borne in mind when reconstructing a species historical record based on floristic data (Pyšek 1991, Pyšek & Prach 1993, Pyšek et al. 2003). In the Czech Republic, the eveness of floristic research may be also partly violated by floristic summer schools organized by the Czech (Czechoslovak) Botanical Society, during which a certain region is throroughly investigated in a systematic manner (Hrouda & Pyšek 2000). Nevertheless, the results of the present study indicate that the distribution of *A. gramineum* in the Czech Republic is stable and increasing.

Seed reproduction

Owing to the fluctuating abundance of *A. gramineum* over long periods, seed production is an important factor in population renewal. There is no literature on the amount of seed produced by *A. gramineum* in the Czech republic. Preliminary field observations by the authors, in shallow littoral habitats of the Pilský and Kuchyňka fishponds, and shores of the Rozkoš reservoir, indicate that a single plant produces from tens to thousands of seeds. Seed production is highly variable and depends on habitat conditions. The aquatic form of *A. gramineum* was reported to produce more seed than the terrestrial form (Wayda 1997). Seeds fall around the adult plant. When they fall into water they float for a long time which is faciliated by the air present in intercellular spaces in the seed coat (Björkqvist 1967). Hydrochory may be an important means of dispersal and spread in this species.

Literature on seed dormancy and conditions necessary for germination is ambiguous. Seeds of *A. gramineum* are reported not to require a long period of cold winter stratification (Glück 1905). Recent research, however, indicates that fresh seed will not germinate, and cold wet stratification (up to six months) enhances germination (Moravcová et al. 2001). In our tests, fresh seeds were dormant, but it was relatively easy to break dormancy (cold wet stratification can be substituted for by dry storage in laboratory conditions or by a short period of fluctuating temperatures). Because of the seed dormancy, *A. gramineum* should germinate in spring, which accords with observed time of seedling establishment in natural conditions and cultivation (Hroudová & Zákravský 1998).

Because the germination tests were performed in different years and with seed from different localities (Table 1), variation in seed dormancy might be influenced by genotype and/or environmental conditions during seed maturation (Bewley & Black 1985, Gutterman 1992, Baskin & Baskin 1999). The conditions during maturation and wintering may influence the germination of seed in spring. In *Trapa natans*, physiologically heteromorphic seed may be produced, some of which germinate in the first spring, while others remain dormant and germinate in subsequent years; the proportion of long-dormant seeds is influenced by environmental conditions during maturation and wintering (Cozza et al. 1994). It is likely that seeds of *A. gramineum* are also sensitive to weather conditions during seed maturation and/or during winter, and that physiologically heteromorphic seed may be produced from year to year.

Seeds of different genotypes may also differ in their germination response to environmental conditions. These differences may be due to an interaction between genetic make-up and environment, hence the germination of seeds from different localities may differ and vary from year to year (Baskin & Baskin 1999). The production of seeds with different germinability represents an important ecological advantage, especially in unpredictable conditions (Gutterman 1992). In *A. gramineum*, a high variation in the response to environmental conditions resulting in variation in the number of seeds that germinate may contribute to irregular seedling establishment in natural habitats.

Rather high temperature requirements are responsible for shifting the maximum germination in *A. gramineum* to late spring, when day temperatures reach 20–25 ºC (or even more). Such conditions may occur from late May to June: in the Czech Republic, a mean daily temperature of 15 °C is attained in the altitudinal range of occurrence of *A. gramineum* from 20 May to 5 June (Götz 1966). However, because of heating of soil surfaces and water layers, the microclimate along shoreline may be entirely different from that where temperature is measured for meteorological purposes. The seeds of *A. gramineum* do not require fluctuating day/night temperatures for germination, but it is induced by flooding (see also Moravcová et al. 2001). Both these features are an adaptation to germination under water. The ability to germinate in the dark when flooded allows seeds to germinate under water or in mud where temperature may be a limiting factor. Mass synchronized germination of seeds of *Alisma gramineum* was observed on sand covered by shallow water (less then 5 cm) in an experimental garden, when seeds were frozen in ice during the preceding winter. In a cultivation experiment, spontaneous germination in water decreased at a depth of 35 cm or deeper (Hroudová & Zákravský 1998).

There is no literature on the formation of persistent seed banks in *A. gramineum*, but the results presented here indicate that some of the seeds remain in the soil. Seed banks play an important role in wetlands since high water levels kill emergent plant species and other species intolerant of deep water, and these species can survive only in the seed bank (Thompson 1992). When the water level declines, bare sediment is rapidly colonized from the seed bank. This accords with frequent occurrence of *Alisma gramineum* on exposed fishpond bottoms or in shallow water near the shoreline; the survival of seeds in bottom sediments appears to be the only way plants could reappear after long periods.

Life cycle

Data on the reproductive traits of *A. gramineum* indicate responses that result to persistence or disappearance of its populations (see Fig. 7). Optimum development of plants occurs on moist mud or in shallow water (0 to 40 cm). Seedlings of *Alisma gramineum* also develop best on moist mud of exposed bottoms or in shallow water (8–10 cm according to Glück 1905) and are able to reach maturity in the first growing season. Seedling establishment is suppressed in water depths of 35–90 cm (Hroudová & Zákravský 1998). Low

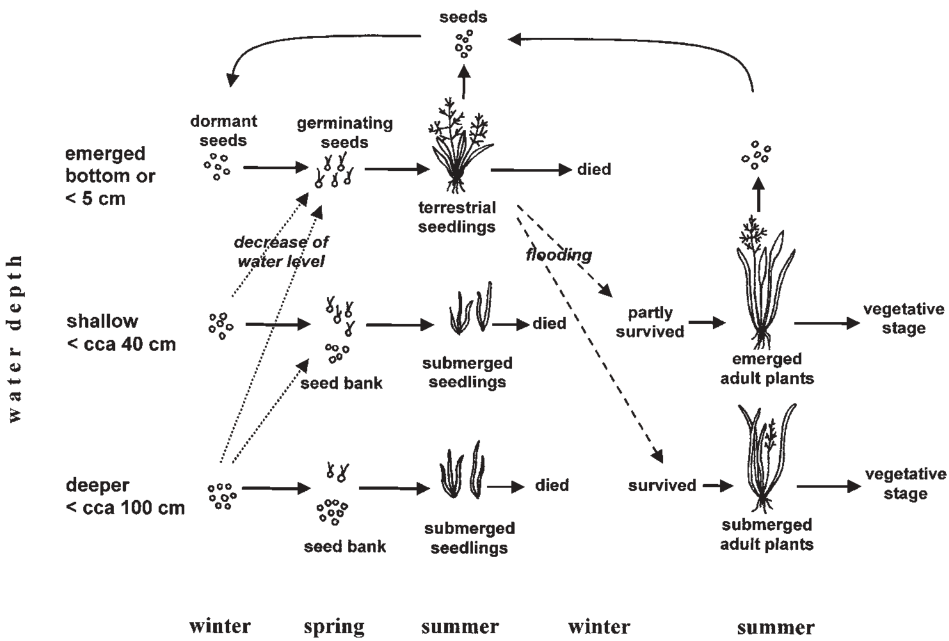

Fig. 7 – Life cycle of *Alisma gramineum* at different water levels, based on germination experiments, experimental cultivation (Hroudová & Zákravský 1998, Moravcová et al. 2001) and field observations.

temperature prevents germination in deep water or mud, where the seedlings die. An early end to the vegetative period is typical of terrestrial plants of this species, especially of seedlings growing in moist mud (Hroudová & Zákravský 1998, Moravcová et al. 2001). Under favourable weather conditions, a small leaf rosette of ribbon-like leaves is produced during September, which enables the plant to continue to photosynthesize and translocate assimilates into underground storage organs (Glück 1905, Hroudová & Zákravský 1998). This contributes to the viability of rhizomes and makes it possible for them to survive over winter.

Winter conditions determine plant survival. Seedlings and plants growing in terrestrial conditions in moist mud usually die during winter, with a few seedlings surviving in mild winter with few frosts (Hroudová & Zákravský 1998). Water depths of 35–90 cm enable vegetative parts (rhizomes) and seedlings to survive over winter. However, the further development of these seedlings is suppressed during the following growing season (Hroudová & Zákravský 1998). Few of the submerged seedlings of *A. gramineum*, which do not produce leaf rosettes at the end of the preceding growing season, survive over winter (Moravcová et al. 2001). This may be due to difference in the underground organs: the rhizome of *A. gramineum* is small and thin in comparison with the tuber-like rhizomes of *A. plantago-aquatica* and *A. lanceolatum* (Glück 1905, Björkqvist 1967).

Irregular occurrence is one of the main features of *A. gramineum*. Temporal fluctuations in its occurrence and colonization of new sites may result from the species' ability to survive under unfavourable conditions, such as long periods of high water levels or complete drying-out of the habitat. *A. gramineum* is well adapted to a fall in water level as it can develop a terrestrial growth form (described as *Alisma arcuatum* Mich.) that is able to complete its whole life cycle growing in mud of exposed bottoms (Fig. 7). In this case, *A. gramineum* behaves as a winter annual (sensu Baskin & Baskin 1999), i.e. survives winter as seed. A special adaptation to terrestrial conditions is the production of a small new leaf rosette at the end of the summer. There is no information on the survival of plants (or rhizomes) of *A. gramineum* on substrates that continue to dry out; the drought threshold and length of dry period necessary to kill plants is unknown. It is likely that rhizomes remain alive in drying mud over summer, even if aboveground parts die. If drainage continues over several years, plants of *A. gramineum* do not re-establish and the soil is colonized by terrestrial species.

A. gramineum responds to flooding by developing ribbon-like leaves and flowers that can produce seed under water (Glück 1905, Glück & Kirchner 1908). The ability to flower decreases with water depth; at depths, below 2 m, plants are sterile, show little leaf growth and have a short vegetative period. A similar response to changes in water level occurs in experiments with seedlings (Hroudová & Zákravský 1998). Plants growing in water behave as perennials, surviving winter season as a rhizome (Fig. 7). The survival in a submerged vegetative form is an important adaptation to periods of high water level. It is unknown how long submerged plants survive; in natural habitats, they can survive submergence for two or three years, while when cultivated in shallow water (< 50 cm), they mostly die after two years (Z. Hroudová, personal observation). Water depth negatively influences plant performance because (i) sprouting is delayed by the cooler bottom layers of water, (ii) more energy is needed to enable leaves to reach the water surface, (iii) assimilation rate of submerged leaves is decreased in turbid water, (iv) flowering is delayed or plants remain sterile, and (v) the mortality of seedlings (if they occur) is high. All these negative features increase with water depth, and a long period of high water may result in a serious weakening and high mortality of plants. Hence for long-term population survival, at least a temporary decrease in water level or exposure of bottom mud is necessary. If high water levels persist for a long period a soil seed bank is the only possible mode of survival. For long-term persistence of the species, periodical recovery of populations by the production of seed, some of which enters the seed bank in the soil, is necessary.

The ability of *A. gramineum* to expand its range when conditions are favourable is another feature determining its irregular occurrence. That plants occur in dense stands is due to the dispersal of seed by water, resulting in masses of seed germinating on recently exposed mud or on mud covered by shallow water, and the ability of seedlings to attain full maturity in the first year of life. These traits are characteristic of R-strategists (sensu Grime 1979). Shores of reservoirs exposed when water level falls or the bottoms of recently drained small fishponds, where competition from other plant species is low, are suitable habitats for seedling establishment of *A. gramineum.* However, maintenance of high water levels in fishponds, canalization of streams, destruction of oxbows and/or their separation from the river prevent seedling establishment and lead to the disappearance of this species in some localities. The ability of *A. gramineum* to survive in human-made habitats (reservoirs, fishponds, flooded sand pits) is important for this species, as these habitats are at present the main localities for persisting (or reappearing) populations.

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Souhrn

Alisma gramineum se v České republice vyskytuje především v nížinách (Polabí, severozápadní Čechy, jižní Morava), zasahuje však i do pahorkatin. Srovnáme-li celkovou četnost výskytu od 19. století, kdy byl tento druh u nás poprvé determinován, s dalšími obdobími (1901–1945, 1946–1970, 1971–2001), nevykazuje klesající tendenci. Nutno ovšem vzít v úvahu různou intenzitu floristického výzkumu v různých obdobích. V Třeboňské pánvi, kde se druh dříve nevyskytoval, se od 70. let minulého století šíří. Vzhledem k tomu, že v ostatních oblastech se vyskytuje převážně na minerálně bohatších podkladech, je možné, že k šíření na Třeboňsku přispěla postupující eutrofizace rybníků. Pro *A. gramineum* je charakteristický nepravidelný výskyt na jednotlivých lokalitách: v některých případech může být submerzní forma přehlížena, jindy však prokazatelně mizí na řadu let. Existují však centra výskytu v některých regionech, kde se v dlouhodobém časovém horizontu (od 19. století) vyskytuje opakovaně a bývá nalézán střídavě na různých lokalitách v závislosti na snížení vodní hladiny. To naznačuje důležitost semenné obnovy populací.

Klíčivost semen *A. gramineum* zvyšuje chladná a vlhká stratifikace. Semena jsou schopna klíčit ve vodě a za určitých podmínek i ve tmě, optimální je stálá teplota 20–25 °C. Charakteristická je velká variabilita jak v množství vyklíčených semen, tak i v reakci na podmínky prostředí. Semena jsou zřejmě citlivá na průběh počasí v jednotlivých letech, jenž ovlivňuje jejich dozrávání i přezimování; jejich reakce může být rovněž ovlivněna genotypem.

V přírodě klíčí druh na jaře v mělké vodě nebo na vlhkém bahně. Na obnaženém dně jsou semenáčky schopny vykvést a produkovat semena během jedné vegetační sezony; za těchto podmínek se *A. gramineum* chová jako jednoletá rostlina, přečkávající zimu pouze semeny. Náhlé vyklíčení ze semen po poklesu vodní hladiny může mít expanzivní charakter. V mělké vodě rostoucí emerzní rostliny představují optimální stadium vývoje; s hloubkou vody se snižuje plodnost rostlin a po určitou dobu jsou schopny přežívat pouze v submerzní formě. Obnova populace po více letech je však zřejmě možná pouze ze semen uložených v podobě semenné banky ve dně.

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Appendix 1. List of localities of *Alisma gramineum* in the Czech Republic. The names of localities are translated from Czech and German.

1. Herbarium specimens examined and localities recorded by authors (Hroudová) and other collaborators (Ducháček, Kurka, Šumberová – only the names are given without a herbarium acronym). Abbreviations of herbaria follow Vozárová & Sutorý (2001).

E x s i c c a t e s : **33. Branžovský hvozd.** SW Bohemia. In the Šepadelský [Všepadelský] fishpond near the village of Chudenice, copious, alt. 475 m (Čelakovský s.d., PRC, BRNU, BRNM) (as *Alisma gramineum* Gmel. f. *angustissimum*), Flora exsiccata Austro-Hungarica, No. 3918; SW Bohemia. In the Šepadelský [Všepadelský] fishpond near the village of Chudenice, copious, alt. 475 m (Čelakovský s.d., PRC, BRNM) (as *Alisma gramineum* Gmel. f. *terrestre*), Flora exsiccata Austro-Hungarica, No. 3917; **36a. Blatensko.** Strakonice district, on emerged moist shore of Velkoláz fishpond W of the village of Láz near the town of Blatná, alt. 500 m (B. Alblová et M. Deyl 1969, BRNU, LIM) (as *Alisma loeselii* Gorski in Eichw.), Plantae Czechoslovacae Exsiccatae, Centuria III, Museum Nationale, Praga, No. 204.

T h e r m o p h y t i c u m : **2a. Žatecké Poohří.** On the shore of the fishpond near the town of Postoloprty (Knaf 1830, PR). – **4a. Lounské středohoří.** Small fishpond in the settlement of Nový Dvůr, by the road between Lenešice and Břvany, ca 6.5 km NW of the town of Louny, alt. 190 m (Hroudová 1991). – **5a. Dolní Poohří.** Pool in the sandy plateau near the crossing from the village of Pistyan [Píšťany] to Lovosice (K. Preis 1937, PRC). – **6. Džbán.** Červený fishpond near the town of Mšec, alt. 410 m (S. Hejný 1946, PR). – **11b. Poděbradské Polabí.** In the „Staré Labe“ oxbow near the town of Nymburk (Velenovský 1895, PRC). – **13a. Rožďalovická tabule.** The village of Charvátce 0.5 km W of the town of Jabkenice, around the fishpond (Dr. J. Wilhelm 1911, PRC); Pilský fishpond ca 4 km N of the town of Rožďalovice, alt. 209 m (Hroudová 1984); Kněžský Dolní fishpond on the S border of the village of Stará Hasina, 1 km N of the village of Rožďalovice, alt. 200 m (Hroudová 1984); the fishpond near the forester’s house near the village of Nouzov, near the village of Dymokury (E. Baudyš 1908, PRC; 1909, PR); Zámecká sádka storage fishpond in the town of Kopidlno, the 5th pond E of the Zámecký fishpond, alt. 220 m (Ducháček 1999, herb. Ducháček, Muzeum Jičín). – **14a. Bydžovská pánev.** Ostruženské fishponds near Jičín (E. Baudyš 1908, PR; PRC); Ostruženský fishpond near the village of Ohaveč near the town of Jičín (E. Baudyš 1911, PR); the fishpond near the spot height of 224 m, near the village of Stará Voda (M. Deyl 1943, PR); the village of Voleč near the town of Pardubice (E. Hadač 1943, MP). – **15a. Jaroměřské Polabí.** In the ditch near the fishpond between the villages of Velký Vřešťov and Bílé Poličany (Ing. V. Kavka 1939, HR). – **15b. Hradecké Polabí.** Hradec Králové: the oxbow near Malšovice suburb (F. Černohous 1978, MP); eastern shore of the Rozkoš dam reservoir near the town of Česká Skalice (J. Krátká 1982, MP); the dam reservoir Rozkoš SE of the town of Česká Skalice, NE shore of the reservoir near the village of Šeřeč, alt. 270 m (Hroudová 1995); Počanka fishpond near the village of Doubravice, near the town of N. Město n. Metují (K. Krčan 1936, 1939, PRC; K. Krčan 1938, 1939, MP; Válek et Krčan 1939, HR; B. Válek 1939, HR; Šourek 1943, BRNM); Počátek [= Počanka] fishpond near the town of Nové Město n. Met. (Válek 1939, MP); southern shore of Počanka fishpond, S of the village of Domkov, alt. 270 m (Šourek 1943, PR, PRC, CB); drained bottom of the fishpond near the village of Doubravice (K. Krčan 1947, BRNM); Broumar fishpond near the town of Opočno, alt. 260 m (Krčan 1937, PR, HR). – **15c. Pardubické Polabí.** Drained bottom of Nadýmač fishpond near the town of Bohdaneč (V. Horák 1933, MP; J. Hadač 1938, MP); the fishpond near „Sádky“ near the town of Bohdaneč (J. Hadač 1935, PRC); Bohdaneč: drained spawning pond between „Zadní zbraň“ and storage ponds (J. Hadač 1935, MP); drained bottom of the fishpond near the road NW of the town of Bohdaneč (opposite the Bohdanečský fishpond), alt. ca 215 m (M. Marek 1980, MP; J. Rydlo1984, ROZ); Smilek fishpond near the village of Horní Ředice (J. Rydlo 1984, ROZ). – **16. Znojemsko-brněnská pahorkatina.** The village of Mikulovice near the town of Znojmo, in muddy bottom of Jezera fishpond, alt. 360 m (J.Horňanský 1943, PRC, BRNM). – **17c. Milovicko-valtická pahorkatina.** Dolní Mušlovský fishpond (Lednické rybníky fishponds) ca 3.5 km ESE of the town of Mikulov, alt. ca. 185 m (D. Šponar 1972, 1973, BRNU; Š. Husák 1973, PR; J. Danihelka 1993, BRNM); Úvalský fishpond (Lednické rybníky fishponds) (Š. Husák 1971, PR). – **18a. Dyjsko-svratecký úval.** The village of Borotice near the town of Znojmo, drainage ditch (Drlík 1950–1953, MZ); the shore of Nesyt fishpond near the village of Sedlec (Dr. Anton Fröhlich 1857, BRNU); saline wetlands on the shore of Nesyt fishpond close to the railway station of Sedlec near the town of Lednice, alt. 180 m (Dostál 1948, PR); NW shore of Nesyt fishpond near the village of Sedlec, alt. 179 m (F. Černoch 1962, BRNM); in Nesyt fishpond (Dr. Anton Fröhlich 1857, BRNU; M. Deyl 1957, PR; S. Hejný 1962, PR; Š. Husák 1971, PR); Lednice: southern shore of Nesyt fishpond, alt. 175 m (J. Zapletálek 1930, BRNU); Lednické rybníky fishponds, E shore of Nesyt fishpond (Kalmus 1864, BRNU; D. Šponar 1972, BRNU); Lednice, emerged bottom near the outlet of Nesyt fishpond, alt. ca. 170 m (Zapletálek 1930, BRNU); Lednické rybníky fishponds, Výtopa fishpond (D. Šponar 1972, BRNU); in wet meadows along Dyje river near the village of Milovice [Mikulovice] near the town of Mikulov (Deyl 1964, PR); Eda fishpond near the village of Hlohovec, 2 km SE of the town of Lednice, alt. 170 m (Hroudová 1972, 1986); Jan fishpond near the village of Hlohovec, 2 km SE of the town of Lednice, alt. 170 m (Hroudová 1972); Bohumír fishpond near the village of Hlohovec, 2 km SE of the town of Lednice, alt. 170 m (Hroudová 1972); Allah fishponds (the upper one) between the towns of Valtice and Lednice (S. Hejný 1962, PR); Allah fishponds between the towns of Valtice and Lednice (S. Hejný 1963, PR); Allach [Allah] fishponds (the middle one) between the towns of Valtice and Lednice (S. Hejný 1962, PR); Lednické rybníky fishponds, Allach [Allah] IV, alt. ca. 177 m (D. Šponar 1972, BRNU; Hroudová 1972); emerged bottom of Střední fishpond near the town of Lednice, alt. 170 m (J. Zapletálek 1931, BRNU); the right shore of Střední fishpond near the town of Lednice, alt. 170 m (J. Zapletálek 1930, BRNU); Mlýnský fishpond near the town of Lednice, along a field way (Rothe 1913, BRNU); Mlýnský fishpond near the town of Lednice (S. Hejný 1962, PR); Mlýnský fishpond near the town of Lednice, in shallow water (ca 1 dm deep) on the shore (Teuber 1913, BRNM); Rakvice, the flooded sand-pit at the SE border of the town, near the road to the town of Podivín, alt. 162 m (Hroudová 1982, 1995); Lednice: the pool near the road from Podivín to Lednice, behind the bridge over Dyje river, alt. 170 m (F. Černoch 1913, BRNM); Podivín, gravel pit about 1250 m NW of the town, alt. 170 m (K. Sutorý 1976, BRNM); in standing water near the town of Podivín (F. Weber 1972, PR); Břeclav: between the villages of Kostice and Lanžhot (J. Podpěra 1921, BRNU); Kostický fishpond near the village of Kostice, alt. 150 m (Š. Husák 1976, PR).

M e s o p h y t i c u m : **24b. Sokolovská pánev.** Emerged bottom of Ovčárenský fishpond near the road SE of the village of Hájek, ca 2.5 km SSW of the town of Ostrov nad Ohří, alt. 410 m (Hroudová 1991); the fishpond within the bend of railway line under the motocross ground area, 1.5 km SW of the town of Ostrov n. Ohří, alt. 450 m (Hroudová 1991); Ostrov n. Ohří, in the fishpond (Ortmann 1820, PRC); Ostrov n. Ohří (Reuss 1840, PR); in Černý fishpond near the town of Ostrov (Reiss s.d., PR); Černý fishpond, ca 0.5 km SW of the town of Ostrov n. Ohří, alt. 410 m (Hroudová 1991, 1994). – **33. Branžovský hvozd.** The Šepadelský [Všepadelský] fishpond near the village of Chudenice, alt. 475 m (Čelakovský1885, PR, PRC, BRNU, BRNM, PL; Čelakovský s.d., PR; L. Čelakovský fil. 1886, PR, PRC, BRNU, PL, MP; L. Čelakovský fil. 1887, PR; J. Roubal 1898, PRC; Roubal 1900, PR; Veselý 1900, PRC); on emerged shore of the Šepadelský [Všepadelský] fishpond near the village of Chudenice, alt. 475 m (as *Alisma arcuatum* Michalet) (Čelakovský 1885, PR); the Šepadelský [Všepadelský] fishpond near the village of Chudenice, alt. 475 m (as *Alisma arcuatum* f. *graminifolia*) (L. Čelakovský fil.1886, PR, PL, MP; 1887, PR). – **35a. Holoubkovské Podbrdsko.** Blatná district: meadows along Jesec brook between the town of Blatná and the village of Řečice (M. Deyl 1972, PR). – **35d. Březnické Podbrdsko.** Kaneček fishpond between the town of Blatná and the village of Paštiky, alt. 430 m (R. Businský 1966, ROZ; B. Deylová 1984, PR); Dražský fishpond near the village of Skaličany (M. Deyl 1973, PR); drained bottom of the Vilímec fishpond N of the village of Buzice (V. Skalický 1957, PR); Hodějovský fishpond at N border of the village of Třebkov, near the road, ca 7 km NW of the town of Písek, alt. 490 m (Hroudová 1981, 1982). – **36a. Blatensko.** Kadovský fishpond near the village of Málkov Lnářský (J. Vaněček 1978, CB); in the fishpond near the village of Lnáře (Čelakovský 1877, PRC); Lípa fishpond near the village of Málkov Lnářský (J. Vaněček 1978, CB); the bottom of drained Velký Kupcový fishpond near the village of Tchořovice (J. Smažík 1980, CB); Kupcovy rybníky fishponds (fishpond No. 10) near the village of Tchořovice (K. Šumberová 2001); Starý Pálenec fishpond between the villages of Tchořovice and Vrbno (V. Skalický 1954, PR); Melec fishpond near the village of Kocelovice (M. Deyl 1972, PR); the fishponds between field biological station and the village of Tchořovice (Velký Pálenec fishpond) (P. Pyšek 1980, ROZ); N shore of Hadí rybník fishpond near the town of Blatná (V. Skalický 1954, PR); NE shore of the greater of Malduchy fishponds near the village of Radomyšl, alt. ca. 465 m (J. Toman 1971, PRC); E shore of the greater of Malduchy fishponds, near the wetland between the greater and the small fishponds (J. Toman 1971, PRC); the village of Radomyšl, NE border of the small of Malduchy fishponds, N of the dam (J.Toman 1971, PRC). – **36b. Horažďovicko.** Malá Strana fishpond near the village of Zbynice, N of the town of Sušice (J. Vaněček 1981, CB). – **37e. Volyňské Předšumaví.** Emerged bottom of drained Křemelný fishpond close to S border of the wood near the road from Strakonice to Sousedovice, alt. ca 421 m (J. Moravec 1950, PR). – **37f. Strakonické vápence.** The village of Osek, Zadní Osecký fishpond S of the Radomyšl railway station (J. Toman 1971, PRC). **37h. Prachatické Předšumaví.** Emerged bottom of Velký Kněžský fishpond near the village of Čichtice, near the village of Strunkovice n. Bl., muddy moist place, alt. ca. 450 m (Hejný 1943, PRC). – **37i. Chvalšinské Předšumaví.** Koubovský fishpond ca 2 km SE of the town of Lhenice (Protected area) (A. Vydrová 1994, ROZ). – **37k. Křemžské hadce.** The fishpond 0.5 km SE of the dam of Křemežský fishpond, near the town of Křemže, alt. 500 m [= Sýkorův fishpond] (M. Lepší 2001, CB); near the shoreline in Sýkorův fishpond S of the settlement of Mříč, near the town of Křemže (A. Vydrová 1995, ROZ). – **38. Budějovická pánev.** Starý fishpond near the village of Jinín near the village of Štěkeň, in deep water (80–130 cm), alt. ca 400 m (S. Hejný 1943, PRC); emerged bottom of the fishpond near the road NW of the village of Cehnice, alt. ca 430–440 m (Moravec 1950, PR); Písecko, Štěkeň (J. Vaněček 1962, CB); Střední Záblatský fishpond near the village of Čejetice, E of the town of Strakonice, alt. 380 m (R. Kurka 1962, CB); in the Šilhavý fishpond near the village of Sudoměř near the village of Štěkeň, in shallow water (20–30 cm), alt. ca. 370 m (S. Hejný 1943, PRC); Miska fishpond near the road between Ražice and Sudoměř, ca 1 km W of the village of Ražice, alt. 390 m (Hroudová 1988); Přední Svinětický fishpond, 1 km N of the village of Svinětice, 4,5 km W of the town of Vodňany, alt. 375 m (Hroudová 1983); emerged bottom of Ražický fishpond near the village of Ražice, alt. ca 370 m (S. Hejný 1943, PRC); Široký fishpond near the farmstead of Dvorce, ca 7 km NW of the town of Vodňany, alt. 420 m (Hroudová 1967, 1988); Rožboud fishpond, 1 km NE of the village of Svinětice, 4 km W of the town of Vodňany, alt. 370 m (Hroudová 1983); in Loviště fishpond near the village of Pražák near the town of Vodňany, alt. 405 m (S. Hejný 1961, PR); Doktorovský fishpond near the town of Vodňany, alt. 395 m (S. Hejný 1943, PRC); Jordanovský fishpond 1 km NW of the town of Vodňany, alt. 395 m (Hroudová 1983); Klokočínský fishpond 3 km NW of the town of Protivín, alt. 370 m (Hroudová 1983); in the drained Újezdecký fishpond near the village of Újezd near the town of Vodňany (S. Hejný 1963, PR); the shore of Nový u Libějovic fishpond near the village of Libějovice (S. Hejný 1964, PR); Kuchyňka fishpond N of the village of Černěves, ca 4 km SSE of the town of Vodňany, alt. 410 m (Hroudová 1981, 1988); Kovanický fishpond near the town of Vodňany (Š. Husák 1971, PR); in Malý Černoháj drained fishpond near the village of Strpí near the village of Radomilice (S. Hejný 1949, PR); in Velký Černoháj fishpond near the village of Strpí near the village of Radomilice (S. Hejný 1961, PR); the border of Černoháj fishpond (M. Lhotská 1962, PR); Dolní Malovický fishpond near the village of Malovice (S. Hejný 1962, PR); Radomilský [Radomilický] fishpond (Š. Husák 1971, PR; Hroudová 1988); Vlhlavský fishpond (S. Hejný 1946, PRC); Koutecký fishpond 7 km ENE of the town of Vodňany, alt. 430 m (Hroudová 1983); Malý [Dolní] fishpond near the village of Novosedly [SW of the village of Dívčice] (S. Hejný 1946, PRC); emerged bottom of Mlýnský fishpond near the village of Sedlec (R. Kurka 1999, CB); Záblatec [Zadní Záblatský] fishpond near the village of Nákří, alt. ca. 400 m (A. Žertová 1962, PR); emerged bottom of Záblatský fishpond near the village of Dubenec near the village of Dívčice (S. Hejný 1962, PR; R. Kurka 1962, CB); Dívčice, the storage fishponds at the E border of the village, ca 10 km ESE of the town of Vodňany, alt. 390 m (Hroudová 1982; J. Rydlo et K. Šumberová 2001, ROZ); the wetland near the village of Pištín (J. Vácha 1935, MP); Bezdrev fishpond ca 3 km W of the town of Hluboká n. Vlt., emerged bottom (B. Jílek 1953, PR; J. Komárek 1953, MZ); the storage fishponds in the village of Čejkovice (Šumberová 2001); České Budějovice, Vrbenské fishponds in the suburb of České Vrbné: Nový Vrbenský fishpond (J. Rydlo 2001, ROZ). – **39. Třeboňská pánev.** Oběšený fishpond near the village of Mláka ca 8 km NE of the town of Třeboň, alt. 445 m (Hroudová 2000); Krajina fishpond 0.5 km S of the village of Vlkov n. Lužnicí, alt. 411 m (Hroudová 1971); the border of the islet in Překvapil fishpond S of the village of Vlkov n. Lužnicí (R. Kurka 1978, CB); in Vlkovský fishpond near the dam, close to the railway station of Vlkov n. Lužnicí, alt. 414 m (Hroudová 1990, 1991); Krásné Pole fishpond NNW of the village of Střîbřec, alt. 440 m (Kurka 1977); Kouškovec fishpond ENE of the village of Střîbřec, alt. 460 m (Kurka 1977); Kovářů Starý (Petrů) fishpond near the village of Mníšek, alt. 470 m (Kurka 1977); Šimků Černá fishpond near the village of Lutová, alt. 445 m (Kurka 1977); Cepáků fishpond 2 km NW of the village of Žíteč, alt. 455 m (Hroudová 1983); Medenice fishpond 1 km NW of the village of Žíteč, 10 km E of the town of Třeboň, alt. 455 m (Hroudová 1983); Pazderňák fishpond at the NE border of the village of Mníšek, alt. 480 m (Kurka 1977); Obecní fishpond SE of the village of Mníšek, alt. 470 m (Kurka 1977); Pazdernický fishpond near the village of Mníšek (Hejný 1978, PR); Blato fishpond near the village of Žíteč, emerged bottom on the place of former duck farm near the dam, alt. 468 m (Hroudová 1981). – **40a. Písecko-hlubocký hřeben.** Hluboká n. Vlt., NE shore of Bezdrev fishpond near the yacht resort, alt. 380 m (B. Jílek 1953, PR). – **41. Střední Povltaví.** Jílové near Prague: the bottom of the „Nebesák“ fishpond near the village of Chleby, alt. ca. 300 m (Medlinová 1946, PRC). – **49. Frýdlantská pahorkatina.** The village of Černousy, flooded field depression on the left side of the road to Boleslav, near the Severočeské dřevařské závody timber industry, alt. ca 210 m (Jehlík 1958, PR). – **52. Ralsko-bezdězská tabule.** Staré Splavy near Jestřebí (Dr. Gustav Lorinser s.d., PR); the shore of Hirschberger fishpond [Máchovo jezero] near Doksy (Dr. Lorinser s.d., PR); Velký fishpond near the town of Doksy [Máchovo jezero] (Dr. C. Mell s.d., PR). – **55e. Markvartická pahorkatina.** Lhotský fishpond near the village of Hlásná Lhota near the town of Jičín (E. Baudyš 1911, PRC, PR); Ostružno near Jičín, the Čeperka, Lhotský and Tureček fishponds near the town of Jičín, alt. 380 m (R. Dvořák 1912, ZMT); the small drained fishpond near the settlement of Pazderna, 0.5 km NW of the village of Liběšice near the town of Kopidlno (D. [Dohnal] 1982, Muzeum Jičín). – **61b. Týništský úval.** The fishpond near the village of Běleč n. Orlicí, near the town of Hradec Králové (J. Krátká 1984, MP). – **62. Litomyšlská pánev.** Dolní Kajzerlík fishpond NW of the village of České Heřmanice (V. Faltys 1969, MP); emerged bottom of the fishpond in the village of Vračovice, alt. 295 m (H. Nováková 1984, ROZ). – **67. Českomoravská vrchovina.** Březina fishpond ca 2 km NNE of the village of Trnava, ca 8 km NE of the town of Třebíč, alt. 495 m (H. Houzarová 1990, ZMT). – **68. Moravské podhůří Vysočiny.** The fishpond near the road 1 km ENE of the village Čížov, E of the town of Vranov n. Dyjí (J. Rydlo 1994, ROZ); Nový fishpond ca 1,6 km NW of the village of Olbramkostel, emerged bottom near the western border of the fishpond, alt. 360 m

(A. Jordánová 1993, MZ); emerged bottom of Vlašňov fishpond, 1 km N of the village of Olbramkostel, alt. 360 m (B. Vocílková 1990, BRNU); Čekal fishpond ca 1,5 km N of the village of Olbramkostel, emerged bottom, alt. 370 m (A. Jordánová 1992, MZ); the small fishpond near the road 0.5 km S of the village of Bojanovice, ca 10 km N of the town of Znojmo, alt. 350 m (K. Sutorý et E. Uhlířová 1983, BRNM); Zahrádka – in the fishpond, near the town of Náměšť nad Oslavou (A. Schwöder 1860, BRNM); Stejskal fishpond near the town of Náměšť nad Oslavou (A. Makowsky 1863, BRNU). – **69a. Železnohorské podhůří.** Slatiňany, drained fishpond near the road to Nasavrky (Červený 1963, CHOM); the fishpond near the village of Kunčí near the town of Chrudim, alt. 280 m (coll.? 1887, PR). – **71b. Drahanská plošina.** Sloup (Wessely 1836, BRNM). – **76a. Moravská brána vlastní.** Dolní Bělotín fishpond near the village of Bělotín, ca 5 km NE of the town of Hranice, alt. 280 m (M. Sedláčková 1992, NJM). – **83. Ostravská pánev.** Bohumín: Šlenčák fishpond near the town of Rychvald, alt. ca 220 m (M. Součková 1950, BRNM); Mělčina fishpond near the settlement of Olšiny, NW of the town of Karviná, alt. 220 m (Hroudová 1989); Louky nad Olzou, Malý Pilarčík fishpond (Slavoňovský 1951, BRNU).

Not determinable localities: **18a. Dyjsko-svratecký úval.** Lednice (Kalmus 1864, BRNM). – **68. Moravské podhůří Vysočiny.** Strutzer (?) Teich (s.d., C. Roemer, Namiest, BRNU).

2. Literature data

Thermophyticum: **2a. Žatecké Poohří.** In the fishpond near the town of Postoloprty (Knaf in Čelakovský 1885, 1886); in the small pool „Na Seníku“ between the villages of Lenešice and Postoloprty (Prokeš 1913). – **7a. Libochovická tabule.** In the pool between the town of Budyně n. Ohří and the village of Mšené (Novák 1923). – **7d. Bělohorská tabule.** In the valley near the town of Unhošť (Čelakovský 1881, 1883). – **8. Český kras.** In the small pond in former brick-clay pit above Chuchle [Prague suburb] (Rohlena 1922). – **9. Dolní Povltaví**. Moist sand-pit S of Motol [Prague suburb] (Veselý 1942). – **11a. Všetatské Polabí.** The village of Tuhaň near the town of Mělník (Čelakovský 1885). – **11b. Poděbradské Polabí.** The town fishpond near the town of Čáslav (Opiz in Čelakovský 1885, 1886). – **12. Dolní Pojizeří.** Mělník district: in the channel between the villages of Velký Borek and Mělnická Vrutice (Veselý 1943); near the town of Mnichovo Hradiště (Čelakovský 1867, 1873). – **13a. Rožďalovická tabule.** Nymburk district: Jakubský fishpond at the E border of the village of Dymokury (Veselý 1943); the fishpond near the forester's house close to the village of Nouzov near the village of Dymokury, towards the settlement of Malý Nouzov (Baudyš 1924). – **14a. Bydžovská pánev.** Jičín district: Ostružna [Ostruženský] fishpond (Baudyš 1915–1917, 1924); Čeperka fishpond near the village of Ostružno (Baudyš 1915–1917, 1924); Turecký [Tureček] fishpond near the village of Ostružno (Baudyš 1924); the western Jinolický fishpond near the town of Jičín (Domin 1917 in Domin. mat.); in the pheasantry near the village of Vesec (Čelakovský 1873, 1881, 1883); near the village of Těšín (Pospích. in Čelakovský 1881, 1883); in the brook between the villages of Volanice and Sběř [Zběř] (Pospích. in Čelakovský 1881, 1883, Vodák in Prokeš & Válek 1946). – **15b. Hradecké Polabí.** The brook near the village of Bolehošť near the town of Opočno (Rohlena 1922); Česká Skalice: the Rozkoš dam reservoir S of the village of Spyta (Šída in Anonymus 2000); along shores of the Rozkoš dam reservoir (Krahulec 1989); in Řemínek small fishpond in Počanka near Doubravice (Krčan & Kopecký 1959). – **15c. Pardubické Polabí.** The small fishponds between Sádky and „Přední Zbraň“ near the town of Bohdaneč (Hadač 1935). – **16. Znojemsko-brněnská pahorkatina.** Znojmo district: in the muddy fishpond „Jezero“ near the village of Mikulovice (Horňanský 1950); Žebětín [Brno suburb], along the small stream in meadows towards the village of Kohoutovice (Staněk in Smejkal 1950); Troubsko [Brno suburb], wet meadow towards the village of Ostopovice (Staněk in Smejkal 1950). – **17c. Milovicko-valtická pahorkatina.** Mušlovský dolní fishpond SE of the town of Mikulov (Husák in Danihelka et al. 1995, Danihelka in Danihelka et al. 1995); Mušlovský horní fishpond E of the town of Mikulov (Husák in Danihelka & Grulich 1996); Úvalský fishpond NE of the village of Úvaly (Husák in Danihelka et al. 1995, Danihelka in Danihelka et al. 1995); the fishpond near the mill of Úvaly (Danihelka in Danihelka et al. 1995). – **18a. Dyjsko-svratecký úval.** The floodplain meadows E of the village of Drnholec (Smejkal 1950); Ivanovice [Brno suburb], along the small stream from Ráječek (Staněk in Smejkal 1950); Nesyt fishpond near the town of Lednice (Zapletálek 1938); southern shore of Nesyt fishpond (Zapletálek in Smejkal 1950); emerged bottom near the outlet of Nesyt fishpond (Zapletálek in Smejkal 1950); Střední fishpond near the town of Lednice (Zapletálek in Smejkal 1950); Mlýnský fishpond near the town of Lednice (Grulich in Danihelka et al. 1995); the small pool near the town of Podivín (Zapletálek in Smejkal 1950). – **20b. Hustopečská pahorkatina.** Černovice [Brno suburb], the ditch in meadows near Ráječek (Staněk in Smejkal 1950). – **21a. Hanácká pahorkatina.** In the bed of Bečva river E of the town of Přerov (Otruba in Smejkal 1950). – **21b. Hornomoravský úval.** Litovel district: on silty sand in the bed of Morava river near the village of Střeň (Otruba in Smejkal 1950); near the village of Chomutov [Chomoutov] (Otruba in Smejkal 1950); N of the town of Olomouc (Otruba in Smejkal 1950).

M e s o p h y t i c u m : **24b. Sokolovská pánev**. The fishpond near the settlement of Rybáře near the town of Karlovy Vary (Presl in Čelakovský 1885, 1886); near the town of Ostrov n. Ohří (Ortmann 1842); the fishpond near the town of Ostrov n. Ohří (Presl in Čelakovský 1885, 1886); Černý fishpond near the town of Ostrov n. Ohří (Reiss in Čelakovský 1885, 1886). – **33. Branžovský hvozd.** The Šepadelský [Všepadelský] fishpond near the village of Chudenice (Čelakovský 1885, 1886, 1887). – **35d. Březnické Podbrdsko.** Hlibenský fishpond near the village of Uzeničky (Hrouda in Hrouda & Skalický 1988). – **36a. Blatensko.** The fishpond N of the village of Kadov (Deyl & Skočdopolová-Deylová 1989); the fishpond near the village of Lnáře (Velenovský in Čelakovský 1881, 1883, 1885, 1886); Velká Kuš [Kuše] fishpond near the village of Vrbno (Veselý 1943, Vaněček in Skalický et al. 1961); Kubov fishpond near the village of Kadov (Vaněček in Skalický et al. 1961); Žoldánka fishpond near the village of Vrbno (Skalický in Skalický et al. 1961); Melec [Měleč] fishpond near the village of Kocelovice (Deyl & Skočdopolová-Deylová 1989); Velký Pálenec fishpond near the village of Vrbno (Deyl & Skočdopolová-Deylová 1989); Radov fishpond near the village of Tchořovice (Hejný in Skalický & Toman 1958); Starý Pálenec fishpond near the village of Vrbno (Skalický and Klásková in Skalický & Toman 1958); Hadí fishpond SW of the town of Blatná (Skalický and Klásková in Skalický & Toman 1958); Velký Kupcov fishpond near the village of Tchořovice (Skalický, Vaněček et al. 1980); Stankovský fishpond between the farm of Paračov and the railway stop of Závišín (Skalická in Skalický et al. 1961); Zadní Topič fishpond near the town of Blatná (Skalický in Skalický et al. 1961); Topič fishpond (Deylová 1972); Velkoláz fishpond near the village of Láz (Deylová 1972); Závist fishpond near the village of Skaličany (Deyl & Skočdopolová-Deylová 1989); Velký Malduch fishpond near the village of Leskovice (Toman in Skalický, Vaněček et al. 1980); Malý Malduch fishpond near the village of Leskovice (Toman in Skalický, Vaněček et al. 1980); Vilímec fishpond near the village of Buzice (Skalický in Skalický & Toman 1958); Rojický fishpond N of the village of Rojice (Toman in Skalický & Toman 1958). – **36b. Horažďovicko.** The storage ponds in the village of Nový Dvůr near the town of Horažďovice (Vaněček 1969); Němeček fishpond near the village of Mečichov (Skalický, Vaněček et al. 1980). – **37f. Strakonické vápence.** Zadní Osecký fishpond S of the railway station of Radomyšl (Toman in Skalický, Vaněček et al. 1980). – **37k. Křemžské hadce.** Sýkorův fishpond S of the village of Mříč (Vydrová 1997). – **38. Budějovická pánev.** The wetland near the village of Pištín (J. Vácha in Rohlena & Dostál 1936). – **39. Třeboňská pánev.** Small shallow fishpond [Votušil] between the villages of Domanín and Kojákovice (leg. R. Černý 1977, cited as „Domanín“ in Chán 1999). – **52. Ralsko-bezdězská tabule.** Hirschberger fishpond [Máchovo jezero] near the town of Doksy (Lorinser in Čelakovský 1867, 1873, 1885, 1886, Wurm 1887, Mikuláš 1929 in Domin. mat.). – **55e. Markvartická pahorkatina.** Lhotský [Lhotecký] fishpond near the town of Jičín (Baudyš 1924). **60. Orlické opuky.** Voděrady near Častolovice (Rohlena in Domin 1905); Rychnov n. Kn. district: near the village of Kvasiny (Pulchart in Hrobař 1936). – **72. Zábřežsko-uničovský úval.** In sand-pits near the town of Olomouc (Otruba in Smejkal 1950). – **74a. Vidnavsko-osoblažská pahorkatina.** Pitárné fishpond near the village of Dívčí Hrad (Hrouda in Hradílek 1999). – **74b. Opavská pahorkatina.** The oxbow of Opava river near the town of Kravaře (Veselý 1950); Přehyně fishpond near the town of Dolní Benešov (Veselý 1950); the fishpond near the village of Děhylov (Veselý 1950). – **83. Ostravská pánev.** In fishponds near the town of Studénka (Otruba in Smejkal 1950); in fishponds near the village of Petřvald (Otruba in Smejkal 1950); in fishponds near the village of Jistebník (Otruba in Smejkal 1950); in Ostravice river near the village of Paseky (Otruba in Smejkal 1950). – **84a. Beskydské podhůří.** On alluvial sand of Lubina river near the town of Příbor (Otruba in Smejkal 1950).