

CYTOGEOGRAPHICAL SURVEY OF *ELEOCHARIS* SUBSER. *ELEOCHARIS* IN EUROPE 1: *ELEOCHARIS PALUSTRIS*

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Abstract: Chromosome numbers for *Eleocharis palustris* subsp. *palustris* (based on 70 samples from Austria, Bulgaria, Croatia, the Czech Republic, Germany, Greece, Hungary, Lithuania, Romania, Russia, Slovakia, Slovenia, and Sweden) and *Eleocharis palustris* subsp. *vulgaris* (based on 74 samples from Austria, the Czech Republic, Denmark, Germany, Ireland, Latvia, Luxembourg, the Netherlands, Portugal, and Sweden) are given. Also the chromosome number estimates based on relative DNA contents of plants from 8 localities *E. palustris* subsp. *palustris* from Croatia, the Czech Republic, Germany, Italy, Israel, and Slovenia, and from 18 localities of *E. palustris* subsp. *vulgaris* from the Czech Republic, Germany and Sweden are included. In *E. palustris* subsp. *palustris*, $2n=16$ prevailed, the mixoploid $2n=15$, 16 was rare and a lone hypoploid $2n=15$ was detected. In *E. palustris* subsp. *vulgaris* $2n=38$ was most frequently detected, the hyperploid $2n=39$ and mixoploid $2n=38$, 39 were common, and the hypoploid $2n=36$ and mixoploids in which $2n$ ranges from 36 to 42 were rarer. Distribution maps based on plants investigated either by chromosome counting or by flow cytometry, augmented by similar data from published sources are given for both subspecies in Europe.

Keywords: Chromosome numbers, *Cyperaceae*, Flow cytometry, Plant geography

Nomenclature: KUBÁT et al. (2002)

INTRODUCTION

Eleocharis R. BR. subser. *Eleocharis* (= *Eleocharis palustris* agg.) is a group of species which are Holarctic in distribution, unlike the other infrageneric taxa of *Eleocharis*, which have centers of species diversity situated in the subtropical and tropical areas of both the Old and New Worlds. Subser. *Eleocharis* is represented by three species and six subspecies in Europe (STRANDHEDE 1966):

E. palustris (L.) ROEM. et SCHULT. (incl. *E. lindbergii* (STRANDH.) TZVELEV)

subsp. *palustris*

subsp. *vulgaris* WALTERS

E. mamillata (H. LINDB.) H. LINDB.

subsp. *mamillata*

subsp. *austriaca* (HAYEK) STRANDH.

E. uniglumis (LINK) SCHULT. (incl. *E. fennica* PALLA and *E. septentrionalis* ZINSERL.).

subsp. *uniglumis*

subsp. *sternerii* STRANDH.

The earliest chromosome numbers from the genus *Eleocharis* were published by PIECH (1924) and HÅKANSSON (1928, 1929). The latter detected two different chromosome

numbers in *E. palustris*, i.e., $2n=16$ and $2n=38$, for the first time. HÅKANSSON (1929) also found a difference in achene size between these two cytotypes, but he did not recommend formal taxonomic treatment of these differences. For *E. uniglumis*, HÅKANSSON (1929) reported $n=23$ (i.e., $2n=46$). More than twenty years later, WALTERS (1949) divided *E. palustris* into two subspecies with different chromosome numbers, $2n=16$ and $2n=38$, based on HÅKANSSON's work (1928, 1929), DOXEY's thesis (1938) and his own karyological investigations. The first discoveries of "high-polyploid" chromosome numbers in *E. uniglumis* were also made by WALTERS (1950) and HARSTHORNE (in DARLINGTON & WYLIE 1955), who recorded $2n=88-92$ or $2n=92$ as apparently randomly occurring somatic chromosome numbers from Great Britain.

An exhaustive taxonomical and karyological revision of *Eleocharis* subser. *Eleocharis* was published by STRANDHEDE (1958, 1960, 1961, 1965a,b,c,d, 1966). He counted chromosomes in about 3500 plants from 1100 localities mainly in northern Europe and detected chromosome numbers of $2n=74-82$ in *E. uniglumis* from the islands of Öland and Gotland. According to STRANDHEDE (1965c, 1966), *Eleocharis* subser. *Eleocharis* is represented by four different ploidy-levels distinguished at the species or subspecies level, i.e.,

$2n=16$: *E. palustris* subsp. *palustris*, *E. mamillata* subsp. *mamillata*, *E. mamillata* subsp. *austriaca*

$2n=38, 39$: *E. palustris* subsp. *vulgaris*

$2n=46$: *E. uniglumis* subsp. *uniglumis*

$2n=74-82$: *E. uniglumis* subsp. *sternerii*.

Most of these taxa have relatively extensive distributions that stretch across the European continent and beyond: *E. mamillata* subsp. *mamillata* and *E. uniglumis* subsp. *uniglumis* – both holarctic, *E. mamillata* subsp. *austriaca* – Euro-Asian (GREGOR 2003); *E. palustris* – sub-cosmopolitan (WALTERS 1980, EGOVA 1981, GONZÁLEZ-ELIZONDO & TENA-FLORES 2000); and *Eleocharis palustris* subsp. *vulgaris* – a somewhat smaller sub-Atlantic distribution (STRANDHEDE & DAHLGREN 1968, WALTERS 1980). *E. uniglumis* subsp. *sternerii* was described by STRANDHEDE (1961) from the Swedish islands of Öland and Gotland. Plants with high chromosome counts were found by the same author in Great Britain and France. BUREŠ (1998) reported similar "high-polyploids" from Austria, Croatia, Hungary, and Slovakia and confirmed the dispersed distribution of this taxon within Europe.

The genus *Eleocharis* is characterized by so-called holocentric chromosomes (first recognized in this genus by BATTAGLIA 1954 and HÅKANSSON 1958), as are all other taxa of the families *Cyperaceae* and *Juncaceae*. Holocentric chromosomes have radically different chromosomal architecture from monocentric chromosomes, because they lack a primary constriction (centromere), and possess instead a diffuse kinetochore along the length of the chromatids (LUCENÓ & GUERRA 1996). Fissions (or fragmentations), fusions or translocations without substantial loss or duplication of the number of genes are important mechanisms of chromosome number change in species with holocentric chromosomes and can play an important role in their evolution. Considerable variability in chromosome numbers in *Eleocharis* subser. *Eleocharis* has been observed by many authors (see e.g. STRANDHEDE 1965, 1966, HÅKANSSON 1958, THIÉBAUD 1970, POGAN 1980), especially in

E. uniglumis. Geographical patterns in distribution or evolution of different cytotypes (caused by fission, fusion or aneuploidy) have also been studied among taxa with holocentric chromosomes in the genus *Carex* (LUCENŐ & CASTROVIEJO 1991, HOSHINO & ONIMATSU 1994, HOSHINO & WATERWAY 1994, OHKAWA et al. 2000).

Chromosome size is also extremely variable in the genus *Eleocharis*. While some species have extremely small ($\ll 1 \mu\text{m}$), numerous (> 100) chromosomes and a small genome size, e.g. *E. sphacelata* R.BR., *E. equisetina* C. PRESL, *E. quinqueflora* (HARTMANN) O. SCHWARZ, other taxa have a few (< 50) extremely large ($> 2 \mu\text{m}$), chromosomes and a large genome size, e.g., *Eleocharis* subser. *Eleocharis*, *E. multicaulis* (SM.) SM., *E. sphacelata* R.BR. (STRANDHEDE & DAHLGREN 1968, BRIGGS 1970, RATH & PATNAIK 1974, BUREŠ et al. 2003).

Natural interspecific hybridization is very frequent in many genera of the *Cyperaceae*. It is documented by many authors not only from the large genus *Carex*, but also in most of the genera of the tribe *Scirpae*. Among the taxa of *Eleocharis* subser. *Eleocharis*, hybrids or probable hybrids have been reported, e.g., by LINDBERG (1902), SAUNTE (1958), LEWIS & JOHN (1961), STRANDHEDE (1965c, 1966), and BUREŠ (1998). Thus, some taxonomists consider hybridization to be one of the root causes of taxonomical difficulties in this group (cf., e.g., WALTERS 1980, KIT TAN 1985). However, bi- and multivalents in the meioses of these hybrids have only been studied in detail by LEWIS & JOHN (1961) and by STRANDHEDE (1965c), who also made crossing experiments followed by tests of pollen viability. STRANDHEDE (1965c) considered *E. palustris* subsp. *vulgaris* to be a hybridogenous species which had originated by fusion of an unreduced gamete of *E. palustris* subsp. *palustris* and a reduced gamete of *E. uniglumis* subsp. *uniglumis* (i.e., $39=16+23$).

The main goals of our investigation were to (a) search for possible new cytotypes; (b) augment earlier knowledge about the distribution of both *Eleocharis palustris* subspecies with karyologically verified data from central and south-eastern Europe; and (c) find putative hybrid populations in areas not studied by STRANDHEDE (1966).

MATERIAL AND METHODS

The plants were collected during 1991–2003 from natural habitats. Taxa of *Eleocharis* subser. *Eleocharis* are clonal plants with a dense network of long rhizomes, usually forming a homogeneous monotypical stand, a few dm to a few m in diameter. Due to this fact, each sample from a locality consisted of approximately 10×10 cm of belowground material from the densest part of the sod. These samples were cultivated in pots approx. 5 cm below the water surface of small ponds in the Botanical Garden of Masaryk University, Brno. The full list of localities is given in Appendix 2. Voucher specimens are deposited in the herbarium of the Department of Botany of Masaryk University, Brno (BRNU).

Root tip cuttings of mature plants were used for chromosome counts. The material was pre-treated at room temperature with a saturated water solution of p-dichlorobenzene for two hours and then fixed in a cold mixture of ethanol and acetic acid (3 : 1) for 24 hours. The fixed material was treated immediately. The root tips were macerated in a mixture of ethanol and hydrochloric acid (1 : 1) for 2 min at room temperature. Temporary slides were made by squashing the cut and stained meristems in lacto-propionic orcein.

Table 1. Occurrence of abnormal chromosome numbers in *E. palustris* subsp. *palustris* – literature and our data summarized. ^a – population from the botanical garden (unknown origin), fr. – fragment.

2n	14	15	16+1fr.	17
Country	Number of localities			
Norway	1	3	.	.
Sweden	.	9	1	3
Finland	.	4	.	1
France	.	2	.	1
Spain	.	1	.	.
Czech Republic	.	2	.	.
Greece	.	1	.	.
Armenia	.	1 ^a	.	.

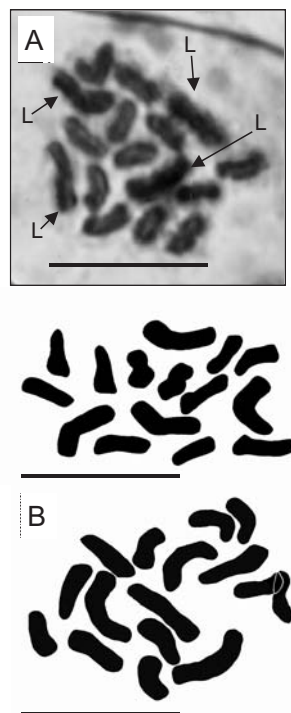


Fig. 1. Somatic metaphases of *E. palustris* subsp. *palustris*. Scale bars 10 μ m. A – $2n=16$ with the typical pattern of 4 longer (L) and 12 shorter chromosomes from the locality Czech Republic, Moravský Krumlov (P10). B – Mixoploid $2n=15, 16$ from the locality Czech Republic, Písek-Staroborský Pond (P22), two metaphases from different roots from the same rhizome – the upper 15 chromosomes, lower 16 chromosomes.

A PA-I ploidy analyzer (Partec GmbH, Münster, Germany) equipped with an HBO-100 mercury arc lamp was used for the flow-cytometric detection of relative DNA content. Sample preparation was carried out in a two-step procedure (OTTO 1990, DOLEŽEL & GÖHDE 1995) in the Laboratory of Flow Cytometry, Department of Botany, Masaryk University Brno. Stem tissues of the analyzed individual and a reference standard (0.5 cm² of leaf blade) were chopped with a new razor blade for about 20 s in a Petri dish containing 0.5 ml of ice-cold Otto I buffer (4.2 g citric acid monohydrate + 1 ml 0.5% Tween 20 adjusted to 200 ml and filtered through 0.22 μ m filter), then 0.5 ml more Otto I buffer was added. The solution was filtered through a nylon cloth (50 μ m mesh size). For DNA staining, 2 ml of Otto II buffer (0.4 M disodium hydrogenphosphate dodecahydrate) including DAPI (4',6-diamidino-2-phenylindole; 4 μ g/ml final concentration) was used. We used specific individual clones of *Eleocharis palustris* subsp. *palustris* (Czech Republic, Moravský Krumlov, $2n=16$, see Appendix 2), for measurement of *E. palustris* subsp. *vulgaris* samples and *E. uniglumis* subsp. *uniglumis* (Hungary, Fülópháza, $2n=46$), for measurement of *E. palustris* subsp. *palustris* samples, karyologically investigated and cultivated in the Masaryk University Botanical Garden, as reference standards for relative DNA content measurement.

RESULTS AND DISCUSSION

Eleocharis palustris subsp. *palustris*

In total, 78 populations of *E. palustris* subsp. *palustris* were studied. Three cytotypes were detected: the prevalent diploid ($2n=16$), a hypoploid ($2n=15$), and a mixoploid ($2n=15, 16$). The most widespread cytotype ($2n=16$) was detected from 67 populations:

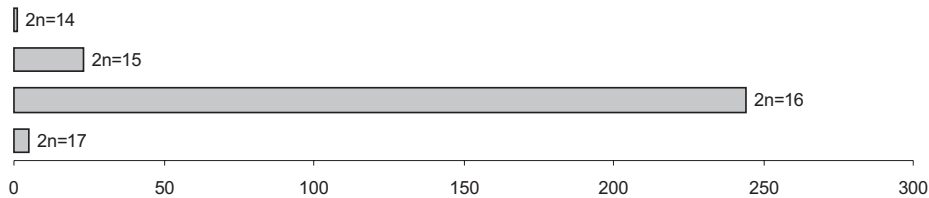


Fig. 2. Chromosome number variability in *Eleocharis palustris* subsp. *palustris* (summarizing all literature and our data, one event = one locality, mixoploids and samples estimated using flow cytometry were excluded). The most frequent cytotype $2n=16$ was detected from Iceland (1 locality), Norway (30 localities) Sweden (72 localities), Finland (32 localities), Lithuania (1 locality), Denmark (1 sample from a botanical garden), the Netherlands (1 locality), Great Britain (4 localities), France (7 localities), Spain (1 locality), Portugal (2 localities), Switzerland (2 localities), Germany (7 localities and 2 samples from botanical gardens), the Czech Republic (27 localities), Slovakia (7 localities), Austria (2 localities), Hungary (7 localities), Romania (10 localities), Italy (3 localities), Croatia (6 localities), Bulgaria (16 localities), Serbia (1 locality), Greece (2 localities), Turkey (1 sample from a botanical garden) and Armenia (1 sample from a botanical garden).

24 populations from the Czech Republic, sixteen from Bulgaria, ten from Romania, six from Croatia, four from Hungary, two from Austria, and one population each from Greece, Lithuania, Slovakia, Sweden, and Russia (Appendix 2, Fig. 1A). This count is a confirmation of data published by various earlier authors from European and extra-European countries (Appendix 1). This chromosome number had not been previously recorded in Austria, Greece, and Lithuania. Data from Hungary, Romania and Bulgaria were published in PIKNER & BUREŠ (2002).

It is very questionable to accept older chromosome counts reported for *E. palustris* (s. l.) as belonging to *E. palustris* subsp. *palustris*, because they can refer to other 16-chromosome taxa of *Eleocharis* subser. *Eleocharis*, i.e., *E. mamillata* subsp. *mamillata* or *E. mamillata* subsp. *austriaca*. For example, KUZMANOV & KOZHUHAROV (1969) and STOEVA (1985) published a chromosome count of $2n=16$ for *E. palustris* from Bulgaria, but both samples were collected in mountains (Rila Mts. and Pirin Mts.) where *E. mamillata* subsp. *austriaca* occurs (GREGOR 2003, BUREŠ unpubl.); in addition, *E. mamillata* s.l. is not included in the basic compendium of Bulgarian flora (PENEV 1964). Likewise POGAN (1971, 1972 and 1974) repeatedly reported $2n=16$ only for *E. palustris* subsp. *palustris* in Poland, including that from the Tatra Mts. where *E. mamillata* subsp. *austriaca* frequently occurs, even though *E. mamillata* (both subspecies) was known at that time from Poland (WALTERS 1959, ŻUKOWSKI 1965). Chromosome numbers of $2n=10$ reported by LEVITSKII (1940) from Kiev and Leningrad probably belong to another taxon of *Eleocharis*.

Only one hypoploid ($2n=15$) was detected, from Greece (Crete). Various aneuploid chromosome numbers were detected by STRANDHEDE (1965a,b,c, 1966) from Sweden, Finland, France, and Spain (Appendix 1). SILVESTRE (1980) found varying chromosome counts ($n=8, 9$) in meiotic metaphases of samples from Spain. The distribution of aneuploids has no obvious geographical pattern (Table 1).

Mixoploid plants were detected in two Czech populations, containing both $2n=16$ and $2n=15$ in the same root-tip (Fig. 1B). STRANDHEDE (1965c) found lower pollen viability in such mixoploids in Sweden (Appendix 1). All known chromosome counts are summarized in a histogram (Fig. 2).

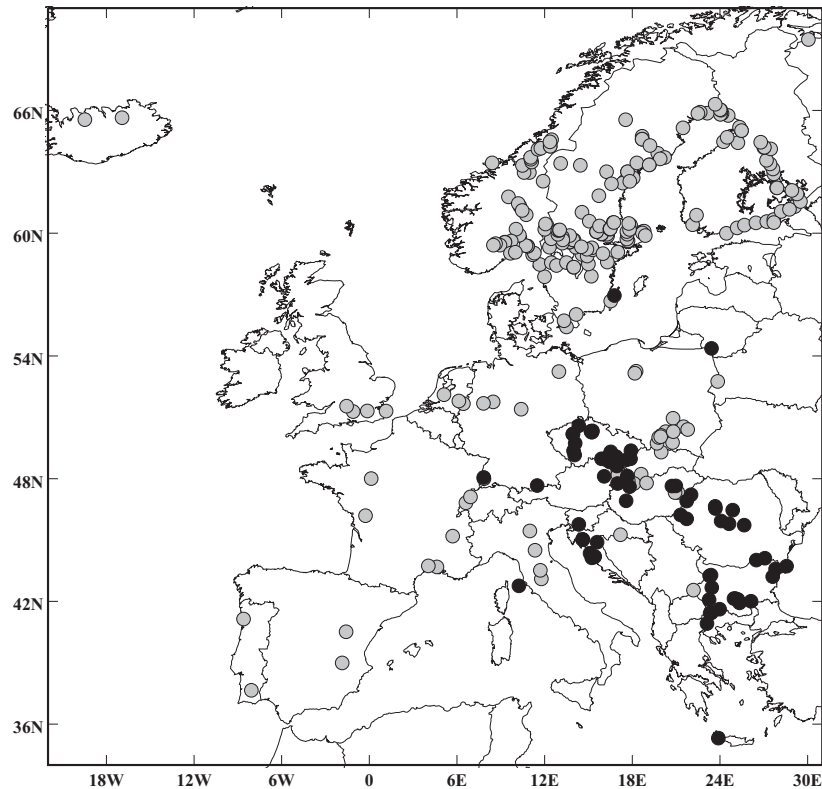


Fig. 3. Distribution of *E. palustris* subsp. *palustris* in Europe based on karyologically investigated plants (chromosome counting or flow cytometry). Literature data – grey circles, our data – black circles. Literature data based on plants for which identification was uncertain (Appendix 1) were excluded. Plants from botanical gardens without original native localization were excluded as well.

Four longer and 12 shorter chromosomes were observed frequently in metaphases of *E. palustris* subsp. *palustris* (Fig. 1A). This karyotype pattern has often been reported before in somatic mitotic metaphases of *E. palustris* subsp. *palustris* and both subspecies of *E. mamillata* by STRANDHEDE (1965c,d) and commented upon by him in detail; furthermore POGAN (1972) also detected this pattern in somatic metaphases of *E. palustris* subsp. *palustris* and HÅKANSSON (1929), STRANDHEDE (1965b) and THIÉBAUD (1970) found it in pollen mitoses of *E. palustris* subsp. *palustris* ($n=8 = 2 \text{ longer} + 6 \text{ shorter chromosomes}$). Various karyotype patterns with combinations of two or three lengths were also detected in North American species of *Eleocharis* subser. *Eleocharis* by STRANDHEDE (1967), HARMS (1968, 1972) and SCHUYLER (1977); and in the only North American 16-chromosome taxon, *E. smallii* BRITTON, STRANDHEDE (1967) reported the same pattern as for European taxa of the same ploidy level.

The chromosomes we observed lacked a localized constriction, as is typical for holocentric types, however some authors from India reported chromosomes with a constriction in *E. palustris* (SAYNAL & SHARMA 1972, BIR et al. 1993). The latter authors also reported 1–2 accessory B-chromosomes in *E. palustris*.

Table 2. *Eleocharis palustris* subsp. *vulgaris*: localities of detected cytotypes from European countries – literature and our data summarized (in mixoploids all numbers are included with weight of one locality). ^a – SAUNTE's (1958) reports of these cytotypes localized “Denmark and Sweden” were excluded. ^b – Cytotypes were detected from non-localized plants cultivated in botanical gardens. Cytotypes with fragments (fr.) were detected from Sweden: 37+1fr. (2 localities), 38+1fr. (3 localities), 39+1fr. (4 localities) and from Finland: 39+1fr. (1 locality).

2n	34	35	36	37	38	39	40	41	42
Country	Number of localities								
Iceland	1
Faeroes	1
Sweden	1	1	1	6	114 ^a	43 ^a	15 ^a	2	.
Finland	.	.	1	1	4	3	3	1	.
Norway	3	4	1	.	.
Denmark	7 ^a	5 ^a	.	.	1
Latvia	1
Germany	.	1	.	1	32 + 7 ^b	15 + 4 ^b	2 + 4 ^b	1 + 2 ^b	.
The Netherlands	6 + 1 ^b	4 + 1 ^b	.	.	.
Great Britain	.	.	.	2 ^b	24 + 3 ^b	1 + 1 ^b	3 + 1 ^b	1 ^b	.
France	.	.	.	1 ^b	2 + 3 ^b
Belgium	1 ^b
Luxembourg	1
Poland	.	.	.	2	10	3 + 1 ^b	3	.	.
Czech Republic	.	.	1	3	49 + 1 ^b	28	7	3	1
Slovakia	1 ^b
Austria	1	1	.	.	.
Ireland	4	2	.	.	.
Portugal	1	1 ^b	1 ^b	.	.

Two populations from Germany, and single populations from the Czech Republic, Italy, Slovenia, Croatia, Bulgaria and Israel were determined as *E. palustris* subsp. *palustris* using flow cytometry. Flow cytometry is better for determination than is chromosome counting, because 16-chromosome *E. palustris* subsp. *palustris* has a smaller DNA content than both subspecies of 16-chromosome *E. mamillata* (BUREŠ et al. 2003).

The distribution of *E. palustris* subsp. *palustris* in Europe, based either on literature reports or our data of karyologically verified material is shown on a map (Fig. 3).

Eleocharis palustris* subsp. *vulgaris

Ninety-three populations of *Eleocharis palustris* subsp. *vulgaris* were studied in total. Although chromosome numbers from 2n=36 to 2n=42 were found (Tab. 2, Fig. 4), cytotype 2n=38 (Fig. 4A) was more widespread (31.5%), which is in agreement with previous reports (Appendix 1). This was confirmed from 23 populations from the Czech Republic, five from Sweden, four from Denmark, and one population each from Austria, Portugal, Latvia and Luxembourg (Appendix 2). It had not been previously found in the last two countries (cf. Appendix 1). The chromosome count 2n=39 (Fig. 4C) was detected from five populations from the Czech Republic and three populations from Denmark, Ireland, and Sweden (Appendix 2), mostly confirming existing literature reports, but previously unknown for the

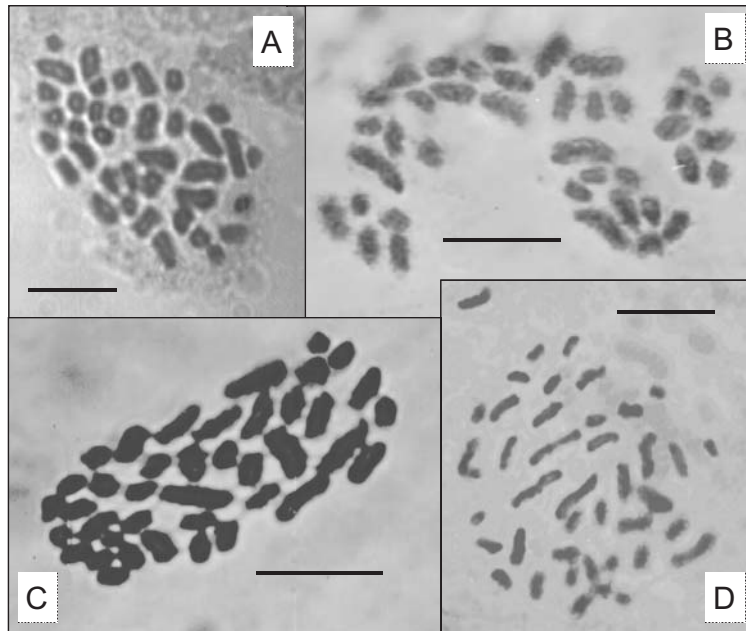


Fig. 4. Various chromosome numbers in somatic metaphases of *E. palustris* subsp. *vulgaris*. Scale bars 10 μ m. A – $2n=38$ from locality in Austria, Gösselsdorf (V24); B – $2n=40$ from the locality in the Czech Republic, Kozičín (V27); C – $2n=39$ from locality in Denmark, Kliplev (V13), D – $2n=41$ from locality in the Czech Republic, Žďár nad Sázavou-Pond Branský (V30).

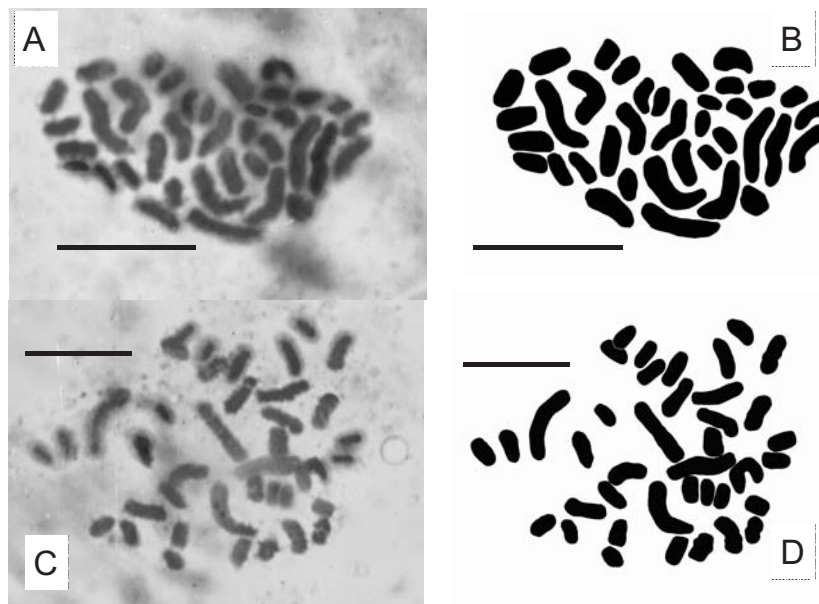


Fig. 5. Somatic metaphases of the most frequent mixoploid $2n = 38, 39$ of *E. palustris* subsp. *vulgaris* from locality Czech Republic, Žďárec (V57). Scale bars 10 μ m. A, B – 38 chromosomes; C, D – 39 chromosomes; metaphases from the same root tip.

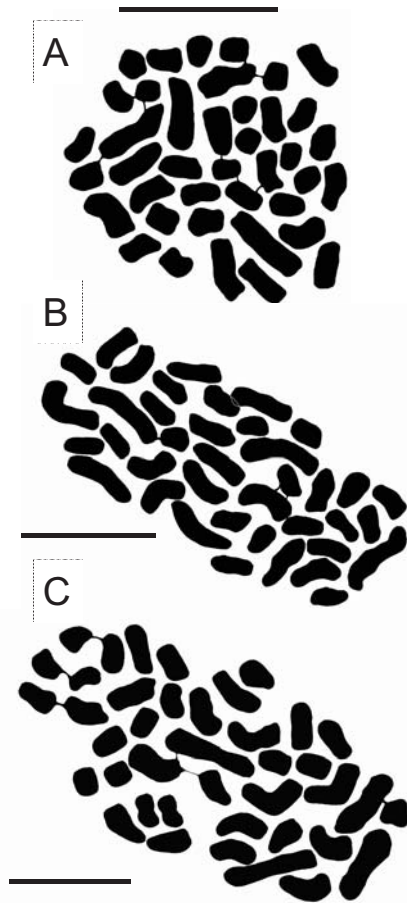


Fig. 6. Somatic metaphases of the mixoploid plant of $2n=38, 39, 40$ of *E. palustris* subsp. *vulgaris* from the locality Czech Republic, Kájov-Nový Pond (V 36). Scale bars 10 μm . A – 38 chromosomes; B – 39 chromosomes; C – 40 chromosomes; metaphases B and C are from the same root tip, metaphase A is from a different root from the same rhizome.

somewhat common hyperploid $2n=39$ and other hyperploid $2n > 39$) is relatively constant and independent of area and of researcher. If we compare the ratios for different areas with representatively high numbers of counted plants, we obtain the same results for Scandinavia, the Czech Republic, Poland, and Germany (Fig. 7). Existence of the same groups of the same cytotypes was documented in North American *Eleocharis macrostachya* BRITTON by HARMS (1968).

A distribution map of all plants of *Eleocharis palustris* subsp. *vulgaris* in which chromosome numbers were counted or DNA contents were measured using DAPI flow cytometry was prepared (Fig. 8). This map is probably the first attempt to depict the whole

Czech Republic (Appendix 1). A hypoploid ($2n=36$), hitherto known only from Sweden and Norway, was also found in the Czech Republic.

Mixoploid plants, in which we found different chromosome numbers either within the same root tip or within different roots growing from the same rhizome, were frequent. The most frequent mixoploid was $2n=38, 39$ (Fig. 5), which we found in 15 populations from the Czech Republic and in one population each from Denmark, the Netherlands and Germany (Appendix 2). This mixoploid was detected in approximately 8% of Scandinavian *Eleocharis palustris* subsp. *vulgaris* by STRANDHEDE (1965c). Other mixoploids were found rarely (Appendix 2): $2n=37, 38$ ($2\times$ from the Czech Republic), $2n=38-40$ ($3\times$ from the Czech Republic, Fig. 6), $2n=38-41$ ($1\times$ from Germany, $2\times$ from the Czech Republic), $2n=38-42$ ($1\times$ from Denmark, $1\times$ from the Czech Republic). Such variable mixoploids were previously reported by STRANDHEDE (1958, 1965c, Appendix 1). They are also frequently reported in various taxa and hybrids of the related genus *Schoenoplectus* (OTZEN 1962).

Seventeen populations from Sweden, two from the Czech Republic and one from Germany were confirmed as *E. palustris* subsp. *vulgaris* using flow cytometry (Appendix 2).

Although the chromosome number is variable, the ratio between the four main groups of detected chromosome numbers (hypoploids $2n < 38$, strongly predominating $2n=38$,

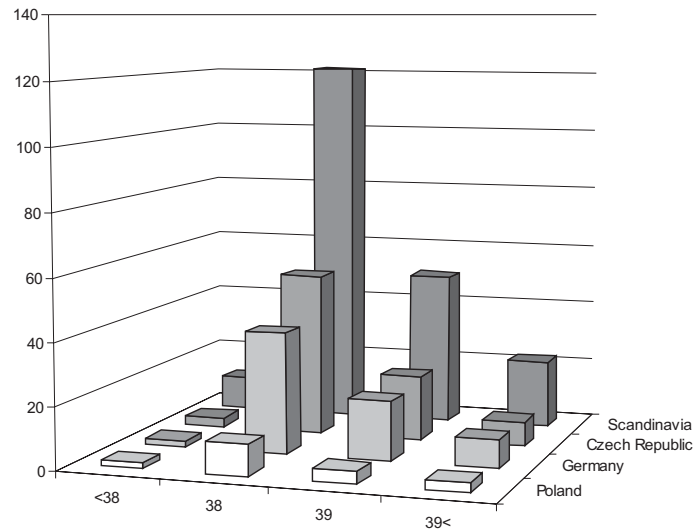


Fig. 7. Histogram comparing four groups of chromosome numbers detected in *Eleocharis palustris* subsp. *vulgaris* by different authors in different areas: Scandinavia (mainly data of STRANDHEDE 1966), Czech Republic (mainly our data), Germany (mainly data of STRANDHEDE 1966), Poland (mainly data of Pogan, Appendix 1). Weight 1 equals one chromosome number from one locality (1 "cytotop"); in mixoploids all numbers are included with weight 1 from one site.

distribution area of this taxon; nevertheless a very good written description of the distribution is given by STRANDHEDE & DAHLGREN (1968). Although from some areas, such as the Iberian Peninsula, France and the British Isles (distribution in Great Britain was published, e.g., by WALTERS (1949) and PRESTON & CROFT (1997)), our data are not representative, we can tell that this subspecies has a typical sub-Atlantic distribution with the eastern boundary running through Austria, the Czech Republic, Poland up to the Baltic countries and southern Finland. Restricting factors of distribution are probably lower annual precipitation, higher average temperatures in July and lower average temperatures in January, but also natural migration barriers, such as the Alps and Carpathians. Fish-pond density in various parts of Europe can also play an important role in the distribution of this taxon. A species with similar ecological preferences and distribution is *Carex elata* (cf. MEUSEL et al. 1965). The northern limit of the *Eleocharis palustris* subsp. *vulgaris* distribution in Scandinavia is restricted by the boundary between temperate and boreal (sub-arctic) climatic zones (northern distribution limit of *Quercus*). Species preferring stagnant water habitats with a similar northern limit of distribution include *Pilularia globulifera*, *Potamogeton crispus*, *Scirpus radicans*, *Isolepis setacea*, *Eleocharis multicaulis*, *Carex acutiformis*, *C. pseudocyperus*, *C. riparia*, *Rumex hydrolapathum*, *Rorippa amphibia*, *Elatine hexandra*, *Hydrocotyle vulgaris*, *Hottonia palustris*, *Lycopus europaeus* and *Utricularia australis*, while the distributions of many other stagnant water species extend further to the north into the boreal climatic zone (cf. MEUSEL et al. 1965). The southeastern limit of distribution of *E. palustris* subsp. *vulgaris* is in part restricted by the boundary between the European temperate and Pannonian phytogeographical provinces.

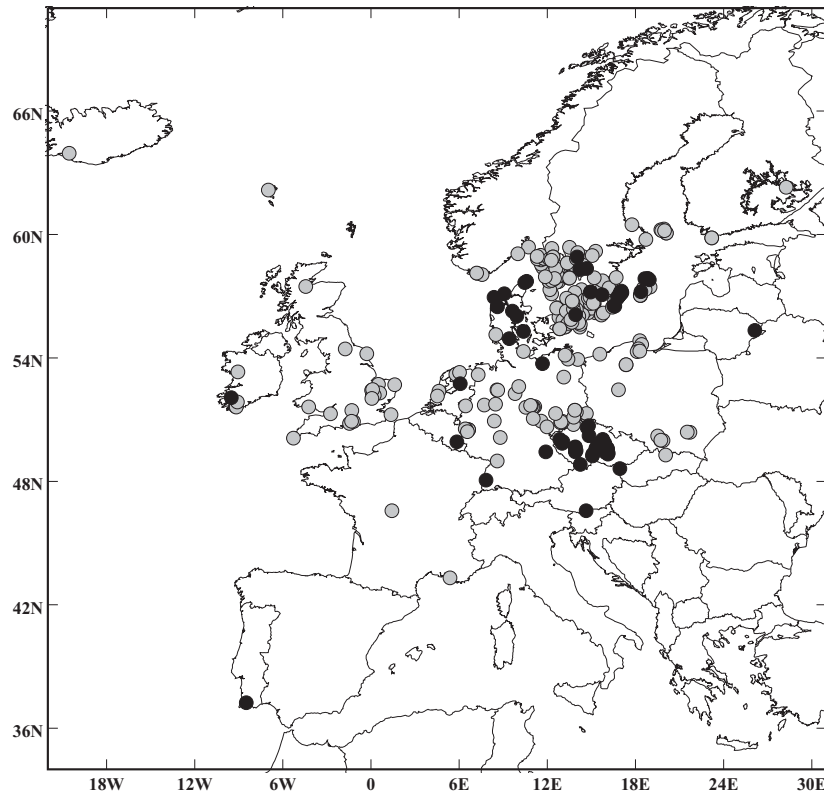


Fig. 8. Distribution of *E. palustris* subsp. *vulgaris* in Europe based on karyologically investigated plants (chromosome counting or flow cytometry). Literature data – grey circles, our data – black circles. Plants from botanical gardens without original native localization were excluded.

HYBRIDS

STRANDHEDE (1966) and LEWIS & JOHN (1961) published intermediate chromosome counts of $2n=27$, $2n=33$ from Sweden and of $2n=22-36$, $2n=27$ from Great Britain (Appendix 1). They considered plants with these chromosome counts to be infraspecific hybrids between *E. palustris* subsp. *palustris* and *E. palustris* subsp. *vulgaris*. We found no such plants, nor did we find plants with chromosome numbers $2n=42$ (or varying around this number) indicative of the interspecific hybrid between *E. palustris* subsp. *vulgaris* and *E. uniglumis* subsp. *uniglumis*. The latter hybrid was recognized by STRANDHEDE (1966) in Finland, Sweden and Germany, and by SAUNTE (1958) under the name *E. palustris* from 8 localities without accurate localization in Denmark and Sweden.

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APPENDIX 1

Previously published data on chromosome numbers of *Eleocharis palustris*. If possible, the locality of investigated plants are given. For a detailed description of the localities of plants karyologically investigated by STRANDHEDE marked “**” see his list of “Base material kept in culture in Lund” in *Opera Bot.* 10/2: 154–178 (STRANDHEDE 1966). Data based on plants for which identification could be uncertain are marked “***”. Data based on plants from botanical gardens, for which the native origins are unknown are marked “****”.

Chrom. No. **Taxon; locality; reference**

Eleocharis palustris subsp. *palustris*

2n=10	Ukraine: Kiev** (LEVITSKII 1940).
2n=12–14	Sweden: Dagsberg in Östergötland (STRANDHEDE 1965c, 1966).
2n=14	Norway (STRANDHEDE 1966)*.
n=7	Switzerland** (THIÉBAUD 1970).
2n=15	Sweden; – Finland (STRANDHEDE 1965a,b, 1966)*. Norway; – France; – Spain (STRANDHEDE 1966)*. – India: Gulmarg** (MEHRA & SACHDEVA 1975). – Central Nepal: Titigaon** (HOSHINO et al. 2000).
2n=15, 16 n=8	Norway; – Sweden; – Finland; – France (STRANDHEDE 1966)*. Poland (PIECH 1924). – Sweden: Lund (HÅKANSSON 1929). – U.S.A.: Wellesley, Lake Waban in Massachusetts ** (HICKS 1929). – Great Britain: Port Meadow in Oxon (LEWIS & JOHN 1961 as subsp. <i>microcarpa</i>). – Switzerland: without localizations from counties of Vaud, Neuchâtel, and Berne** (THIÉBAUD 1970). – India: Tangmarg in Kashmir** (MEHRA & SACHDEVA 1975). – Spain: Punta Umbría, Laguna del Portil in Huelva (SILVESTRE 1980). – Central Nepal** (HOSHINO et al. 2000).
2n=16	Romania (AVDULOV 1931). – Great Britain: River Thames in Kew (DOXEY 1938 sec. WALTERS 1949). – Ukraine: Kiev**; – Russia: Leningrad** (LEVITSKII 1940). – Japan** (TANAKA 1942). – Hungary*** (PÓLYA 1948). – Great Britain: Graveney Marches near Whitstable in East Kent; – Hagley Pool, Berks in Oxon (WALTERS 1949 as subsp. <i>microcarpa</i>). – Sweden and Denmark (SAUNTE 1958). – Greenland** (JÖRGENSEN et al. 1958). – Iceland; – Sweden; – Norway; – Finland; – Denmark***; – the Netherlands; – France; – Spain; – Portugal; – Germany; – Czech Republic; – Slovakia; – Hungary; – Italy; – Croatia***; – Serbia; – Greece; – Turkey, European part***; – Armenia*** (STRANDHEDE 1966)*. – Central Canada (LÖVE & RITCHIE 1966). – Bulgaria: Rila Mts.** (KUZMANOV & KOZHUHAROV 1969). – Poland: Fordon near Bydgoszcz (POGAN 1971). – Poland: Huta Komorowska near Rzeszów (POGAN 1971, 1972). – Poland: Košne Hamry near Zakopane; Maków Podhalański; – Gródek on the Dunajec; – Tyniec near Kraków; – Zakrzówek near Kraków; – Nowy Korczyn near Busko; – Primeval forest of Białowieża; – Fordon near Bydgoszcz (POGAN 1972). – Poland: Siedliska Sławeckie; – Tarnówka near Kraków; – Klonów near Tunel; – Zawidza in Kielce distr.; – Košne Hamry in the Tatra Mts.** (POGAN 1974). – India: Ranchi in Hindustan** (SAYNAL & SHARMA 1972). – Slovakia: Nature reserve Šúr (MURÍN 1974). – Slovakia: Záhorská nížina lowland, Nature reserve Abrod (ZÁBORSKÝ 1978). – Slovakia: Devín, bank of gravel pit (MURÍN & FERÁKOVÁ 1981). – Canada: SE of Middleboro in Manitoba ** (LÖVE & LÖVE 1981). – Russia: Far East** (KOZHEVNIKOV et al. 1986).
2n=16+fr.	Sweden (STRANDHEDE 1966)*.
n=8+1B	India: Patiala in Punjab** (BIR et al. 1993).
2n=16, 17	Sweden (STRANDHEDE 1966)*.
2n=17	Sweden; – Finland; – France (STRANDHEDE 1966)*.
n=9	U.S.A.: Wellesley, Spot Pond in Massachusetts ** (HICKS 1929). – Switzerland** (THIÉBAUD 1970). – Spain: Punta Umbría, Laguna del Portil in Huelva (SILVESTRE 1980).

Eleocharis palustris* subsp. *vulgaris

- 2n=35 Sweden; – Germany (STRANDHEDE 1966)*.
 2n=36 Sweden; – Finland (STRANDHEDE 1966)*.
 2n=37 Sweden (STRANDHEDE 1961, 1966)*. – Finland; – Great Britain***; – France***; – Germany; – Poland (STRANDHEDE 1966)*. – Great Britain (DOXEY 1938 sec. WALTERS 1949).
 2n=37+fr. Sweden (STRANDHEDE 1966)*.
 2n=37, 38 Sweden; – Great Britain*** (STRANDHEDE 1966)*. – Poland, Karwia (POGAN 1972)
 2n=37–39 Great Britain*** (STRANDHEDE 1966)*.
 2n=37–40 Belgium (STRANDHEDE 1966)*.
 n=19 Sweden: Holmsjö in Blekinge (HÅKANSSON 1928, 1929). – Great Britain: Port Meadow in Oxon (LEWIS & JOHN 1961).
 2n=38 Great Britain, northern England (DOXEY 1938 sec. WALTERS 1949). – Great Britain: Hagley Pool in Berks (WALTERS 1949). – Great Britain: Hauxton in Cambs (WALTERS 1949, 1950 sec. www.BSBI.org.uk)*. – Great Britain: Hatchet Pond near Bealieu in S Hants; – Wickham in S Hants; – East Winch Common in W Norfolk; – Hacklinge Marshes, 2.5 mi S of Sandwich in E Kent; – Gower, Llanmadoc in Glam; – Middleton in Teesdale, Balder Beck in NW Yorks; – Beaulieu in Easternness; – Bletchley in Berks; – N Somerset; – Cavenham, 7 mi NW of Bury St. Edmund in W Suffolk; – Hickling Priory in E Norfolk; – Dernford in Cambs; – Fulbourn in Cambs; – Quy Fen in Cambs; – Wicken Fen in Cambs; – Filey Brig headland (WALTERS 1950 sec. www.BSBI.org.uk). – Iceland (LÖVE & LÖVE 1956). – Sweden and Denmark (SAUNTE 1958). – Sweden; – Finland; – Faerøerne; – Norway; – Ireland; – Great Britain; – the Netherlands; – Belgium***; – France***; – Germany; – Poland; – Czech Republic; – Slovakia (STRANDHEDE 1966)*. – Poland: Jastrzębia Góra; – Mrzezino near Puck; – Lake Klasztorne; – Lake Wygoda; – Zagacie near Kraków; – Huta Komorowska near Rzeszów (POGAN 1972). – Great Britain: Loch Morlich in Easternness (BAILEY & GORNALL sec. www.BSBI.org.uk). – Ireland: Skibbereen in W Cork; – near Lough Kyne in W Cork; – near Lough Ballyally in W Cork (BAILEY & GORNALL sec. www.BSBI.org.uk).
 2n=38, 39 Norway; – Sweden (STRANDHEDE 1961, 1966)*. Finland; – the Netherlands; – Germany (STRANDHEDE 1966)*. – Great Britain, northern England (DOXEY 1938 sec. WALTERS 1949).
 2n=38, 40 Great Britain: Loe Pool, near Helston in W Cornwall; – Lymington in S Hants (WALTERS 1950 sec. www.BSBI.org.uk).
 2n=38–40 Norway; – Portugal*** (STRANDHEDE 1966)*.
 2n=38+fr. Sweden (STRANDHEDE 1966)*.
 2n=39 Great Britain, northern England (DOXEY 1938 sec. WALTERS 1949). – Sweden and Denmark (SAUNTE 1958). – Sweden (STRANDHEDE 1961, 1966)*. – Norway; – Finland; – Ireland; – Great Britain***, the Netherlands***; – Poland***; – Portugal***; – Germany (STRANDHEDE 1966)*. – Poland: Lake Karlikowskie; – Sidzina near Kraków; – Płoki near Siersza (POGAN 1972).
 2n=39+fr. Sweden; – Finland (STRANDHEDE 1966)*.
 2n=39, 40 Sweden (STRANDHEDE 1966)*.
 n=20 Great Britain: Holmsley Bog in Hants (DAVIES 1956, 1953 as *E. uniglumis*).
 2n=40 Sweden and Denmark (SAUNTE 1958). – Sweden; – Finland; – Great Britain***; – Portugal***; – Germany (STRANDHEDE 1966)*. – Poland: Babule near Huta Komorowska; – Lake Mielenko near Kartuzy; – Zagacie near Kraków (POGAN 1972).
 2n=40, 41 Great Britain, northern England (DOXEY 1938 sec. WALTERS 1949).
 2n=41 Sweden; – Finland; – Germany*** (STRANDHEDE 1966)*.

***Eleocharis palustris* subsp. *palustris* x subsp. *vulgaris* and backcrosses**

- 2n=22–36 Great Britain: Port Meadow in Oxon (LEWIS & JOHN 1961).
 n=11–18 Great Britain: Port Meadow in Oxon (LEWIS & JOHN 1961).

- 2n=27 Great Britain: Port Meadow in Oxon (LEWIS & JOHN 1961). – Sweden: Skärplinge in Uppland (STRANDHEDE 1965c, 1966).
 2n=33 Sweden: Silbodal in Värmland (STRANDHEDE 1965c, 1966).
 2n=34 Sweden: Kävlinge in Skåne (STRANDHEDE 1965c, 1966).

***Eleocharis palustris* subsp. *vulgaris* x *E. uniglumis* subsp. *uniglumis* and backcrosses**

- 2n=38–52 Great Britain: Hacklinge Marshes, 2.5 mi S of Sandwich in E Kent (WALTERS 1950 sec. www.BSBI.org.uk).
 2n=40, 42 Great Britain: Gower, Llanmadoc in Glam (WALTERS 1950 sec. www.BSBI.org.uk).
 2n=40–43 Great Britain: Hagley Pool, Berks in Oxon (WALTERS 1950 sec. www.BSBI.org.uk).
 2n=41+fr. Sweden: Hede, Kärnsjön, Staen in Bohuslän (STRANDHEDE 1966).
 2n=42 Sweden: Ramkvilla church in Småland (STRANDHEDE 1965c, 1966). – Great Britain: Midlothian***; – Germany: Deutschbaselitz in Sachsen; – Altenberg in Sachsen; – Zeulenroda in Thüringen; – France: Loire Inferieure*** (STRANDHEDE 1966).
 2n=42+fr. Sweden: Lake Mullsjön near Hjo, Kullebäcken in Västergötland (STRANDHEDE 1965c, 1966).
 2n=42, 43 Germany: Euskirchen, Kirchheim in Eifel (STRANDHEDE 1966).
 2n=43 Sweden: Lake Viaredsjön in Västergötland (STRANDHEDE 1965c, 1966). – Ö. Nöbbelöv in Brantevik (STRANDHEDE 1966). – Great Britain: Hagley Pool, Berks in Oxon (STRANDHEDE 1966). – Germany: Altenberg in Sachsen (STRANDHEDE 1966).
 2n=44 Sweden: Lake Mullsjön near Hjo in Västergötland (STRANDHEDE 1965c, 1966).

APPENDIX 2

List of localities of karyologically investigated plants. For some collectors, the following abbreviations are used: P. B. (P. Bureš), I. B. (I. Burešová), M. B. (Michaela Burešová), R. P. (R. Pikner) and K. K. (K. Kratochvílová). For the Czech Republic, the abbreviation Cz is used; the abbreviation FCM is used for samples detected by flow cytometry. Number of counted metaphases (m.) is mentioned in brackets.

Taxon; Locality	2n (number of metaphases)	Coordinates
<i>E. palustris</i> subsp. <i>palustris</i>		
Sweden, Köping (Öland Island), Önnelöv: wet grassy meadow near the parish border of Alböke – S.-O. STRANDHEDE 11 Sept. 1996	16 (2 m.)	56°57'04" N 16°46'47" E
Lithuania, Šeštokai (distr. Marijampolė): ditch in the village – V. Grulich Sept. 1995	16 (2 m.)	54°22'05" N 23°25'50" E
Germany, Gundelfingen (Bundesland Baden-Württemberg): campground 3 km WNW of the village – S. D. Stoneberg Holt 16 June 2002 (from the same loc. subsp. <i>vulgaris</i> was also collected)	ca. 16 (FCM)	48°03'42" N 7°49'10" E
Germany, Arznbach (Bundesland Bayern), pasture in valley S of the village – P. Šmarda 17 June 2002	ca. 16 (FCM)	47°39'48" N 11°29'32" E
Cz, Ústěk (distr. Litoměřice): pond Chmelář – P. B. & I. B. 10 July 1993	16 (7 m.)	50°35'11" N 14°20'11" E
Cz, Kopidlno (distr. Jičín): pond Zámecký – P. B. 29 July 1993	16 (3 m.)	50°20'04" N 15°16'23" E
Cz, Hasina (distr. Rožďalovice): pond on the N edge of the village – P. B. 29 July 1993	16 (2 m.)	50°19'16" N 15°10'24" E
Cz, Rožďalovice: bank of the river Mrlina in the town – P. B. 29 July 1993	16 (7 m.)	50°18'11" N 15°10'25" E
Cz, Břístev (distr. Rožďalovice): ditch along the road 1.5 km SW of the village – P. B. 30 July 1993	16 (15 m.)	50°16'49" N 15°14'57" E
Cz, Viničná Lhota (distr. Rožďalovice): pond Komárovský – P. B. 30 July 1993	16 (6 m.)	50°16'30" N

Cz, Lodenice (distr. Kladno): pond Lodenický – P. B. & I. B. 10 July 1993	16 (1 m.)	15°12'18" E 50°11'13" N 13°56'16" E
Cz, Mšecké Žehrovice (distr. Kladno): shore of the pond Markův – P. B. & I. B. 10 July 1993	16 (3 m.)	50°10'26" N 13°55'28" E
Cz, Kotečnice (distr. Příbram): pond Hluboký – P. B. & I. B. 9 July 1993	16 (3 m.)	49°43'57" N 14°05'39" E
Cz, Ratiboř (distr. Vsetín): wet place along the brook Ratibořka, 0.3 km N of the edge of the village – M. Chytrý 22 June 1996	16 (11 m.)	49°22'05" N 17°54'53" E
Cz, Písek: shore of the pond Staroborský between the town of Písek and the village of Sedlice – P. B. & I. B. 9 July 1993	15 (1 m.), 16 (3 m.)	49°21'37" N 13°58'58" E
Cz, Kuřim (distr. Brno): wet meadow along the road from the village to Zlobice Hill – P. B. 23 May 1993	16 (12 m.)	49°18'41" N 16°31'30" E
Cz, Brno: W shore of the reservoir Kníničská přehrada – P. B. 29 June 1994	16 (5 m.)	49°13'52" N 16°30'36" E
Cz, Bílsko (distr. Bavorov): shore of the pond on the E edge of the village – P. B. & I. B. 31 July 1993	16 (1 m.)	49°09'32" N 14°03'58" E
Cz, Kobeřice (distr. Slavkov): pond Horáček 2.5 km SW of the village – P. B. 24 Oct. 1992	16 (4 m.)	49°04'35" N 16°53'52" E
Cz, Moravský Krumlov: bank of the river Rokytá, near the bridge in the town – P. B. 27 May 1993	16 (9 m.)	49°02'52" N 16°18'39" E
Cz, Pavlice (distr. Znojmo): nature reserve Pavlické louky – B. Gruna 22 July 1996	16 (3 m.)	48°58'22" N 15°53'49" E
Cz, Horní Němčí (distr. Uherský Brod): valley of the brook Kazivec – P. B. & M. Hájek 6 Oct. 1994	16 (6 m.)	48°55'36" N 17°37'42" E
Cz, Starý Hrozenkov (distr. Uherské Hradiště): quarry NE of the village – O. Rotreklová June 2001	ca. 16 (FCM)	48°58'24" N 17°52'18" E
Cz, Oleksovice (distr. Znojmo): shore of the pond N of the village – P. B. & I. B. Sept. 1995	16 (2 m.)	48°54'35" N 16°15'21" E
Cz, Nejdek (distr. Mikulov): wet place N of "Azant" near the village – J. Danihelka 28 June 1994	16 (6 m.)	48°49'09" N 16°46'34" E
Cz, Nový Přerov (distr. Mikulov): bank of the River Dyje in the village – M. Hanušová 1 Aug. 1993	16 (2 m.)	48°48'34" N 16°28'08" E
Cz, Lanžhot (distr. Hodonín): inundated sandy place S of the town – P. B. 13 Aug. 1991	16 (11 m.)	48°43'03" N 16°57'57" E
Cz, Lanžhot (distr. Hodonín): place called Doubravka in the meadow 4 km S of the town – V. Řehořek Aug. 1997	15 (1 m.), 16 (4 m.)	48°41'20" N 16°56'05" E
Cz, Lanžhot (distr. Hodonín): confluence of the rivers Morava and Dyje, place called Melambon – M. Chytrá 10 Sept. 1995	16 (5 m.)	48°40'32" N 16°55'25" E
Cz, Lanžhot (distr. Hodonín): confluence of the rivers Morava and Dyje – M. Chytrá 23 Sept. 1993	16 (4 m.)	48°37'18" N 16°56'24" E
Cz, Lanžhot (distr. Hodonín): gravel pit called Dědova pískovna near the confluence of the rivers Morava and Dyje – V. Řehořek Aug. 1997	16 (5 m.)	48°38'14" N 16°57'31" E
Slovakia, Čierna Voda (distr. Bratislava): saline meadow at SE edge of the nature reserve Svätôjurský Šúr – P. B. 20 June 1997	16 (14 m.)	48°07'34" N 17°39'07" E
Austria, Tadten (reg. Burgenland, Neusiedlersee Lake): saline meadow on the N shore of the Schochstolacke Lake – P. B. 17 July 1997	16 (12 m.)	47°45'55" N 16°59'05" E
Austria, Grosshönniggraben (Wienerwald Highlands): wet meadow at the S edge of the village – R. P. 6 July 1999	16 (3 m.)	8°07'03" N 16°04'45" E
Hungary, Pér (distr Győr): inundated place 1 km WNW of the village – P. B. & R. P. 1 July 1998	16 (5 m.)	47°37'10" N 17°47'50" E
Hungary, Tiszafüred (Heves county): S of the road between the lakes Poroslói and Tiszavalki, 3 km N of the town – P. B. & R. P. 2 July 1998	16 (8 m.)	47°38'30" N 20°44'30" E
Hungary, Sóskás (Borsod-Abaúj-Zemplén county): inundated place on the left of the road 3 km SW of the village – P. B. & R. P. 2 July 1998	16 (4 m.)	48°12'30" N 20°46'50" E
Hungary, Monostorapáti (Veszprém county): ditch along the road near the church in the village – P. B. & R. P. 3 July 1998	16 (2 m.)	46°55'10" N 17°33'30" E
Italy, Marina di Campo (Elba Island): ditch along the road at the E edge of the village – P. B. 17 Aug. 2001	ca. 16 (FCM)	42°45'49" N 10°14'23" E
Slovenia, Postojna (Notranjsko county): Cerniško jezero Lake E of the village	ca. 16 (FCM)	45°45'47" N

– O. Rotreklová 24 June 2003		14°20'33" E
Croatia, Krk (Krk Island): wet meadow on the shore of Lake Ponikve – P. B. 13 Aug. 1997	16 (1 m.)	45°01'57" N 14°35'00" E
Croatia, Punat (Krk Island): reservoir in pasture between the Hills Veli vrh and Obzova, near the village – P. B. 13 Aug. 1997	16 (2 m.)	45°01'17" N 14°37'35" E
Croatia, Plitvica (Mala Kapela Mts., Plitvička jezera Lakes): shore of the Proščansko jezero Lake 5 km S of the village – P. B. & I. B. 14 Aug. 1998	16 (2 m.)	44°53'47" N 15°35'42" E
Croatia, Poveljana (Pag Island): exposed bottom of the Veliko blato Lake 4 km E of the village – P. B. 10 Aug. 1998	16 (3 m.)	44°21'06" N 15°06'51" E
Croatia, Suhovare (distr. Zadar): S shore of the reservoir 2 km S of the village – P. B. 10 Aug. 1998	16 (10 m.)	44°09'53" N 15°23'59" E
Croatia, Jovići (distr. Zadar): shore of the pond near the road in the village – P. B. 10 Aug. 1998	16 (2 m.)	44°07'53" N 15°13'50" E
Croatia, Rupalj (Dalmacia, distr. Zadar): exposed river bottom by the road Poličnik – Posedarje, 0.5 km N of the village – P. B. 9 Aug. 1998	ca. 16 (FCM)	44°11'48" N 15°25'55" E
Romania, Akpașu de Jos (Sibiu county): wet meadow 1 km NNW of the village – R. P. & Z. Mahdal Aug. 1998	16 (1 m.)	45°47'35" N 24°37'06" E
Romania, Mindra (Sibiu county): shore of the reservoir 1 km S of the village – R. P. & Z. Mahdal Aug. 1998	16 (3 m.)	45°55'44" N 24°04'44" E
Romania, Martinești (Cluj-Napoca county): shore of the reservoir W of the village – R. P. & Z. Mahdal Aug. 1998	16 (4 m.)	46°38'58" N 23°40'52" E
Romania, Cefa (Bihor county): saline meadow 1 km NW of the village – R. P. & Z. Mahdal Aug. 1998	16 (2 m.)	46°54'22" N 21°43'03" E
Romania, Sălard (Bihor county): wet places in the meadow on the SW edge of the village – R. P. & K. K. 3 Aug. 1999	16 (1 m.)	47°12'56" N 22°01'15" E
Romania, Arad (Arad county): wet meadow on the NW edge of the town – R. P. & K. K. 20 July 1999	16 (2 m.)	46°13'31" N 21°18'42" E
Romania, Șistarovăț (Arad county): wet places in the meadow near the road from the town of Lipov, 1 km N of the village – R. P. & K. K. 20 July 1999	16 (4 m.)	46°02'06" N 21°43'43" E
Romania, Harmăn (Brașov county): wet ditch in the meadow 1 km NW of the village – R. P. & K. K. 31 July 1999	16 (5 m.)	45°43'51" N 25°39'10" E
Romania, Trei Sate (Mureș county): wet meadow 3 km SW of the village – R. P. & K. K. 2 Aug. 1999	16 (4 m.)	46°27'46" N 24°52'23" E
Romania, Cheia (Cluj county): Valley of Turda – R. P. & K. K. 2 Aug. 1999	16 (2 m.)	46°32'41" N 23°41'23" E
Bulgaria, Cherkaski (Stara Planina Mts.): wet meadow 1 km W of the village – R. P. & K. K. 22 July 1999	16 (3 m.)	43°17'06" N 23°23'00" E
Bulgaria, Glavatsi (Stara Planina Mts.): wet places 0.5 km NE of the village – R. P. & K. K. 22 July 1999	16 (1 m.)	43°15'00" N 23°17'47" E
Bulgaria, Kazichene (Sofia county): wet ditch along the road on the W edge of the village – R. P. & K. K. 22 July 1999	16 (1 m.)	42°40'19" N 23°26'55" E
Bulgaria, Marikostinovo (Sandanski county): wet meadow 1 km SW of the village – R. P. & K. K. 24 July 1999	16 (5 m.)	41°25'26" N 23°19'49" E
Bulgaria, Hursovo (Sandanski county): wet ditch along the road on the S edge of the village – R. P. & K. K. 24 July 1999	16 (4 m.)	41°26'51" N 23°25'16" E
Bulgaria, Sadovo (Plovdiv county): wet places in the meadow 2 km E of the village – R. P. & K. K. 25 July 1999	16 (3 m.)	42°08'28" N 24°57'12" E
Bulgaria, Popovica (Plovdiv county): shore of the lake on the W edge of the village – R. P. & K. K. 26 July 1999	16 (3 m.)	42°08'28" N 25°03'18" E
Bulgaria, Biala Reka (Plovdiv county): wet ditch in the meadow 1 km W of the village – R. P. & K. K. 26 July 1999	16 (2 m.)	42°05'50" N 25°13'30" E
Bulgaria, Satovcha (Rodopi Mts., Dospat county): wet place in the meadow 4 km E of the village – R. P. & K. K. 25 July 1999	16 (2 m.)	41°37'13" N 23°58'50" E
Bulgaria, Haskovo (Rodopi Mts.): bank of the river in the W part of the village of Mineralni Bani – R. P. & K. K. 26 July 1999	16 (1 m.)	41°55'40" N 25°20'54" E
Bulgaria, Cherepovo (Sakar Mts., Topolovgrad county): shore of the reservoir 0.5 km SE of the village – R. P. & K. K. 26 July 1999	16 (6 m.)	42°00'34" N 26°07'37" E
Bulgaria, Devnya (Varna county): wet place in the meadow 2 km E of the village – R. P. & K. K. 29 July 1999	16 (2 m.)	43°12'52" N 27°36'30" E

Bulgaria, Durankulat (Dobrudzha county): margin of wetland near the camp 4 km ENE of the village – R. P. & K. K. 30 July 1999	16 (4 m.)	43°43'28" N 28°33'46" E
Bulgaria, Dobrich (Dobrudzha county): wet meadow on the W edge of the town – R. P. & K. K. 30 July 1999	16 (3 m.)	43°35'21" N 28°48'55" E
Bulgaria, Srebrna (Silistra county): W shore of the Srebrna Lake – R. P. & K. K. 30 July 1999	16 (2 m.)	44°06'35" N 27°04'07" E
Bulgaria, Nova Cherna (Tutrakan county): moors at the road 4 km E of the village – R. P. & K. K. 30 July 1999	16 (5 m.)	44°01'03" N 26°29'34" E
Bulgaria, Cherna Mesta (Rodopi Mts.): spring meadow NE of the village – M. Hájek & P. Hájková 7 July 2003	ca. 16 (FCM)	42°04'55" N 23°15'58" E
Greece, Karteraí (Central Macedonia county): meadow 2 km E of the village – V. Růžička & V. Šuk 13 May 2000	16 (1 m.)	40°55'06" N 23°06'14" E
Greece, Omalós (Crete Island): reservoir 3 km SSW of the village on the road to the village of Ayioi Theódhoroi – K. Šumberová 21 Apr. 2000	15 (9 m)	35°18'55" N 23°53'33" E
Israel, Central Golan Heights – T. Pavlíček June 2002	ca. 16 (FCM)	32°58'13" N 35°44'31" E
Russia, S Siberia, Bajkal Lake: peninsula Svjatoj Nos – M. Chytrý Aug. 1993	16 (8 m.)	53°36'58" N 108°57'14" E
<i>Eleocharis palustris</i> subsp. <i>vulgaris</i>		
Sweden, Svanshals (E of the Vättern Lake, Östergötlands county): S shore of the Tåkern Lake – M. Štech 19 July 1995	38 (4 m.)	58°20'48" N 14°40'00" E
Sweden, Vinslöv (SE of Hässleholm, Skånes county): bank of flooded gravel-pit by the village – P. B. & M. B. 15 July 2001	ca. 38–39 (FCM)	56°06'07" N 13°55'13" E
Sweden, Stenbrohult (Småland county): shore of Möckeln Lake by the churchyard with the grave of Linnaeus' father – P. B. & M. B. 15 July 2001	ca. 38–39 (FCM)	57°04'11" N 15°43'05" E
Sweden, Hjo (Västra Götalands county) S shore of Mulsjön Lake – P. B. & M. B. 16 July 2001	ca. 38–39 (FCM)	58°18'55" N 14°12'54" E
Sweden, Askeviksbadet (between Mariestad and Kristinehamn, Västra Götalands county): E shore of Vänern Lake – P. B. & M. B. 16 July 2001	ca. 38–39 (FCM)	58°54'33" N 14°01'52" E
Sweden, Böda (Öland Island): brackish shore, the boat landing at Nabbelund – S.-O. STRANDHEDE 11 Sept. 1996	38 (2 m.)	57°15'04" N 17°02'47" E
Sweden, Ramkvilla (Småland county): grassy boat landing place in Sjöborg – S.-O. STRANDHEDE 13 Sept. 1996	38 (4 m.)	57°12'04" N 14°56'53" E
Sweden, Högby (Öland Island): sandy shore on beach of the boarding house at Hornsviken Lake – S.-O. STRANDHEDE 11 Sept. 1996	38 (1 m.)	57°09'27" N 17°02'42" E
Sweden, Pernäs (Öland Island): muddy lake shore of the Knisa mosse Lake – S.-O. STRANDHEDE 11 Sept. 1996	38 (1 m.)	57°04'06" N 16°55'45" E
Sweden, Sten(sa) (Öland Island): NE muddy shore of the Fröslundamossen Lake – S.-O. STRANDHEDE 11 Sept. 1996	39 (3 m.)	56°31'00" N 16°35'51" E
Sweden, Binnerbäck (Öland Island): shallow sandy depression at the E shore of Horns Sjön Lake – P. B. & M. B. 26 July 2001	ca. 38–39 (FCM)	57°11'57" N 16°58'16" E
Sweden, Munkegard (Öland Island): shallow depression – ephemeric reservoir in pasture N of road at Lötörps campground – P. B. & M. B. 26 July 2001	ca. 38–39 (FCM)	57°09'33" N 17°01'48" E
Sweden, Högby (Öland Island): shallow depression in pasture S of Sandbysbadets campground – P. B. & M. B. 26 July 2001	ca. 38–39 (FCM)	57°10'40" N 17°04'24" E
Sweden, Pernäs (Öland Island): depression in pasture at homestead Nörra Holm ENE of the village – P. B. & M. B. 26 July 2001	ca. 38–39 (FCM)	57°04'36" N 16°57'33" E
Sweden, Föra (Öland Island): shallow depression on N shore of Lake Alverviken – P. B. 27 July 2001	ca. 38–39 (FCM)	57°01'28" N 16°52'34" E
Sweden, Folberga (Öland Island): shallow depression in pasture on E edge of Fisk Mossen Swamp between Folberga and S Greda – P. B. 27 July 2001	ca. 38–39 (FCM)	56°59'30" N 16°51'20" E
Sweden, Uggletorp (Öland Island): by the Road No. 136, 2 km S of village – P. B. & M. B. 17 July 2003	ca. 38–39 (FCM)	56°58'55" N 16°48'35" E
Sweden, Resmo (3.5 km NE of Mörbylanga, Öland Island): shallow depression S of Möckelmossen Lake in Stora Alvaret Reserve, 4.5 km E of the village – P. B. & M. B. 17 July 2003	ca. 38–39 (FCM)	56°31'41" N 16°31'14" E
Sweden, Hangvar (Gotland Island): swamps E of the road in the reserve	ca. 38–39 (FCM)	57°51'12" N

Hal – Hangvars, NW of the village – P. B. 22 July 2001		18°38'44" E
Sweden, Valleviken (Gotland Island): western shore of Fardumeträsk Lake – P. B. 22 July 2001	ca. 38–39 (FCM)	57°47'58" N 18°56'02" E
Sweden, Stockvike (Gotland Island): N shore of lake S of the village – P. B. & M. B. 23 July 2001	ca. 38–39 (FCM)	56°58'55" N 16°48'35" E
Sweden, Djupvik (Gotland Island): disturbed places on the shore of lake S of the village – P. B. & M. B. 13 July 2003	ca. 38–39 (FCM)	57°51'56" N 18°50'48" E
Sweden, Hemse (Gotland Island): shallow depression by Road No. 142 at the small village Alva – P. B. & M. B. 14 July 2003	ca. 38–39 (FCM)	57°13'13" N 18°22'09" E
Denmark, Skagen (Vendsyssel county): coast at the top of the Peninsula Skagen – P. B. & I. B. 8 Aug. 1994	38 (2m.), 39 (1m.), 42 (1 m.)	57°43'36" N 10°35'30" E
Denmark, Hulsig (Vendsyssel county): lake by the road to the town of Skagen – P. B. & I. B. 8 Aug. 1994	38 (2 m.)	57°39'49" N 10°27'39" E
Denmark, Vust (Thy county): Lundfjord Lake – P. B. & I. B. 8 Aug. 1994	39 (2 m.)	57°07'00" A 09°04'02" E
Denmark, Vorupor (Thy county): lake W of the village – P. B. & I. B. 8 Aug. 1994	38 (2 m.)	56°56'44" N 08°22'46" E
Denmark, Struer (Harsyssel county): Kilen Lake – P. B. & I. B. 9 Aug. 1994	39 (1 m.)	56°29'11" N 08°36'15" E
Denmark, Gronbaek (N of the town of Silkeborg, Jylland county): Alling S- Lake – P. B. & I. B. 7 Aug. 1994	38 (3 m.)	56°16'36" N 09°37'07" E
Denmark, Skanderborg (Jylland county): Skanderborger Sø Lake – P. B. & I. B. 7 Aug. 1994	38 (1 m.)	56°01'54" N 09°55'50" E
Denmark, Norre Soby (S of the town of Odense, Fyn Island): pond in the village – P. B. & I. B. 9 Aug. 1994	39 (2 m.)	55°17'12" N 10°22'12" E
Denmark, Kliplev (Jylland county): Hostrup Sø Lake – P. B. & I. B. 7 Aug. 1994	38 (1 m.), 39 (4 m.)	54°56'21" N 09°24'22" E
Latvia, Palūšē (distr. Ignalina): shore of Lake Lūšiai – V. Grulich Aug. 1994	38 (6 m.)	55°20'22" N 26°07'52" E
Ireland, Killarney [Cill Áirne] (distr. Tralee [Tráighlí]): shore of the lake near the town – V. Grulich 10 Aug. 1996	39 (3 m.)	52°04'16" N 9°30'51" W
Netherlands, Giethoorn (Overijssel county): lake S of the village – P. B. & I. B. 10 Aug. 1994	38 (2 m.), 39 (1 m.)	52°44'38" N 6°04'39" E
Luxembourg, Bavigne: lake W of the village – P. B. 11 Aug. 1994	38 (2 m.)	49°55'08" N 5°50'45" E
Germany, Sternberg (Bundesland Schleswig-Holstein): pond by the road on the W edge of the town – P. B. & I. B. 6 Aug. 1994	38 (1 m.), 40 (1 m.), 41 (1 m.)	53°43'08" N 11°40'45" E
Germany, Amberg (Bundesland Bayern): pond near the road from the town to the village of Schwandorf – P. B. & I. B. 12 Aug. 1994	38 (3 m.), 39 (1 m.)	49°25'55" N 11°53'13" E
Germany, Gundelfingen (Bundesland Baden-Württemberg) campground 3 km WNW of the village – S. D. Stoneberg Holt 16 June 2002 (from the same loc. subsp. <i>palustris</i> was also collected)	ca. 38–39 (FCM)	48°03'42" N 7°49'10" E
Cz, Tišová (distr. Mariánské Lázně): pond 1 km SW of the village – V. Řehořek 9 July 1996	38 (2 m.)	50°02'26" N 12°50'58" E
Cz, Krsy (distr. Planá): pond in the valley of the brook Dolský potok – P. B. 16 May 1992	38 (4 m.)	49°55'32" N 13°03'17" E
Cz, Šipín (distr. Planá): meadow in the valley of the brook Hadovka 2 km WSW of the village – P. B. 16 May 1992	38 (3 m.)	49°51'03" N 13°00'25" E
Cz, Stráž pod Ralskem (distr. Česká Lípa): pond Horecký – P. B. 10 July 1993	38 (5 m.), 39 (3 m.)	50°42'09" N 14°48'25" E
Cz, Hradčany (distr. Mimoň): pond Hradčanský – P. B. & I. B. 10 July 1993	38 (2 m.)	50°37'06" N 14°42'33" E
Cz, Hrabanov (distr. Nymburk): wet meadow Černava – O. Rotreklová 28 May 1999	ca. 38–39 (FCM)	50°12'56" N 14°50'00" E
Cz, Pardubice: wet places in the park at the castle in the town – P. B. 29 June 1993	39 (2 m.)	50°02'30" N 15°46'32" E
Cz, Kunčičky (distr. Chrudim): pond on the NW edge of the village – P. B. 12 June 1993	38 (2 m.)	49°54'15" N 15°49'51" E
Cz, Lukavice (distr. Chrudim): pond between the villages of Lukavice and Lukavička – P. B. 12 June 1993	38 (3 m.)	49°53'11" N 15°50'15" E

Cz, Šiškovice (distr. Chrudim): pond Brožek – P. B. 25 July 1992	38 (1 m.), 39 (1 m.)	49°52' 51" N 15°46' 49" E
Cz, Radochlín (distr. Chrudim): pond Housírek – P. B. 23 Sept. 1993	36 (2 m.)	49°52' 15" N 15°50' 06" E
Cz, Libáň (distr. Chrudim): pond Hluboký – P. B. 1 June 1993	38 (3 m.)	49°51' 36" N 15°49' 21" E
Cz, Havlovice (distr. Chrudim): N shore of the pond Hoříčka – P. B. 12 June 1993	39 (2 m.)	49°51' 08" N 15°54' 04" E
Cz, Nasavrky (distr. Chrudim): pond on the S edge of the village – P. B. 12 June 1993	38 (2 m.)	49°50' 22" N 15°48' 05" E
Cz, Ctětín (distr. Chrudim): pond 0.3 km W of the village – P. B. 12 June 1993	39 (5 m.)	49°49' 26" N 15°50' 23" E
Cz, Podmokly (distr. Golčův Jeníkov): pond Nový – P. B. & J. BUREŠ 23 July 1993	38 (2 m.)	49°49' 51" N 15°26' 28" E
Cz, Nová Ves (distr. Chotěboř): meadow in the valley of the river Doubrava 1.5 km E of the village – P. B. 23 July 1993	38 (4 m.), 39 (1 m.), 40 (1 m.)	49°45' 31" N 15°39' 03" E
Cz, Jarošov (distr. Chotěboř): pond on the S edge of the village – P. B. 26 July 1993	38 (2 m.)	49°45' 13" N 15°34' 39" E
Cz, Podmoklany (distr. Chotěboř): pond on the SW edge of the village – P. B. Sept. 1993	38 (3 m.)	49°43' 13" N 15°46' 13" E
Cz, Žďárec nad Doubravou (distr. Chotěboř): pond near the railway 1.1 km N of the village – P. B. 4 June 1993	38 (7 m.), 39 (5 m.)	49°42' 30" N 15°48' 49" E
Cz, Možděnice (distr. Hlinsko): pond Kaprový – P. B. July 1995	38 (1 m.), 39 (1 m.)	49°45' 39" N 15°47' 46" E
Cz, Chlum (distr. Hlinsko): pond Jordán – P. B. 4 June 1993	38 (8 m.)	49°43' 08" N 15°51' 31" E
Cz, Zalíbené (distr. Hlinsko): peat-moor on S edge of the village – P. B. 8 Sept. 1991	37 (2 m.), 38 (5 m.)	49°43' 00" N 15°54' 05" E
Cz, Benátky (distr. Hlinsko): pond on the brook Slubice, 0.8 km SSE of the village – P. B. 4 June 1993	38 (3 m.), 40 (2 m.)	49°42' 29" N 15°50' 43" E
Cz, Herálec (distr. Žďár nad Sázavou), reservoir in the part of the village called Famílie – P. B. 25 Aug. 1991	37 (5 m.), 38 (3 m.)	49°41' 44" N 15°58' 51" E
Cz, Staré Ransko (distr. Hlinsko): pond Pobočenský – P. B. 4 June 1993	38 (3 m.), 39 (1 m.)	49°41' 00" N 15°48' 57" E
Cz, Krucemburk (distr. Hlinsko): pond Řeka – P. B. 5 June 1993	38 (5 m.)	49°40' 38" N 15°50' 26" E
Cz, Kozičín (distr. Příbram): reservoir Pilská – P. B. & I. B. 9 July 1993	38 (1 m.), 39 (2 m.), 40 (1 m.), 42 (1 m.)	49°40' 33" N 49°39' 56" N
Cz, Světlá nad Sázavou: pond in the park at the castle on the S edge of the town – P. B. 25 July 1993	38 (4 m.)	49°39' 56" N 15°24' 32" E
Cz, Láz (distr. Příbram): pond Lázský – P. B. & I. B. 9 July 1993	38 (5 m.)	49°39' 34" N 13°53' 45" E
Cz, Radostovice (distr. Světlá nad Sázavou): pond on the N edge of the village – P. B. 26 July 1993	39 (3 m.)	49°38' 27" N 15°23' 59" E
Cz, Broumova Lhota (distr. Humpolec): pond Ředkovský – P. B. 26 July 1993	38 (3 m.), 39 (1 m.), 40 (1 m.)	49°38' 00" N 15°26' 46" E
Cz, Tři Studně (distr. Nové Město na Moravě): pond Sykovec – P. B. 5 June 1993	38 (1 m.), 39 (2 m.), 40 (1 m.)	49°36' 35" N 16°02' 14" E
Cz, Staré Hutě (distr. Humpolec): pond Pařez – P. B. 26 July 1993	38 (2 m.), 39 (5 m.)	49°36' 27" N 15°19' 04" E
Cz, Studnice (distr. Hlinsko): S shore of the reservoir Hamerská nádrž – P. B. 26 Aug. 1991	38 (7 m.), 39 (2 m.)	49°36' 19" N 16°05' 26" E
Cz, Kaliště (distr. Humpolec): pond U Málků – P. B. 26 July 1993	38 (1 m.)	49°36' 04" N 15°18' 37" E
Cz, Nové Město na Moravě: pond at the homestead Skalský dvůr – P. B. 15 July 1993	38 (2 m.)	49°33' 52" N 16°04' 09" E
Cz, Brunka (distr. Humpolec): pond Peruš – P. B. 26 June 1993	38 (6 m.)	49°33' 39" N 15°20' 07" E
Cz, Žďár nad Sázavou: pond Branský – P. B. 5 June 1993.	38 (5 m.), 39 (3 m.), 41 (7 m.)	49°33' 36" N 15°56' 56" E

Cz, Radostín (distr. Žďár nad Sázavou): pools in the moor called Borky, E of the village – P. B. 20 Sept. 2001	ca. 38–39 detected by FCM	49°39'17" N 15°53'18" E
Cz, Nové Město na Moravě: small pond below ponds Křivka and Trnka – P. B. 15 July 1993	38 (4 m.), 39 (2 m.)	49°33'11" N 16°05'42" E
Cz, Vatín (distr. Žďár nad Sázavou): pond Jetel – P. B. 20 July 1992	39 (3 m.)	49°31'26" N 15°57'58" E
Cz, Uzeničky (distr. Blatná): pond Hlibeňský – P. B. & I. B. 9 July 1993	38 (3 m.), 39 (1 m.)	49°29'50" N 13°57'28" E
Cz, Skaličany (distr. Blatná): pond Závist – P. B. & I. B. 9 July 1993	38 (4 m.), 39 (2 m.)	49°26'09" N 13°54'56" E
Cz, Netín (distr. Velké Meziříčí): pond Vrkoč – P. B. 20 July 1992	38 (3 m.), 39 (1 m.)	49°24'17" N 15°57'07" E
Cz, Křižanov: pond by the road to the village of Ořechov – P. B. 20 July 1992	38 (1 m.)	49°22'57" N 16°06'40" E
Cz, Kadolec (distr. Křižanov): pond in the village – P. B. 8 May 1993	38 (2 m.)	49°22'28" N 16°08'29" E
Cz, Ruda (distr. Velká Bíteš): pond Puštěnec – P. B. 21 June 1992	38 (8 m.)	49°19'31" N 16°07'23" E
Cz, Kamenice nad Lipou: pond Pecovský – P. B. & I. B. 8 July 1993	38 (2 m.)	49°18'58" N 15°05'04" E
Cz, Nová Včelnice (distr. Jindřichův Hradec): pond Velký Pohonč – P. B. & I. B. 8 July 1993	38 (1 m.), 39 (2 m.), 40 (1 m.), 41 (1 m.)	49°14'06" N 15°04'21" E
Cz, Kájov (distr. Český Krumlov): pond Nový – P. B. & I. B. 8 July 1993	38 (4 m.), 39 (1 m.), 40 (1 m.)	48°49'23" N 14°14'25" E
Cz, Lanžhot (distr. Hodonín): confluence of the rivers Morava and Dyje – M. Chytrá 23 Sept. 1993	38 (3 m.)	48°37'10" N 16°56'18" E
Austria, Gösselsdorf (Kärnten): N shore Gösselsdorfer See Lake – P. B. & I. B. July 1994	38 (2 m.)	46°34'16" N 14°38'01" E
Portugal, Odelouca (reg. Algarve): alluvium of the Ribeira de Odelouca River 4 km N of the bridge between the villages of Odelouca and Porto de Lagos – K. Šumberová 31 Mar. 2000	38 (3 m.)	37°14'19" N 8°29'58" W

