

THE GENUS *BOLBOSCHOENUS* (CYPERACEAE) IN POLAND

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Abstract. Presented here is the first revision of Polish *Bolboschoenus* (Asch.) Palla (Cyperaceae), recognizing four species in Poland: *B. laticarpus* Marhold, Hroudová, Zákravský & Ducháček, *B. maritimus* (L.) Palla, *B. planiculmis* (F. Schmidt) T. V. Egorova, and *B. yagara* (Ohwi) Y. C. Yang & M. Zhan. The paper provides a key for identification of *Bolboschoenus* species, and covers morphology, variability, distribution, habitat and chromosome numbers. Three species, *B. laticarpus*, *B. planiculmis* and *B. yagara*, are reported from Poland for the first time.

Key words: *Bolboschoenus*, taxonomy, variability, habitat, distribution, chromosome number, Poland

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INTRODUCTION

Bolboschoenus (Asch.) Palla is a genus widely distributed around the world, comprising about 15 species. Recently, Browning and Gordon-Gray (2000) proposed dividing the genus into three morphologically recognizable groups, with some continent specific species (Eurasia, North America, Africa, Australia, New Zealand). In Europe a single widely distributed species *Bolboschoenus maritimus* (L.) Palla (= *Scirpus maritimus* L.) was formerly recognized, sometimes with a few intraspecific taxa (e.g., Foerster 1972; Norlindh 1972; Schultze-Motel 1980; Casper & Krausch 1980). In *Flora Europaea*, DeFilipps (1980) placed taxa we consider to be the separate genus *Bolboschoenus* within the genus *Scirpus* L. s.l. and recognized in Europe only *Scirpus maritimus* L., with the two subspecies subsp. *maritimus* and subsp. *affinis* (Roth) Norl.

Considerable developments in the taxonomic treatment of the genus *Bolboschoenus* were initi-

ated by Oteng-Yeboah (1974), who incorporated fruit characters into the classification of the *Bolboschoenus*, extended later by Browning and collaborators to members of the genus in Africa (Browning & Gordon-Gray 1993, 1999; Browning *et al.* 1998), North America (Browning *et al.* 1995), Australia and New Zealand (Browning *et al.* 1997a), and partially in Europe (Browning *et al.* 1996; Browning *et al.* 1997b). Simultaneously, Hroudová and collaborators dealt with the *Bolboschoenus* taxa in Central Europe in terms of their morphological and ecological differentiation (Hroudová *et al.* 1997, 1998a, b, 1999a; Zákravský & Hroudová 1996), chromosome numbers (Jarolímová & Hroudová 1998), taxonomy and distribution (Hroudová *et al.* 1999b, 2001; Hroudová 2002; Ducháček 2002; Marhold *et al.* 2004). Recently *Bolboschoenus* was also critically revised in the former Soviet Union (Egorova & Tatanov 2002, 2003; Tatanov 2003a, b, c, 2004a, b) and Japan (Hayasaka & Ohashi 2002), following a new concept of species delimitation.

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European *Bolboschoenus* plants with trigonous fruits were determined by Browning *et al.* (1996) to be identical with the Asian species *B. yagara* (Ohwi) A. E. Kozhev., and other similar plants with wide fruits as the 'putative hybrid *B. maritimus* × *yagara*.' This differentiation was subsequently accepted by some authors in Germany (Kiffe 1997, 2000; Wisskirchen & Haeupler 1998; Gregor 1999; Senghas & Seybold 2000; Jäger & Werner 2002) and Austria (Hohla 2001, 2002). *Bolboschoenus yagara* was found to be present also in the Czech Republic (Hroudová *et al.* 2001; Hroudová 2002), while the putative hybrid *B. maritimus* × *B. yagara* sensu Browning *et al.* (1996) appeared to be a stable taxon with a characteristic distribution area and habitats, and was recently described as the new species *Bolboschoenus laticarpus* (Hroudová *et al.* 2001; Marhold *et al.* 2004).

Two taxa from previous classifications of the genus *Bolboschoenus* in Central Europe (e.g., Casper & Krausch 1980) have been divided: *B. maritimus* subsp. *maritimus* is now treated as two separate species, *B. yagara* and *B. laticarpus*; and *B. maritimus* subsp. *compactus* (Hoffm.) Drobov is now treated as *B. maritimus* and *B. planiculmis*.

In Poland, only *B. maritimus* (frequently misspelled as *Bulboschoenus*) has been recognized so far (e.g., Raciborski 1919; Piotrowska 1966; Szafer *et al.* 1976; Mirek *et al.* 2002). In his monograph of the subfamily Cyperoideae in Poland, Żukowski (1969) concludes that the species is extremely variable, and provides three varieties which may well be treated as forms because of their overlapping variability: var. *maritimus*, var. *compactus* (Hoffm.) G. F. Mey, and var. *monostachyus* G. F. Mey. No recent thorough study of *Bolboschoenus* exists for Poland. Only Klimko and Kreft (1999) studied in detail the variability of nutlet and glume characters of several maritime and inland populations of *B. maritimus*.

Examination of herbarium specimens from different herbaria and living plants led us to identify four species of *Bolboschoenus* occurring in Poland: *B. laticarpus*, *B. maritimus*, *B. planiculmis*, and *B. yagara*. In this paper we provide

a key for their identification, and characterize their morphology variability, distribution, habitat and chromosome numbers.

MATERIAL AND METHODS

The study is based on material in the herbaria B, BIL, BP, BRNM, BRNU, GLM, GZU, JE, KRA, KRAM, LBL, LI, LOD, M, PR, PRA, PRC, SLO, SZCZ, TRN, UGDA, W, WA and WRSŁ (abbreviations follow Holmgren *et al.* 1990; Mirek *et al.* 1997), as well as our own collections. Live populations of *Bolboschoenus* were thoroughly studied in 2003, especially in the southern part of Poland, in a cooperative project of the Institute of Botany, Academy of Sciences of the Czech Republic, and the W. Szafer Institute of Botany, Polish Academy of Sciences.

Chromosome numbers were counted from live plant material brought from natural habitats in Poland and cultivated in the experimental garden of the Institute of Botany of the Academy of Sciences of the Czech Republic in Průhonice. Chromosome counts of meiotic chromosomes were made, using young spikelets at the stage of emerging styles in the lower flowers. The tissue was slightly broken to accelerate penetration of the fixative solution. The sampled material was fixed in a mixture of ethanol and glacial acetic acid (3:1) and stained in lacto-propionic orcein. The gametic number (*n*) is given. Since agmatoploidy may occur in the families Juncaceae and Cyperaceae, and hybridization is probable within the genus *Bolboschoenus*, the somatic number is not necessarily twice the gametic number in all cases. Voucher specimens are deposited in PRA.

The names of macroregions in the lists of localities of *Bolboschoenus* species in Poland follow Kondracki (1981).

IDENTIFICATION KEY TO POLISH SPECIES OF THE GENUS *BOLBOSCHOENUS*

1. Achenes triangular in cross section, exocarp thinner than mesocarp 2
- 1* Achenes not triangular in cross section, exocarp thicker than or as thick as mesocarp 3
 2. Achenes narrow (1.6–1.8 mm wide), equilaterally triangular in cross section; exocarp very thin, formed of isodiametric cells *B. yagara*
 - 2* Achenes broad (2.0–2.4 mm wide), wide-based triangle in cross section (rarely nearly flattened or only slightly convex to subtrigonal on abaxial side); exocarp thin but visibly developed, formed

of isodiametric to slightly elongated cells

. *B. laticarpus*

3. Achenes convex on abaxial side, lenticular, plano-convex to subtrigonal in cross section; exocarp twice thicker than sclerenchymatic mesocarp, styles predominantly trifid *B. maritimus*

3*. Achenes concave to flattened on abaxial side, oval, concave or plano-concave in cross section; exocarp as thick as sclerenchymatic mesocarp, wider over angles than on concave faces, styles predominantly bifid *B. planiculmis*

***Bolboschoenus yagara* (Ohwi) Y. C. Yang
& M. Zhan (Figs 1a–d & 2a)**

Acta Biol. Plateau Sin. 7(1987): 14. 1988.

≡ *Scirpus yagara* Ohwi, Mem. Coll. Sci., Kyoto Imp. Univ., Ser. B 18: 110–111. 1944. ≡ *Bolboschoenus fluviatilis* subsp. *yagara* (Ohwi) T. Koyama, Acta Phytotax. Geobot. 31: 140. 1980. – INDICATIO LOCOTYPICA: Kyoto. – HOLOTYPE: [Kyoto Imperial University, Cultivated in the Botanical Garden], 3.7.1931, *J. Ohwi s.n.* (KYO!).

= *Bolboschoenus maritimus* var. *desoulavii* Drobov, Trudy Bot. Muz. Akad. Nauk 11: 91–92. 1913. INDICATIO LOCOTYPICA: Primorskaya obl. Post' Sanzhan' na r. Sungari (Desulavi, A. N.). – HOLOTYPE: Post' Sanzhan' na Sungari, 27.6.1903, *N. Desoulavy 510* (LE!).

Perennial plants with underground rhizomes bearing spherical to ellipsoid tubers; tubers up to 3–4 cm in diameter. Plants 0.8–1.3(–1.6) m tall. In flowering shoots the leaf-bearing part of the stem prevails; upper leafless part is (1/10–)1/5–1/4(–1/3) of total stem length. Inflorescence consists of a central group of clustered, sessile spikelets and of (1)3–7(12) rays bearing 1–3(5) spikelets; rays with one spikelet frequently present; rays mostly more than twice the length of sessile spikelets. Styles always trifid. Achene narrowly obovate to elliptic in outline, 3.2–4.0 mm long and 1.6–1.8 mm wide, with elongated beak on summit and with well-developed edge on abaxial side; in cross section nearly equilaterally triangular. Achene surface smooth or with a fine network of cell outlines (at 20× magnification), dark brown to black at maturity (Fig. 2a). Perianth bristles persistent up to maturity. Pericarp contains very thin exocarp consisting of isodiametric cells only partly filled

with air; sclerenchymatic mesocarp thick; exocarp thickness ca 1/10 to 1/15 of mesocarp thickness.

CHROMOSOME NUMBER. $n = 55$.

SPECIMENS EXAMINED. POLAND. Small fishpond SE of Wola, ca 2 km N of Brzeszcze, 2003, leg. *Z. Hroudová, P. Zákravský & J. J. Wójcicki*. – Fishponds ca 1 km E of Ruda Milicka village, ca 6 km E of Milicz, 2003, leg. *Z. Hroudová & P. Zákravský*. – Fishpond near road from Police to Żeleźniki, ca 1 km ESE of Police, ca 11 km SE of Milicz, 2003, leg. *Z. Hroudová & P. Zákravský*. – Staw Żimiec fishpond at NE border of Grabek, ca 11 km NNE of Twardogóra, 2003, leg. *Z. Hroudová & P. Zákravský*. – Fishpond ca 1.5 km ESE of Gadkowiec, ca 6 km SW of Sulmierzyce, 2003, leg. *Z. Hroudová & P. Zákravský* (Fig. 3). – Staw Sieczkowski fishpond at NW border of Gaški, ca 9 km ESE of Żmigród, 2003, leg. *Z. Hroudová & P. Zákravský*. – Small fishpond near road at S border of Żeleźniki, ca 13 km SE of Milicz, 2003, leg. *Z. Hroudová & P. Zákravský*.

VARIABILITY. The plants of *B. yagara* are moderately variable in morphology, and the main distinguishing characters (fruit shape and anatomy) are consistent. The sessile spikelets in the inflorescence are usually much fewer than the spikelets on the rays; sometimes only one sessile spikelet is formed. The plants with an inflorescence containing only rays bearing one spikelet are identical with *B. maritimus* var. *desoulavii* described by Drobov (1913) from the Far East, and sometimes treated as a separate species. However, this character has no taxonomic value (see also Tatanov 2003a). Inflorescence development depends on habitat conditions: water and nutrient availability influence quantitative characters, especially number and length of rays, and number of spikelets in fascicles on rays. Plants growing in nutrient-poor habitats may produce inflorescences composed of a few rays (2–3), while those in nutrient-rich habitats may produce well-developed rays bearing fascicles of spikelets; only rarely is 2nd-order branching found on rays. The lowest ray in the inflorescence is sometimes attached in the axil of the uppermost leaf, distant from the other rays; 2nd-order branching is occasionally found on this lowest ray, resembling a small separate inflorescence.

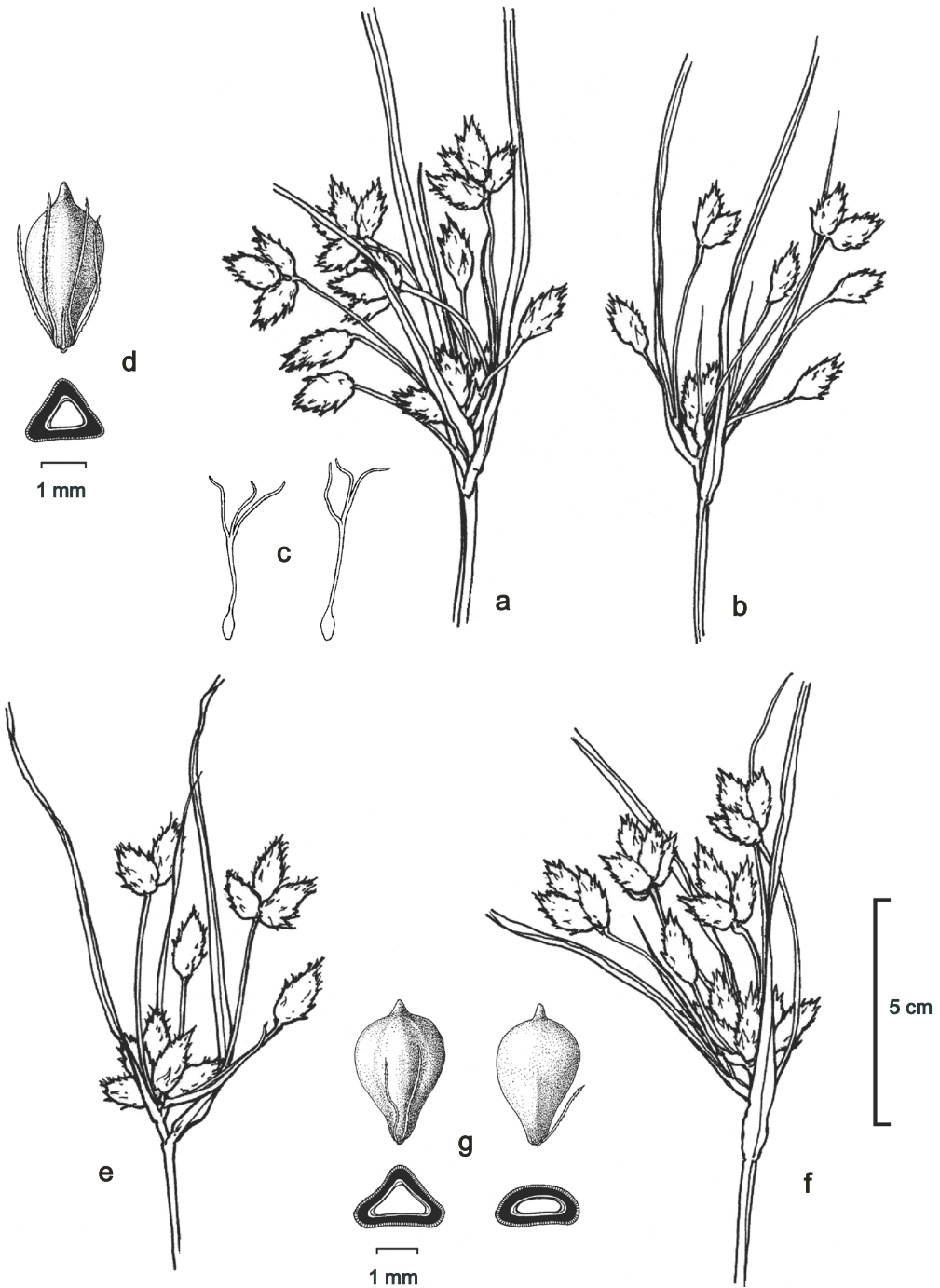


Fig. 1. a–d – *Bolboschoenus yagara* (Ohwi) Y. C. Yang & M. Zhan: a & b – inflorescence (Nowe Dwory, Wola), c – pistils with trifold styles, d – achene (view on abaxial side and cross section); e–g – *Bolboschoenus laticarpus* Marhold, Hroudová, Zákravský & Ducháček: e & f – inflorescence (Kazimierza Wielka, Łąki), g – achene (view on abaxial side and cross section). Del. Z. Hroudová.

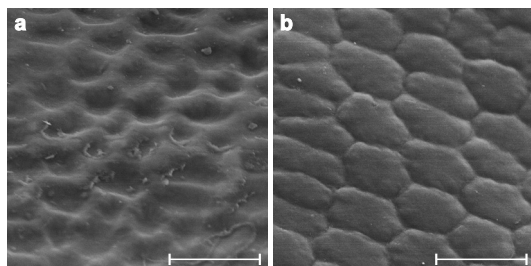


Fig. 2. Scanning electron micrographs of exocarp surface. a – *Bolboschoenus yagara* (Ohwi) Y. C. Yang & M. Zhan (Nowe Domy, PRA), and b – *Bolboschoenus maritimus* (L.) Palla (Rewa, PRA). Scale bars = 50 μ m. Phot. J. Machač.

HABITAT. *Bolboschoenus yagara* is a plant species typical of freshwater habitats with standing water, growing frequently on acid, base-poor substrates. It inhabits mainly the littoral zone in shallow fishponds with fluctuating water level, where temporary draining of the bottom initiates sprouting of shoots from tubers deposited in the bottom, and crowded vegetative multiplication of plants. Extensive stands of *B. yagara* may arise on emerged moist bottom, as well as in shallow water the year after summer draining. A good example was the extremely dry year 2003, when the fishponds, especially small ones, were almost entirely overgrown by *B. yagara* stands following sharp drops of water levels. This was observed often, especially in the fishpond region around the town of Milicz. Stands of *B. yagara* covering whole fishponds are mentioned also on some herbarium sheets (e.g., Sośnica near Przemyśl, 18 Aug. 1993, K. Zarzycki, KRAM 424500). The species can survive long-term high water levels only in the dormant tuber stage at the bottom. Besides fishponds, *B. yagara* may also occur in other littoral habitats with fluctuating water levels, such as pools, oxbows or shallow bays of rivers (e.g., near Nieboczowy). These habitats were probably the natural sites inhabited by *B. yagara* before construction of fishponds.

DISTRIBUTION IN POLAND. *Bolboschoenus yagara* is distributed in the southern part of Poland (Fig. 4) and reaches the northern limit of its continuous distribution in Central Europe there. It is a typical plant of flat landscape with numerous

fishponds. Most of its known localities are concentrated north of Wrocław. Localities scattered along the upper courses of the Nysa Łużycka, Odra, Wisła and San Rivers are linked with those in other Central European fishpond basins (Hroudová *et al.*, manuscript).

EXSICCATES. POLAND. A. Callier. Flora Silesiaca exsiccata No. 106: *Scirpus maritimus* L. Militsch [Milicz]: Graben an den Fischhaeltern, alt. 100 m, 17°16'E/51°31'N, Callier 8 July [18]89 (JE). – Flora silesiaca exsiccata. 1297. *Bulboschoenus maritimus* (L.) Palla. Silesia Inferior. Nowy Zamek apud Milicz, palat. Wrocław. Ad ripam stagni, alt. 100 m, 17°22'E/51°34'N, 18 July 1982, E. Koziol (W 13728, WRSŁ).

OTHER MATERIAL SEEN. POLAND. WAŁ TRZEBNICKI BELT. Przychowa near Ścinawa, oldbed of Odra river, 23 July 1993, 16°26'E/51°27'N, E. Koziol (WRSŁ). – NIZINA ŚLĄSKO-ŁUŻYCKA. Henndorfer Teich [Jędrzychowice near Zgorzelec], alt. 200 m, 15°1'E/51°9'N, July [18]63, Hieronymus (GLM 14154); Görlitz: Langer Teich bei Henndorf. [Jędrzychowice near Zgorzelec], alt. 200 m, 15°1'E/51°9'N, 7 Aug. [18]93, E. Barber (GLM 45986); Haynau, Schlossteich [Chojnów], alt. 140 m, 15°56'E/51°9'N, 15 Aug. [18]84, Rakete (GLM 105696). – OBNIŻENIE MILICKO-GŁOGOWSKIE DEPRESSION. S of Koniówko, 'Stawy Koniowskie', W fishpond, ca 10 km E of Żmigród, alt. 104 m, 17°5'E/51°27'N, 27 Aug. 2003, Z. Hroudová & P. Zákravský (KRAM 523022, PRA); 'Stawy Koniowskie', middle fishpond, 17°5'E/51°27'N, 27 Aug. 2003, Z. Hroudová & P. Zákravský (KRAM 523021, PRA); 'Stawy Ko-



Fig. 3. Meiotic chromosomes of *Bolboschoenus yagara* (Ohwi) Y. C. Yang & M. Zhan (Gadkowice). Scale bar = 10 μ m. Phot. V. Jarolímová.

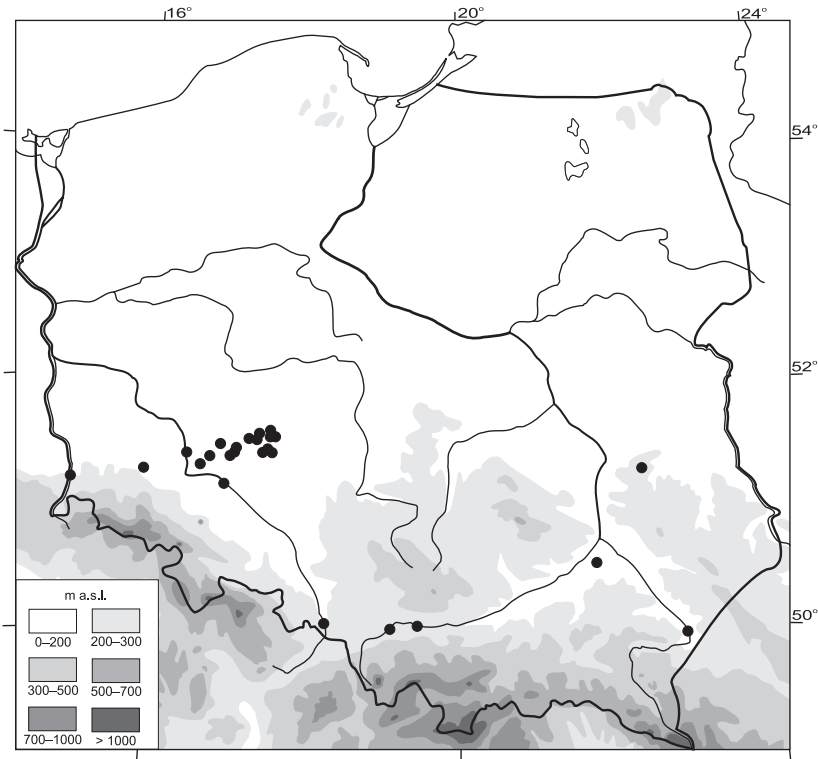


Fig. 4. Distribution of *Bolboschoenus yagara* (Ohwi) Y. C. Yang & M. Zhan in Poland.

niowskie', E fishpond, 17°5'E/51°27'N, 27 Aug. 2003, Z. Hroudová & P. Zákravský (KRAM 523023, PRA); 'Staw Sieczkowski' fishpond at NW border of Gaški, ca 9 km ESE of Żmigród, alt. 73 m, 17°2'E/51°26'N, 27 Aug. 2003, Z. Hroudová & P. Zákravský (KRAM 523024, PRA); Fishpond near the road at NW border of Ligota Strupińska, ca 11 km SW of Żmigród, alt. 126 m, 16°48'E/51°24'N, 30 Aug. 2003, Z. Hroudová & P. Zákravský (KRAM 523041, PRA); Fishpond near the road at N border of Nowe Domy, ca 3.5 km NNE of Żmigród, alt. 91 m, 16°55'E/51°31'N, 30 Aug. 2003, Z. Hroudová & P. Zákravský (KRAM 523039, PRA); Fishpond near the road ca 1 km SE of Nowe Domy, ca 3 km NE of Żmigród, alt. 82 m, 16°56'E/51°31'N, 30 Aug. 2003, Z. Hroudová & P. Zákravský (KRAM 523032, PRA); Fishpond near the road from Żmigród to Milicz, ca 2.5 km W of Łąki, alt. 89 m, 17°6'E/51°30'N, 30 Aug. 2003, Z. Hroudová & P. Zákravský (KRAM 523040, PRA); Fishpond near the road ca 0.5 km SW of Górka, ca 8 km S of Sulmierzyce, alt. 113 m, 17°31'E/51°32'N, 31 Aug. 2003, Z. Hroudová & P. Zákravský (KRAM 523038, PRA); Fishpond 'Staw Jan', E border of Joachimówka, ca 8 km S of Sulmie-

rzyce, alt. 109 m, 17°30'E/51°32'N, 31 Aug. 2003, Z. Hroudová & P. Zákravský (KRAM 523033, PRA); First (eastern) fishpond at E border of Joachimówka, ca 9 km of Sulmierzyce, alt. 112 m, 17°30'E/51°32'N, 31 Aug. 2003, Z. Hroudová & P. Zákravský (KRAM 523037, PRA); Fishpond at SE border of Joachimówka, ca 9 km SSW of Sulmierzyce, alt. 106 m, 17°29'E/51°32'N, 31 Aug. 2003, Z. Hroudová & P. Zákravský (KRAM 523036, PRA); Third (middle) fishpond at S border of Joachimówka, ca 9 km SSW of Sulmierzyce, alt. 105 m, 17°29'E/51°32'N, 31 Aug. 2003, Z. Hroudová & P. Zákravský (KRAM 523035, PRA); Fourth fishpond at S border of Joachimówka, ca 9 km SSW of Sulmierzyce, alt. 102 m, 17°29'E/51°32'N, 31 Aug. 2003, Z. Hroudová & P. Zákravský (KRAM 523034, PRA); Fishpond at E border of Ruda Milicka, ca 5 km E of Milicz, alt. 108 m, 17°21'E/51°32'N, 28 Aug. 2003, Z. Hroudová & P. Zákravský (KRAM 523028, PRA); Fishpond near the road, ca 1 km E of Ruda Milicka, ca 6 km E of Milicz, alt. 108 m, 17°21'E/51°32'N, 28 Aug. 2003, Z. Hroudová & P. Zákravský (PRA); Fishponds ca 1 km E of the village of Ruda Milicka, ca 6 km E of Milicz, alt. 106 m, 17°21'E/51°32'N, 28 Aug. 2003,

Z. Hroudová & P. Zákravský (KRAM 523027, PRA); Fishpond ca 1.5 km SE of Ruda Milicka, ca 6 km E of Milicz, alt. 108 m, 17°21'E/51°32'N, 28 Aug. 2003, Z. Hroudová & P. Zákravský (KRAM 523026, PRA); Stawno near Milicz, 'Nowy Świat', 17°16'E/51°32'N, 13 July 1973, E. Koziol (WRSL 93973); Fishpond ca 1.5 km ESE of Gądkowice, ca 6 km SW of Sulmierzyce, alt. 110 m, 17°29'E/51°34'N, 28 Aug. 2003, Z. Hroudová & P. Zákravský (PRA); Fishpond W of Rybakówka, ca 2 km ESE of the village of Gądkowice, alt. 105 m, 17°29'E/51°34'N 28 Aug. 2003, Z. Hroudová & P. Zákravský (KRAM 523025, PRA); Small fishpond near the road at S border of Żelezniki, ca 13 km SE of Milicz, alt. 118 m, 17°25'E/51°27'N, 29 Aug. 2003, Z. Hroudová & P. Zákravský (KRAM 523031, PRA); [*]² Fishpond near the road from Police to Żelezniki, ca 1 km ESE of Police, ca 11 km SE of Milicz, alt. 117 m; 17°23'32.6"E/51°27'18.4"N, 29 Aug. 2003, Z. Hroudová & P. Zákravský (PRA); [*] Fishpond 'Biały Most' near the road from Grabownica to Drożdżęcín, ca 10 km N of Twardogóra, alt. 121 m, 17°28'58.5"E/51°27'02.5"N, 29 Aug. 2003, Z. Hroudová & P. Zákravský (PRA); [*] 'Staw Żimiec' fishpond at NE border of Grabek, ca 11 km NNE of Twardogóra, alt. 124 m, 17°30'48.8"E/51°27'12.1"N, 29 Aug. 2003, Z. Hroudová & P. Zákravský (PRA); [*] Fishpond ca 0.5 km N of SW border of Czesławice (Janisławice), ca 14 km NE of Twardogóra, alt. 117 m; 17°29'05.2"E/51°32'29.2"N, 31 Aug. 2003, Z. Hroudová & P. Zákravský (PRA); Koniowo near Trzebnica, 17°3'E/51°26'N, 16 July 1991, T. Macicka (WRSL 82986); Puditsch [Budziez, NW of Trzebnica], alt. 100 m, 16°55'E/51°22'N, July 1878, Schwan (W 8883). – NIZINA ŚLĄSKA LOWLAND. Wołów near Wrocław, 16°39'E/51°20'N, 2 July 1976, E. Koziol (WRSL 93586); Vratislaviae [Wrocław], ad fl. Oder versus Hortum Zoologicum, alt. 100 m, 17°2'E/51°6'N, 22 July 1882, Uechtritz (M 80438); Oxbow of Odra river ca 1 km NW of Nieboczowy, ca 7 km SSE of Racibórz, alt. 180 m, 18°15'E/50°3'N, 26 Aug. 2003 Z. Hroudová & P. Zákravský (KRAM 523030, PRA); – KOTLINA OŚWIECIMSKA BASIN. Wola near Miedźna, alt. 220 m, 19°7'E/50°0'N, 20 Aug. 1996, A. Rostański (B); Small fishpond SE of Wola, ca 2 km N of Brzeszcze, alt. 233 m, 19°9'E/50°0'N, 25 Aug. 2003, Z. Hroudová, P. Zákravský & J. J. Wójcicki (KRAM 523029, PRA); Spytkowice, small pond near Institute of Zootechnic, alt. 240 m, 19°30'E/49°59'N, 19 Aug. 1958, R. Rozmus (KRAM 21684); – WYŻYNA LUBELSKA UPLAND. Wrotków near Lublin, Bystrzyca valley, alt.

205 m, 22°33'E/51°12'N, 4 July 1998, M. Panasiuk (LBL). – KOTLINA SANDOMIERSKA BASIN. Buda Stalowska near Tarnobrzeg, Staw Pańska Łąka II fishpond, alt. 160 m, 21°48'E/50°28'N, 29 July 1995, M. Wrzesień (LBL); Staw Cyranki I fishpond, alt. 160 m, 21°48'E/50°28'N, 29 July 1995, M. Wrzesień (LBL – two sheets); Stary Staw fishpond, alt. 160 m, 21°48'E/50°28'N, 24 July 1995, M. Wrzesień (LBL); Sońnica near Przemyśl, alt. 178 m, 22°52'E/49°54'N, 18 Aug. 1993, K. Zarzycki (KRAM 424500, KRAM).

Bolboschoenus laticarpus Marhold, Hroudová, Zákravský & Ducháček (Fig. 1e–g)

Phyton (Horn) 44: 7. 2004. – INDICATIO LOCOTYPICA: E Bohemia, Jílovka fishpond near road from Bukovka to Lázně Bohdaneč, 1 km SE of the village Bukovka, alt. 225 m, 50°6'N, 15°38'E. – HOLOTYPE: E Bohemia, Jílovka fishpond near road from Bukovka to Lázně Bohdaneč, 1 km SE of the village Bukovka, alt. 225 m, 50°6'N, 15°38'E, 5.9.2002, Z. Hroudová & P. Zákravský s. n. (PRA!).

= *Scirpus maritimus* var. *cymosus* Rchb. Fl. Germ. Excurs. 1: 79. 1830. = *Bolboschoenus maritimus* subsp. *cymosus* (Rchb.) Soják Čas. Nár. Mus., Odd. Přír. 141: 62. 1972. = *Scirpus maritimus* f. *cymosus* (Rchb.) T. Koyama, Canad. J. Bot. 40: 936. 1962. = *Bolboschoenus maritimus* var. *cymosus* (Rchb.) Kit Tan & Oteng-Yeb., Fl. Turkey 9: 64. 1985. – INDICATIO LOCOTYPICA: [Central Europe]. – LECTOTYPE: (Marhold et al. 2006): Schkuhr, Bot. Handbuch vol. 1, pl. 8 'Scirpus maritimus.' 1787–1791.

– *B. maritimus* × *B. yagara* sensu Browning et al. (1996).

– *B. yagara* × *B. koshewnikowii* sensu Hroudová in Kubát et al., Klíč ke květ. ČR: 795. 2002.

Plants with underground rhizomes bearing spherical to elongated (ellipsoid) tubers (1.5–) 2–3 cm in diameter. Plants (0.3–)0.7–1.1(–1.5) m tall. In flowering shoots, the upper leafless part of stem is ca 1/3 of total stem length. Inflorescence consists of central group of (1–)2–7(–13) clustered, sessile spikelets and (1–)2–5(–7) rays bearing fascicles of 2–4(–8) spikelets, more rarely single spikelets. Styles trifid, frequently also flowers with bifid styles present in the same inflorescence. Achene obovate to broadly obovate in outline, narrowed at basal part, apical part suddenly narrowed into a beak, 3.1–3.7 mm long, 2–2.4 mm wide,

² [*] – Plants cultivated in Průhonice.

trigonus, with low edge on abaxial side which may be sometimes nearly round, dark brown to black at maturity. Perianth bristles persistent up to maturity, sometimes caducous. Achene surface smooth, sometimes faint cell outlines detectable as a fine network (at 20× magnification) (similar as in *B. maritimus*, depending on development of the exocarp layer). Fruits wide-based triangular in cross section, pericarp formed by thin exocarp (epidermis), thick sclerenchymatic mesocarp and thin sclerenchymatic endocarp. Exocarp consists of one layer of isodiametric to slightly elongated air-containing cells; exocarp thickness *ca* 1/3 of mesocarp thickness.

CHROMOSOME NUMBERS. $n = 54, 55, (55?)$

SPECIMENS EXAMINED. $n = 54$. POLAND. Small fishpond near road at SE border of Krośnice, *ca* 8 km SE of Milicz, alt. 128 m, 2003, *leg. Z. Hroudová & P. Zákravský*. – Fishpond near branch road to Potasznia, *ca* 1 km SW of Górká, *ca* 8 km of Sulmierzyce, alt. 108 m, 2003, *leg. Z. Hroudová & P. Zákravský*.

$n = 55$. N of Pławowice, middle fishpond among three, *ca* 1.5 km W of Bobin, 190 m, 2003, *leg. Z. Hroudová, P. Zákravský & J. J. Wójcicki*. – NE border of Niezgoda, Staw Niezgoda fishpond, *ca* 9 km NE of Żmigród, 2003, *leg. Z. Hroudová & P. Zákravský*.

$n = 54 (55?)$. – Irregularities in meiosis observed, variation in bivalent size. Fishpond *ca* 1.5 km S of Sanie near Żmigród, alt. 85 m, 2003, *leg. Z. Hroudová & P. Zákravský*.

VARIABILITY. The inflorescence structure of *B. laticarpus* varies mostly in the number of rays and the number of spikelets on rays. Some rays may bear only one spikelet, but spikelet fascicles usually prevail on rays. In most cases the number of sessile spikelets in the inflorescence is nearly the same or slightly less than the number of the spikelets on rays. Inflorescence development is influenced by nutrient supply; poor nutrient supply limits the development of rays and spikelets on rays, and under extreme conditions an inflorescence formed of only sessile spikelets may arise. Long spikelets (*macrostachyate* form over 2 cm in length) are relatively rare, and the spikelets are usually entirely fertile. Plants may vary in the proportion of flowers with bifid styles

in the inflorescence; sometimes only trifid styles are present, but individual populations may differ in this character. A small proportion of achenes nearly flat or only slightly convex on the abaxial side may be present in the same inflorescence, corresponding to the presence of flowers with bifid styles. The persistence of perianth bristles also varies. They are sometimes persistent at maturity, but sometimes caducous. These variable characters, intermediate between *B. yagara* and species with compact inflorescences – *B. maritimus* or *B. planiculmis* – suggest the possible hybrid origin of *B. laticarpus*.

HABITAT. *Bolboschoenus laticarpus* is a freshwater plant species with a wide ecological amplitude. It inhabits littoral zones of standing waters with fluctuating water levels, especially fishponds and other reservoirs, riverbanks and oxbows, and also summer-drying, temporarily flooded field depressions and channels or ditches. It is a typical plant of river floodplains. *Bolboschoenus laticarpus* is able to inhabit various substrates, but avoids highly saline habitats. Like *B. yagara*, *B. laticarpus* can endure periods of unfavorable habitat conditions (high water level or drying) in the stage of dormant underground tubers, and produces well-developed stands on wet emerged bottoms and/or in shallow littorals.

DISTRIBUTION IN POLAND. *Bolboschoenus laticarpus* is distributed in fishpond areas and along rivers, and seems to be the most frequent member of the genus *Bolboschoenus* in Poland (Fig. 5). It is widespread throughout the country, with more numerous localities grouped in the environs of Wrocław and Kraków, and the middle and lower Vistula River. The wide distribution of *B. laticarpus* evidently results from its ability to spread by river currents and its tolerance to a wide range of habitat conditions.

EXSICCATES. POLAND. Exsiccata Toruniensia imprimis plantas Poloniae Septentrionalis continetia. 12. *Bolboschoenus maritimus* (L.) Palla ssp. *maritimus* (ssp. *eumaritimus* Hejný). Polonia septentrionalis: urbs Toronium (Toruń), suburbium Rybaki. In ripa meandri mortui fluminis Vistulae ad viridarium urbanum versam, alt. 20 m, 18°37'E/53°0'N, 23 July 1973, *W. Gugnacka*

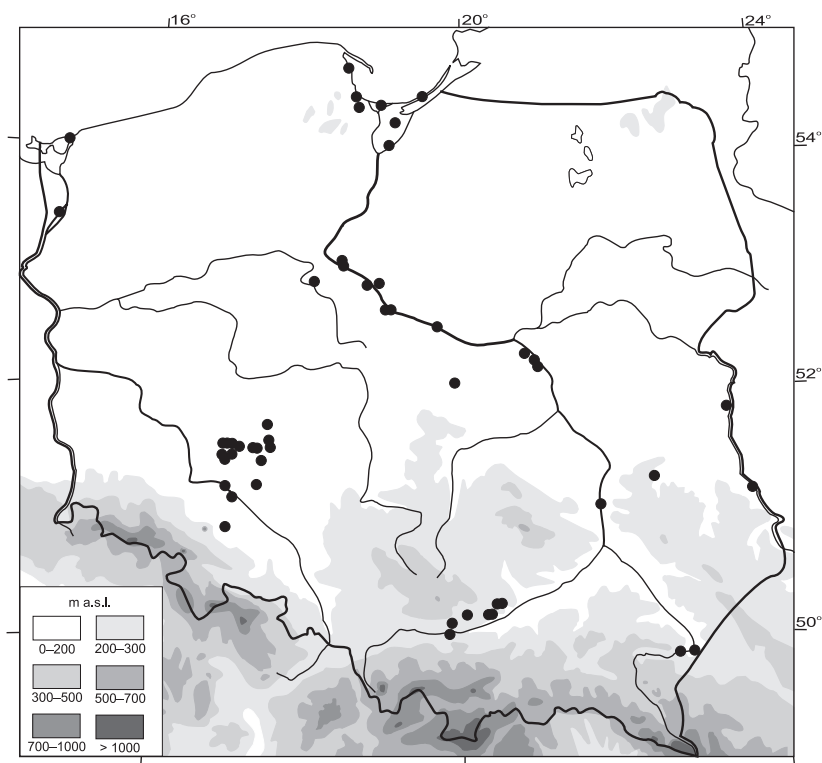


Fig. 5. Distribution of *Bolboschoenus laticarpus* Marhold, Hroudová, Zákravský & Ducháček in Poland.

(BRNM 544174, KRAM 216373, LOD 58592, LBL, PRC, WA 68148). – Flora Poloniae exsiccata ab Instituto botanico Academiae Scientiarum Poloniae edita. 489. *Bolboschoenus maritimus* (L.) Palla. Poloniae meridionalis districtus Kazimierza Wielka: pagus Kazimierza Mała. In fossa ad pedes collis, alt. 182 m, 20°31'E/50°15'N, 12 July 1972, T. Tacik & A. Palkowa (BRNU 469759, GZU, W 1997–02747, WRSL).

OTHER MATERIAL SEEN. POLAND. POBRZEŻE SZCZECIŃSKIE SEA-COAST. Śtětín [Szczecin], alt. 0 m, 14°34'E/53°25'N, 26 Aug. 1948, *Reitmayerová* (BRNM 78179; mixed sheet with *B. maritimus*); Wolin, Międzywodzie, on canal connecting Jezioro Koprowskie lake and Dziwnów canal, alt. 0 m, 14°45'E/54°1'N, 21. 7. 1951, J. Mądałski (KRAM 465468); Flora Pomorza Zachodniego, s.d., W. Bacieczko (SZCZ). – POBRZEŻE GDAŃSKIE SEA-COAST. Dolina Redy valley, W of Rewa, alt. 20 m, 18°26'E/54°41'N, 4 Aug. 1971, M. Jończak (UGDA); Danzig [Gdańsk], alt. 0 m, 18°40'E/54°24'N, 1836, *Klinsmann* (B); Westerplatte [Gdańsk], alt. 5 m 18°41'E/54°24'N, July 1869, *Steffens* (JE); Miko-szewo, bay near 'Bursztynowa Droga', alt. 0 m,

18°57'E/54°20'N, 18 Aug. 1969, E. Koteja (KRAM 238568, 225572, 225573); Mierzeja Wiślana, st. 15, alt. 3 m, 18°57'E/54°21'N, 13 July 1976, M. Michel (UGDA); Bei Kahlberg [Krynica Morska], alt. 0 m, 19°27'E/54°23'N, Aug. 1931, M. Trosche (KRA 210879); Kahlberg [Krynica Morska], alt. 0 m, 19°27'E/54°23'N, s.d., s.coll. (KRA 21897); Tiegenhof [Nowy Dwór Gdański], alt. 0 m, 19°7'E/54°13'N, 12 July 1913, R. Gross (B); Marienburg [Malbork], an der Nogat, alt. 5 m, 19°2'E/54°2'N, 17 July [18]91, R. Gross (B); – NIZINA POŁUDNIOWO-WIELKOPOLSKA LOWLAND. Krotoschin: Tomnitz [Tomnice near Krotoszyn], alt. 120 m, 17°30'E/51°42'N, Aug. 1912, H. Bothe (B); Schwarzwasser bei Tomnitz [Tomnice near Krotoszyn], alt. 120 m, 17°30'E/51°42'N, 28 Aug. 1909, Bothe (B). – PRADOLINA TORUŃSKO-EBERSWALDZKA VALLEY. Toruń, on Wisła river, alt. 30 m 18°36'E/53°0'N, 12 July 1922, s.coll. (WA 39527); Ciechocinek, park, alt. 40 m 18°47'E/52°53'N, July 1912, s.coll. (WA 39531); Nowogródek on Wisła river [near Czernikowo], 18°51'E/52°53'N, July 1889, A. Zalewski (WA 39490); Kulin near Włocławek, on Wisła river alt. 40 m, 19°8'E/52°40'N, 15 July 1963, M. Ceynowa (TRN); Surround-

- ings of Płock, alt. 50 m, 19°42'E/52°32'N, July 1936, *H. Wiśniewska* (WA 39523); Szpetal Dolny [Włocławek], alt. 40 m, 19°5'E/52°40'N, 1916, *R. Kabendza* (WA 39505). – POJEZIERZE WIELKOPOLSKIE LAKE LAND. Rąbin near Inowrocław, alt. 60 m 18°14'E/52°47'N, 7 July 1959, *J. Wilkoń-Michalska* (TRN); NIZINA ŚRODKOWOMAZOWIECKA LOWLAND. Near Łowicz, alt. 60 m, 19°54'E/52°7'N, s.d., *Szubert* (WA 39508); Surroundings of Warszawa, alt. 60 m, 20°59'E/52°18'N, 1869, *Cybulski* (WA 39492); [Warszawa] Młociny, on Wisła river, alt. 60 m, 20°55'E/52°19'N, Oct. 1967, *H. Tomaszewicz* (WA 64640); Warszawa, on Wisła river near Gdański bridge, alt. 60 m, 21°1'E/52°15'N, 23 Sept. 1967, *Z. Podbielkowski* (WA 64649). – OBNIŻENIE MILICKO-GŁOGOWSKIE BASIN. Osiek near Milicz, alt. 80 m, 17°1'E/51°28'N, 30 Sept. 1965, *M. Ciaciura* (KRAM 357892); Fishpond ca 1.5 km S of Sanie near Żmigród, alt. 85 m, 16°56'E/51°25'N, 27 Aug. 2003, *Z. Hroudová & P. Zákravský* (KRAM 523015, PRA); [*] Small forest fishpond ca 1 km S of Sanie, ca 4 km S of Żmigród, alt. 90 m, 16°56'22,7"E/51°25'25,1"N, 27 Aug. 2003, *Hroudová & Zákravský* (PRA); [*] NE border of Niezgod, 'Staw Niezgod' fishpond, ca 9 km NE of Żmigród, alt. 84 m, 17°02'35,9"E/51°31'07,3"N, 30 Aug. 2003, *Hroudová & Zákravský* (PRA); ca 1.5 km ESE of Radziądz near Żmigród, fishpond near the road W of the fishpond Jeleń II, alt. 90 m, 16°59'E/51°30'N, 27 Aug. 2003, *Z. Hroudová & P. Zákravský* (KRAM 523013, PRA); Small fishpond at W border of the fishpond Jeleń II, ca 6 km NE of Żmigród; alt. 83 m, 16°59'E/51°31'N, 30 Aug. 2003, *Z. Hroudová & P. Zákravský* (KRAM 523009, PRA); [*] Fishpond at S border of Pogórzyno, ca 5 km S of Milicz, alt. 154 m, 17°17'44,7"E/51°28'53,3"N, 28 Aug. 2003, *Hroudová & Zákravský* (PRA); [*] Small fishpond near the road at SE border of Krośnice, ca 8 km SE of Milicz, alt. 128 m, 17°22'00,6"E; 51°28'04,8"N, 29 Aug. 2003, *Hroudová & Zákravský* (PRA); [*] Fishpond W of Brzostowo, ca 8 km NW of Twardogóra, alt. 118 m, 17°25'10,2"E/51°26'06,7"N, 29 Aug. 2003, *Hroudová & Zákravský* (PRA); [*] Fishpond at W border of Brzostowo, ca 8 km NW of Twardogóra, alt. 122 m, 17°25'12,4"E/51°26'03,1"N, 29 Aug. 2003, *Hroudová & Zákravský* (PRA); Fishpond W of Rybakówka, ca 2 km ESE of Gadkowice near Milicz, alt. 105 m, 17°29'E/51°34'N, 28 Aug. 2003, *Z. Hroudová & P. Zákravský* (KRAM 523016, PRA); Fishpond near the road at N border of Nowe Domy, ca 3.5 km NNE of Żmigród, alt. 91 m, 16°55'E/51°31'N, 30 Aug. 2003, *Z. Hroudová & P. Zákravský* (KRAM 523010, PRA); Fishpond near the road ca 1 km SE of Nowe Domy, ca 3 km NE Żmigród, alt. 82 m, 16°56'E/51°31'N, 30 Aug. 2003, *Z. Hroudová & P. Zákravský* (KRAM 523019, PRA); Fishpond near the road from Żmigród to Milicz, ca 2.5 km W of Łąki, alt. 89 m, 17°6'E/51°30'N, 30 Aug. 2003, *Z. Hroudová & P. Zákravský* (KRAM 523011, PRA); Fishpond near the road at NW border of Ruda Sułowska, ca 10 km W of Milicz, alt. 95 m, 17°7'E/51°31'N, 30 Aug. 2003, *Z. Hroudová & P. Zákravský* (KRAM 523018, PRA); Fishpond near the road ca 1 km NW of Ruda Sułowska, ca 11 km W of Milicz, alt. 95 m, 17°6'E/51°31'N, 30 Aug. 2003, *Z. Hroudová & P. Zákravský* (KRAM 523020, PRA); Fishpond near the branch road to Potasznia, ca 1 km SW of Górka, ca 8 km of Sulmierzyce, alt. 108 m, 17°31'E/51°32'N, 31 Aug. 2003, *Z. Hroudová & P. Zákravský* (KRAM 523012, PRA); Fishpond near the road ca 1 km SW of Górka, ca 8 km S of Sulmierzyce, alt. 103 m, 31 Aug. 2003, 17°31'E/51°31'N, *Z. Hroudová & P. Zákravský* (KRAM 523008, PRA); Fifth (western) fishpond at SW border of the village of Joachimówka, ca 10 km SW of Sulmierzyce, alt. 98 m, 17°29'E/51°32'N, 31 Aug. 2003, *Z. Hroudová & P. Zákravský* (KRAM 523007, PRA); Third (middle) fishpond at S border of Joachimówka, ca 9 km SSW of Sulmierzyce, alt. 105 m, 17°29'E/51°32'N, 31 Aug. 2003, *Z. Hroudová & P. Zákravský* (PRA); NIZINA ŚLĄSKA LOWLAND. Zwischen Schmarsee u. Bohrau an den Ufern der Oelse [between Smardzów and Borowa, NE of Wrocław], alt. 130 m, 17°20'E/51°12'N, June 1842, s.coll. (GLM 142048); Wrocław, on Odra river opposite to the cathedral, alt. 100 m, 17°3'E/51°6'N, 25 Aug. 1952, *S. Marek* (KRAM 357900, 357899, 357898, 357897; in no. 357897 some fruits flattened); Wrocław, Mielizna Odry shallow, alt. 100 m, 17°1'E/51°7'N, 10 Oct. 1952, *T. Kowal* (KRAM 357893, 357894; in no. 357894 flattened fruits); Rędzin near Wrocław, 16°58'E/51°10'N, 25 June 1964, *H. Radomska* (WRSL 16675); Stogi near Strzelin, W of the village, alt. 167 m 67°59'E/50°51'N, 7 Sept. 1965, *J. Serwatka* (KRAM 355661). – [*] NIECKA NIDZIAŃSKA BASIN. N of Pławowice, middle of three fishponds, ca 1.5 km W of Bobin, 190 m, 20°24'47,2"E/50°10'50,2"N, 24 Aug. 2003, *Z. Hroudová, P. Zákravský & J. J. Wójcicki* (PRA); Pławowice near Brzesko Nowe, alt. 226 m, 20°24'E/50°10'N, 5 Aug. 1969, *A. Sendel* (KRA 137051); Kazimierza Mała near Kazimierza Wielka, alt. 182 m, 20°31'E/50°15'N, 12 July 1972, *T. Tacik & A. Palkowa* (BP 600881, KRA 72162, TRN); Kazimierza Mała, valley of Nidzica river, alt. 180 m, 20°31'E/50°15'N, 12 July 1972, *A. Palkowa & T. Tacik* (JE); Kazimierza Wielka, fishpond in the town, alt. 166 m, 20°29'E/50°16'N, 24 Aug. 2003, *Z. Hroudová, P. Zákravský & J. J. Wójcicki* (KRAM 523017, PRA); S border of the village of Wolwanowice between Bobin

and Kościelec, alt. 180 m, 20°25'E/50°11'N, 24 Aug. 2003, Z. Hroudová, P. Zákravský & J. J. Wójcicki (KRAM 523014, PRA); Grabowiec [near Łuczyce], alt. 270 m, 20°5'E/50°10'N, 10 July 1970, M. Raciniowska (TRN). – BRAMA KRAKOWSKA GATE. Skawina, W of Samborek, alt. 240 m, 19°50'E/49°58'N, 27 Aug. 1949, B. Pawłowski (KRAM 373064). – WYŻYNA KRAKOWSKO-CZĘSTOCHOWSKA UPLAND. [Kraków] Mydlniki alt. 221 m, 19°51'E/50°5'N, 19 July 1990, Lanczowska (KRAM 399094). – WYŻYNA LUBELSKA UPLAND. Lublin, valley of Bystrzyca river near Park Ludowy, alt. 160 m, 22°34'E/51°15'N, 4 Aug. 1999, E. Golińska (LBL); Popów near Józefów, on Wisła river, alt. 130 m, 21°49'E/50°59'N, 22 July 1959, D. Fijałkowski (LBL). – POLESIE PODLASKIE. Sławatycze, on Bug river, alt. 140 m, 23°33'E/51°45'N, 26 Aug. 1963, D. Fijałkowski (LBL). – WYŻYNA ZACHODNIOWOŁYŃSKA UPLAND. Husynne on Bug river near, alt. 160 m, 23°51'E/51°8'N, s.d., K. Łapczyński (WA 39501). – KOTLINA SANDOMIERSKA BASIN. Ostrów Dolny [near Przemyśl], 22°44'E/49°48'N, 26 Aug. 1988, J. Kędzierska (KRAM 394923); Hurko near Przemyśl, alt. 180 m, 22°55'E/49°47'N, 22 Aug. 1973, J. Piórecki (KRA 72882).

***Bolboschoenus maritimus* (L.) Palla**

(Figs 2b & 6a–f)

in Hallier & Brand, Syn. Deutsch. Schweiz. Fl., ed. 3, 3: 2532. 1905.

≡ *Scirpus maritimus* L. Sp. Pl.: 51. 1753. – INDICATIO LOCOTYPICA: Habitat in Europae litoribus maritimis. – LECTOTYPE (Smith & Kukkonen 1999: 356): Herb. Celsius 2: 212 (UPS). – EPITYPE: (Smith & Kukkonen 1999: 356): [Sweden] E. Roslagen, par. Börstill, 2 km W. Kallö, near Husbacka 14.10.1995 Nilsson 9515 (UPS; ISOEPI TYPE PR!).

= *Scirpus compactus* Hoffm. Deutschl. Fl.: 25. 1800. ≡ *Bolboschoenus maritimus* subsp. *compactus* (Hoffm.) Hejny in Dostál. Květ. ČSR: 1844. 1950. ≡ *Scirpus maritimus* f. *compactus* (Hoffm.) Junge Jahrb. Hamburg. Wiss. Anst. Beih. 25(3): 259, 1908. – INDICATIO LOCOTYPICA: [Germany]. – LECTOTYPE: (Marhold et al. 2006): Vahl, 1787, Fl. Danica, no. 937. – EPITYPE: (Marhold et al. 2006): [Sweden] E. Roslagen, par. Börstill, 2 km W. Kallö, near Husbacka 14.10.1995, Nilsson 9515 (UPS; ISOEPI TYPE PR!).

Perennial plants with richly branched underground rhizomes bearing spherical to ellipsoid tubers (1–)2–4 cm in diameter. Plants (0.3–)0.7–1.0(–1.5) m tall. In flowering shoots the upper leaf-

less part of the stem is usually 1/3–1/2 of total stem length. Inflorescence either head-like, consisting only of clustered, sessile spikelets, or formed of a central group of 3–7(–10) sessile spikelets and 1–2(–4) rays each bearing 1–4(–5) spikelets. Styles trifid, but frequently some flowers with bifid styles also present in the same inflorescence. Achenes elliptical, obovate to broadly obovate in outline, 3.0–3.2 mm long, (1.8–)2.1–2.3 mm wide, with short beak on summit, on abaxial side round or with round edge, sometimes lenticular. Perianth bristles caducous. Achenes mostly medium brown to rusty brown, rarely dark brown at maturity, with well-visible polygonal network structure on surface (anticlinal cell walls depressed) (Fig. 2b). Cross section of achenes oval, flat-convex to sub-trigonal, pericarp formed of thick exocarp layer consisting of cylindrical cells radially elongated and filled with air, and sclerenchymatic mesocarp and endocarp; exocarp mostly ca twice as thick as mesocarp.

CHROMOSOME NUMBER. $n = 55$.

SPECIMENS EXAMINED. POLAND. Owczary near Busko, 2003, leg. Z. Hroudová & P. Zákravský (Fig. 7).

VARIABILITY. *Bolboschoenus maritimus* is highly variable in inflorescence morphology and structure, and in fruit shape. The inflorescence may vary from a branched one with 2–4 rays bearing 2–4 spikelets to a head-like inflorescence with only sessile spikelets; an extreme case is the occurrence of only one sessile spikelet, sometimes treated as the *monostachyate* form (Fig. 6b). An inflorescence with only one spikelet is frequently formed in young plants flowering for the first time, or in plants under a shortage of water or nutrients. In other cases the plants may form narrow, cylindrical, very long catkin-like spikelets (2–4 cm), with a great proportion of sterile flowers. This aberration corresponds to the *macrostachyate* form also found in other *Bolboschoenus* species (Browning et al. 1998; Egorova & Tatanov 2002; Tatanov 2003b). Spikelet length generally depends on habitat and weather conditions during the growing season, but the influence of genotype should not be ruled out; differences between plants from various localities persisted to some extent in

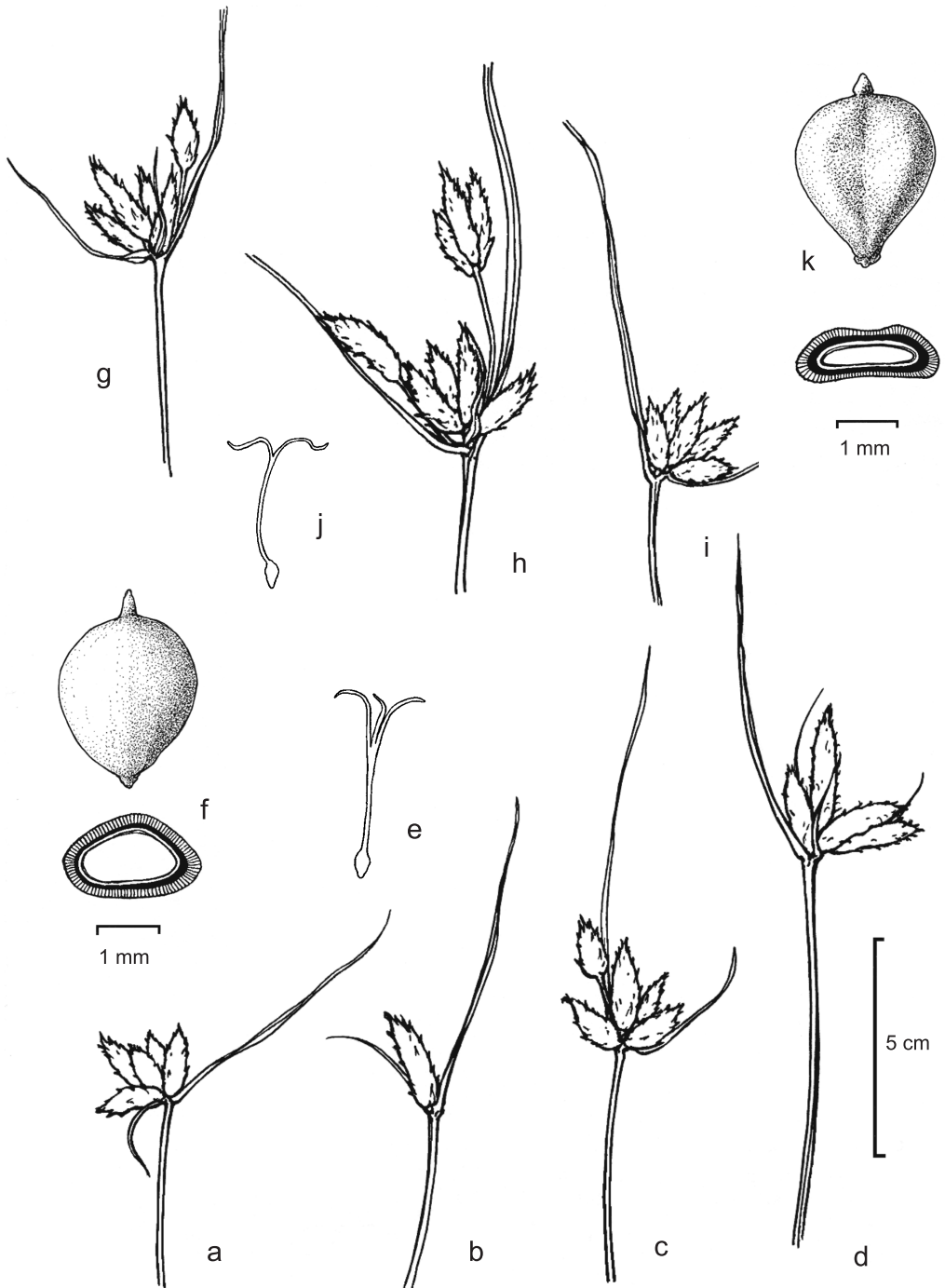


Fig. 6. a–f – *Bolboschoenus maritimus* (L.) Palla: a–d inflorescence (a & b – Łeba, c – Owczary, d – Kórnik), e – pistil with trifid style, f – achene (view on abaxial side and cross section); g–k – *Bolboschoenus planiculmis* (F. Schmidt) T. V. Egorova: g–i inflorescence (g – Kaszyce Wielkie, h & i – Kazimierza Wielka), j – pistil with bifid style, k – achene (view on abaxial side and cross section). Del. Z. Hroudová.

cultivated plants as well (Hroudová, unpublished data). Fruit shape may vary markedly within and between populations of *B. maritimus*. In addition to round or subtrigonal achenes, achenes that are almost flat to only slightly convex on the dorsal side may occur in the same infructescence. Their proportion is often related to the presence of flowers with trifid and bifid styles (flat achenes originate from flowers with bifid styles). Plants with only bifid styles are infrequently found: some flowering plants with bifid styles collected in Gdańsk (Danzig: Am Loch bei Weichselmünde, 1872, *C. Baenitz*, PRC, BRNM 08180/38, 08170/38, W 8886, 8887; Danzig: Strand bei Neufahrwasser, 1871, *C. Baenitz*, LI, B) were determined as *Bolboschoenus* cf. *planiculmis* (based on style branching), but other plants from the same locality (Danzig: Am Loch bei Weichselmünde, 1872, *C. Baenitz*, W 19030, BP 34370, 34376, 34407) had convex fruits, leading to their determination as *B. maritimus*. Because some of the fruiting plants had bifid styles associated with somewhat flattened fruits (e.g., sheet W 34376), we suppose that all these plants collected in Gdańsk originated from a population of *B. maritimus* with bifid styles, not from a mixed population of *B. maritimus* and *B. planiculmis*. Exocarp layer thickness and its relation to mesocarp thickness vary in *B. maritimus* fruits as well, but generally the exocarp is thicker.

HABITATS. *Bolboschoenus maritimus* is predominantly a halophyte, but it can also survive and grow in non-saline habitats. It inhabits brackish sites along seacoast as well as inland saline habitats; it may be found in wet field depressions drying in summer, on banks of rivers close to their outlets to the sea, in channels and lakes (especially those close to the sea). Sometimes the species invades man-made secondary habitats (e.g., near railway lines, drainage ditches). *Bolboschoenus maritimus* is well adapted to fluctuations of water level, especially to summer drying connected with increased concentrations of salt ions in the soil.

DISTRIBUTION IN POLAND. The documented localities of *B. maritimus* are scattered west of the Vistula River (Fig. 8). Further localities should be

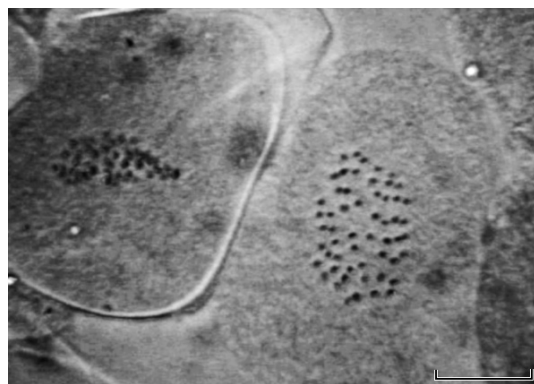


Fig. 7. Meiotic chromosomes of *Bolboschoenus maritimus* (L.) Palla (Owczary). Scale bar = 10 μ m. Phot. V. Jarolímová.

found especially along the Baltic coast. Its natural inland distribution is probably limited mainly by the availability of proper habitats.

EXSICCATES. POLAND. A. Kneucker. *Cyperaceae* (exclus. *Carices*), *Restionaceae* et *Juncaceae* exsiccatae. IV. Lieferung. 1902. No. 97. *Scirpus maritimus* (L.) f. *monostachys*. Salzhaltige Wiesen am rechter Swineufer oberhalb Swinemünde [Świnoujście] in Pommern, alt. 1 m, 14°15'E/53°54'N, 25–28 June 1901, A. Lüderwaldt (B, GZU 014111, 014152, PR, PRC, W 1569); Begleitpflanzen: *Schoenoplectus tabernaemontani*, *Blysmus rufus*, *Spergularia salina* etc. – A. Callier. Flora silesiaca exsiccata. Nr. 106. *Scirpus maritimus* L. Militsch [Milicz]: Bahnhof, alt. 100 m, 17°16'E/51°51'N, 8 July [18]89, Callier (WA 81020).

OTHER MATERIAL SEEN. POLAND. POBRZEŻE SZCZECIŃSKIE SEA-COAST. Am Swineufer bei Swinemünde [Świnoujście], alt. 0 m, 14°15'E/53°54'N, 5 Sept. [18]68, s.coll. (JE); Dünen, alt. 0 m, 14°24'E/53°55'N, Aug. [18]91, R. Ruthe (JE); Swineufer bei Westswine [Świnoujście-Płachcin Uznam], alt. 0 m, 14°15'E/53°53'N, 30 Sept. [18]93, R. Ruthe (WA); Swineufer, alt. 0 m, 14°15'E/53°54'N, 12 July [18]93, R. Ruthe (WA); 30 Sept. 1893 (B); 30 Oct. [18]93 (LI); 3 Oct. 1894 (BP 34400, JE, PRC, PR); 3 Oct. [18]94 (WA 102197); 13 Aug. 1896 (KRA 210835, WA); Świnoujście, alt. 0 m, 20 July 1966, 14°21'E/53°51'N, H. Piotrowska (UGDA); between park and see, alt. 0 m, 14°16'E/53°55'N, 27 Aug. 1963, H. Piotrowska (UGDA – two specimens); Odra-Port, alt. 0 m, 14°15'E/53°54'N, 25 July 1962, H. Piotrowska (UGDA – two specimens); Uznam, near Bożyce, on Kanał Piastowski, alt. 0 m, 14°19'E/53°50'N, 14 Aug. 1956, H. Piotrowska (UGDA); Wolin, Dziwnowo, Dziwna river estuary, alt.

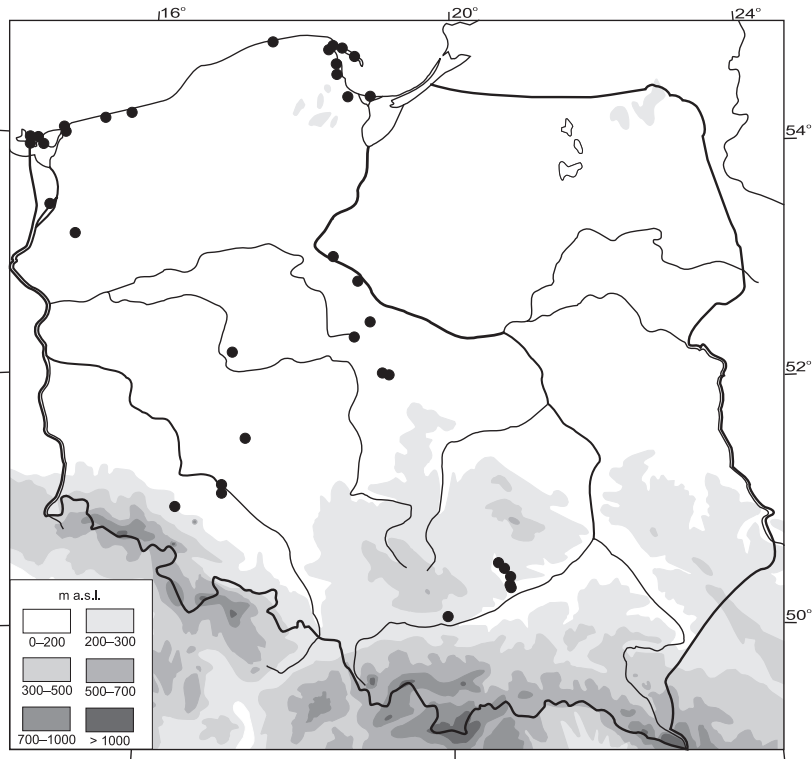


Fig. 8. Distribution of *Bolboschoenus maritimus* (L.) Palla in Poland.

0 m, 14°45'E/54°1'N, 16 Aug. 1958, *H. Piotrowska* (UGDA); E of Lubin, on Zalew Szczeciński bay, alt. 0 m, 15 July 1951, 14°29'E/53°52'N, *H. Piotrowska* (UGDA); Bei Kalkofen am Vietziger See [near Mieliń], alt. 0 m, 14°15'E/53°53'N, July 1889, *Winkelmann* (JE); Wrzosowo – Żółcino near Kamień [Pomorski], alt. 0 m, 14°48'E/54°1'N, 24 July [19]71, *M. Jasnowski* (SZCZ); Dziwnów near Kamień Pomorski, alt. 0 m, 14°47'E/53°58'N, 16 Aug. 1949, *J. Mowszowicz* (LOD 132416); Berg-Dievenow [Dziwnów], alt. 0 m, 14°46'E/54°1'N, 4 Aug. 1936, *H. Reichenbach* (JE); Štětín [Szczecin], alt. 0 m, 14°34'E/53°25'N, 26 Aug. 1948, *Reitmayrová* (BRNM 78179; mixed sheet with *B. laticarpus*); Turze near Pyrzyce, SW of Jezioro Miedwie lake, alt. 0 m, 14°53'E/53°13'N, 30 July 1954, *J. Mądałski* (KRAM 465474); between Mrzeżyn and Trzebusz, alt. 0 m, 15°16'E/54°7'N, 30 Aug. 1968, *H. Piotrowska* (UGDA); Kołobrzeg, E of Prośnica river estuary, alt. 0 m, 15°35'E/54°11'N, 14 July 1947, *J. Mądałski* (KRAM 465473). – POBRZEŻE KOSZALIŃSKIE SEACOAST. Łeba, on Łeba, alt. 0 m, 17°33'E/54°46'N, 30 July 1953, *J. Mądałski* (KRAM 465460); on channel between the lake and sea, alt. 0 m, 17°32'E/54°46'N,

29 Aug. 1955, *A. & J. Kornasiowie* (KRA 60591); Jezioro Łebsko lake, ca 3 km SW of Łeba, alt. 0 m, 17°31'E/54°42'N, 1983, *P. Zákravský* (PRA); Jastarnia (Hel), alt. 10 m, 18°40'E/54°42'N, 13 July 1922, *J. Zabłocki* (KRAM 219378); Gniezdzewo near Puck, ca 1 km SE of the village, alt. 0 m, 18°24'E/54°45'N, 5 Sept. 1969, *J. Mądałski* (KRAM 465454); Półwysep Hel peninsula, between Wielka-Wieś [Władysławowo] and Chałupy, alt. 0 m, 18°27'E/54°47'N, 20 Aug. [19]62, *W. Raclawska* (LOD 132415); Władysławowo, 'Słone Łąki' reserve, 18°24'E/54°47'N, *M. Piątek & J. Cabala* (KRAM 531117, PRA); N of Rewa, 'Beka' reserve, 18°26'E/54°38'N, *M. Piątek & J. Cabala* (KRAM 531116, PRA); Rewa, 'Mechelińskie Łąki' reserve, 18°28'E/54°37'N, *M. Piątek & J. Cabala* (KRAM 531118, PRA); Danzig [Gdańsk], bei Weichselmünde [Wisłoujście], alt. 5 m, 18°40'E/54°24'N, 8 July [18]72, *C. Baenitz* (BP 34370, 34376, 34407, W 19030); Gdańsk, alt. 5 m, 18°41'E/54°24'N, 1929, *U. Nürnberg* (B). – PRADOLINA TORUŃSKO-EBERSWALDZKA VALLEY. Thorn [Toruń], Ufer am Jakobsfort, alt. 40 m, 18°36'E/53°0'N, 19 July 1885, *G. Froelich* (WA 26567); alt. 30 m, 18°36'E/53°0'N, 19 July 1885, *G. Froelich*

(JE); Ciechocinek, alt. 40 m, 18°48'E/52°53'N, 1873, *K. Łapczyński* (WA 39516, 39499); 5 Aug. 1881, *F. Karo* (WA 39512); July 1889, *A. Zalewski* (WA 39491, 39503); July 1912, *K. Rouppert* (BRNU 261313, KRA 68978); s.d., *K. Rouppert* (KRA 68977); July 1912, s.coll. (GZU 14143); s.d., s.coll. (WA 39530); 14 Aug. 1973, *L. Fagasiewicz* (LOD 89292). – POJEZIERZE WIELKOPOLSKIE LAKELAND. Kórnik, on Jezioro Kórnickie lake, alt. 60 m, 17°8'E/52°15'N, 1983 *P. Zákravský* (PRA); Świętosławice near Babiak, NE of Jezioro Brdowskie lake, alt. 100 m, 18°44'E/52°23'N, 30 July 1983, *L. Samosiej* (LOD 84589); N of Jezioro Borzymowskie lake [S of Włocławek], alt. 80 m, 18°59'E/52°29'N, 19 June [19]83, *L. Samosiej* (LOD 84588). – NIZINA ŚRODKOWOMAZOWIECKA LOWLAND. Błonie near Łęczyca, alt. 120 m, 19°8'E/52°5'N, 19 Sept. [19]52, *L. Fagasiewicz* (LOD 132411); Łęczyca-Leszczce, alt. 110 m, 19°13'E/52°4'N, 16 July 1961, *R. Olaczek* (LOD 132413). – NIZINA ŚLĄSKA LOWLAND. Breslau [Wrocław], Eisenbahn, 17°2'E/51°6'N 11 Aug. 1871, *Uechtritz* (BRNM 08163/38); am Wege nach Oltaschin [Wrocław-Oltaszyn], alt. 100 m, 17°2'E/51°4'N, s.d., *Penbak?* (B). – POGÓRZE ZACHODNIO-SUDECKIE FOOTHILLS. Striegau, Ausstuf an der Eisenbahn bei Haidau [Międzyrzecze near Strzegom], alt. 200 m, 16°21'E/50°57'N, 28 July 1870, *J. Zimmermann* (GLM 115474, Hb. Wenck). – BRAMA KRAKOWSKA GATE. [Kraków] Kapelanka, alt. 220 m, 19°56'E/50°6'N, 15 June 1910, *A. Żmuda* (WA 39520). – NIECKA NIDZIĄSKA BASIN. Wolica Siesławska near Busko Zdrój, alt. 240 m, 20°43'E/50°28'N, 30 Sept. 1955, *A. Jasiewicz* (KRAM 67221, 67223, 429116); Owczary near Busko, alt. 220 m 20°45'E/50°27'N, 6 June 1957, *Z. Kucowa* (KRAM 95537); 30 Aug. 1974, *R. Ochrya* (KRAM 226836); alt. 212 m, 20°45'25,9"E/50°26'47,2"N, 24 Aug. 2003, *Z. Hroudová, P. Zákravský & J. J. Wójcicki* (PRA); Chotel Czerwony near Wiślica, alt. ca 180 m, 20°43'E/50°23'N, 7 July 2005, *M. Piątek* (KRAM 531119, PRA), 2 Sept. 2005, *J. J. Wójcicki & M. Piątek* (KRAM 531112, 531113, PRA); Gadawa, 20°48'E/50°23'N, 2 Sept. 2005, *J. J. Wójcicki & M. Piątek* (KRAM 531114, 531115, PRA).

Bolboschoenus planiculmis (F. Schmidt) T. V. Egorova
(Fig. 6g–k)

Rast. Centr. Azii 3: 20. 1967.

≡ *Scirpus planiculmis* F. Schmidt, Reis. Amur-Land., Bot.: 190, 1868. – INDICATIO LOCOTYPICA: Ssussuja-Mündung auf schammigem Boden. – LECTOTYPE: (Egorova & Tatanov 2003: 140): Ssussuja Mündung auf schlammigen [sic!] Boden, 10.8.1861, *F. Schmidt*

s.n. (LE!). – EPITYPE: (Egorova & Tatanov 2003: 140): Yuzhnyi Sakhalin, Anivskii zaliv, okolo sel. Sinba (Dachnoe), primorskie plavni (*M. G. Popov s. n.* 12. 9. 1948 LE!).

= *Scirpus koshevníkovi* Litv. ex Kots, Bull. Soc. Nat. Mosc. 57: 220. 1882. ≡ *Bolboschoenus koshevníkovi* (Litv. ex Kots) A. E. Kozhev., Sosud. Rast. Sovet. Dal'nego Vostoka 3: 189. 1988. – INDICATIO LOCOTYPICA: Oblast' Voiska Donskago bliz stantsii Uryupinskoi. – NEOTYPE: (Egorova & Tatanov 2003: 141): Novotscherkassk, ad ripam fluvii Axaj, 9.6.1911, *A. Jakushev s.n.* (LE!).

= *Scirpus biconcavus* Ohwi, Mem. Coll. Sci., Kyoto Imp. Univ., Ser. B 18: 109–110, 1944. – INDICATIO LOCOTYPICA: Yezo: Nemuro. – HOLOTYPE: Nishiwada, prope Nemuro, Yezo, 10–11.9.1931, *J. Ohwi s.n.* (KYO!).

Plants with a richly branched underground rhizome system bearing numerous, mostly small, spherical to ellipsoid tubers 0.5–1.5 cm in diameter. Plants (0.2–)0.5–0.9(–1.1) m tall. In flowering shoots the upper leafless part of the stem is usually 1/3 to 1/2 (sometime more) of total stem length. Inflorescence head-like, consisting of only sessile spikelets or else formed of a central group of 3–7(–11) clustered, sessile spikelets and of 1–2(–4) rays bearing single spikelets or fascicles of 2–3(–5) spikelets. Styles bifid; rarely, some flowers with trifid styles present in the same inflorescence. Achenes obovate to broadly obovate in outline, 3.1–3.8 mm long, 2.2–2.5 mm wide, with short beak on summit, concave on abaxial side. Perianth bristles caducous. Achene surface shows a well-visible polygonal network structure (anticlinal cell walls depressed); achenes ocher or light brown to rusty brown at maturity. In cross section, achenes biconcave to flat-concave, with angles radially elongated. Pericarp with well-developed exocarp consisting of air-filled, radially elongated cylindrical cells, and sclerenchymatic mesocarp and endocarp. Exocarp approximately as thick as mesocarp, wider over angles than on concave faces.

CHROMOSOME NUMBER. $n = 54$.

SPECIMENS EXAMINED. POLAND. Small fishpond at NW border of Kaszyce Wielkie near Trzebnica, 2003, leg. *Z. Hroudová & P. Zákravský*. – Kazimierza Wielka, fishpond in town, 2003, leg. *Z. Hroudová*,

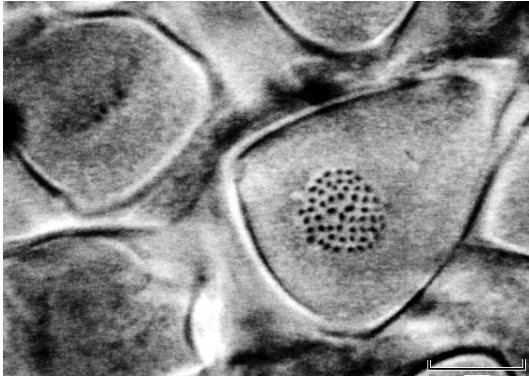


Fig. 9. Meiotic chromosomes of *Bolboschoenus planiculmis* (F. Schmidt) T. V. Egorova (Krościna Mała). Scale bar = 10 μ m. Phot. V. Jarolímová.

P. Zákravský & J. J. Wójcicki. – Small fishpond at S border of Krościna Mała ca 1 km W of Prusice, 2003, leg. *Hroudová & Zákravský* (Fig. 9).

VARIABILITY. Plants of *B. planiculmis* vary in inflorescence structure, from simple head-like ones, occasionally formed by only one spikelet, to branched ones with 3–4 rays. Ray and spikelet length varies as well; spikelets are sometimes long (more than 2 cm long – *macrostachyate* form). This character is evidently influenced by habitat conditions. The number of styles may also vary. Besides flowers with bifid styles, some flowers with trifid styles may be present in the same inflorescence and even in one spikelet. Variation in the number of style branches corresponds to achene shape. Some fruits are very slightly concave to flattened, exceptionally even convex to subtrigonal on the abaxial side. Concave fruits have been found to originate from flowers with bifid styles, while convex fruits develop from flowers with trifid styles (Ducháček 2002).

HABITAT. This species occupies habitats with fluctuating water levels, such as shallow fishponds, lakes, river banks, ditches and temporarily flooded depressions. *Bolboschoenus planiculmis* is quite able to survive in terrestrial conditions on open soil of shores after water recedes, and in temporarily wet depressions drying in summer; thus it is well adapted to secondary habitats. Unlike *B. yagara*, it usually does not form extensive stands

over whole fishponds, but forms a belt along the shoreline. *Bolboschoenus planiculmis* tolerates a wide range of soil chemistry. It may occur on base-poor substrates as well as in slightly saline habitats. Owing to the smaller size of the plants, the occurrence of this species may be limited by competition from other plants, especially in the reed belt; this would explain its adaptation to using temporarily free niches.

DISTRIBUTION IN POLAND. The localities of *B. planiculmis* in Poland known to date are rare (Fig. 10). More numerous stations are concentrated in the fishpond area in the environs of Milicz, while others are widely scattered in the Polish lowlands. The only known locality in the Polish Carpathians, from the vicinity of an artificial water reservoir in Tęgoborze, does not exceed 270 m a.s.l. The species may be overlooked in natural habitats, especially when sterile, but the observed distribution may be the actual one because *B. planiculmis* attains northern limit of its European distribution in Poland.

MATERIAL SEEN. POLAND. POBRZEŻE SZCZECIŃSKIE SEA-COAST. Śtětín [Szczecin], on Odra river, alt. 0 m, 14°34'E/53°25'N, 28 Aug. 1948, *Reitmayerová* (BRNM 78180). – PRADOLINA TORUŃSKO-EBERSWALDZKA VALLEY. Toruń, on Wisła river, alt. 30 m, 18°38'E/53°1'N, July 1922, s.coll. (WA 39532). – OBNIŻENIE MILICKO-GŁOGOWSKIE BASIN. Kaszyce Milickie near Milicz, SE of the village, alt. 80 m, 17°0'E/51°26'N, 30 Sept. 1965, *M. Ciaciura* (KRAM 357890); Small fishpond at NW border of Kaszyce Wielkie near Trzebnica, alt. 90 m, 17°1'E/51°25'N, 27 Aug. 2003, *Z. Hroudová & P. Zákravský* (KRAM 523006, PRA); Zielony Dąb [Osiek] near Milicz, alt. 80 m, 17°08'E/51°36'N, 30 Sept. 1965, *M. Ciaciura* (KRAM 357891); Glumbowitz a. Wohlau [Głębowice, Wołów], alt. 80 m 16°44'E/51°27'N, Aug. 1891, *Schwarz* (M 80439, PRC); [*] Small fishpond at S border of Krościna Mała ca 1 km W of Prusice, alt. 105 m; 16°56'39,5"E/51°22'16,3"N, 27 Aug. 2003, *Z. Hroudová & P. Zákravský* (PRA). – NIZINA ŚLĄSKO-ŁUŻYCKA LOWLAND. Bei Oslau [Osła near Bolesławiec], alt. 120 m, 15°45'E/51°19'N, June 1835, *Winkler* (PR). – NIZINA PÓLNOCPODLASKA LOWLAND. Białystok Centralny, alt. 160 m, 23°9'E/53°8'N, 27 June 1972, *A. Sokołowski* (BIL 48159). – POJEZIERZE LITEWSKIE LAKE LAND. Palki [peninsula] near Augustów, alt. 120 m, 23°01'E/53°50'N, 6 Aug. 1971, *A. Sokołowski* (BIL

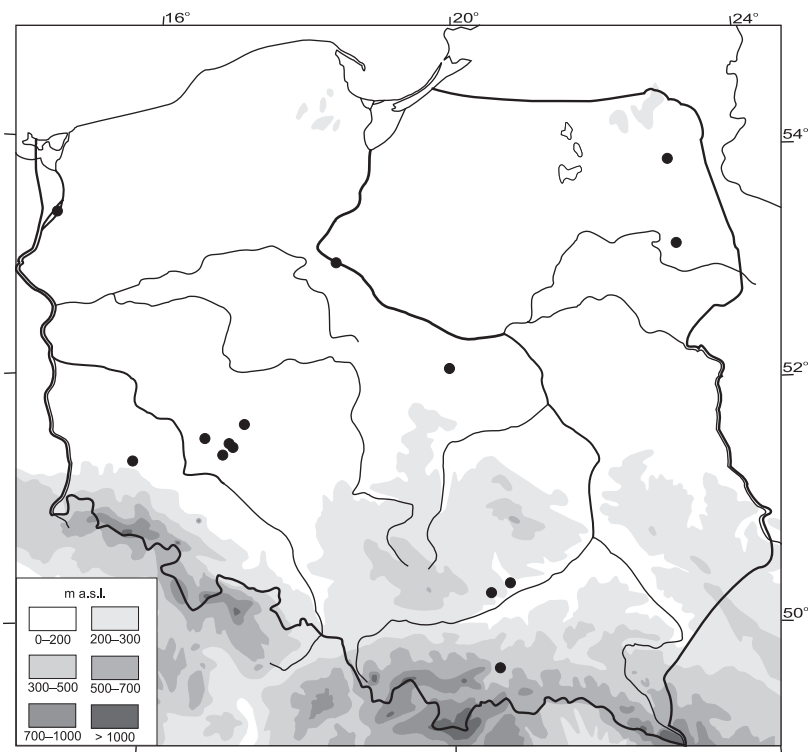


Fig. 10. Distribution of *Bolboschoenus planiculmis* (F. Schmidt) T. V. Egorova in Poland.

42842). – NIZINA ŚRODKOWOMAZOWIECKA LOWLAND. Pilaszków near Pruszków, alt. 60 m, 19°53'E/52°5'N, 26 Sept. 1966, K. Nowak (WA 77332). – NIECKA NIDZIAŃSKA BASIN. Kazimierza Wielka, fishpond in the town, alt. 166 m, 20°29'E/50°16'N, 24 Aug. 2003, Z. Hroudová, P. Zákravský & J. J. Wójcicki (KRAM 523005, PRA); Chotel Czerwony near Wislica, alt. ca 180 m, 20°43'E/50°23'N, 2 Sept. 2005, J. J. Wójcicki & M. Piątek (KRAM 531106–531111, PRA); Szczerbaków, 20°39'E/50°20'N, 2 Sept. 2005, J. J. Wójcicki & M. Piątek (KRAM 531120, 531121, PRA – intermediate forms between *B. planiculmis* and *B. maritimus*) – POGÓRZE ŚRODKOWOBESKIDZKIE FOOT-HILLS. Zbiornik Rożnowski reservoir, Tęgoborze, alt. 260 m, 20°39'E/49°43'N, 18 Aug. 1973, S. Loster (KRA 128174); 21 Aug. 1973, S. Loster (KRA 128173).

DISCUSSION

The variability in fruit shape and anatomy found within *Bolboschoenus maritimus* s.l. by other authors in the past corresponds well with the char-

acters of the taxa recognized at present. In his studies on the fruit anatomy of European genera of several subfamilies of the family Cyperaceae, including *B. maritimus* s.l., Marek (1958) confirmed the difference between the genera *Bolboschoenus* and *Schoenoplectus* based on pericarp structure. In terms of the recent classification, the drawings of the pericarp in cross section in his paper do not represent characters of *B. maritimus* s.str., but more probably *B. laticarpus*. At the same time, in his paper on fruit morphology of the same representatives of the family Cyperaceae, Kowal (1958) distinguished two morphotypes of fruits of *B. maritimus*, plano-convex and trigonous, but no taxonomic value was attributed to this character. Unfortunately, no voucher material is listed in either paper. In a recent paper by Klimko and Kreft (1999), probably only populations of *B. maritimus* s.str. were studied, and therefore no significant differences in fruit shape between coastal and inland populations were found.

In the Polish plants of the genus *Bolboschoenus*, the range of variation of inflorescence morphology, fruit shape and fruit anatomy is comparable with that of plants from surrounding Central European countries. Fertile plants were reliably determinable in most cases. With the exception of the plants from Gdańsk given above, trifid styles prevailed in *B. maritimus*, as is typical of most European populations of this species (according to Browning *et al.* 1996, trifid styles are more common in Europe, while bifid styles prevail in North American populations of *B. maritimus*). In *B. laticarpus*, flattened achenes were found in addition to trigonous ones in some plants, especially in the vicinity of Wrocław (e.g., *leg. Marek* 1952, KRAM 357897; *leg. Kowal* 1952, KRAM 357894), and achene shape also varied in plants from the Milicz area (see Fig. 1g). The puzzling variability observed in some *Bolboschoenus* populations may be related to possible hybridization, but this process is poorly studied so far.

Various chromosome numbers are provided for *B. maritimus* s.l. in the literature: for example, $2n = 76-77$, 80, 86, 104, 110 by Casper and Krausch (1980), or $2n = 104$ by Rothmaler (1982) for Central Europe (for complete list of published chromosome numbers, see Jarolímová & Hroudová 1998). Counting of chromosomes in *Bolboschoenus* is difficult, as in other members of the family Cyperaceae, and counting of haploid numbers in meiosis appeared to be a better method than counting somatic chromosomes. Jarolímová (in Jarolímová & Hroudová 1998) counted chromosome numbers in *Bolboschoenus* taxa from 85 localities in Europe, and only haploid numbers $n = 54$ and $n = 55$ were found, consistent with the chromosome counts presented in this paper. Using the currently accepted taxonomic classification, they found only $n = 55$ in *B. yagara*; $n = 54$ was typical of *B. planiculmis* (only occasionally $n = 55$); $n = 54$ and 55 , with $n = 54$ prevailing, were found in *B. laticarpus*; and $n = 54$ and 55 , with $n = 55$ prevailing, were found in *B. maritimus*. From Poland, they found chromosome number $n = 54$ in *B. maritimus* s.str. in plants from two localities (Łeba and Kórnik lakes). The newly counted number $n = 55$ in *B. maritimus* from Owczary

near Busko, however, is partly inconsistent with the number $2n = ca\ 55-60$ previously reported from this locality (Jankun 1985). Interestingly, the two chromosome numbers $n = 54$ and 55 found in *B. laticarpus*, as well as the occurrence of meiotic irregularities, support the hybrid origin of this species, and the frequent occurrence of $n = 54$ suggests its possible relation with *B. planiculmis*.

Central Europe is an important area where the distributions of some *Bolboschoenus* taxa overlap (Hroudová *et al.*, manuscript). Such a pattern of distribution is a result of complex Quaternary history, and landscape that provides highly diversified habitats including freshwater littoral habitats, temporarily flooded field depressions, and salt marshes, combined with various mineral substrates and different climatic conditions. All members of *Bolboschoenus* recognized in Poland are distributed exclusively in lowlands below 300 m a.s.l. (Figs 4, 5, 8, 10). *Bolboschoenus planiculmis* and *B. laticarpus*, concentrated in the center of the continent, reach their northern limits of geographical distribution in Poland. *Bolboschoenus maritimus*, distributed west of the Vistula River, continues along the coastal region in Germany, while *B. yagara* is concentrated in flat fishpond basins in the south of the country, a landscape typical of the species in Central Europe (e.g., Upper Lusatia, South Bohemia, Styria).

The habitats of all species recognized in Poland are characterized by fluctuating water levels, as in the other European regions, but there are marked differences in the habitats of individual species. *Bolboschoenus yagara* grows in littoral habitats, mostly in fishpond areas, *B. laticarpus* predominantly occupies river floodplains, *B. planiculmis* is scattered along shores of small shallow fishponds or summer-drying pools and flooded depressions, while *B. maritimus* prefers mostly saline habitats. Temporary emergence of the bottom provides appropriate conditions for seed germination and seedling establishment, as well as for vegetative reproduction. Two growing seasons of moist emerged bottom are necessary for seedlings of *B. yagara* to attain fruiting stage (Hroudová *et al.* 1996); this rarely occurs in fishponds, and thus vegetative reproduction prevails there.

There is a great lack of herbarium specimens of *Bolboschoenus* from lake districts in northern Poland (Figs 4, 5, 8, 10; see also Zajac & Zajac 2001), only a few flowering, indeterminable plants were collected so far. This may be due in part to differences in the practices of collectors and the intensity of floristic investigations at regional level. Another possibility is that the occurrence of *Bolboschoenus* species in lake districts really is rare, and related to the ecological requirements of these species. Stabilized water levels in lakes, leading to the development of extensive reed stands, limits the spread and development of *Bolboschoenus* populations. *Bolboschoenus* can take advantage of temporary open niches after water level declines, and without water level fluctuations it is usually suppressed by reed (*Phragmites australis*). Reeds are a strong competitor growing at the same range of depth as *Bolboschoenus* species. This is one possible explanation of its distribution gap in these regions, but the problem requires further studies.

ACKNOWLEDGEMENTS. We are grateful to the Directors and Keepers of the herbaria B, BIL, BP, BRNM, BRNU, GLM, GZU, JE, KRA, KRAM, LBL, LI, LOD, M, PR, PRA, PRC, SLO, SZCZ, TRN, UGDA, W, WA and WRSL for making specimens available for study, to Eva Zamazalová for cultivating the plants in the experimental garden in Průhonice, to Jiří Machač for processing the photographs, and to Zbigniew Mirek and Zbigniew Szelać for valuable suggestions on the manuscript. This work was funded by the Polish Academy of Sciences under its scientific exchange program, the Grant Agency of the Academy of Sciences of the Czech Republic (grant no. A 6005905) and the Academy of Sciences of the Czech Republic (grant nos. AV0Z 6005908 and KSK 6005114).

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Received 16 February 2005