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ELEOCHARIS MAMILLATA – DISTRIBUTION AND INFRASPECIFIC DIFFERENTIATION

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Abstract: *Eleocharis mamillata* is a widespread species in the temperate zone of Eurasia and North America. Populations in mountainous areas of Europe and Asia (the Pyrenees, Alps, Carpathians, Balkans, Ural, Caucasus, Altai) can be separated as subspecies *austriaca* differing mainly by the stylopodium shape from the nominate subspecies. Clear morphological criteria to create a separate infraspecific taxon in East Asia could not be found.

Keywords: *Cyperaceae, Eleocharis austriaca, E. ussuriensis, E. leptostylopodiata*

INTRODUCTION

Most problems concerning the central and north European species of *Eleocharis* subser. *Eleocharis* (= *E.* subser. *Palustres* SVENSON) seemed to be solved by the exhaustive work of STRANDHEDE (1961, 1966). Only *Eleocharis mamillata* subsp. *austriaca* remained somewhat unclear. During a survey of *E. mamillata* in Hesse/Germany (GREGOR & BARTH 1998) some populations could neither be ascribed to subsp. *mamillata* nor to subsp. *austriaca*. Therefore, it seemed worthwhile to investigate the taxonomic value of the subsp. *austriaca*.

Eleocharis austriaca and related taxa

HAYEK (1910) mentions weaker palisade parenchyma, grey-green culms, always 6 perigon bristles, and the base of style (stylopodium) not clearly separated from the nut in the protologue of *Eleocharis austriaca* as differentiating characters from *E. palustris*. *E. austriaca* was separated by him from *E. mamillata* by stiffer, grey-green culms, 15–20 vascular bundles, a better developed palisade parenchyma, and a higher stylopodium (swollen lower part of the style attached to the fruit). Except for the culm colour and bristle number these characters were confirmed by later authors (e.g. STRANDHEDE 1966). Material distributed in the "Flora stiriaca exsiccata" (collected by Karl Fritsch) on which the name *E. austriaca* is based partly does not belong to *E. austriaca*. According to WALTERS (1953), the sheets in Lund (L) and Göteborg (GB) are mixed collections of *E. austriaca* and *E. mamillata*. Two sheets in Berlin (B), one in London (BM), and one in Vienna (W) belong to *E. mamillata* s.str. One sheet in Graz (GZU 014585) belongs to *E. austriaca*, another one (GZU 014586) contains *E. austriaca* and *E. mamillata* s.str. The lectotype in Helsinki (H) selected by WALTERS (1953) is in accordance with the protologue, except for the culm-colour (light green) and the number of bristles (mostly 5).

BEAUVERD (1921) described *Eleocharis benedicta* from Lac Bénit in the French Alps south of Lake of Geneva. STRANDHEDE (1966) studied material from the type locality and considered it to belong to *E. mamillata* subsp. *austriaca*. Beauverd was not aware of the close relationship between *E. benedicta* and *E. mamillata*, erroneously attributing to the latter persistent bracts. *E. austriaca* is not mentioned by him. The shape of the stylopodium of *E. benedicta* ranges, according to BEAUVERD (1921), from less high than broad to as high as broad. In material from the type locality STRANDHEDE (1966: 108) measured a stylopodium with a length of 0.5 and a width of 0.4 mm. My own measurements of a specimen from the type locality revealed a ratio of 1.07 : 1 (see Appendix). According to the protologue the stylopodium shape is in the intermediate range between subsp. *mamillata* and subsp. *austriaca*. So, *E. benedicta* should not be considered synonymous with *E. austriaca*. If this is accepted, the first combination in the rank of subspecies for the taxon with high stylopodia would be *Scirpus palustris* subsp. *benedictus* (DOUIN 1931).

FRITSCH (1926) placed *E. austriaca* together with other "grey-green forms" of *E. palustris* s.l. under *E. glaucescens* (WILLD.) SCHULT. The holotype of *Scirpus glaucescens* in the Willdenow-herbarium in Berlin (B) consists of an immature plant with two spikes. "Habitat in America boreali" is marked on the sheet.

ZINSERLING (1935) did not mention *E. austriaca*, but described two species similar to *E. mamillata*: *E. ussuriensis* from the Russian Far East with short conical stylopodia (height/width: 1.2–1.5/1) and *E. leptostylopodiata* from the Ural with narrow conical stylopodia (height/width: 2–3/1).

WALTERS (1953) confirmed most of Hayek's characters of *E. austriaca,* stressing its intermediate position between *E. mamillata* and *E. palustris*. He found new characters differentiating *E. austriaca* and *E. mamillata* from *E. palustris*: the number of epidermal cell rows between fibre-rows (= collenchyma strands) as 3–5 versus 1–3, and the form of the stomata: guard cells longer than subsidiary cells (short side convex) versus guard cells shorter than subsidiary cells (short side concave). *E. leptostylopodiata* is regarded as "possibly identical" to *E. austriaca*, later (WALTERS 1959) as synonymous.

STRANDHEDE (1961, 1966) found the number of achenes per centimetre in the spike helpful for the differentiation of the subspecies: approx. 60 in subsp. *austriaca* versus approx. 42 in subsp. *mamillata*. The most important character to distinguish the two subspecies proved to be the stylopodium shape: mamillate in subsp. *mamillata* with a mean height-width ratio of 0.75 : 1; elongated triangular in subsp. *austriaca* with a mean height-width ratio of 1.5 : 1. *E. leptostylopodiata* and *E. ussuriensis* are regarded as synonyms of *E. mamillata* subsp. *austriaca*.

EGOROVA (1976) regarded *E. austriaca* and *E. leptostylopodiata* as synonymous. In the Russian Far East, northern China, Japan, and Korea *E. mamillata* subsp. *ussuriensis* is differentiated from the nominate subspecies by short conical broad-based stylopodia. *Eleocharis mamillata* var. *cyclocarpa* KITAGAWA is regarded as synonymous with *E. mamillata* subsp. *ussuriensis*.

MATERIAL AND METHODS

Present study is based on about 600 specimens of *Eleocharis mamillata* from the public herbaria and private collections mentioned in the Acknowledgements. The following characters were recorded for each specimen: length and width of achene and stylopodium, number of hypogynous bristles, number of vascular bundles of a fertile stem and number of achenes per cm in the spike (receptacle density). Five ripe fruits (in some cases only 3) from one specimen were measured. The number of vascular bundles and the stem-diameter were measured once, at a height of about 2/3 of the stem. The achene-length was measured without a short stalk, which is sometimes present. Two-cleft or three-cleft bristles were counted as 2 or 3 bristles. Receptacle density was only measured on spikes that had shed their fruits and glumes. This state is only reached in mature spikes, collected late in season. Most herbarium specimens have been collected at an earlier state of development.

Correlations between parameters were tested by Spearman's correlation coefficient (r_S). Using a graphic adaptation ("full width at half maximum") described by BRANDT (1999) normal-distributions were calculated from the data of the stylopodium shape. Principal components analysis (PCA) was performed using SPSS. The maps were produced with BRAHMS (Botanical Research And Herbarium Management System) and MUSICA.

RESULTS AND DISCUSSION

Principal components analysis

The first three principal components (PCs) explain 78% of the total variance (46.8%, 19.6%, and 11.5% for PC1, PC2, and PC3 respectively). PC1 has high positive loadings for stylopodium height/stylopodium width, fruit density, number of vascular bundles, and stylopodium height and high negative loadings for stylopodium width, stylopodium width/achene width and number of bristles; PC2 has high positive loadings for achene height and achene width (Fig. 1). The scatter diagram of the first two components (Fig. 2) distinguishes subsp. *mamillata* and subsp. *austriaca* as differentiated by stylopodium shape (see below). The two groups are connected by intermediates. Parameters with high loadings on PC1 will be discussed further. Height (1.31 mm ± 0.1 s.d.) and width (1.13 mm ± 0.09 s.d.) of the achenes that have high positive loadings on PC2 are not correlated with the stylopodium shape.

Of all parameters, only the stylopodium shape (stylopodium height by stylopodium width) shows a bimodal distribution with peaks at about 0.725 and 1.4 (Fig. 3). However, the stylopodium shape generally has a high variation. In a cultivated specimen from the Rhön in Thuringia/Germany 120 measurements had an arithmetic mean of 1.37 with a standard deviation of 0.16 and extreme values of 1.04 and 1.79. According to BRANDT (1999), two normal distributions with arithmetic means of 0.725 ± 0.11 s.d. and 1.4 ± 0.15 s.d. can be calculated. The peak at 0.725 corresponds to subsp. *mamillata*, the peak at 1.4 to subsp. *austriaca*. Accordingly, specimens with a stylopodium shape of 0.96 or less are regarded as subsp. *mamillata* and those with a stylopodium shape of 1.11 or more as subsp. *austriaca*. Approx. 8% (36 of 464) of the measurements fall in the range 0.97–1.1.

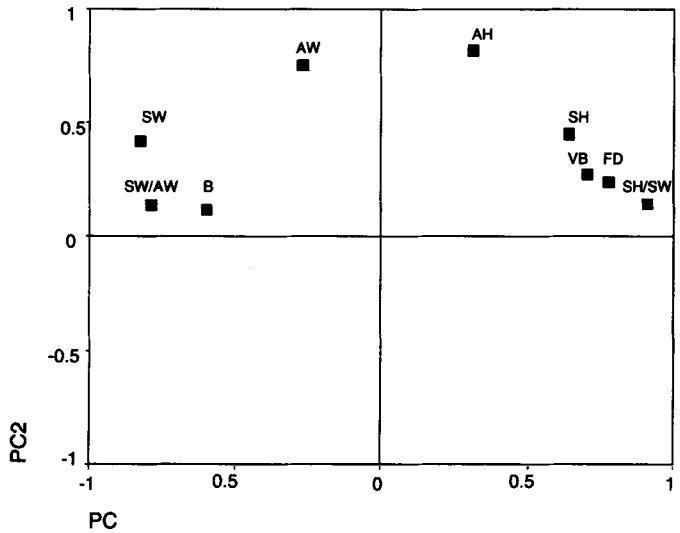


Fig. 1. PCA, character loadings; varimax rotation, eigenvalue 1.1; $n = 119$. AH – achene height, AW – achene width, B – number of bristles, FD – fruit density, SH – stylopodium height, SW – stylopodium width, VB – number of vascular bundles.

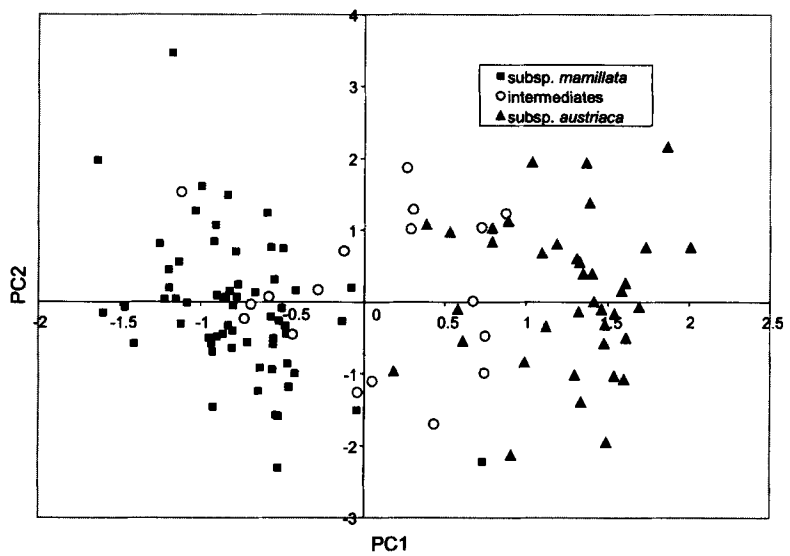


Fig. 2. PCA, scatter diagram; $n = 119$. Assignment to subsp. *austriaca*, subsp. *mamillata* and intermediates according to stylopodium shape.

The relative stylopodium width (= stylopodium width by achene width) (Fig. 4) shows a rather strong positive correlation with the stylopodium shape ($r_S = 0.65$; $P \leq 0.01$). Specimens with a relative stylopodium width of more than 0.5 can be attributed to subsp. *mamillata*, those with a relative stylopodium width of less than 0.4 to subsp. *austriaca*.

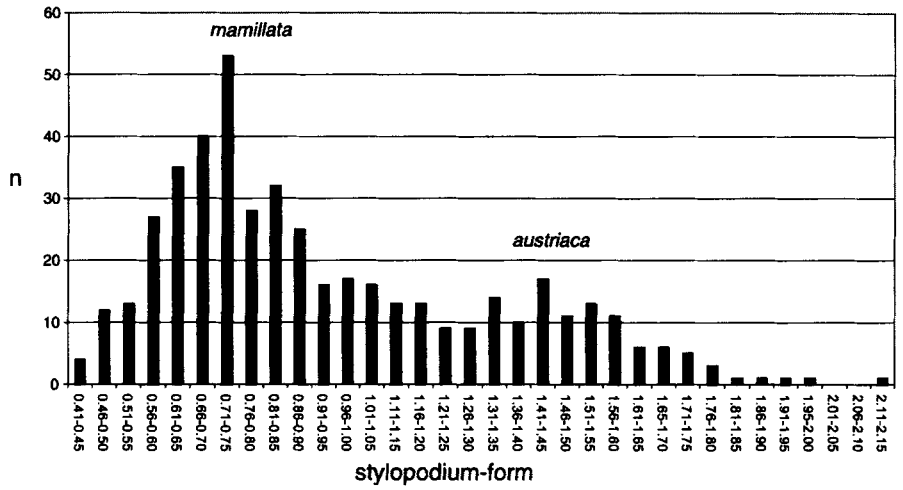


Fig. 3. Stylopodium shape (stylopodium height by stylopodium width); $n = 463$, mean value of measurements of (3–)5 fruits.

The number of vascular bundles (Fig. 5) is positively correlated with the stylopodium shape ($r_S = 0.49$; $P \leq 0.01$). Subsp. *mamillata* tends to have fewer vascular bundles than subsp. *austriaca*.

The number of hypogynous bristles (Fig. 6) is negatively correlated with the stylopodium shape ($r_S = -0.49$; $P \leq 0.01$). Subsp. *mamillata* tends to have more bristles than subsp. *austriaca*.

The receptacle density (fruits per cm; Fig. 7) is positively correlated with stylopodium shape ($r_S = 0.567$; $P \leq 0.01$). Two peaks are discernable: one at 42–45 (subsp. *mamillata*) and one at 66–69 (subsp. *austriaca*).

In summary, the following characters for the two subspecies can be given:

	subsp. *austriaca*	subsp. *mamillata*
stylopodium shape	> 1.1	< 0.97
relative stylopodium width	< 0.4	> 0.5
vascular bundles	> 16	< 13
fruit density	> 70	< 46

Because of the great variation in all characters, identification of plants should be done carefully. Measuring of one spike might not be sufficient. Intermediates between the two subspecies occur regularly.

Taxonomy

The results suggest two infraspecific taxa in *Eleocharis mamillata*. Specimens with high stylopodia occur nearly exclusively in mountain areas of Europe and Asia. It seems appropriate to recognize them as a geographic subspecies (subsp. *austriaca*) with an

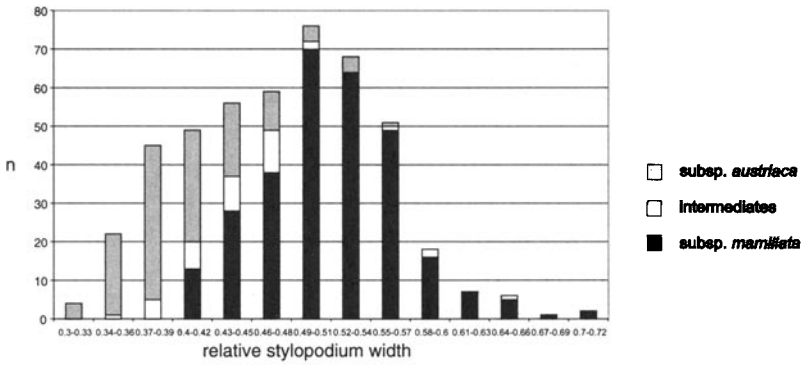


Fig. 4. Relative stylopodium width (= stylopodium width by achene width); $n = 463$, mean of measurements of (3 –)5 fruits.

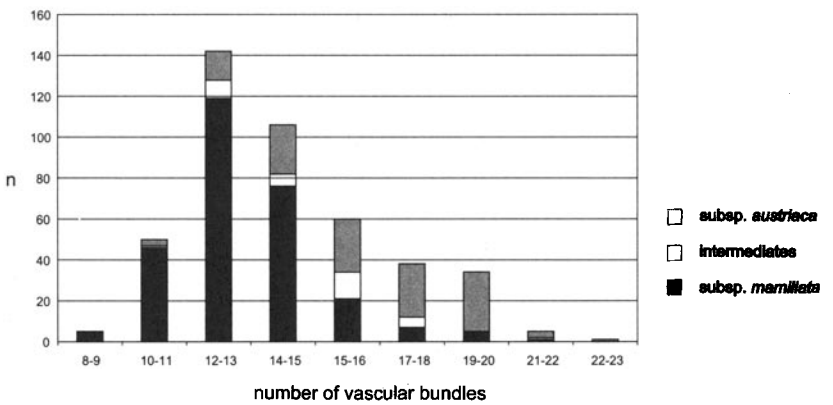


Fig. 5. Number of vascular bundles; $n = 441$.

incoherent area as was already done by STRANDHEDE (1966). Intermediates occur frequently near the range of subsp. *austriaca*, but also in East Asia where subsp. *austriaca* is absent.

Most specimens from East Asia could not be separated from the nominate subspecies. But, as there was only a limited number of specimens available this should be proved with a wider selection of material.

Eleocharis mamillata **(H. LINDB.) H. LINDB. Herb. Norm. 4383 ejusque Sched. Herb. Norm. 44: 108, 1903, "*Heleocharis mamillata*"**

≡ *Scirpus mamillatus* H. LINDB. Acta Soc. Fauna Fl. Fenn. 23(7): 4, 1902, "*Scirpus* (*Heleocharis*) *mamillatus*".
Lectotypus (STRANDHEDE 1966: 144): Herbarium Normale, editum ab I. Dörfler, no. 4383, *Heleocharis mamillata* H. LINDBERG (filius) n. sp.! Fennia. Savonia borealis. In fossa limosa prope "Jorois." (VIII. 1902 H. LINDBERG H).

≡ *Scirpus palustris* subsp. *mamillatus* (H. LINDB.) MELA et CAJANDER Suomen Kasvio: 110, 1906 [citation according to STRANDHEDE 1966].

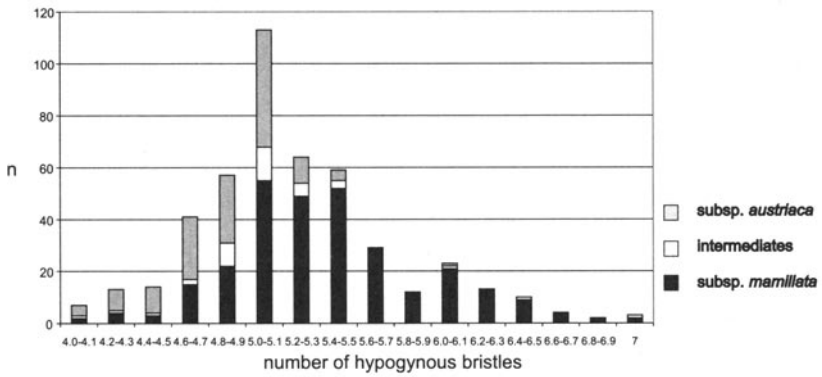


Fig. 6. Number of hypogynous bristles; $n = 464$, mean of measurements of (3–)5 fruits.

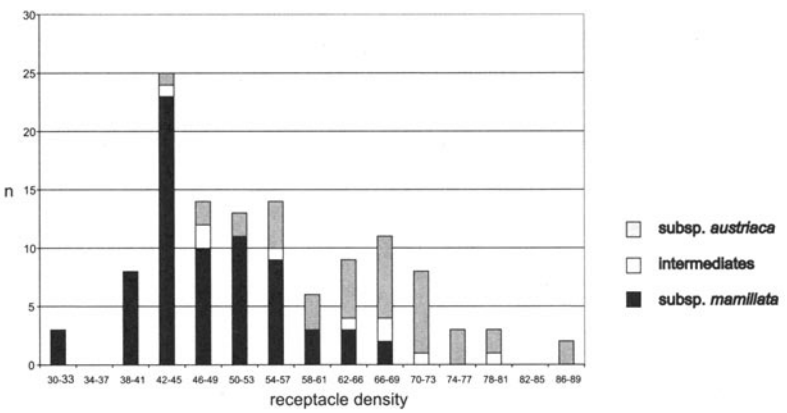


Fig. 7. Receptacle density (fruits per cm); $n = 120$.

≡ *Eleocharis palustris* var. *mamillata* (H. LINDB.) SYR. Ill. Fl. Moskovsk. Gub.: 170, 1906, "*Heleocharis palustris β. mamillatus*".

≡ *Eleocharis palustris* subsp. *mamillata* (H. LINDB.) BEAUVERD Bull. Soc. Bot. Genève Sér. 2, 13: 263, 1921.

≡ *Eleocharis palustris* var. *palustris* f. *mamillata* (H. LINDB.) KRYLOV Fl. Zapad. Sib. 3, 393, 1929, "*Heleocharis palustris* var. *communis* f. *mammillatus*".

= ? *Eleocharis ussuriensis* ZINSERL. Fl. URSS 3: 581, 1935, "*Heleocharis ussuriensis*". Holotypus: [Russia] In valle fl. Rakovka, prope Nikolsk-Ussurijsk, No. 907 (1913 V. L. KOMAROV LE).

≡ *Eleocharis mamillata* f. *ussuriensis* (ZINSERL.) Y.L. CHANG in Y.L. CHANG et Y.L. YANG, Fl. Pl. Herb. Chinae Bor.-Or. 11: 32, 1976.

≡ *Eleocharis mamillata* subsp. *ussuriensis* (ZINSERL.) T.V. EGOROVA Fl. Eur. URSS 2: 113, 1976.

= ? *Eleocharis mamillata* var. *cyclocarpa* KITAG. Lin. Fl. Manshur.: 119, 1939. Typus: not selected.

= ? *Eleocharis satoi* OHWI Acta Phytotax. Geobot. 2: 28, 1933.
Typus: not selected.
- *Eleocharis macrostachya* auct. non BRITTON IN SMALL Fl. S. E. US, 184, 1903: FERNALD et BRACKET 1929.

Note: The name *Heleocharis mamillatus* was invalidly published by LINDBERG (1902) as a synonym of *Scirpus* (*Heleocharis*) *mamillatus* referring to "LINDB. fil. apud Soc. p. F. et Fl. Fenn., 3. 5. 1902". At this date he probably presented his new species at a session of the society. Centuria 44 of the "Herbarium Normale" was issued in January 1903 (GREGOR & BARTH 1998). A bill for the herbarium Haussknecht is dated "Wien, den 16. I. 1903". It was received in the London Natural History Museum on the 31st of January 1903. STRANDHEDE's (1965) choice of lectotype is correct even as number 4383 of "Herbarium Normale" appeared after (probably in January 1903) Lindberg's article in the "Acta Societatis pro Fauna et Flora Fennica" (between October and December 1902). In the later publication a group of collections was cited from: "Savonia bor., Jorois, Järvikylä, allgemein in Torfteichen, Wassertümpeln und auf sumpfigen Uferwiesen mit *Carex rostrata* und *Equisetum limosum*, 8. 1902, H. L." Number 4383 of the "Herbarium Normale" is part of this collection.

Eleocharis mamillata subsp. *austriaca* (HAYEK) STRANDH. Opera Bot. 9(2): 9, 1965.

≡ *Eleocharis austriaca* HAYEK Fl. Stiriac. Exs., 922, 1910; Schedae Fl. Stiriac. Exs. 19/20: 8, 1910, "*Heleocharis austriaca*".
Lectotypus (WALTERS 1953: 284): [Austria] Stiria media, in stagno exsiccato ad pagum St. Peter prope urbem Graz, 370 m (VI. 1906 K. FRITSCH H!).
= *Eleocharis leptostylopodiata* ZINSERL. Fl. URSS 3, 581, 1935.
Holotypus: Baschkiria, Canton Zalair, jug. Irendyk, No. 515 (O. E. KNORRING LE)
- *Eleocharis glaucescens* auct. non (WILLD.) SCHULT. Mant. 2: 89, 1824: FRITSCH 1926.

Note: PODPĚRA (1929) included *Heleocharis austriaca* HAYEK under the letter D in *Heleocharis palustris* R.BR. besides *Heleocharis eupalustris* SYME (as A), *Heleocharis mamillata* LINDB. f. (as B) and *Heleocharis glaucescens* SCHULT. (as C). He did not indicate the rank of these taxa and thus did not make the combination *Eleocharis palustris* subsp. *austriaca* as stated by STRANDHEDE (1966).

Eleocharis mamillata subsp. *mamillata vergens* ad subsp. *austriaca*

Eleocharis benedicta BEAUVERD Bull. Soc. Bot. Genève Sér. 2, 13: 245, 264, 1921.
Locus typicus according to protologue: En cordon littoral submergé d'*Equisetum limosum* du lac Bénit, 1500 m d'alt., massif des Vergys, Haute Savoie.
≡ *Scirpus palustris* subsp. *benedictus* (BEAUVERD) DOUIN Fl. Compl. Fr. 11: 81, 1931.

Note: The exact taxonomic position of *Eleocharis benedicta* depends on the choice of a lectotype. STRANDHEDE (1965: 145) indicated a specimen from the Herbarium Boissier in G (No. 4277. Haute Savoie: plage limoneuse du lac Bénit, ... , 15.8.22) as holotype. This is unacceptable as this specimen was collected after the description of *Eleocharis benedicta*.

Distribution of *Eleocharis mamillata* subsp. *mamillata*

LINDBERG (1902) regarded *Eleocharis mamillata* to be confined to northern Europe: Finland, central Sweden, southern Norway, the Russian part of Karelia and Ingermanland (SW of St. Petersburg). HAYEK (1910) was the first to mention it from the Alps. FERNALD & BRACKETT (1929) considered *E. macrostachya* synonymous with *E. mamillata* reporting it from Illinois to British Columbia, south to Louisiana, Texas, Mexico, and southern California. At least two of their cited specimens actually belong to *E. mamillata* (MACOUN *34773 & 78193*). However, the type of *E. macrostachya* (NY, "collected by Edward Palmer in the Indian Territory, chiefly on the False Washita, between Fort Cobb and Fort Abruckle, 1868"; fruits with four hypogynous bristles, stylopodium separated from the nut) and certainly the majority of the specimens cited by them do not belong to *E. mamillata*. ZINSERLING (1935) states a large distribution area of *E. mamillata*: European part of Russia, west and central Siberia, and upper Amur basin. HULTÉN & FRIES (1986) mapped a continuous distribution in north, central and eastern Europe, a couple of isolated areas in Siberia, Korea, north eastern China, Japan (Kyushu, Honshu, Hokkaido), two localities in Alaska and one in British Columbia.

The examined herbarium specimens confirm and extend the already huge distribution area of this taxon (maps 1 and 2) that stretches from central Europe through Eurasia to Korea and Japan. In North America it extends from Alaska to Quebec. The distribution coincides generally with the temperate vegetation zone, approx. between 50° and 60° N. On the western sides of the continents, distribution extends into the boreal zone with northernmost stations in Alaska at 66° N (14.VII.1975 J. & C. TAYLOR *19612* NY) and in Scandinavia at 67° N (9.VIII.1927 MONTELL STU). In East Asia, the range extends further south. In Japan the southernmost seen specimen was from the Tokyo Prefecture (10.VII.1915 MAKINO MO) at 36° N. According to OHWI (1965), it also occurs further south in Kyushu.

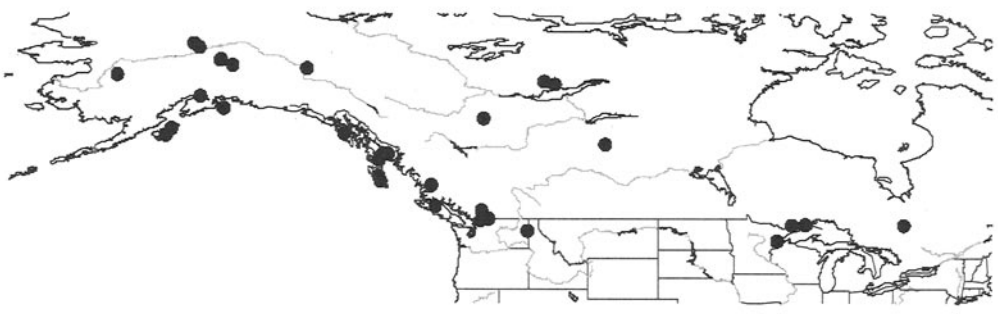
Eleocharis mamillata in East Asia

KITAGAWA (1939) described *Eleocharis mamillata* var. *cyclocarpa* from Manchuria, as differing from the nominate subspecies by round lense-shaped nuts and broad stylopodia distinctly "acuminate-constricted". KITAGAWA (1939) and OHWI (1944, 1965) report *E. mamillata* var. *cyclocarpa* as the only variant in Manchuria, Hokkaido, Hondo, Kyushu, Sakhalin, and Korea; TSIN & FA-TSUAN (1961) as the only variant in China. *E. ussuriensis* is regarded by OHWI (1944) as synonymous with *E. mamillata* var. *cyclocarpa*.

According to EGOROVA (1976, 1980, 1981), *Eleocharis mamillata* subsp. *ussuriensis* has a wide distribution in the south of the Russian Far East, north-eastern China, Korea, and Japan. The stylopodia of subsp. *ussuriensis* shall be slightly less broad than high (0.4–0.5 × 0.5–0.6 mm), a stylopodium shape allegedly hardly found in Europe. Subsp. *austriaca* is similar and intermediates occur. Egorova is ambiguous about the occurrence of subsp. *mamillata* in East Asia.

The limited number of examined herbarium sheets from East Asia shows a considerable percentage of specimens with conical stylopodia (stylopodium shape between 0.9 and 1.1): 27% (n = 22) in the Russian Far East, 50% (n = 10) in Japan. In North America, the corresponding figure was 15% (n = 34), and in Russia outside the Far East 12% (n = 42). As

Map 1. Distribution of *Eleocharis mamillata* subsp. *mamillata* in Eurasia. Specimens with an intermediate stylopodium shape between subsp. *mamillata* and subsp. *austriaca* from East Asia are included.



Map 2. Distribution of *Eleocharis mamillata* subsp. *mamillata* in America.

Map 3. Distribution of *Eleocharis mamillata* subsp. *austriaca*. Type locality of *E. leptostylopodiata* in the Ural is included.

the majority of the seen specimens from East Asia is, however, not distinguishable from European, west or central Siberian or North American subsp. *mamillata*, it seems inappropriate to identify a geographical variant or subspecies in East Asia.

Distribution of *Eleocharis mamillata* subsp. *austriaca*

Many authors mention this taxon from mountain areas of Europe: the Pyrenees (WALTERS 1963), Alps and surrounding mountain areas (HAYEK 1910, WALTERS 1953, HOLUB 1964, STRANDHEDE 1966, BERTANI 1988, BUREŠ 1999), and the Carpathians (WALTERS 1959, HOLUB 1964, ŻUKOWSKI 1965, EGOROVA 1976, DANYLYK 1995, BUREŠ 1999). SOÓ (1973) lists a few records from Hungary, WALTERS (1963) one from Bosnia-Herzegovina, and STRANDHEDE (1961) three from Norway. Records from northern England and southern Scotland are given by WALTERS (1963), ROBERTS (1977), and CORNER (1975). NOVIKOV & TICHOMIROV (1980) record it from the Ryazanskaya area southeast of Moscow. According to ZINSERLING (1935), *E. leptostylopodiata* has a highly disjunct distribution in the European part of Russia, the Ural, Siberia (Altai), the Amur region, and the Caucasus. BUBNOVA (1986) maps about 15 records from an area between Novosibirsk, Krasnoyarsk and the Altai. EGOROVA (1991) mentions it from Zakatal'skii Raion in Azerbaijan. A record from Bulgaria (Hisar, distr. Karlova) by URUMOV (1928) for "*Heleocharis palustris* ssp. *mamillata*" might belong to subsp. *austriaca* as the nominate subspecies is so far not recorded from Bulgaria.

The majority of the examined herbarium specimens comes from the Alps and river valleys originating from that region. The occurrence in other European mountain areas (the Pyrenees, Carpathians, Balkan mountains) and the Caucasus was confirmed (map 3). Central European hill regions, such as Harz, Rhön, Bavarian forest and Eifel also revealed a number of records. In northern Germany a couple of populations exist at low altitudes, e.g. at the "Wahner Heide" near Cologne (WOLFF & KORNECK 1984). Three specimens originate from western Siberia north of the Altai.

No plants from Norway or northern England/Scotland were examined. Drawings of plants from northern England (WALTERS 1963, ROBERTS 1977) show plants with a stylopodium about as high as broad which should assign these plants as intermediates between the two subspecies.

Some specimens with a stylopodium shape of more than 1.1 do not fit into this picture (see Appendix). Due to the great variation of the stylopodium shape (Fig. 4) this is not unexpected. Most of these specimens show number of vascular bundles or fruit densities typical for subsp. *mamillata*.

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APPENDIX

A selection of the seen specimens is given in the form: locality (date, collector & collection-number (if present), herbarium abbreviation, vascular bundles/stylopodium shape/stylopodium width by achene width/number of bristles/number of vascular bundles (stem diameter in mm)/receptacle density. – Localities are mostly given in abbreviated form. For a specimen in the private herbarium of the collector no indication of the herbarium is made. The distinction between the two subspecies is made strictly by the stylopodium shape (see above).

Eleocharis mamillata subsp. *austriaca*

Bulgaria: Montes Pirin: opp. Banko: lacus Vasilashki ezera (14.VIII.1990, I. ŠTĚPÁNEK, B, 1.73/0.32/4.2/15(1.7)/-).

France: Kiesgruben nördlich des Waldes bei Fuchs am Buckel (4.VIII.1904, ?, STR, 1.27/0.43/4.8/16(2.0)/48). Ober-Elsaß: Kiesentnahmestelle östlich Daubensand (1.X.1977, D. KORNECK, KR, 1.26/0.48/5/ca. 20 (2.2)/-). **Georgia:** Kazbegi: gorge SE of village (14.VII.1975, I. KUKKONEN *12111*, H, 1.62/0.36/4.8/12(1.2)/-). Distr. Chokhatauri: montes Meskhetskii khrebet: in vicinitate pagi Bakhmaro (21.VII.1979, V. VAŠÁK, W, 1.25/0.37/5/16(1.5)/-).

Germany: Lower Saxony: Osterrode: Teich im Uferbachtal östlich Badenhausen (23.VI.1990, G. DERSCH, 1.79/0.36/4.2/19(1.9)/-). **Northrhine-Westfalia:** Bergisches Land: Genkel Talsperre (30.VIII.1967, A. SCHUMACHER, HBG, 1.36/0.45/4.8/16(2.2)/58). Wahner Heide (5.IX.1982, P. WOLFF *D-R22*, 1.39/0,41/5/18(1.9)/66). Sandgrube ne Grenzkrug (30.IX.1986, E. FOERSTER *860930.2a*, 1.55/0.42/5/?/54). Bergisches Land: Mündungsgebiet des Leienbaches in die Agger bei Derschlag Kloster (6.VIII.1989, K. KIFFE, 1.53/0.38/5/17(1.9)/-). Hochsauerlandkreis: Marsberg, Kiessee an der Diemel bei Westheim (26.VIII.1989, U. RAABE, 1.19/0.37/5.2/20(2.5)/-). **Rhineland-Palatinate:** Süd-Eifel, Kolk in Grube zwischen Bergweiler und Hupperath (25.IX.1988, D. KORNECK, Herbarium Peter Wolff, 1.59/0.47/6/16(1.5)/69). **Saarland:** N Kraftwerk Ernsdorf (30.IX.1995, P. WOLFF *D-S410*, 1.5/0.5/4.6/19(2.2)/66). **Saxony-Anhalt:** Oberharz: Königshütte, Südufer der Talsperre Mandelholz (22.IX.1985, W. ILLIG, HAL, 1.42/0.34/5/17(2.1)/69). **Thuringia:** Thüringer Wald: Humbachs Teich ca. 1.5 km WSW Cottendorf (13.IX.1992, M. SCHNITTLER *1988*, JE, 1.16/0.5/5.2/12(1,2)/-). Grenzstreifen östlich Tann (11.VII.1996, T. GREGOR *500*, FULD, 1.27/0.43/4.2/23(2.5)/ca. 75). Hochrhön: Teiche am W Ortsrand Frankenheim (24.IX.1999, C. AHRNS, 1.12/0.47/4.9/19(1.9)/ ca. 54). Dittersdorf (VII.1881, C. HAUSSKNECHT, JE).

Romania: In rippio arenosis fluvii Temis ad Lagro? (Sept., HEUFFEL, GOET, 1.51/0.4/5/?/-).

Russia: Tomsk. Guv.: R. Tomi (?, ?, MW, 1.18/0.39/4.4714(1.2)7-). Kemerovskaya oblast': Mariinskii rajon. Okr. s. B. Antives (13.VIII.1946, T. GREKHOVA & I. KUZMINOVA, MHA, 1.39/0.37/5/12(1.2)/76). Novosibirskaya oblast': Maslyaninskii r-on: okr. Priicka Egor'evskii: 8 km po doroge na d. Aleksandrovsku (26.VII.1986, I.M. KRASNOBOROV, MW, 1.24/0.38/4.6/14(17)/-).

Spain: Montes Pirineos, ad fossam in prato udo, 4 km ad septentr. a summi collis Pico de Aneto (VIII.1997, J. NĚMEC, Herbarium P. Bureš, 1.44/0.35/?/13(?)/-).

Specimens with an "*austriaca* type" *stylopodium*, but assignment to subsp. *austriaca* very dubious

Japan: Mombetsu (18.VII.1887, FAURIE *725*, F [& WU], 1.24/0.45/4.8/18(2.2)/-). Abaschiro (20.VIII.1892, FAURIE *3573*, WU, 1.31/0.53/5/16(2.4)/48). Environs de Akkashi (28.VIII.1892, FAURIE *8666*, WU [& F], 1.48/0.55/4.6/17(1.2)/-).

Russia: Moskovskaya obl.: Serpukhovskii r-n. (10.VII.1946, B. SMIRNOV, V. VEKHOV & I. MEDVEDEVA, MHA, 1.34/0.34/5/12(2.0)/-). Primor'e, Srednii Sikhotè-Alin', pravyi bereg r. Gadumi, Otmel', 1 km bliz s. Bogopol' (21.VII.1973, M.A. KUBRESHOV, MW, 1.45/0.495/4.6/12(1.2)/-). Mordovskaya ASSR: Bol'she Bereznyasovskii r-n: v 8 km yuzhnee s. Simkino (24.VI.1989, S. MATOROV, MW, 1.37/0.34/4.6/12(1.5)/-).

USA: Alaska : Beetles Quad, No name creek, Mi 79 Dalton Hwy (28.VII.1986, D.F. MURRAY *8976*, ALA, 1.18/0.42/5.2/10(1.7)/42). Alaska : Ophir Quad., Innoko River, vic. Grouch Creek (16.VII.1987, J. DELAPP *648*,

ALA, 1.21/0.45/5.3/10(1.3)/-). Alaska: Dixon Entrance Quad., Prince of Wales Island, Kendrick Bay (12.VIII.1993, M.C. STENSVOLD *6244*, ALA, 1.13/0.46/5/12(1.8)/-).

Intermediates between subsp. *austriaca* and subsp. *mamillata*

Canada: Vegetation Survey along the Mackenzie River, Yellowknife Highway N.W.T. (20.VII.1961, J.W. THIERET & R J. REICH *7831*, F, 1.01/0.48/5/10(1.1)/-).

China: Nanking (10.V.1928, Y.L. KENG *1547*, B, 1.02/0.57/4/18(1.6)/-).

France: Haute Savoie: Lac Bénit (VIII., ?, HBG, 1.07/0.39/5/12(1.3)/-). Jura: Lac de Lamoura (9.VII.1964, S. VAUTIER et al., MHA, 0.97/0.4/4.8/16(1.8)/-).

Mongolia: Mir. Kobdoskii aimak: 75 km na jug ot g. Kobdo: yuzhnoe poberezh'e ozera Chara-us-nur (10.VIII.1982, I.A. TUBANOV *7568*, MW, 1.08/0.48/5.2/16(1.9)/-).

USA: Alaska : Ketchikan Quad., Muskeg ponds N of Lake Ella (15.VII.1993, J. DELAPP & M. DUFFY *93-506*, ALA, 1.04/0.41/4.8/12(1.4)/-).

Eleocharis mamillata subsp. *mamillata*

Belarus: Gomel'skaya obl.: Khvoinikskii r-n: v 3 km yu-z pos. Khv. Polyana (21.VIII.1987, A. SKURATOVIC, MW, 0.84/0.55/5/?/39).

Canada: British Columbia: Chilliwack Valley (25.VII.1901, J.M. MACOUN *34773*, GH, 0.67/0.44/4.2/11(1.2)/-). Lake House, Skagit River (9.VII.1905, J.M. MACOUN *78193*, B, 0.84/0.49/4/10(1.1)/-). Bella Coola (9.VII.1926, B. MCAVOY 35, UBC, 0.49/0.56/5/10(1)/-). Queen Charlotte Islands: about three miles north of Moresby, logging camp (21.VIII.1957, J.A. CALDER *23666* & R.L. TAYLOR, UC, 0.96/0.47/4.6/10(1.7)/38). Queen Charlotte Islands: Moresby Island, about three miles south of mouth of Copper Creek (28.VI.1957, J.A. CALDER *21894*, D.B.O. SAVILE & R.L. TAYLOR, B [& W], 0.76/0.45/4.6/12(1.8)/-). Vancouver Island: area of lakes on Tsitika River plateau west of Mount Cain (VIII.1973, H. ROEMER *129*, UBC, 0.63/0.53/4.2/12(1.2)/-). Kotcho Lake, 100 mi NE of Fort Nelson (14.VII.1983, A.A. ROSE *83195*, UBC, 0.93/0.44/4.6/8(1.0)/-). **Northwest Territories:** Mackenzie District: Yellowknife (25.VII.1949, W.J. CODY & J.B. MCCANSE, CAS, 0.75/0.48/5/12(1.7)/-). **Ontaria:** Thunder Bay City: NW side of expressway in Northwood area of Intercity fen (13.VIII.1979, C.E. GARTON *19091*, UC, 0.75/0.59/4.8/12(1.6)/48). Thunder Bay Dist.: Buda L. access road, 4 km SE of bridge over Weikwabinowaw River (1.VII.1981, C.E. GARTON *20215*, UBC, 0.64/0.47/5/12(1.1)/-). **Quebec:** Canton de Roquemaure : Cté d'Abitibi-ouest (24.VII.1980, C. GAUVIN & D. BERTHIAUME *80-42*, MT, 0.71/0.43/5/12(1.7)/-). **Sasketchewan:** La Loche, 7 mi S-Se, Mile 60 N, Hwy. 155 (28.VI.1971, V.L. HARMS *17625*, MT, 0.81/0.5/4/12(0.9)/-). **Yukon Territory:** Hunker Creek at Independence Cr. (13.VIII.1951, J.D. CAMPBELL 142, MT, 0.74/0.42/5.2/14(2.0)/-).

Finland: Lapponia kemensis, Muonio, Valkiajärvi (9.VIII.1927, J. MONTELL, STU, 0.72/0.44/5.6/14(2.2)/-).

France: Sundgau: Terr. de Belfort: Leval: Fischteich (26.VIII.1967, D. KORNECK, STR, 0.52/0.56/5/16(1.6)/-). Bas-Rhin: N Dambach (29.VIII.1982, P. WOLFF *F-60*, 0.63/0.5/5.6/12(1.4)/45). Bas-Rhin: NE Obersteinbach, Teichboden (1.XI.1984, P. WOLFF *F-183*, 0.74/0.48/6.2/12(2.0)/54).

Germany: Mecklenburg-Western Pomerania: Westendorfer Haussee bei Feldberg (19.V.2000, H. HENCKER, 0.6/0.55/4.7/10(0.9)/-).

Kazakhstan: Karsaki raion: verchov'e r. Sar-Turgai v gorakh Ulutau (22.VII.1929, N. PAVLOV, MW, 0.59/0.55/5.2/10(0.7)/-).

North Korea: Kaipsang (3.VII.1901, U. FAURIE, B, 0.9/0.41/5/18(2.5)/-). Kyojo [Kyonson] (11.VII.1930, J. OHWI *2315*, F, 0.86/0.55/5/14(2.0)/-).

Japan: Tokyo Pref.: Mitaka City: Inokashira (10.VII.1915, T. MAKINO *230129*, MO, 0.82/0.62/5/20(4.9)/-).

USA: Alaska: Margin of small lake near Yes Bay (28.VII.1895, T. HOWELL *1684*, NY, 0.84/0.46/4.6/12(1.6)/-). Back Bay (28.VII.1895, M.W. GORMAN *124*, NY, 0.77/0.51/4.6/10(1.1)/-). Small lake back of Yes Bay (8.VIII.1895, E. HULTÉN, UC, 0.89/0.43/5/10(1.2)/-). Kodiak Island (7.VII.1936, I.W. HUTCHINSON *302*, BM,

0.73/0.41/4.7/12(1.3)/-). Ditch near lake Anchorage (20.VII.1943, C.L. YORK *316*, LL [& LL, MO], 0.79/0.44/4.8/16(2.4)/-). Smith Lake Area, College (17.VIII.1965, V.L. HARMS *4971*, GH, 0.67/0.51/4.4/16(1.7)/-). 2 miles south of [Polar] Circle (14.VII.1975, J. & C. TAYLOR *19612*, NY, 0.64/0.49/5/12(2.2)/-). Fairbanks Quad.: Goldstream Valley (16.VIII.1988, C.L. PARKER *88-190*, MO, 0.84/0.46/5.2/12(2.8)/-). Big Delta Quad.: Birch Lake (29.VIII.1989, C. PARKER *2207*, ALA, 0.61/0.44/5/12(2.0)/-). Seward Quad.: Montague Island, Hanning Bay (13.VIII.1993, M. DUFFY *93-1027*, ALA, 0.6/0.47/4.6/10(1.3)/-). **Minnesota:** Oatka Bay Adition: Duluth (25.VIII.1937, O. LAKELA *2303*, UC, 0.8/0.49/5/12(1.5)/ca. 40). **Washington:** Spokane County: Newman See (9.VII.1916, W.N. SUKSDORF, B, 0.77/0.52/4.75/10(1.2)/-). Whatcom County: Mount Baker National Forest (6.IX.1943, W.C. MUENCHER *16181*, UC, 0.72/0.53/5/13(23)/-).