

***Conocephalum salebrosum* (Marchantiopsida, Conocephalaceae) - a new Holarctic liverwort species**

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Abstract. Detailed analysis of 270 specimens of *Conocephalum conicum* (L.) Dumort., mainly from the POZW Herbarium revealed some diagnostic differences between two cryptic species originally detected on the basis of isozyme studies. Several diagnostic characters were found in the structure of the archegoniophore, sporophyte and sterile thallus. The most reliable diagnostic features are size and structure of stomatal apparatus of the archegoniophore 'heads', type of junction of the air chamber walls with epidermal cells, and the thallus surface details. On the basis of morphological and anatomical diagnostic characters, two formerly cryptic species are recognized following the rules of formal taxonomy. The lectotype of *C. conicum* preserved in FI was found to possess characteristics of cryptic species *C. conicum*-species L. Accordingly, the species previously named as *C. conicum*-species L must bear the name *Conocephalum conicum* (L.) Dumort. No published name was related to *C. conicum* - species S, which is therefore described as a new species: *Conocephalum salebrosum* Szweykowski, Buczkowska & Odrzykoski. Both species are fully described and their diagnostic characters are illustrated. Distribution maps for both species are given.

Key words: Bryophyta, liverworts, *Conocephalum conicum*, *Conocephalum salebrosum*, diagnostic characters, morphological differences, cryptic species.

Introduction

The common and widely distributed liverwort *Conocephalum conicum* (L.) Dumort. is regarded as taxonomically uniform throughout temperate and boreal regions of the Northern Hemisphere (e.g. Müller 1951–1958, Schuster 1992, Paton 1999). Nevertheless, the morphospecies has a complex genetic structure and is known to consist of six cryptic species with more restricted geographical distributions. Genetic distances between these cryptic species are similar to or higher than those between morphologically distinct species of other liverwort genera (Szweykowski and Odrzykoski 1990, Odrzykoski and Szweykowski 1991, Akiyama and Hiraoka 1994).

The discovery of two cryptic species within the *C. conicum* complex in Europe dates back to the first studies of genetic differentiation of this species in Poland (Szweykowski and Krzakowa 1979). Two species were detected as genetic races (L and S) and later named

[†]The first draft of this paper has been prepared by late Professor Jerzy Szweykowski. His sudden death in a car accident in November 2002 obligated junior authors to finish a manuscript and send it for publication (KB, IJO).

cryptic species: *C. conicum* (L.) Dumort.–species L and *C. conicum* (L.) Dumort.–species S, according to the informal nomenclature by Odrzykoski and Szweykowski (1991).

The geographical range of species L is probably restricted to Europe, whereas species S has a wider holarctic distribution. Both occur in moist, shaded and usually calcareous habitats. When growing together they exhibit only slight differences in microhabitat preferences and species S appears to be more tolerant to xeric habitats than species L (Szweykowski et al. 1981; Odrzykoski 1987, 1995).

Living plants can usually be discriminated on the basis of differences in size and the texture of the thallus surface: large and shining versus small and dull. Some other morphometric differences have been detected and shown to persist in a greenhouse culture (Szweykowski and Bobowicz 1978, 1979). Unfortunately, the absence of clear morphological or anatomical diagnostic differences in herbarium specimens (Szweykowski and Bobowicz 1983) caused difficulties in the recognition of these cryptic species according to the ICBN rules (Greuter et al. 2000).

Morphological investigation of a large number of *Conocephalum* Hill samples identified during our isozyme studies led to the detection of several discrete morphological and anatomical characters which separate the cryptic species. In this paper we describe *Conocephalum conicum*–species S as a new species and discuss morphological differences between the new species and *C. conicum* s. str.

Materials and methods

The plants used in this study were collected from natural populations in different parts of Europe (for a complete list of collection sites, see Appendix 1). Each sample was divided into two parts: one was used for greenhouse culture and isozyme analysis; the second was deposited as a voucher at POZW Herbarium.

The morpho-anatomical studies were carried out in two stages. In the first stage herbarium samples of cryptic species originally identified on

the basis of isozyme markers were used to search for diagnostic morphological and anatomical features. A total of 270 colonies (samples) were studied in the first stage: 61 fertile (41 of species L and 20 of species S) and 209 sterile (66 of species L and 143 of species S). In the second stage, characters chosen in the first stage were used for identification of type specimens and other herbarium samples. A total of 324 dried herbarium specimens from: BG, FI, G, KRAM, M, O, PI, STR, W and POZW were studied (see Appendix 2).

From each sample, five thalli and at least three with archegoniophores (in the case of fertile samples) were randomly taken. In order to correlate the traits of the sterile thallus with corresponding archegoniophores, both were analyzed from the same plant. Each thallus with an archegoniophore was identified from a small fragment using isozyme markers (Odrzykoski 1995), and the remaining parts were fixed in 70% ethanol (archegoniophore) or dried (thallus). The 'heads' of archegoniophores were studied using longitudinal sections, and the stalks using cross sections (Table 1, Fig. 1). Thallus cross-sections were made approximately 8–10 mm from the thallus apex. A total of 30 characters (22 quantitative and 8 qualitative) were examined (Table 1). The texture of the dorsal surface of the thallus (character no. 1), was checked after a careful moistening of the dried herbarium specimen. The thallus was placed on a piece of wet blotting paper with rhizoids and ventral scales down and without moistening the upper surface. Thalli treated in this manner regain, after ca 1h, their typical texture and are shining or dull exactly as when alive.

Measurements of 22 quantitative characters were made under a light or a dissecting microscope on five individual thalli and at least three archegoniophores. For each of 22 characters, a mean value (from five measurements made on each individual thallus), was calculated except for length of thallus, which was measured only once. Descriptive statistics and multivariate analyses (Principal Component Analysis "PCA" and Discriminant and Variance Analysis) were performed using STATISTICA 6.0 for Windows.

Results

Our studies reveal some morpho-anatomical differences between the two cryptic species of the *Conocephalum conicum* complex. Differ-

Table 1. List of characters used in biometrical analyses of two species of *Conocephalum*

No.	Character	Method of observation
<i>Sterile thallus</i>		
1	Texture of dorsal thallus surface	in plane view
2	Width of thallus	“_”
3	Length of thallus	“_”
4	Number of air chambers between costa and thallus margin, Fig. 1d	“_”
5	Length of air chambers	“_”
6	Width of air chambers	“_”
7	Diameter of air chamber pores	“_”
8	Width of thallus hyaline margin	“_”
9	Structure of dorsal thallus surface (limits between particular air chambers)	in plane view and in cross section
10	Structure of junction of walls between air chambers with dorsal epidermis	“_”
11	Outer epidermal cell walls	“_”
12	Type of thallus margin	“_”
13	Shape of the hyaline apical cells underlying the pores	“_”
<i>Archegoniophore</i>		
14	Epidermis of archegoniophore air chambers	longitud. section
15	Length of archegoniophore stomatal apparatus	“_”
16	Width of archegoniophore stomatal apparatus	“_”
17	Number of cells on cross section of stalk	cross section
18	Diameter I of stalk (on cross section). Fig. 1g	“_”
19	Diameter II of stalk (on cross section). Fig. 1g	“_”
<i>Sporophyte</i>		
20	Longer diameter of spores	
21	Length of elaters	
22	Width of elaters	
23	Length of epidermal cells of capsule wall	
24	Width of epidermal cells of capsule wall	
25	Width of thickenings of epidermal cells of capsule wall	
26	Distance between thickenings of epidermal cells of capsule wall	
27	Length of inner cells of capsule wall	
28	Width of inner cells of capsule wall	
29	Width of thickenings inner cells of capsule wall	
30	Distance between thickenings of inner cells of capsule wall	

ences were found in the structure of archegoniophores and sporophytes, as well as in sterile thalli (Table 2). Additionally, both species differ significantly with respect to 11 quantitative characters (Table 3). The PCA of 61 fertile samples based on 22 quantitative characters shows the existence of a distinct morpho-anatomical gap between the studied species. The studied samples were divided

into two distinct groups corresponding to groups delimited on the basis of isozyme analyses (Fig. 2). The characters most strongly correlated with the 1st PCA axis were 15, 2, 4, 3 and with the 2nd PCA axis 20, 16, thus these characters were recognized as diagnostic ones (Table 3). Statistically significant Mahalanobis' distance between the species equal to 44.99 ($p \leq 0.001$) and

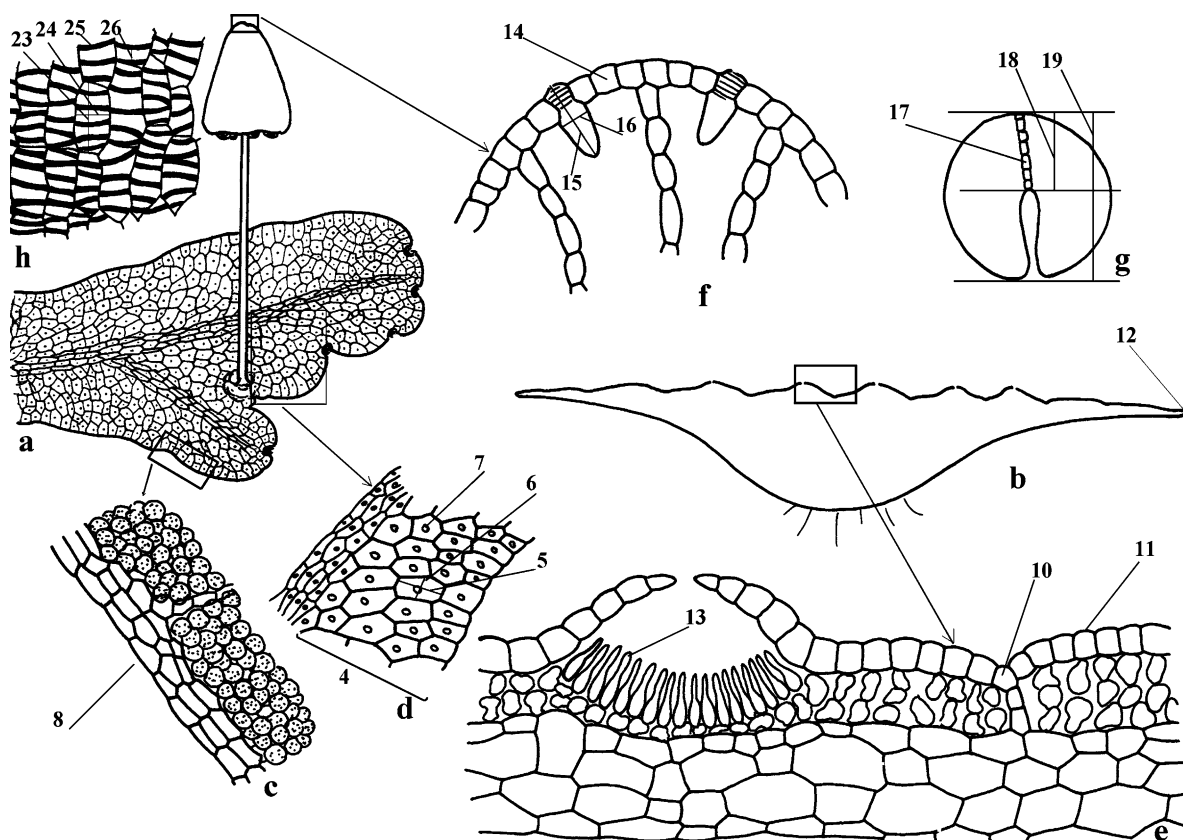


Fig. 1. Diagram showing the methods of measurement: **a** general view, **b**, **e** thallus cross section, **c** hyaline thallus margin, **d** number of air chambers between the costa and thallus margin, **f** longitudinal section of archegoniophore 'head', **g** cross section of archegoniophore stalk, **h** capsule wall

value of statistics F equal to 68.27 ($p \leq 0.001$) in Variance Analysis confirms differences between the species.

A strong correlation between features of the archegoniophore and sterile thallus was also observed. All plants of cryptic species *S* had a longer stomatal apparatus in the archegoniophore 'head', were dull and had an uneven thallus surface (Tables 2, 3; Fig. 3b). In these plants the dorsal epidermis at the junction of the air chamber walls with the epidermis, was distinctly lowered and the highest cells of the walls were inserted between the epidermal cells (Fig. 4d). The plants identified as cryptic species *L* had a smaller stomatal apparatus and a smooth shiny thallus surface (Tables 2, 3; Fig. 3a). The dorsal epidermis of these plants was usually flat, the highest cells of the air

chamber walls only touching the epidermal cells (Fig. 4c). The diagnostic characters (Tables 2, 3) were used during examination of the type specimens and other herbarium samples (see Appendix 2).

***Conocephalum conicum* (L.) Dumort.** Comment. Bot.: 115. 1822 [*Conocephalus conicus*] – *Marchantia conica* L., Sp. Pl. 2: 1138. 1753 – TYPE CITATION: Habitat in Europae locis umbrosis, ripis elevatis; in addition, references to Columna (1606), Bauhin (1623), Micheli (1729) and Dillenius (1741) are provided. Lectotype (*vide* Proskauer 1958: p. 126): the specimen corresponding to the drawing No. 1 in Micheli's (1729), Nov. Plant. Gen.: 3. Hepatica no. 1. tab. 2, fig. 1 (FI!).

The lectotype consists of several thalli (Fig. 6a, b), including several female thalli with archegoniophores. Owing to the great historical

Table 2. Description of 8 qualitative characters in two species of *Conocephalum*. Diagnostic characters are bolded

No.	Character	<i>C. conicum</i>	<i>C. salebrosum</i>
<i>Sterile thallus</i>			
1	Texture of dorsal thallus surface	Shiny (Fig. 3a)	Dull (Fig. 3b)
8	Width of thallus hyaline margin	Broad, usually 3–4 ± elongated cells; rarely fewer (Fig. 4e)	Narrow, usually 1 or 2 ± elongated cells; rarely more (Fig. 4f)
9	Structure of dorsal thallus surface (limits between particular air chambers)	Smooth, limits between particular air chambers usually shallow or indistinct (Fig. 4a)	Uneven, limits between particular air chambers very distinct or deep (Fig. 4b)
10	Structure of the junction of air chamber wall with dorsal epidermis	Highest cell of air chamber wall not inserted, only touching the dorsal epidermal cells (Fig. 4c)	Highest cell of air chamber wall inserted between the dorsal epidermal cells (Fig. 4d)
11	Outer epidermal cell walls	Flat (Fig. 4a)	Inflated (Fig. 4b)
12	Type of thallus margin	Usually plane or recurved (Fig. 4g)	Inflexed or rarely plane (Fig. 4h)
13	Shape of the hyaline apical cells underlying the pores	Flask-shaped	Pyriiform
<i>Archegoniophore</i>			
14	Epidermis of archegoniophore air chambers	Usually bistratose (Fig. 5a)	Usually unistratose (Fig. 5b)

value of the collection, cross-sections could not be made and only characters which could be studied without cross-sectioning the plants were analyzed. The plants have a wide thallus, ranging from (4-)8-9-(-13) mm, with the mean value equalling 9.0 mm with 6–8-(-9) rows of air chambers between the costa and the margin. The hyaline thallus margin is broad, consisting of (3-)4-5 rows of ± elongated cells. The dorsal surfaces of the thalli are nearly entirely even, and the borders between the air chambers are indistinct. All features that we could analyze are characteristic of cryptic species L (Odrzykoski and Szweykowski 1991).

***Asterella kiaerii* Kaal.** Nyt Mag. Naturv. 33: 78, 1893 – TYPE CITATION: [Norway, Hordaland] ‘i en underjordisk hule paa øen Lammetun i Dalsfjorden i Søndfjord (60°15’ n. br.) af. kaptein Landmark (27de august 1880)’ – holotype 6690 (O!); isotype M-5537 (BG!) and syntype M-5538 (BG!) [the original labels of the holotype and isotype were dated 27/7

1880 instead of 27de august 1880 published by Kaalaas (1893)].

All specimens consist of very small plants which are only 2–4 mm wide (Fig. 6c), and have 3–4 rows of air chambers between the costa and the thallus margin. The hyaline thallus margin in relation to the whole thallus width is broad, usually formed of 2 rows of cells. The dorsal surface of the thallus in plane view is nearly completely even. The type of junction between the air chamber walls and the epidermis could not be studied because the thalli were unable to regain turgor and, consequently, a cross section was impossible to do. The plants are morphologically similar to sample no. 30 – from Isle of Man (POZW No. 29212) Fig. 6d, identified using isozyme markers as cryptic species L (see also Fig. 3e, 3f in Odrzykoski and Szweykowski 1991). All specimens, despite their small size, correspond with cryptic species L (Odrzykoski and Szweykowski 1991).

Table 3. Descriptive statistics of 22 quantitative characters of two species of *Conocephalum*, all measurements except of character no. 2 and 3 were done in μm . Statistical significance * - $p \leq 0.05$, ** - $p \leq 0.01$, ns - $p \geq 0.05$. Diagnostic characters are bolded

No.	Character	<i>C. conicum</i>			<i>C. salebrosum</i>			t-test		
		mean	min-max	\pm SD	V%	mean	min-max		\pm SD	V%
	Sterile thallus	N = 66				N = 143				
2	Width of thallus (mm)	12.4	7–20	2.1	17.12	8.3	5–12	1.4	17.68	*
3	Length of thallus (mm)	50.5	20–110	22.8	45.15	37.3	15–90	14.8	39.68	*
4	Number of air chambers between costa and thallus margin	6.3	5–8	0.8	12.7	4.8	3–7	0.7	14.6	**
5	Length of air chambers	1211.3	500–2250	296.3	24.46	1207.1	750–1750	218.0	18.01	ns
6	Width of air chambers	730.2	375–1375	205.6	28.16	748.1	375–1250	161.7	21.61	ns
7	Diameter of air chamber pores	367.5	250–450	74.6	20.30	347.5	225–450	71.2	20.49	ns
	Archegoniophore	N = 41				N = 20				
15	Length of archegoniophore stomatatal apparatus	86.5	66–121	8.8	10.17	121.2	99–165	11.1	9.16	**
16	Width of archegoniophore stomatatal apparatus	56.2	33–77	8.5	15.12	62.8	44–88	7.2	11.46	*
17	Number of cells on cross section of stalk	21.5	19–24	1.25	5.8	19.8	17–24	1.7	8.6	*
18	Diameter I of stalk	738.1	706–749	28.8	3.9	557.6	417–642	67.6	12.1	*
19	Diameter II of stalk	1203.0	1123–1284	59.8	5.0	849.5	663–1016	118.6	14.0	*
	Sporophyte	N = 41				N = 20				
20	Longer diameter of spores	73.2	53–97	9.2	12.57	68.9	53–88	5.2	7.55	*
21	Length of elaters	232.0	132–374	45.3	19.53	222.0	99–286	23.8	10.72	ns
22	Width of elaters	14.1	9–31	4.6	32.62	13.7	7–22	2.2	16.06	ns
23	Length of epidermal cells of capsule wall	68.4	48–95	12.8	18.71	70.5	45–100	15.7	22.27	ns
24	Width of epidermal cells of capsule wall	30.0	19–40	5.0	16.67	28.7	21–36	4.0	13.94	ns
25	Width of thickenings of epidermal cells of capsule wall	2.61	2.1–4.8	0.5	19.23	2.52	2.1–3.6	0.3	12.0	ns
26	Distance between thickenings of epidermal cells of capsule wall	22.2	14–29	3.3	14.86	17.6	12–24	3.6	20.45	*
27	Length of inner cells of capsule wall	70.3	48–95	13.1	18.63	70.3	45–102	15.4	21.91	ns
28	Width of inner cells of capsule wall	30.0	19–40	4.7	15.67	27.5	21–36	4.3	15.64	ns
29	Width of thickenings inner cells of capsule wall	3.82	2.4–4.8	0.9	23.68	3.31	2.1–4.8	1.0	30.30	ns
30	Distance between thickenings of inner cells of capsule wall	20.2	12–36	4.4	21.78	14.2	12–17	1.6	11.27	*

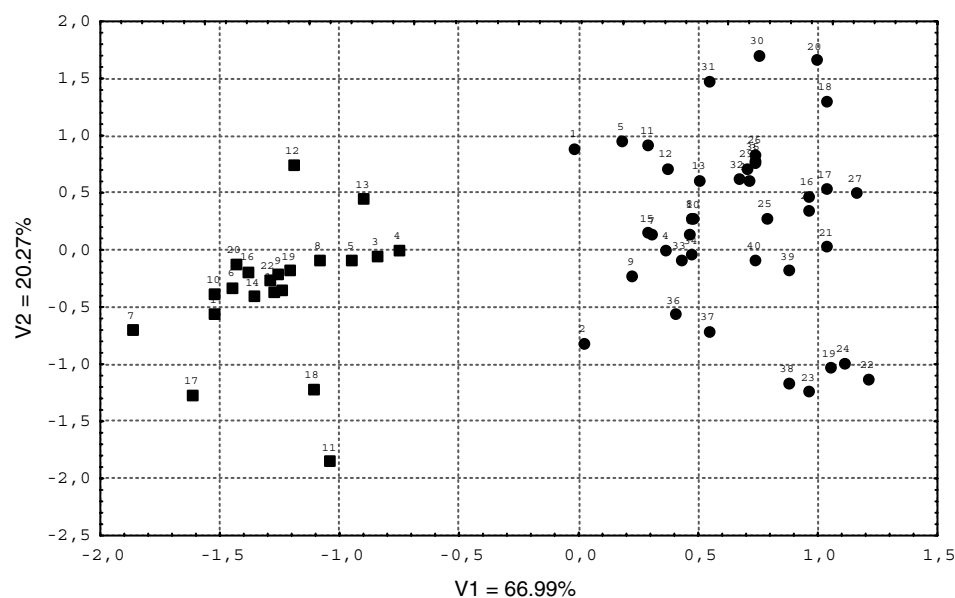


Fig. 2. Scatter plot of 61 samples of *Conocephalum conicum* s.l. (41 of *C. conicum*—circles, and 20 of *C. salebrosum*—squares) in the 1st and 2nd PCA axes explaining 87.26% of total variation included in the 22 analyzed characters

***Fegatella japonica* Steph.** Hedwigia 22: 50, 1883 – TYPE CITATION: ‘leg. Goering. No. 64, Japonia’. Holotype—21963 (G!), in spite of its different number (97 instead of 64 published by Stephani) its appearance is in accordance with description (Stephani 1883).

The type consists of only one male, rather large, 6 cm long, 11 - 13 mm wide plant (Fig. 6e), with 6-7 rows of air chambers between the costa and the thallus margin.

The hyaline thallus border (seen in plane view) is broad and formed of 3-4 rows of \pm isodiametric cells. The dorsal surface of the thallus in plane view is uneven, the limits between the air chambers are distinct, the epidermis at the junction between the air chamber walls and the epidermis is lowered. The combination of these characters indicates that this plant does not belong to either cryptic species L or species S. Probably it belongs to

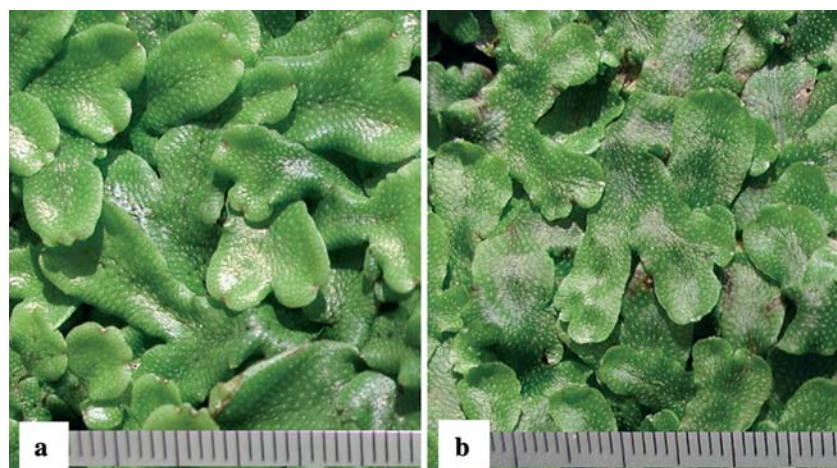


Fig. 3. Texture of thallus dorsal surface: **a** *C. conicum*, **b** *C. salebrosum*

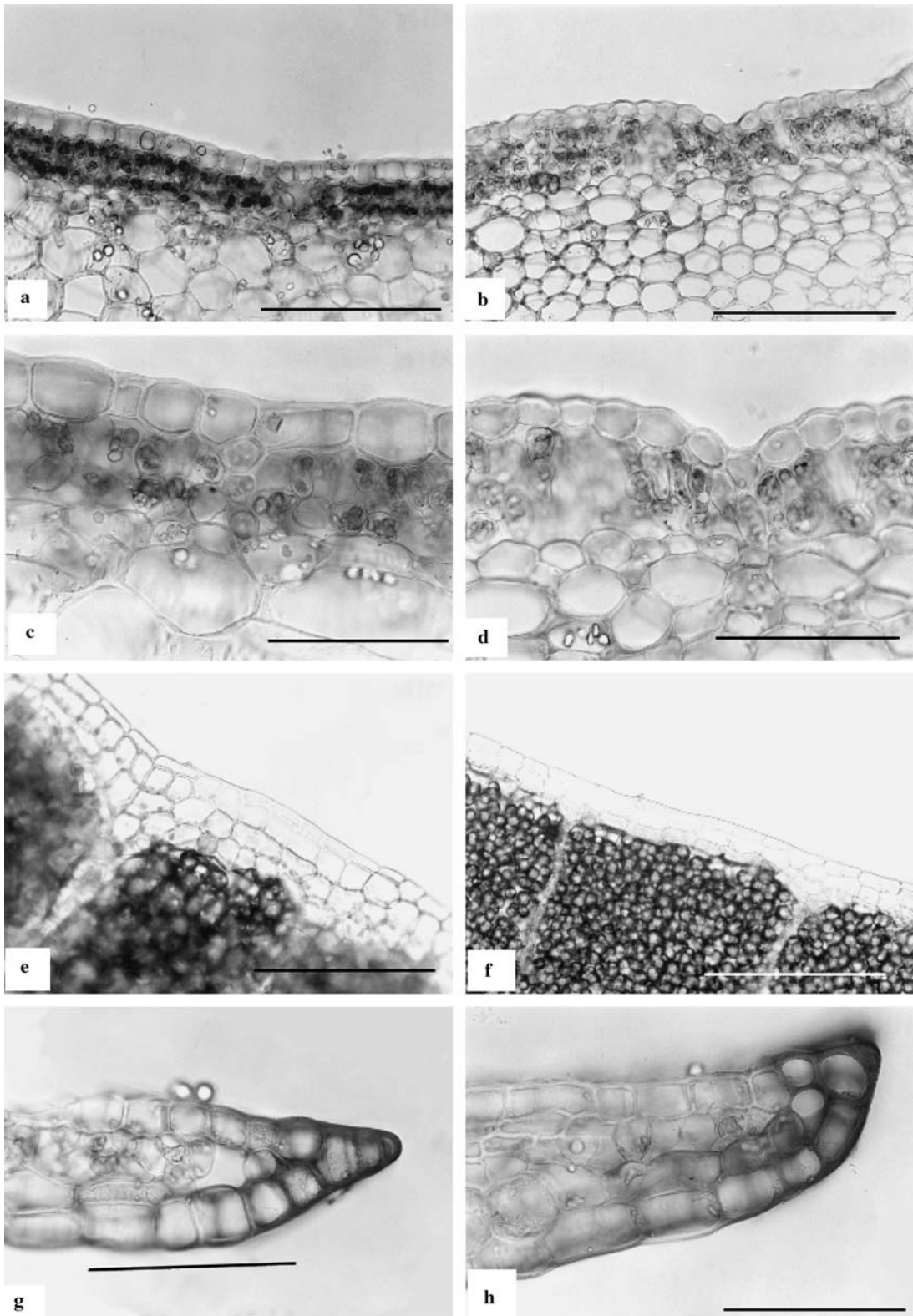


Fig. 4. Diagnostic characters of sterile thallus of *C. conicum* (a, c, e, g) and *C. salebrosum* (b, d, f, h); a, b cell walls of outer epidermis; c, d junction of air chamber wall with epidermis; e, f hyaline margin of thallus; g, h type of thallus margin (cross section). Bar for a, b, e, f = 200 μ m, for c, d, g, h = 100 μ m

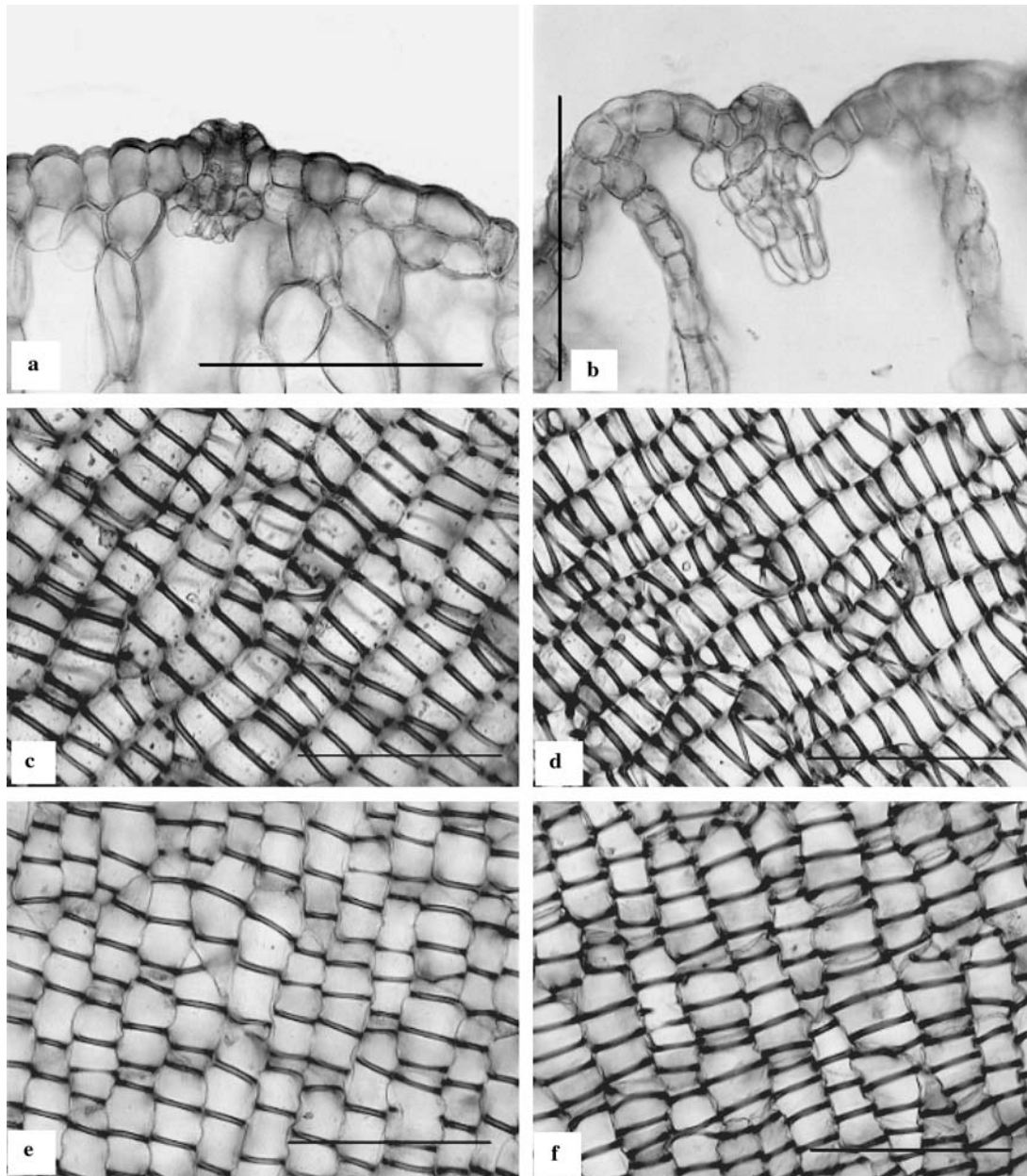


Fig. 5. Diagnostic characters of archegoniophores and sporophytes of *C. conicum* (a, c, e) and *C. salebrosum* (b, d, f); a, b stomatal apparatus, c, d epidermal cells of capsule wall, e, f inner cells of capsule wall. Bar for a, b = 200 μ m, for c, d, e, f = 100 μ m

one of two other cryptic species that occur in Japan, species J or F (Odrzykoski and Szweykowski 1991, Akiyama and Hiraoka 1994, Akiyama et al. 1998).

All of several synonyms published for *C. conicum* (Bonner 1962-1963), including

Fegatella officinalis (Raddi 1818), *Conocephalum trioicum* (Wiggers 1780), *Conocephalus nemorosus* (Hübener 1834), *Conocephalus vulgaris* (Bischoff 1835) and *Conocephalus officinalis* (Trevisan 1874), proved to be illegitimate. Our conclusions from examination of the type

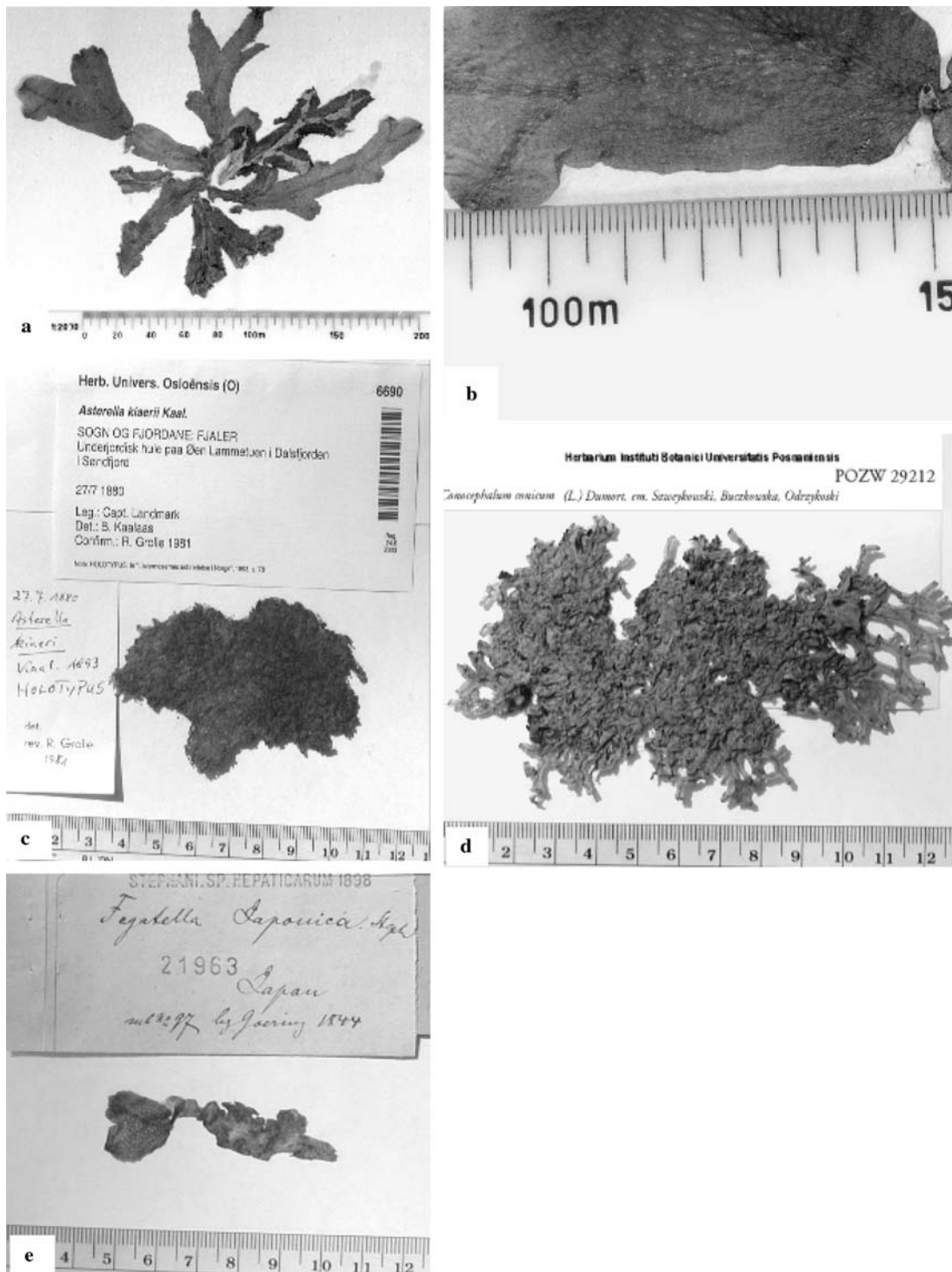


Fig. 6. The type specimens of *Conocephalum conicum* (a, b, c, e): a, b—lectotype of *C. conicum* (L.) Dumort., c holotype of *Asterella kiaerii* Kaal., e holotype of *Fegatella japonica* Steph., d specimen of *C. conicum* from Isle of Man (POZW 29212)

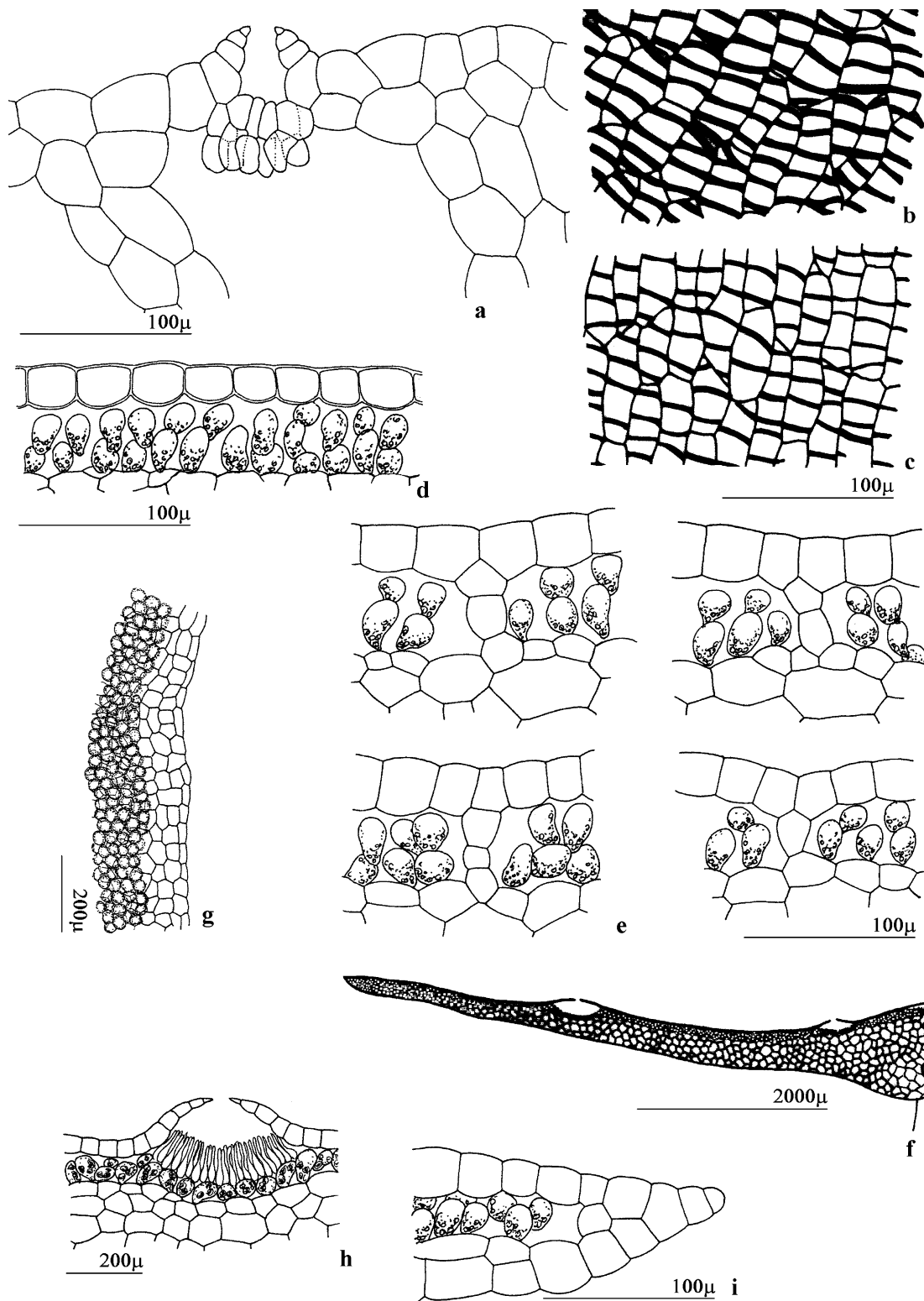


Fig. 7.1. *Conocephalum conicum* (L.) Dumort.: **a** archegoniophore stomatal apparatus, **b** inner capsule wall, **c** epidermal capsule wall, **d** dorsal epidermis of thallus, **e** junction of air chamber wall with epidermis, **f** scrap of thallus cross section, **g** thallus hyaline margin, **h** thallus stomatal apparatus, **i** thallus hyaline margin (cross section)

specimens is that cryptic species L should bear the name *Conocephalum conicum* (L.) Dumort. and species S should bear a new name - *Conocephalum salebrosum* Szweykowski, Buczkowska & Odrzykoski.

Differential description of both species

Conocephalum conicum (L.) Dumort. (Fig. 7.1)

Diagnosis. Dorsal surface of thallus distinctly shining, thallus large (2-)–5–11 cm long, 7–18 mm wide, usually with 6–8 (rarely fewer) air chamber rows between costa and thallus margin. Thallus border formed by 3–4 rows of hyaline, ± elongated cells. Dorsal surface of thallus nearly completely even. Limits between air chambers indistinct. Highest cells of air chamber walls not inserted but touching epidermal cells. Outer epidermal cell walls completely flat and reflecting light to observer, resulting in shiny surface. Stomatal apparatus of archegoniophore ‘heads’ rather small, 66–121 µm long, 33–77 µm wide, with their lowest cells relatively short and diverging in various directions. Epidermis of archegoniophore air chambers usually formed of two cell layers.

Sterile thallus. Dorsal surface of thallus of living plants and of herbarium specimens after delicate moistening (see Materials and methods) distinctly shining (Fig. 3a). Thallus rather large, (2-)–5–11 cm long, 7–18 mm wide. Air chambers on dorsal thallus surface form distinct rows running nearly parallel to each other and to thallus margin. Number of air chamber rows between costa and thallus margin usually 6–8, rarely fewer (Table 3). Thallus border (in plane view) formed of 3–4 rows of hyaline, ± elongated cells (Fig. 4e). Dorsal surface of thallus in plane view, as well as in cross-section, nearly completely even; epidermis not distinctly furrowed at border of particular air chambers (Fig. 4a). Highest cells of air chamber walls not inserted but only touch lower cell wall of epidermis (Fig. 4c). Therefore, epidermis at these junctions is not at all or only indistinctly lowered, resulting in flat surface of thallus (Fig. 4a). Outer epider-

mal cell walls are completely flat (Fig. 4a), and as result, whole epidermis is smooth and reflects light to observer, making shining surface. Apical cells of assimilators under stomata are usually elongate, and flask-shaped, and thallus margin (in cross-section) is plane or recurved (Fig. 4g).

Archegoniophore. Stomata of archegoniophore ‘heads’ differ profoundly from those of sterile thalli. The latter consist of simple pores surrounded by concentric rings of elongate cells, but ‘heads’ of archegoniophores have complex, barrel-shaped stomata resembling those in *Marchantia* L., with their lower part being more developed. Stomata of archegoniophore ‘heads’ in *Conocephalum conicum* rather small, 66–121 µm long (86.5 on average) and 33–77 µm wide (56.2 on average) (Table 3). Their lowest cells relatively short and variously oriented (Fig. 5a). Epidermis of archegoniophore air chambers usually formed of two cell layers (Fig. 5a). Archegoniophore stalk rather thick (Table 3).

Sporophyte. Thickenings of capsule inner wall incrassate (Fig. 5e, Table 3), mean of spore’s longer diameter 68.5 µm (Table 3). Chromosome number $n=9$ (Szweykowski et al. 1983). This species corresponds to the cryptic *C. conicum* - species L of Szweykowski and Odrzykoski (1991) and Odrzykoski (1995).

Geographical distribution. The species is known so far only from Europe, where it reaches the Caucasus Mts. and seems to be more frequent southward. It is already known from: Norway, Finland, Great Britain, Ireland, Belgium, France, Germany, Czech Republic, Austria, Hungary, Romania, Italy, Portugal, Spain, Croatia, Bulgaria, Greece, Ukraine (see Appendix 2 and Fig. 8.1 in this paper and Odrzykoski and Szweykowski 1991). In Poland it is known from the lowlands to the foothills and from low elevations in mountainous areas in the Tatry Mts., Sudety Mts., Beskidy and Bieszczady Zachodnie Ridges, where it is found only below 1100 m. For details of the geographical distribution in Poland, see Odrzykoski (1995) and Appendix 1.

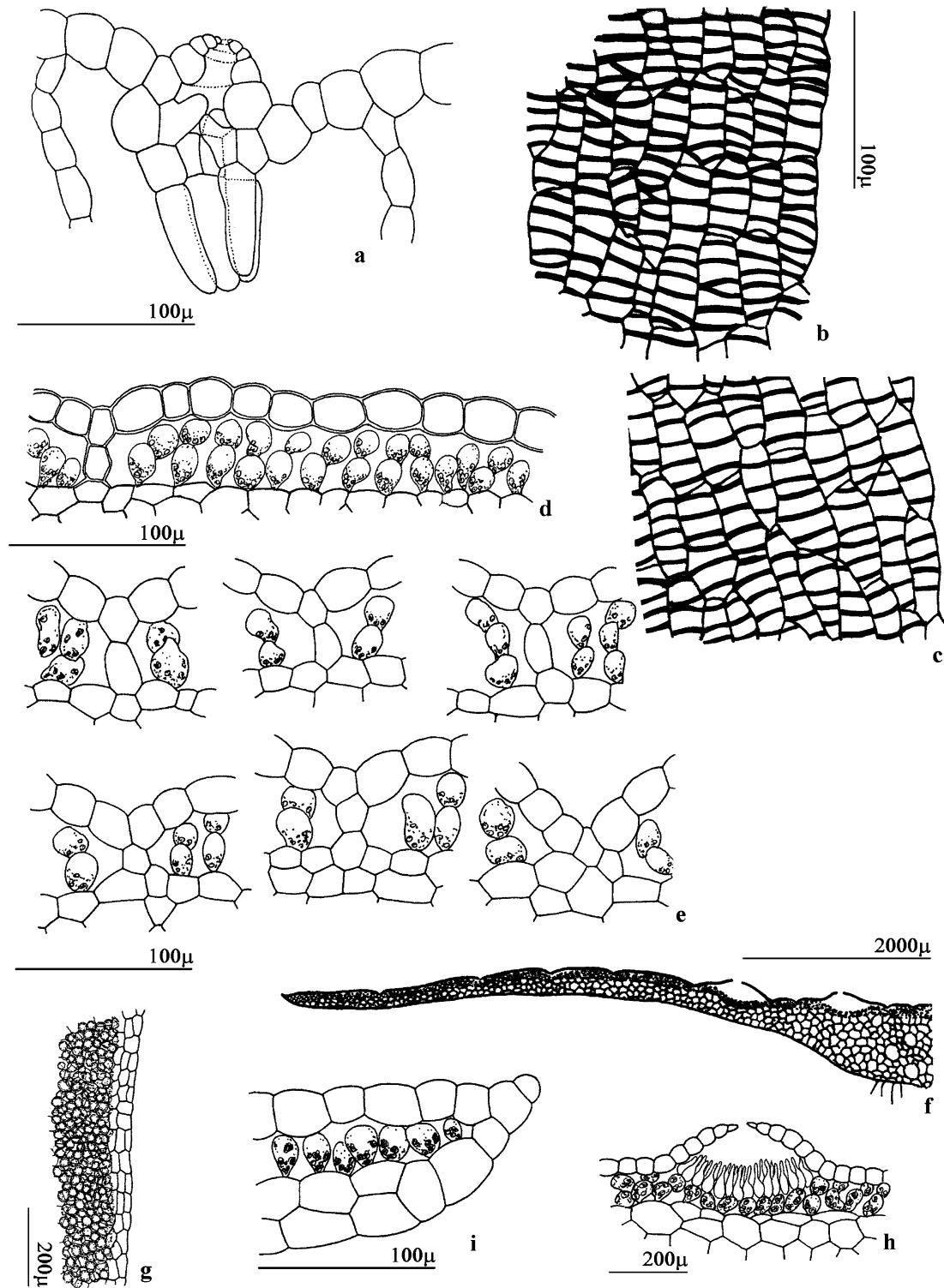


Fig. 7.2. *Conocephalum salebrosum* Szweykowski, Buczkowska & Odrzykoski: **a** archegoniophore stomatal apparatus, **b** inner capsule wall, **c** epidermal capsule wall, **d** dorsal epidermis of thallus, **e** junction of air chamber wall with epidermis, **f** scrap of thallus cross section, **g** thallus hyaline margin, **h** thallus stomatal apparatus, **i** thallus hyaline margin (cross section)

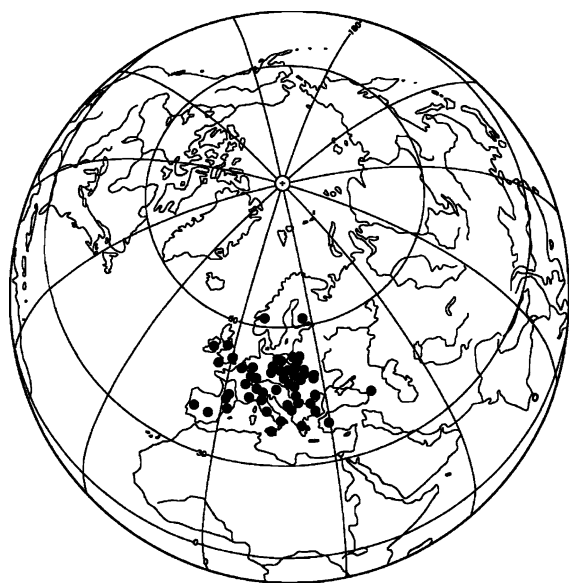


Fig. 8.1. Distribution map of *C. conicum* (L.) Dumort

DNA sequences. A sample no. 043 from our greenhouse collection (see Odrzykoski and Szweykowski 1991) has been used for sequencing of the 5' flanking region and *psbA* gene (Kim et al. 2001). A sequence was deposited in DDBJ (Acc. No. AB020589).



Fig. 8.2. Distribution map of *C. salebrosum* Szweykowski, Buczkowska & Odrzykoski

***Conocephalum salebrosum* Szweykowski, Buczkowska & Odrzykoski, sp. nov. (Fig. 7.2)**

Diagnosis. *Facies dorsalis thalli obscura et aspera, marginibus inter cavitatis aeriferis distinctissimis. Thallus parvus, (2-)3-5(-9) cm longus, 5-12 mm latus, cavitatis aeriferis 4-5, rarissime 6 in thallis magnis, in seriebus inter costam et marginem thalli dispositis, marginibus hyalinis, angustatis, cellulis plus minusve elongatis, 1-2-seriatis. Cellulae altissimae cavitatis aeriferae inter cellulis epidermalibus insertae. Epidermis primum visum verrucosae propter parietes cellularum epidermalium externarum valde inflatis. Stomata capituli archegoniophoris magna, 99-165 μm longa, 44-88 μm lata, cellulis infimis plerumque elongatis, fasciculo distincto formantibus. Epidermis capituli archegoniophoris plerumque unistratosa.*

Type. Poland, Western Carpathians, Tatry Mountains, Kościeliska Valley, Wąwóz Kraków gully; on moist humus covering shady calcareous rocks, alt. 1050 m; 26 April 2002, leg. K. Buczkowska & A. Bączkiewicz, POZW 39644 - holotype. Isotypes: KRAM, BM, FI, G, MHA, O, JE, NY, herb. Schuster.

Sterile thallus. Dorsal surface of thallus of both living plants and herbarium specimens after delicate moistening dull (Fig. 3b). Thallus smaller, (2-)3-5(-9) cm long and 5-12 mm wide, usually only 4-5 (up to 6 in exceptionally large thalli) rows of air chambers between the costa and thallus margin (Table 3). Hyaline thallus border (in plane view) usually narrow, composed of 1-2 rows of \pm elongate cells (Fig. 4f). Epidermis at border between particular air chambers distinctly furrowed; dorsal surface of thallus in plane view and in cross-section clearly uneven. Highest cells of air chamber walls in cross-section inserted between epidermal cells (Fig. 4d). Junction in such places lowered and remaining epidermis appears elevated (Fig. 4b, d). Apical cells of air chamber walls easily seen in plane view as rows of smaller cells forming rhomboidal pattern situated in rather deep furrows (Fig. 4d). Outer epidermal cell walls distinctly inflated, giving epidermis 'verrucose' appearance (Fig. 4b). Epidermal

surface disperses light that falls on thallus surface and gives dull effect. Apical cells of assimilators under stomata usually pyriform, and thallus margin seen in cross-section usually inflexed or rarely plane (Fig. 4h).

Archegoniophore. Stomata of archegoniophore 'heads' relatively large (Table 3) and their length ranges from 99–165 μm (121.2 on average) and width from 44–88 μm (62.0 on average). Lowest cells usually elongate and arranged parallel to each other and to long axis of apparatus, forming rather distinct fascicle (Fig. 5b). Epidermis of archegoniophore 'heads' usually unistratose. Archegoniophore stalk rather thin (Table 3).

Sporophyte. Thickenings of inner wall of capsule thinner and closer to each other than those in *C. conicum* (Fig. 5f, Table 3). Mean of spore's longer diameter equal to 68.5 μm (Table 3). Chromosome number $n = 9$ (Szweykowski et al. 1983). This species corresponds to the cryptic *C. conicum* - species S of Szweykowski and Odrzykoski (1991) and Odrzykoski (1995).

Geographical distribution. Holarctic, with known locations in Europe including Scandinavia, East Asia (Himalaya Mts., China, Japan) and North America, see Fig. 8.2, Appendix 2 and Szweykowski and Odrzykoski (1991). In Poland a rather frequent species, occurring from the northern lowlands (Western Pomerania, Masurian Lakeland) through the central plains to the higher elevations in mountains including Tatry Mts., Sudety Mts., Beskidy, and Bieszczady Zachodnie Ridges, where it grows also above 1000 m. In the Tatry Mts. it reaches an elevation of about 1800 m. The geographical distribution in Poland is discussed in detail in Odrzykoski (1995), see also Appendix 1.

DNA sequences. Samples no. 031 and 127d from our greenhouse collection (see Odrzykoski and Szweykowski 1991) have been used for sequencing of the 5'flanking region and *psbA* gene and sequences were deposited in DDBJ, Acc. No. AB020582, AB020583 (Kim et al. 2001). Two additional samples of this species have been used for sequencing: clones T921-2

and TC from Japan studied by Akiyama and Hiraoka (1994) as plants with multilocus genotype T (DDBJ, Acc. No. AB020603, AB020602).

Key to European species of the genus *Conocephalum* (based on sterile thalli)

Dorsal thallus surface of living plants and dried herbarium specimens after delicate moistening distinctly shining; number of air chamber rows between costa and thallus margin usually 6–7 (rarely fewer); hyaline margin of thallus broad, usually consisting of 3–4 cell rows; outer epidermal cell walls flat; dorsal thallus surface usually even, limits between particular air chambers lying at same level as rest of epidermis; highest cells of air chamber walls usually not inserted into epidermal layer *Conocephalum conicum*

Dorsal thallus surface in living plants and dried herbarium specimens after delicate moistening dull; number of air chamber rows between costa and thallus margin usually 4–5 (rarely more); hyaline border of thallus narrow, usually consisting of 1–2 cell rows; outer epidermal cell walls \pm inflated; dorsal thallus surface uneven, highest cells of air chamber walls inserted between epidermal cells and seen as rows of smaller cells on thallus surface; these rows of inserted cells situated at lower level than rest of epidermal cells, thus forming deep furrow that marks limits between particular air chambers very distinctly *Conocephalum salebrosum*

Discussion

The application of molecular markers in bryophyte taxonomy has revealed numerous cases of morphologically cryptic species (e.g. Boisselier-Dubayle and Bischler 1998, Shaw 2000). One of the first examples was the discovery of cryptic species within thallose liverwort *C. conicum* (Szweykowski and Krzakowa 1979, Odrzykoski and Szweykowski 1991, Akiyama and Hiraoka 1994), but several other cases have been found within other

liverwort genera such as: *Pellia* Raddi (Zieliński 1987), *Riccia* L. (Dewey 1989), *Aneura* (L.) Dumort. (Szweykowski and Odrzykoski 1990, Andrzejewska 2000), *Corsinia* Raddi and *Reboulia* Raddi (Boisselier-Dubayle and Bischler 1998, Boisselier et al. 1998) *Porella platyphylla* (L.) Pfeiff. (Therrien et al. 1998), *Conocephalum japonicum* (Thunb.) Grolle (Miwa et al. 2003) and *Dumortiera hirsuta* (Sw.) Nees (Akiyama et al. 2003).

Cryptic species have usually been discovered in the course of population genetic studies, but some have also recently been detected during phylogenetic analysis of DNA sequences, particularly in mosses (Shaw 2000). As in the present study, detailed morphological analysis of the relevant specimens may lead to the discovery of previously overlooked morphological differences. Frequently, they can be recognized only after employing various genetic markers, but additional studies often reveal differences in morphometric characters (e.g. Akiyama and Hiraoka 1994, Akiyama et al. 2003), geographical distributions, or ecological preferences. It has not been possible in all cases, however, to find reliable morphological characters to identify herbarium specimens. This causes serious problems not only in determination of the vast number of preserved herbarium specimens, but also is a serious barrier to formal taxonomic recognition of cryptic species. According to the rules of the International Code of Botanical Nomenclature, after splitting one species must bear the name of the species described first. Therefore, it is first necessary to find some diagnostic morpho-anatomical characters that can be scored in dried herbarium specimens including the type. This could be very difficult or even impossible for some bryophytes due to the simple morphology of their gametophytes and the ease with which they can be modified by the environment. A possibility for identification on the basis of some sequences amplified from herbarium specimens may overcome these difficulties in the future (e.g. de Castro and Menale 2004).

In the case of the two cryptic species of *Conocephalum conicum* found in Europe, some morphological differences including texture of dorsal thallus surface, overall size and ventral scales were first observed in a common garden experiment (Szweykowski and Bobowicz 1978, 1979), but discrete morphological characters which would allow proper identification of plants in a herbarium were not found (Szweykowski and Bobowicz 1983). The present studies carried out on larger sample of plants separated into cryptic species L and species S showed that these species do differ significantly in several qualitative and quantitative characters and that in fact no morphologically cryptic taxa are in hand. Diagnostic differences are related to the structure of the sterile thallus and archegoniophore, as well as the sporophyte (structure of the capsule wall and diameter of spores). Combining these characters allows proper identification of both living plants and dried herbarium specimens.

The most reliable diagnostic features are size and structure of the stomatal apparatus of archegoniophore 'heads'. In thallose liverworts the stomatal apparatus of the thallus and of the archegoniophore 'head' differs profoundly (Müller 1951-1958). In *Conocephalum* the stomata of the thallus are simple pores surrounded by concentric rings of elongated cells (Müller 1951-1958, Schuster 1992, Paton 1999), whereas, the archegoniophore 'heads', although formed from similar tissues as the sterile thallus, have a rather complicated structure. They are similar to the barrel-shaped stomata found in the thallus of *Marchantia* or *Preissia* Corda (Müller 1951-1958, Schuster 1992, Paton 1999), but their lower part in *Conocephalum* is much more developed and consists of several cells.

We found a strong correlation between features of archegoniophores and sterile thalli. Because most herbarium specimens are sterile, this correlation is very important for taxonomic practice. The most useful character of the thallus is texture of its dorsal surface

(shining or dull), which permits identification of samples at first glance in the field with high reliability. Moreover, several other characters such as number of air chambers between the costa and the thallus margin, structure of the dorsal thallus surface or type of junction of air chambers walls with the epidermis, are stable enough to allow unambiguous recognition of more than 95% of herbarium specimens, even from old collections. The oldest specimen classified in this way was collected in 1824.

Detection of diagnostic, morphological and anatomical differences has given an opportunity to identify type specimens and, in fact, to describe the discussed species according to the ICBN rules. The lectotype of *Conocephalum conicum* in Florence (FI) belongs without any doubt to *C. conicum* - species L, although not all diagnostic characters could be checked. No published name was related to *C. conicum* - species S, which is therefore described as *C. salebrosum*.

We did not perform any special studies of ecological differentiation between the two European species, but our preliminary observations suggests that *C. conicum* grows more frequently along streams. When both species grow sympatrically *C. salebrosum* is generally not so closely bound to wet places and can grow in limestone areas on roadsides (Odrzykoski 1987, 1995). Ecological differences are evident when plants are cultivated in a glasshouse; under such conditions *C. salebrosum* seems to be more tolerant of desiccation.

Appendix 1. List of samples isozymatically identified and used in morpho-anatomical studies. Each entry lists: identification number in this study, locality, collector name, date of collection. All specimens in POZW.

Conocephalum conicum

POLAND: ZACHODNIOPOMORSKIE PROV.: 34350 Puszcza Goleniowska Natl. Res., Gowienica River, KB,JS&HB 1993, 34375 Radowo Małe, Piaskowa River, KB&JS,HB 1993, 34379 Radowo Małe,

Ukleja River, JS,KB&HB 1993; **POMORSKIE PROV.:** 32201 Chojnice, Stawek lake near Asmus, JS, KB&HB 1992, 32202 Brusy Orla Struga stream, JS,KB&HB 1992; **KUJAWSKO-POMORSKIE PROV.:** 32174 Tuchola, Stążka stream, JS,KB&HB 1992; **WARMIŃSKO-MAZURSKIE PROV.:** 30709 Berkowo - Elk road, drainage ditch, JS 1988, 30827a Elbląg, Bażantarnia, I. Odrzykoski 1989, 32242 Gołdap, Pogorzelska Struga River, JS, KB&HB 1992, 32252a, 32253 Dubeninki, Czerwona Struga Natl. Res., JS,KB&HB 1992, 32257 Dubeninki, Rominta River, JS, KB&HB 1992; **PODLASKIE PROV.:** 30987 Pietronajc lake near Nowa Wieś village, JS, HB&ECH 1991, 30989, 30992 Kaletnik River near Lipnicki Las village, JS,HB&ECH 1991; **WIELKOPOLSKIE PROV.:** 30734, 30736, 30737, 30748, 30749, 30750 Diabli Skok Natl. Res. near Szwecja, JS 1987, 39050 small stream at Kobyla Góry near Ostrzeszów, Ł. Kaczmarek 1999; **DOLNOŚLĄSKIE PROV.:** 35277 Jawor, Wąwóz Myśluborski, Jawornik stream, 275m, KB&JS 1993; **GÓRY KACZAWSKIE MTS.** 35220 Dziki Wąwóz gully, 300m JS&KB; **KARKONOSZE MTS.** 31277 Chojnik Mt., 925m, JS&AB 1991; **MAŁOPOLSKIE PROV.:** **TATRA MTS.:** 23823, 24701 Kościelisko, Z. Mirek, 1985, 30691 Spadowiec stream, 1050m, JS,HB&IF 1987, 30702 Koziarski Żleb, Przednia Kopa Sołtysia, 1075m, JS&KB 1988, 30703 Dol. Filipka, 1075m, JS&KB 1988, 30726 Przyporniak stream, 935m, JS&KB 1988, 32719 Sichański Potok JS&AB 1992, 32827, 32821, 32872 Dol. Filipka, Żleb za Skałą, 925–1075m, JS&ECH 1992, 32844 Przybylanka stream, 940m, JS&AB 1992, 32851 Dol. Chochołowska, Wielka Dol. Sucha, 1025m, JS&AB 1992, 34691 Małe Ciche village, Zgorzeliski Potok, 920m, JS 1993, 34511 Męcicki Żleb, 970m, JS&ECH 1993; **PODKARPACKIE PROV.:** **PUSZCZA SOLSKA NATL. RES.** 27131 Łosiniecki stream near Susiec, JS 1989, 29208 Biedaczów near Łañcut, small stream, I.Odrzykoski 1980; **BIESZCZADY MTS.** 24125 upper part of Górna Solinka River, 660m, JS&HB 1985, 24217 Wołosatka stream, 790m, JS&HB 1985, 26183 Pszczeliny, slope above Wołosate village, 600m, JS&HB 1985, 26584, 26589, 26626, 26752 Terebowiec stream, 675–875m, JS&IF 1986, 32776 Hnatowe Berdo Mt., stream 730m, KB,ECH&JS 1992, 32781, 32792 Otryt Ridge Ridge, Hulskie Res., 525–540m, JS,ECH&KB 1992, 32793 Tworylczyk stream, 600m, KB, JS&ECH 1992, 32815 Góra Solinka River, Moczarne, 775m, JS,KB&ECH 1992, 34750 Pszczeliny, Wołosatka stream, 660m,

KB&JS 1993, 36447 Hnatowe Berdo Mt., W slope, 750m, KB&JS 1994, 36456, 36457, 36458 Górna Solinka River, Moczarnie, 675m, JS&KB 1994, 37254 Beniowa, Negryłów stream, 750m, KB&JS 1995, 37471 Wielki Lutowy stream, 750m, KB&JS 1995; **FRANCE:** 29211, 30717 Lotaryngia, Forbach, R. Mues, L. Urbaniak 1987; **GREAT BRITAIN:** 29210 Sonning, Berkshire Co., E. Watson 1978, 29212 Scotland, Isle of Man, E. Watson 1979; **ITALY:** 29207 Prato near Florence, Buti stream, J. Rafiński 1979, 29209 Stressa, Alps, Maggiore lake, I. Odrzykoski 1979.

Conocephalum salebrosum

POLAND: ZACHODNIOPOMORSKIE PROV.: 30844, 30848, 30851, 30852 Barwice, Dębno lake, JS,AB&HB 1991, 34351 Stepnica, Gowienica River, HB,JS&KB 1993, 34353 Węgorzyno, Brzezińska Węgorza River, JS,HB&KB 1993, 34372 Resko, Piaskowa River, KB, HB&JS 1993, 34378, 34379b Radowo Małe, Ukleja River, JS,KB&HB 1993, 34382 Radowo Małe, Piaskowa River, KB,JS&HB 1993; **POMORSKIE PROV.:** 34186 Kościerzyna, Jez. Szarlota lake, KB,JS&HB 1993, 34241 Dziemiany-Lipusz, Wda River, KB,JS&HB 1993, 34278 Nowa Karczma-Liniewo, Jez. Grabówko lake, KB,JS&HB 1993; **WARMIŃSKO-MAZURSKIE PROV.:** 30707 Wydminy, Berkowo-Ełk road, drainage ditch, JS 1988, 30708 Dywity, near Olsztyn, JS 1988, 30827b Elbląg, Bażantarnia, I. Odrzykoski 1989; 32252b, 32258, 32260 Dubeninki, Rominta River, JS,KB&HB, 1992, 32227, 32328 Dubeninki, Puszcza Romincka Natl. Res., Żytkiejmska Struga River, KB,JS&HB 1992, 32217 Gołdap, Puszcza Romincka Natl. Res., HB,JS&KB 1992, 32235, 32236, 32238 Gołdap, Dzięgielka River, JS,HB&KB 1992, 32245 Gołdap, Pogorzelska Struga River, JS,KB&HB 1992, 32266 Gołdap, Rezerwat Boczek Natl. Res., JS,KB&HB 1992; **PODLASKIE PROV.:** 28684 Sejny, Jez. Pomorze lake, JS&KB 1990, 30978, 30981 Suwałki, Jez. Pierty lake, JS,HB&ECH 1991; **WIELKOPOLSKIE PROV.:** 30715 Jez. Kubek lake near Sieraków, SL 1986, 30732, 30733, 30735, 30738, 30741, 30742, 30743, 30744, 30746, 30747, 30750 Diabli Skok Natl. Res. near Szwecja, JS 1987, 33857 Nowa Wieś near Poznań, KB 1992, 33858, 33859 Radojewo near Poznań, KB 1992; **LUBELSKIE PROV.:** 27143, 27148 Czartowe Pole Res., Sopot River near Józefów, JS&HB 1989; **DOLNOŚLĄSKIE**

PROV.: **KARKONOSZE MTS.** 31278 Zachełmie Dolne, stream, 380 m, JS&AB 1991; **GÓRY KACZAWSKIE MTS.** 35060 Dziki Wąwóz gully, 300m, KB&JS 1993; **MAŁOPOLSKIE PROV.:** 29204 Wąwóz Bolechowicki Natl. Res. near Kraków, I. Odrzykoski 1979; **BESKIDY RIDGES: BESKID ŻYWIECKI** 39039 Babia Góra Range, Markowy Stawek, Cyl Mt., 1125m, JS 1999; **TATRA MTS.** 32836 Hala Gąsienicowa, Kopa Magury, 1550m, JS&AB 1992, 34528 Potok Głęboki, 890m, JS&ECH 1993, 31281 Dol. Białki, stream, 1020m, JS 1991, 30714 Dol. Filipka, Filipczński stream, 950m, JS&KB 1988, 29279 Dol. Waksmundzka, 1280m, JS,ECH&KB 1990, 33001, 33012 Dol. Białki, Las Palenica, 1050–1060m, ECH&JS 1992, 32818, 32868, 32870, 32871 Dol. Filipka, Żleb za Skalką, 930-1280m, JS&AB 1992, 32730 Dol. Skalnite, Sucha Woda stream, 930m, AB&JS 1992, 32744 Dol. Suche Wody, 1025m, JS&AB 1992, 33124 Rusinowa Polana, 1280m, JS&ECH 1992, 32826 Gęsia Szyja Mt., 1440m, JS&AB 1992, 30706, 30713 Koziański Żleb, Przednia Kopa Sołtysia, stream, 970-1000m, KB&JS 1988, 30711 Przednia Kopa Sołtysia, Sucha Woda stream, 950m, KB&JS 1988, 30705, 30712 Przyporniak stream, 910–975m, JS&KB 1988, 27423 Dol. Kryta, stream, 1100m, JS&ECHKB 1989, 30698 Dol. Miętusia, Wielka Świstówka, 1420m, JS,HB&IF 1987, 30695 Spadowiec stream, 1025m, JS,HB&IF 1987, 30704 Dol. Chochołowska, Wyżni Potok Chochołowski stream, 1440m, JS,KB&HB 1988, 24653, 24691 Dol. Jaworzynka, Żleb pod Czerwienią, 1430–1450m, JS&IF 1985, 22902 Dol. Jaworzynka, Kopa Magury, 1430m, JS&MK 1984, 30694 Dol. Kondratowa, Długi Żleb, 1675m, JS,HB&IF 1987, 29451 Dol. Kościeliska, Kominiarski Wierch, 1505m, JS,KB&AB 1990, 29447 Dol. Kościeliska, Wściekły Żleb, 955m, KB,JS&AB 1990, 27422 Dol. Kryta, stream, 1100m, KB,ECH&JS 1989, 22913, 30697 Dol. Miętusia, Wantule, 1225–1260m, JS&MK 1984, 1987, 22816, 22907 Dol. Miętusia, Wielka Świstówka, 1410–1450m, JS&MK 1984, 34478 Dol. Olczyńska, Pióro Mt., 950m, JS&ECH 1993, 29452 Dol. Pyszniańska, Potok Dolinczański stream, 1230m, KB,JS&AB 1990, 22841, 22843, 22862 Dol. Smytnia, 1080-1390m, JS&MK 1984, 27420, 27421 Dol. Starorobociańska, 1100-1150m, JS,KB&ECH 1989, 32837 Dol. Chochołowska, Wielka Dol. Sucha, 1025m, JS&ECH 1992, 34763 Dol. Kościeliska, Pisaniarski Żleb, 1100m, JS&AB 1993, 34574, 34580, 34587 Dol. Spadowiec, 970-

1110m, JS&AB 1993, 34596 Kobylarzowy Żleb, 1470m, JS&AB 1993, 29448 Dol. Kościeliska, Kominiarski Wierch Mt., 1520m, KB,JS&AB 1990, 34473 Kończysta Turnia, 1190m, JS&ECH 1993, 34519 Męcicki Żleb, Siwa Polana, 1025m, JS&ECH 1993, 30692 Mała Dolinka, Żleb Kirkora, 1320m, JS,HB&IF 1987, 30696 Polana Waksmundzka, 1375m, JS,HB&IF 1987, 33554 Przybylanka stream, Polana Kosarzyska, 830m, JS&AB 1992, 29259 Polana pod Wołoszynem, 1230m, KB,JS&ECH 1990, 30693 Wielkie Koryciska, 1025m, JS,HB&IF 1987, 27419 Wydarty Żleb, 1325m, KB,JS&ECH 1989, 30718 Wyznia Dol. Chochołowska, Długi Uplaz, 1410m, JS,HB&IF 1987, 29449, 29450 Zadnia Sucha Dol. Smreczyńska, Zadnie Nadspady, 1220-1300m, JS,KB&AB 1990, 27418 Kobyle Głowy, 1150m, JS,ECH&KB 1989, 30701 Żleb pod Wysranki, 1150m, JS&IF 1986, 30699, 30719 Żleb Wielki Ciemniak, 1065-1095m, JS,HB&IF 1987, 34723 Żleb Żeleźniak, 1080m, JS&AB 1993, 23626 Kościelisko, W slope of Butorów, 1100m, Z. Mirek 1985, 29471 Chowańcówka stream, 1015m, KB,ECH&JS 1990, 29457, 29496 Sołtysówka stream, 925-970m, ECH,JS&KB 1990, 29495 Wierch Poroniec Mt., 1025m, KB,JS&ECH 1990; **PODKARPACKIE PROV.:** **BIESZCZADY MTS.** 26650 Bukowe Berdo Mt. 1250m, JS&IF 1986, 26591, 26763, 26747 Terebowiec stream, 750-945m, JS&IF 1986, 32804 Góra Solinka River, Moczarne, 775m, JS,KB&ECH 1992, 32795, 32796 Tworylczyk stream, 610-620m, KB,JS&ECH 1992, 34732 Hnatowe Berdo Mt., 1125m, JS&KB 1993, 24203 Pszczeliny, Wołosaty stream, 600m, JS& HB 1985, 26612, 34741, 34744, 34759 Pszczeliny, Wołosaty stream, 630-1120m, JS&IF 1986, KB&JS 1993, 32814 Otryt Ridge, Hulskie Res., 520m, JS,ECH&KB 1992, 32777 Hnatowe Berdo Mt., 730m, KB,JS&ECH 1992, 32802 Smerek Mt., 970m, JS,ECH&KB 1992, 26616 Wołosate peat bog, 725m, JS&IF 1986; **GREAT BRITAIN:** 35293 England, Yorkshire, Hackfall Woods, 1993; **BELGIUM:** 29206 Ardennes, Vallee de la Warche, Robertville, G. Raeymaekers 1979; **GERMANY:** 29205 Harz, Treseburg, R. Fritch 1980; **USA:** 227 Illinois, Carbondale, R. Schuster, 230 Wyoming, Firehole Canyon, Yellowstone Natl. Park, R. Duell, 357 White Water Falls, NC, I. Odrzykoski 1994, 358 Dry Falls, NC, I. Odrzykoski 1994; **INDIA:** 127 Darjeeling City, Himalaya, Assam, KG, 359 Uthar Pradesh, S.D. Tewari, **CHINA:** 468 Pearl Beach

Falls, R. Wyatt 1997, Wolong Nature Park, R. Wyatt 1997.

Appendix 2. List of studied herbarium specimens. Each entry lists: identification number in this study, locality, collector name, date of collection or collector number, acronym of herbarium where material is deposited. Unless otherwise stated, specimens are housed in POZW. Samples with archegoniophores are marked with an asterisk.

Conocephalum conicum

POLAND: ZACHODNIOPOMORSKIE PROV.: 4614 Szczecin, Winkelmann 1893; 4717 Choszczno, Drawa River, JS 1960, 4764 Sławno, Wielin Natl. Res., JS 1966; **POMORSKIE PROV.:** 35782 Kamienica River near Borzytuchom village, JS,KB&HB 1995; **WARMIŃSKO-MAZURSKIE PROV.:** 4727 Elbląg, Bażantarnia Wood, T. Wojterski 1962, 4708 Wąwóz Stoliński near Kadyny village, JS 1957, 4709 stream in Kadyny village, JS 1957, 4710 Lębork, stream in Osowo Lęborskie, JS 1956; 9821, 44859, 134392 Hep. Polonica Fasc. XI 252, Pomorze Wschodnie, Elbląg, Las Bażantarnia, T. Wojterski 1962 (**KRAM**); **WIELKOPOLSKIE PROV.:** 4623 Kępno, stream near Ostrzeszów, F. Krawiec 1934; **LUBELSKIE PROV.:** **ROZTOCZE** 4661 Zamość, Szczebreszyn, Szperówka, JS 1952, 4754, 4755 Susiec near Tomaszów Lubelski, K. Karczmarz 1965; 43134, Tomaszów Lubelski, K. Karczmarz 1965 (**KRAM**); **DOLNOŚLĄSKIE PROV.:** 4650 Lwówek Śląski, Dresler 1873; **GÓRY KACZAWSKIE MTS.** 4662 Złotoryja, Połom Mt. Near Wojcieszów, 490 m, JS 1957; **GÓRY STŌOWE MTS.** 4635 road Karłów-Radków, 500 m, JS 1948, 4634 stream in Nowy Karłów, 700 m, JS 1948, 4641 stream in Radkowo, 520 m, JS 1948; **GÓRY SOWIE MTS.** 4762 stream between Rymarz and Słoneczna Mt., 830 m, JS 1954, 4766 Kalenica Mt., 745 m, JS 1954, 4765 stream between Kalenica and Popielak Mt., 590 m, JS 1954; **OPOLSKIE PROV.:** 130828 Hep. Macroreg. Merid. Poloniae Exsiccati Fasc. X 140, Opole Plain, Kokotek near Lubliniec, K. Jędrzejko, W-71, 1989 (**KRAM**); **ŚLĄSKIE PROV.:** 89317 Hep. Macroreg. Merid. Poloniae Exsiccati Fasc. IV 46, Kwaczała near Chrzanów, K. Jędrzejko arnowiec 1985 (**KRAM**), 130830 Hep. Macroreg. Merid. Poloniae Exsiccati Fasc. X 142, Szymocice near Nędza, A. Stebel W-85, 1991 (**KRAM**); **MAŁOPOLSKIE PROV.:**

OŚWIĘCIM BASIN 130825 Hep. Macroreg. Merid. Poloniae Exsiccati Fasc. X 137, Wilamowice Foothills, Janowice, K. Jędrzejko & A. Stebel W-30, 1994 (**KRAM**), 130826 Hep. Macroreg. Merid. Poloniae Exsiccati Fasc. X 138, Wilamowice Foothills, Pisarzowice near Wilamowice, K. Jędrzejko & A. Stebel W-34, 1992 (**KRAM**), 130834 Hep. Macroreg. Merid. Poloniae Exsiccati Fasc. X 146, Wilamowice Foothills, Harszówki near Kety, H. Klama, A. Stebel, J. Żarnowiec drzejko W-116, 1991 (**KRAM**); **BESKIDY RIDGES.: BESKID WYSOKI:** 4729 Polica Range, stream from Zimna Dziura, 800 m, T. Wojterski 1964; 134344 Hep. Polonica Fasc. XIII 301, Polica Range, 880 m, T. Wojterski 1964 (**KRAM**), 142241 Polica Range, Polica Mt., N slope, over Budownia Mt., 800m, L. Stuchlik 1958 (**KRAM**), 142547 Polica Range, Polica Mt, NW slope, 1220m, L. Stuchlik 1966 (**KRAM**), 130827 Hep. Macroreg. Merid. Poloniae Exsiccati Fasc. X 147, Polica Range, N slope of Polica Mt., valley of Skawica Górna stream, H. Klama & J. Żarnowiec W-47, 1989 (**KRAM**); **BESKID ŚLĄSKI** 74458 Hep. Macroreg. Merid. Poloniae Exsiccati Fasc. II 16, Brenna, K. Jędrzejko & H. Klama 1982 (**KRAM**), 130824 Hep. Macroreg. Merid. Poloniae Exsiccati Fasc. X 136, Bystra near Bielsko-Biała, 500m, A. Stebel W-17, 1993 (**KRAM**); **BESKID ŻYWIECKI:** 130832 Hep. Macroreg. Merid. Poloniae Exsiccati Fasc. X 144, Babia Góra Range, Zawoja-Markowe Rówienki, J. Żarnowic & A. Stebel W-94, 1990 (**KRAM**), 130835 Hep. Macroreg. Merid. Poloniae Exsiccati Fasc. X 147, Korbielów-Kamienna, 650m, A. Stebel W-121, 1992 (**KRAM**), 4649 Babia Góra Range, Czatoża, 800 m, T. Wojterski 1954, 44832 Hep. Polonica Fasc. III 51, Babia Góra Range, Czatoża, 800m, T. Wojterski 1954 (**KRAM**); **BESKID MAŁY** 89260 Hep. Macroreg. Merid. Poloniae Exsiccati Fasc. VI 76, Żarnówka Duża Słowiaki, 315m, K. Jędrzejko, H. Klama & J. Żarnowiec 1986 (**KRAM**), 130829 Hep. Macroreg. Merid. Poloniae Exsiccati Fasc. X 141, Rzyki-Jagódki, valley of Rzyczanka stream, 505m, H. Klama, J. Żarnowic & A. Stebel W-84, 1991 (**KRAM**); **BESKID MAKOWSKI** 89289 Hep. Macroreg. Merid. Poloniae Exsiccati Fasc. III 31, Cicha (hamlet), 750m, K. Jędrzejko, H. Klama arnowiec 1984 (**KRAM**); **BESKID ŚREDNI** 95245, Harbutowice, Pasma Babicy, 520m, H & T. Tacik 1964 (**KRAM**), **BESKID NISKI** 43118 Dukla, Z. Waclawska 1954 (**KRAM**), 43123 Dukla, Z. Waclawska 1954 (**KRAM**), 43124 Folusz near Dukla, Z. Waclawska 1954 (**KRAM**), 43126 Łazy

near Rymanów, Z. Waclawska 1954 (**KRAM**), 43117 Iwonicz Zdrój, Z. Waclawska 1954 (**KRAM**); **GORCE MTS.** 130833 Hep. Macroreg. Merid. Poloniae Exsiccati Fasc. X 145, valley of Koninki stream, 750 m, K. Jędrzejko & J. Żarnowiec W-99, 1990 (**KRAM**); **PODKARPACKIE PROV.: POGÓRZE PRZEMYSKIE** 99324, Rybotycze, 15 km SW of Przemyśl, H. Bednarek-Ochyra 1989 (**KRAM**); **BIESZCZADY MTS.** 4705 Bereżki village Wołosaty stream, 600 m, JS 1958, 4702 Stuposiany village, JS 1958, 4722 Beskidnik stream, 800 m, M. Mendelak 1965, 36726 Caryńczyk stream, M. Mendelak 1965, 4704b Pszczeliny village, stream, 650 m, JS 1958, 4721 Pszczeliny village, 700 m, M. Koźlicka 1965, 4723a Solinka River under Mylnów Wierch Mt., 900 m, J. Krenz 1965, 37471 Moczarne, potok Wielki Lutowy stream, 750m, KB&JS 1995, 37254 potok Negryłów near Beniowa village, 750m, KB&JS 1995, 37977 tributary of San River near Sianki village, 780m, KB,HB&JS, 37944 Beskid Wołowy Mt., potok Szczawianka stream, 800m, JS,KB&HB, 4716 Smerek Mt., 800 m, S. Lisowski 1955; **NORWAY:** 6690 Song og Fjordane: Fjaler, Underjordisk hule paa Øen Lammetum i Dalsfjorden i Søndfjord (60°15'N), Capt. Landmark, 27 Juli 1880 (**holotype O**); M-5537 Song og Fjordane, Fjaler, [Askvoll,], auf der kleinen Insel Lammetum an der Westkøste Norwegens. Capt. Landmark, 27 Juli 1880, (**isotype BG**), M-5538 Song og Fjordane, Fjaler, [Askvoll,], Lammetun i Askvold, Søndfjord, B. Kaalaas 18 July 1892 (**syntype BG**); **FINLAND:** 60946 Kb, Tohmajärvi: high, oligotrophic, NE exposed cliffs of Havukkavaara hill, 4106 dupl., R. Fagerstén **BELGIUM:** 46416 Auderghem, environsde Bruxelles, M. Couteaux No. 1187, 1953 (**KRAM**); **GREAT BRITAIN:** 4693 Ireland, Tyrone, Fitzgerald 1958, M-0060705 Penzance, Cornwall (Gottsche & Rabenh., Hepat. Eur. 329, W. Curnow (**M**); 123012 Anglia, England, East Suffolk, (vice county 25), Fort. Grid ref. TG 284332, H & R. Ochyra No. 475A/97, 1997 (**KRAM**); **GERMANY:** 4630 Darmstadt, H. Schenck 1916, 4685 Hessen, G.Roth 1883, 4625 Berthelsdorf, Breutel; M-0060755 Baden-Württemberg, Memmingen, Brunnentobel, 720m, Holler 1895 (**M**), M-0060762 Mark Brandenburg, Eberswalde, H. Paul 1902 (Schiffner: Hepat. Eur. Exs. 1205) (**M**), M-0060770 Hannoverae (Ehrhart: Plant. Crypt. Exs. 235) (**M**); 1 Heiligenberg, H. Chermeson 1927 (**STR**), 6 Freiburg? 1862 (**STR**), 10a Salem, (Jack, Leiner u. Stizenberger, Kryptogamen

Badens. 362), Jack 1858 (**STR**), 11 Berthelsdorf (N. ab. E. Hapat. Europ. IV. P. 181, no. 241), Breutel (**STR**), 22 Kaiserstuhl, Eiskenberg 1866 (**STR**); **CZECH REPUBLIC**: 4652 Opava, 300 m, J. Duda 1955, 4651 Moravia, Staré Hamry, J. Duda 1951; M-0061252 Altvatergebirge, Goldenstein, Schenk 1934 (**M**), M-0060732 Höllengrund bei B. Leipa, 250m (Bauer: Bryotheca Bohem. 173), A. Schmidt 1898 (**M**); 88339 Opp. Fulnek: vallis rivi prope locum Pocheta, 380m, J. Duda 1972 (**KRAM**), 88340 Opp. Nový Jičín: pag. Libhost, N, 400m, J. Duda 1981 (**KRAM**); **UKRAINE**: 4681 Zerov 1935, 4683 Zerov, 1954; **FRANCE**: M-0061249 Cherbourg, Le Jolis 1850 (**M**), M-0061250 Le ou. De Beauv..., A. Boullu (**M**), M-0060724 Vosges (Mougeot, Nestler & Schimper: Stirp. Crypt. Vosges-Rhen. 247) (**M**); 4 Doubs 270m, (no. 427), Killian 1932 (**STR**), 18 Vosges, Mougeot (**STR**), 21 Vosges, Schimper, Bonjean (**STR**); **AUSTRIA**: 4687 Tirol, Th. Suse 1897, M-0061258 Niederösterreich, Hollabrunn, Hardegg 420m, Grützmänn 1953 (**M**); 7515 Fl. Österreich Küstenland, Görz?, Loitlesberger 1901 (**W**); **HUNGARY**: 4656* com. Baranya, 250 m, A. Boros 1953, 4653 com. Haves, 400 m, A. Boros 1928, 4655 com. Veszprem, 300 m, A. Boros 1954, 4657 com. Zala, 200 m, A. Boros 1953; **ROMANIA**: M-0060741 Transsilvania, Hunedoara, ca 280m, (Fl. Roman. Ex. Univ. Napoc. 3044b), P. Pteancu 1943 (**M**); 43447 Fl. Romaniae Exsiccata, 3044 b, Transsilvania, distr. Hunedoara. Ad terram in valle Săcămasul prope pag. Dumbrăvita, ca. 280m, P. Pteancu 1943 (**KRAM**); **SPAIN** 4694 Gerona, Pineda, P. Montserrat 1950; **PORTUGAL**: 4695 Tras-os-montes, Serra de Montesinho – Vale da Coma, E. Mendez & C. Romariz 1953; **ITALY**: M-0060722 Reggio Calabria, a Gallico supr. (Erb. Critt. Ital., Ser. II 1202), Macchiati 1881 (**M**), M-0060721 Liguria occid., Pegli (Exs. 180), Baglietto 1859 (**M**), M-0060723 I. Elba, Porto Azzurro, 150m, P. Thyssen, 1964 (**M**), M-0061248 Südtirol, Algund bei Meran, H. Hertel 1981, No. 23453 (**M**); **CROATIA**: 9191 Dalmatia, bie Beržović J. Baningartues & Schiffner (**W**); **BOSNIA**: M-0061253 Travnik, O. Sendtner 1847 (**M**); **BULGARIA**: 43125 Flora Bulgarica Exsiccata, M. Stara Planina Orientalis, ca 160m, Sl. Petrov 1955 (**KRAM**); **GREECE**: M-0061254 Peleponnese, Taygetos, 1400m, Froehlich no. 21663, 1958 (**M**); **TURKEY**: 138976 Flora of Madran Mountain (Western Turkey), C11, Aydin: Bo-

zdoğan, Altintas köyü, dere kenari islak kaya üzerinden, ca 900m, A. Erdag 2000 (**KRAM**).

Moreover several specimens probably from Italy, however without any data except name of species originally wrote by G. Raddi or G. Savi (information from Dr. Lucia Amadei curator of the herbarium) were also checked: 59 Italia? (**PI**); 60 Italia? (**PI**); 57 Italia? G. Savi (**PI**); 58 Italia? G. Raddi (**PI**); 49 Italia? G. Savi (**PI**); 50 Italia G. Savi (**PI**);

Conocephalum salebrosum

POLAND: **ZACHODNIOPOMORSKIE PROV.**: 4715 Szczecin, Beach Forest, JS 1959; 122051 Szczecin, Beach Forest, “Bukowe Zdroje” res., E. Fudali 1996 (**KRAM**), 129474 Szczecin, Beach Forest, “Zródliskowa Buczyna” res., E. Fudali 1997 (**KRAM**); **WARMIŃSKO-MAZURSKIE PROV.**: 30710 Dywity, near Olsztyn, JS 1988; **PODLASKIE PROV.**: 4763 Bielsk Podlaski, Białowieża Natl. Park, JS 1953, 27184, 27192 Stary Folwark, Kamionka River, JS&HB 1989; **POMORSKIE PROV.**: 4618 Kartuzy, tributary of Łeba River, Z. Czubiński 1936; **WIELKOPOLSKIE PROV.**: 4624 Starczanowo near Poznań, F. Krawiec 1928, 4619 Białośliwia, mixed forest near Piła, F. Krawiec 1935; **ŁÓDZKIE PROV.**: 4679 Łódź, stream in Modlica, T. Chmielewski 1955; **DOLNOŚLĄSKIE PROV.**: **GÓRY STOŁOWE MTS.** 4642, 4647 Wambierzyce, quarry, 600 m, JS 1947, 4638 Radkowo, waterfall, 520m, JS 1948, 4636 Szczeliniec, stream, 660 m, JS 1949, 4637 Darnkowski stream, 625m, JS 1949, 4640, 4648 Karłów, stream, 640 m, JS, 4643 Duże Torfowisko Batorowskie peat bog, Czerwony Potok stream, 700m, JS 1951; **GÓRY BIALSKIE MTS.** 4733 Morawka stream, 770m, W. Koła 1961, **GÓRY ORLICKIE MTS.** 4742 Zieleniec peat bog, W. Koła 1964; **GÓRY KACZAWSKIE MTS.** 4663 Jawor, Jawornik stream in Wąwóz Myśluborski gully, 330 m, JS 1957; 4731 Oleśnica, W. Koła 1960; **ŚLĄSKIE PROV.**: 74441 Hep. Macroreg. Merid. Poloniae Exsiccata Fasc. I 2, Upper Silesian Industrial district, Antoniów near Dąbrowa Górnicza-Ząbkowice, K. Jędrzejko, J. Żarnowiec & H. Klama 1982 (**KRAM**), 89259 Hep. Macroreg. Merid. Poloniae Exsiccata Fasc. IV 77, Zagórze near Chrzanów, K. Jędrzejko, H. Klama arnowiec 1987 (**KRAM**), 89265 Hep. Macroreg. Merid. Poloniae Exsiccata Fasc. VII 92, Kwaczała near Chrzanów, K.

- Jędrzejko 1987 (**KRAM**); **ŚWIĘTOKRZYSKIE PROV.:** 4770, 4771, 4772 Kielce, Silnica River, K. Karczmarsz 1940, 30723 Kielce, Zagaje Grzegorzewickie, Dobruchno River, JS&HB 1986; 74379 Wyżyna Sandomiersko-Opatowska, Karwów near Opatów, R. Ochyra, nr 88.82, 1982 (**KRAM**); **MAŁOPOLSKIE PROV.:** **OŚWICIM BASIN** 130823 Hep. Macroreg. Merid. Poloniae Exsiccata Fasc. IX 135, Wilamowice Foothills, Krzywa near Czechowice-Dziedzice, K. Jędrzejko & A. Stebel W-3, 1993 (**KRAM**); **JURA KRAKOWSKA** 43105, 43114 Mników near Kraków, B. Szafran 1945 (**KRAM**), 43107, 43111, 43116 Las Walski near Kraków, B. Szafran 1946 (**KRAM**), 12193 Ojców (**KRAM**), 43135, 43136, 43138, 43143, 43145, 44697 Piaskowa Sakła near Ojców, Prądnik stream, A. Pałkowa, 1957–58 (**KRAM**), 43137, 43139, 43140, 43148 Ojców near Skała Dolina Sąspowska, A. Pałkowa 1956 (**KRAM**), 95265 Dolina Sąspowska, near wąwóz Jamki, H. Trzcinka-Tacik 1966 (**KRAM**), 43141 Ojców near Skała, las near GrotaŁokietka, A. Pałkowa 1956 (**KRAM**), 43142, 43146 Ojców near Skała, Wąwóz Jamki, A. Pałkowa 1957 (**KRAM**), 43144 Ojców near Kraków, Wąwóz Korytania, A. Pałkowa 1956 (**KRAM**), 43147 Ojców near Skała, Brama Krakowska, A. Pałkowa 1956 (**KRAM**), 43184 Skorocice near Busko-Zdrój, B. Szafran 1946 (**KRAM**); 89329 Hep. Macroreg. Merid. Poloniae Exsiccata Fasc. VII 91, Paczółtowice near Krzeszowice, “Dolina Raclawki” res., H. Klama & J. Żarnowiec 1987 (**KRAM**); **BESKIDY RIDGES: BESKID WYSOKI** 142495 Polica Range, Polica Mt., N slope, 1095m, L. Stuchlik 1966 (**KRAM**), 142531 Polica Range, Polica Mt., N slope, 1305m, L. Stuchlik 1966 (**KRAM**), 142548 Polica Range, Polica Mt., N slope, 1200m, L. Stuchlik 1956 (**KRAM**), 142553 Polica Range, Polica Mt., N slope, 1305m, L. Stuchlik 1965 (**KRAM**); **BESKID ŚLĄSKI** 89277 Hep. Macroreg. Merid. Poloniae Exsiccata Fasc. V 61, valley of the Biała Wisielka stream, K. Jędrzejko, H. Klama arnowiec 1985 (**KRAM**); **BESKID SĄDECKI** 4632 Krynica, Parkowa Mt., JS& AS 1950; 44729 Krynica, Parkowa Mt., 1956 (**KRAM**); **BESKID NISKI:** 43119 Teodorówka near Dukla, Z. Waclawska 1954 (**KRAM**), 43121 Góra Cergowa near Dukla, Z. Waclawska 1954 (**KRAM**), 43122 Puławy near Rymanów, Z. Waclawska 1954 (**KRAM**); **GORCE MTS.** 4769 Obidowiec Mt., 950 m, JS 1960; 9519 Ochotnica, J. Kornaś 1965 (**KRAM**), 9524 Ochotnica Górna, dolina pot. Jaszczce, 820m, J. Kornaś 1962 (**KRAM**), 9625 valley of Piekieleko, 760m, J. Kornaś 1962 (**KRAM**), 9663 valley of Jamne stream, 990m, J. Kornaś 1963 (**KRAM**); **PIENINY Mt.** 4698 Zamkowa Góra Mt., 760m, JS 1956; 12329 E slope of ... gully, 1948 (**KRAM**), 43110, 12450 Pieniński stream, 1948 (**KRAM**), 43109 Wysoki Dział, B. Szafran 1949 (**KRAM**); **TATRA Mts.** 31316 Opalony Wierch Mt. 1315m, JS&AB, 1991, 31320 Dol. Roztoki, 1290m, JS&AB 1991, 4667, 4761 Dol. Strążyska, Sikława, 1100m, 1948, 1958, 4669 Dol. Kościeliska, Wąwóz Kraków gully, JS 1948, 30727 Czubik Mt, 1710m, KB,JS&HB 1988, 4671 Dol. Jarząbcza, 1465m, JS 1957, 30725 Dol. Kościeliska Przednie Nadspady, 1280m, JS&IF 1986, 4676 Dol. Starorobociańska, 1100m, JS 1958, 4760, 26804, 26805 Dol. Wielka Rówień, Giewont Mt, 1100–1300m, JS 1959, H. Klama 1987, 25657, 25658 Dol. Strążyska, Mała Dolinka, 1225–1300m, JS&MK 1983, 25659, 25661 Dol. Małej Łąki, 1550–1650m, JS&MK 1983, 25660 Dol. Białego Potoku, 1200m, JS&MK 1983, 22879, 22905, 22912 Dol. Miętusia, Wyżnia Świstówka, 1420–1725m, JS&MK 1984, 23568 Dol. Miętusia, Wantule, 1330m, JS&IF 1985, 23214 Dol. Jaworzynka, Żlab pod Czerwienią, 1560m, JS&MK 1984, 24093 Suchy Żleb Kalacki, 1360m, JS&IF 1985, 23593 Kościelisko, Butorów Mt., 970m, Z. Mirek 1985, 26111 Kościelisko, between Czajki and Pająkówk, 930–1020m, Z. Mirek 1985; 43112 F. Lilienfeld–Hep. Poloniae Exsiccatae Nr. 53b, Wąwóz Kraków in Dolina Kościeliska, F. Lilienfeldówna 1912 (**KRAM**), 44743 Dolina do Białego, 941–1079m, I. Szyszyłowicz 1887 (**KRAM**); **PODKARPACKIE PROV.:** **BIESZCZADY Mts.** 4678 Urycz, Schodnicy, S. Fedorowicz 1910, 4701 Bukowe Berdo Mt., 1150m, JS 1958, 4704a Pszczeliny stream, 650 m, JS 1958, 4706 Magura Stuposiańska, stream, 700 m, JS 1958, 4723b Solinka river near Młynów Wierch, 900 m, J. Krenz 1965, 26141 Górna Solinka stream, 520 m, JS,HB 1985, 30720, 30721, 30722 Halicz Mt., 1260–1300m, JS&HB 1985, 36276, 36282 Cisna, Smerek stream, 840–850 m, JS&KB 1994, 36353 Krzemień Mt., 1175m, KB&JS 1994, 36446, 36452 Hnatowe Berdo Mt., 760–1170m, KB&JS 1994, 37193 Smerek Mt., 1125m, JS&KB 1995, 37255 Beniowa, Negrylów stream, 750m, KB&JS 1995; 43113 F. Lilienfeld Hep. Poloniae Exsiccatae Nr. 53a, Urycz ob. Schodnicy, S. Fedorowicz 1910 (**KRAM**); 1886–12272 Skrobaczów near Wiśla River, Breidler owicz 1886 (**W**); **NORWAY:** M-0060700 Hordaland, O. Balle 1977 (**M**); **SWEDEN:**

4689 Gastrikland, Gävle, Tolvforsravinen, S. Arnell 1955, 4617 Skane Skäralid, K. Löfvander 1912, M-0060702 Suecia boreal., (Gäfle) (M), M-0060703 Dalsland, S. Bergström 1914 (M), M-0060704 Skåne, Fogelsång, H. Möller 1893 (M); 114205 Hep. Exsiccatae S.O. Lindbergii 298, Gästrikland: 'Gefle, Talfors, sandbl. Lera i skugga' 60°40'N 17°09'E, R. Hult 1872 (KRAM), 135139 Gästrikland: Gävle, K. Fr. Thedenius 1837 (KRAM); **DENMARK:** 39329 Sjælland, Furesøens Sydskrænt, C. Jensen 1891 (KRAM), 39414 Zealand: at Avnsø by Hvalsø, distr. 44, C. Jensen 1896 (KRAM), 39415 Zealand: the south slope of lake Furesø, distr. 45a, C. Jensen 1891 (KRAM), 43127 Bryophyta Danica Exsiccata, 5a, Zealand: brook at Langtved, C. Jensen 1904 (KRAM), 43128 Bryophyta Danica Exsiccata, 5b, Zealand: slope of lake Furesø, Aug. Hesselbo 1902 (KRAM); **RUSSIA** M-0060743 Lettland, Kurland, Kr. Friedrichstadt, (Bryotheca Baltica 154), Mikitowicz 1907 (M), M-0060742 Siberia, gub. Primorskaja, Ssichote-Alinj., Schischkin 1924 (M); **BELGIUM:** M-0060726 Anvers, Schouten, Vandenbroeck 1882 (M); **LUXEMBOURG:** 123072 Grand-Duchy of Luxemburg, Gutland, Consdorf, 300m, T. Arts nr 18790 (KRAM); **GERMANY:** 38751, 38752 Harz, Z. Szweykowska-Kulińska 1999, 4686* Saksonia, Proschdorf, W. Krieger, 4626 Baden, near Salem, Jack & Leiner 1858, 4741 Garmisch, J. Dornunller 1899; 2 Eisenach, H. Chermeson 1899 (STR), 5 Heidelberg, 1849 (STR), 7 Frankfurt, 1847 (STR), 10b Tobel bei Constanz (Jack, Leiner u. Stizenberger, Kryptogamen Badens. 362), Leiner 1858 (STR), 20 Lauenbürg, Wallroth 1824 (STR); Montis Tauni, Hep. Germ. 76, Hübener (HEID); 59758 Stiria Orientalis: in valleculis umbrosis supra oppidum Hartberg, 400-600m, J. Baumgartner, 1943 (KRAM), 96370 Baden-Württemberg, Voralpines Hügel- und Moorland Kreis Ravensburg, TK 8123/4c Weingarten, Kleintobelschlucht bei Ravensburg, 470-500 m, Schäfer, nr. 98, 1977 (KRAM); **CZECH REPUBLIC:** 4680* Staré Hamry, Cerná stream, 550m, J. Duda 1956; M-0060730 Bot. Garten Prag, (Bauer: Bryotheca Bohem. 281), E. Bauer 1900 (M), M-0060731 Bot. Garten Prag (Schiffner: Hepat. Eur. Exs. 1206), V. Schiffner 1902 (M); 88237 Bauer, Bryotheca Bohemica, No. 173, In Tümpeln im Höllengrunde bei Leipa, 250m, A. Schmidt 1898 (KRAM), 88326 Opp. Žilina: pag. Višňové, convallis Višňovska dolina, 800-900m, J. Duda 1985 (KRAM), 73184 Moravia septentr.,

distr. Šuperk, mts. Králický Sněžník, loc. Tvarožné diry, in declive merid. Montis Kralicky Sněžník, 870m, J. Váňa (KRAM); **SLOVAKIA:** 4746 Wielka Fatra Mt, 1000m, JS 1958, 4749 Słowacki Raj cave, 500m, JS 1958; M-0060727 Kohlbachthal, 1700m, Wilms 1882 (M), M-0060728 Karpathen Kalchbrenner (Gottsche **UKRAINE:** 4682* Zerov 1952, 4684 Zerov 1956; 8660, 43131 Godovica near Lwów, J. Krupa 1883-84 (KRAM), 44775 las Rudnowski near Lwów, 1889 (KRAM); **FRANCE:** M-0061251 Lothringen, Freiberg 1915 (M); 3 Strasbourg, H. Chermeson 1927 (STR), 19 Vosges, Mougeot 1875 (STR); 76231 Bryophyta Vogesiaca Exsiccata, Fasc. I nr. 8, Frankreich Dép. Haute-Saône, Corravillers, an Brückengemäuer aus Zement im Ort ca. 400m, J. Frahm 1985 (KRAM); **SWITZERLAND:** M-0060712 Gurten bei Bern (Wartmann & Schenk: Schweizer Krypt. 578), L. Fischer 1866, (M), M-0060714 Lugano, Osteno, M. Fürbringer 1909 (M), M-0060707 Helvetia, Kt. St. Gallen, Martinstobel, C. Correns 1884 (M), M-0060708 Helvetia, Kt. Uri, Wirtshaus zum Tell, 1400m, C. Correns 1884 (M); 9 Gurten bei Bern (Wartmann u. Schenk, Schweizerische Kryptogamen, 578), Fischer 1866 (STR), 17 Amsoldingen?, J. Mueller AARG (STR); **AUSTRIA:** 4688 Niederdonau, Dürental near Weissebach, 600-700m, J. Baumgartner 1943; M-0061257 Salzburg, V. Schoenau 1936 (M), M-0061255 Steiermark, Trieben, Fehlner 1883 (M), M-0061256 Tirol, Steineracher Padastertal, 1300m, Steiner 1964 (M); 81679 Niederösterreich: Kalte rinne im Semmerringebiet ca 800m, J. Froehlich 1961 (KRAM); **HUNGARY:** 4737 com. Hont, Bacina River near Kiralyhaza, 600m, A. Boros 1957, 4732 com. Heves, Sasko Mt. near Paradu, 850m, A. Boros 1953; **ROMANIA:** M-0060740 Muntenia, Prahova, m. Bucegi, ca 110m, (Fl. Roman. Ex. Univ. Napoc. 3044a), P. Cretzoiu 1940 (M); 14994 Fl. Romaniae Exsiccata, 3044 a, Muntenia, distr. Prahova, M-tibus Bucegi, valle Jepi, ca 110m, P. Cretzoiu 1940 (KRAM); **BOSNIA:** 43115 Flora von Bosnien, Travnik: Popara, Brandis 1889 (KRAM); **USA:** 43132 New Mexico, Sandoval Co.: Arch springs, T. 19 N., R. 2 W., Sec. 5 or 6, L. Weber 1963 (KRAM), 56246 Michigan, Cheboygan Co.: Reeses Bog, Burt Lake, H. Crum 1982 (KRAM), 59066 Yukon, Vicinity of Watson Lake campground, Mile 632 Alaska Hwy., I.A. Worley, S Thorpe, 4892, 1967 (KRAM), 139009 New York, Essex County, Chilson, Eagle Lake, S.J. Smith 52227, with D.J. Starck 1976

(**KRAM**), 139015 New York, Greene County, Catskill Mountains, Stony Clove, S.J. Smith nr 48354, with J.W. Herrick 1972 (**KRAM**); **CAN-ADA**: 43133 Ontario: on damp rotten log, Eugenia Falls, Grey County, H. Crum 11567, 1961 (**KRAM**); **JAPAN**: 48674 Kyushu, Myazaki-ken, Nichinan-shi, Obi, 20m alt., Z. Iwatsuki & M. Mizutani, 1977 (**KRAM**); **OTHER SPECIMENS** without complete data: 4629 leg. Lorch; 14 Herb. Wallroth (**STR**); 15 Herb. Wallroth (**STR**); 12 (Hepat. p. 546 Rabenh. Krypt. Flor. II 3 p. 10) (**STR**); 8 Flora Julico-Alpina 1843 (**STR**), 16 p. 82 no. 917, 1824 (**STR**); 13 Stempisch; Volk; 1880 (**STR**), 14 XX, Wallroth (**STR**).

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